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Mate guarding constrains foraging activity of male baboons

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Abstract. For many species, mate guarding results in dramatic departures from normal behaviour that reflect compromised attention to feeding and other activities. Such departures have previously been difficult to document in primates, however. Data were gathered on two aspects of male behaviour that were predicted to be constrained during consortships, individual travel distance and duration of feeding bouts, for wild male baboons, *Papio cynocephalus*, in and out of mate-guarding episodes. In each case, consorting males were compared with themselves outside of consortships, and, in the case of distance travelled, they were compared also with non-consorting males matched for sample time and location. Males travelled significantly shorter distances while consorting than while not consorting, with the result that consorting males travelled distances similar to those travelled by females. Males also had significantly shorter feeding bouts while consorting. The shorter travel distances and feeding bouts experienced by consorting males may represent important constraints on male foraging activity, and probably result in decreased energy intake during mate guarding. Seasonal and non-seasonal breeding patterns will have different consequences for the magnitude of fluctuations in energy stores and depletions experienced during mate guarding, and costs of mate guarding in species that breed non-seasonally will be more difficult to document because they are necessarily smaller and temporally dispersed. When considered across the lifespan, however, mate guarding costs to non-seasonal breeders may equal or exceed costs to seasonal breeders.

Mate guarding, when it occurs over short, concentrated periods of breeding, imposes constraints on males that often result in dramatic departures from normal behaviour. These constraints may entail extreme energetic costs or may compromise the male's ability to engage in other important activities such as thermoregulation or predator avoidance (dragonflies, *Sympetrum* spp.: Singer 1987; Convey 1989; blackbirds, *Turdus merula*: Cuthill & Macdonald 1990; mountain sheep, *Ovis canadensis* and *O. dalli*: Geist 1971; elephant seals, *Mirounga angustirostris*: LeBoeuf 1974; red deer, *Cervus elaphus*: Clutton-Brock et al. 1982; elephants, *Loxodonta africana*: Poole 1989). Indeed, it may be a general rule across a wide range of taxa that animals incur a variety of costs when they mate-guard. Primates ought to be no exception. Although short-term guarding of reproductive females is not the prevailing mating pattern among primates, it occurs in a number of species that live in multi-male, multi-female groups, including savannah baboons (Hall & DeVore 1965; Seyfarth 1978), rhesus macaques, *Macaca mulatta* (Carpenter 1942; Altmann 1962; Lindburg 1971), Japanese macaques, *M. fuscata* (Enomoto 1974), chimpanzees, *Pan troglodytes* (Tutin 1979), mantled howler monkeys, *Alouatta palliata* (Carpenter 1934; Crockett & Eisenberg 1987), and spider monkeys, *Ateles* spp. (Robinson

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& Janson 1987). Such mate guarding typically occurs in the context of consortships, periods of sexual activity and close, persistent following of a female by a male that involves exclusion of other males from access to the female. Mate guarding in this sense functions to protect or guard the male's own interests and does not necessarily accrue any benefit to the guarded female. Because consorting requires careful monitoring and following of the consort partner's movements, and involves excluding potential rivals from access to the partner, it may impose constraints on males that translate into decreased energy consumed (e.g. a reduction in quality or quantity of food consumed) or increased energy expended (e.g. an increase in distance travelled or in vigilance activities). Although mate guarding in many species also involves an increased risk of injury associated with challenges from competing males, we focus here on behavioural constraints associated with energy and not with morbidity and mortality risks due to fighting.

Few data are available to support the supposition that mate guarding imposes energetic costs on male primates, however, and some authors have suggested that consortships may not entail serious costs (Rasmussen 1980; Bercovitch 1983). Packer (1979) found that consorting male baboons spent less time feeding than nonconsorting males, but two other detailed studies of how time was apportioned for male baboons found no significant changes in time spent feeding or moving during consortships relative to other times (Bercovitch 1983; Rasmussen 1985). Bercovitch further reported no increase in time spent being vigilant during consortships, although time spent in social activities increased significantly during consortships in both studies.

The absence of a strong effect of mate guarding on how much time males spend feeding or moving is somewhat puzzling. Are primates exempt from the energetic costs of mate guarding found in so many other animals? There are two possible answers. Consortships among primates may be cooperative endeavours involving both the male and the female, so that potential energetic costs are reduced or avoided for both partners. Cooperative consortships certainly occur (Seyfarth 1978; Rasmussen 1983; Smuts 1985), and they may contribute to the apparent absence of a cost to males during consortships. None the less, consortships are often aggressively challenged by competing males and frequently end as a result of these challenges (Packer 1977; Smuts 1985; Noë & Sluijter 1990). Therefore, maintaining even cooperative consortships is likely to involve careful attendance to the movements of both the female consort partner and competing males; several studies report that proximity during consortships is primarily maintained by following rather than by herding or leading, and that males follow females rather than the reverse (Saayman 1970; Hausfater 1975; Seyfarth 1978; Rasmussen 1986).

The other possibility is that the constraints experienced by consorting males are simply not reflected in activity profiles. The behaviour patterns of mate-guarding males might be compromised in a number of ways that incur energetic costs, including (1) increases in distance travelled due to increased time spent moving, (2) increases in distance travelled arising from more rapid travel, (3) increases in positional and activity changes associated with following females and being alert to the possibility of challenges from males, (4) decreases in food intake due to decreased time spent feeding, (5) decreases in food quality due to compromised attention or to constraints on movement during foraging and (6) decreases in feeding rate (i.e. bite rate), again due to compromised attention or constraints during foraging. The first three possible costs represent increases in energy expended, and the last three represent decreases in energy consumed. The first and fourth proposed costs should be reflected in activity profiles, but the other four have unpredictable relationships to overall time spent in various activities. For instance, a male may expend more calories during consortships without spending more time moving, by covering more ground when he does move (he may increase his pace rate). Alternatively, a male may consume fewer calories during consortships without spending less time feeding if he cannot feed as efficiently (if his bite rate drops). Whether these costs were incurred through energy intake or expenditure, the energetic cost of the mate guarding would not be revealed in data on activity budgets.

Here we present results of a study on wild baboons in which we examined two aspects of male behaviour that we predicted would be constrained during consortships, distance travelled and feeding bout lengths. Distance travelled represents a major form of energy expenditure for savannah-foraging animals with a large day range. We reasoned that, while consorting, males are faced both with the problem of meeting their own feeding requirements, by moving from food patch to food patch, and with the need to follow the foraging path of their consort partner. Therefore, males could either follow only the foraging path of their consort partner and of necessity compromise their own foraging, or they could attempt to follow a foraging path similar to their normal path and thereby compromise following the female to some extent. In the first case, travel distance for consorting males would match female travel distance, which we predicted would be shorter than normal male travel distance (males are twice as large as females and have greater energetic needs; Coelho 1985; Watts 1985; Altmann & Alberts 1987; Strum 1991). In the second case, because the males are periodically moving between food and female, they would travel greater distances while consorting than while not consorting. Feeding bout lengths are direct measures of how long an animal feeds without interruption; although males often glance up to monitor their surroundings while feeding, any interruptions beyond brief glancing will be reflected in shorter feeding bouts. We tested the prediction (Rasmussen 1985) that the need to monitor and follow partner movements results in frequent feeding interruptions as males track their partner's activities, and thus in shorter feeding bouts for consorting males, even if overall time spent feeding does not change for males in consort. Finally, we also examined activity budgets for males in and out of consortships for comparison with past studies, and we discuss our results in the light of these comparisons.

METHODS

Study Subjects

We studied adult baboons living in three social groups (Hook's, Alto's and Lodge groups) in and around Amboseli National Park, a semi-arid savannah in southern Kenya (Altmann & Altmann 1970; Western & van Praet 1973). All study groups have a typical baboon social organization: males disperse as they approach maturity and females remain in the natal group. Further, male–male competition determines access to cycling females similarly in both groups, such that high-ranking males have priority of access to consorting females (Hausfater 1975; Altmann et al., in press). Members of all groups are subjects of long-term studies on demography and behaviour, and all individuals are individually recognized and habituated to observers. Two of the study groups (Hook's and Alto's group) subsist entirely on wild foods; the third (Lodge group) forages part of the time at a garbage dump adjacent to a tourist lodge. The difference in food source affects activity budgets (Altmann & Muruthi 1988; Muruthi et al. 1991), body size and composition (Altmann et al. 1993), and energy expenditure but not intake for adult females (Altmann & Muruthi 1988; Muruthi et al. 1991). Specifically, females in Lodge group are larger and fatter, spend less time feeding, travel shorter distances during the day, and expend fewer calories than females in Hook's group, but they do not consume more calories.

Data Collection

We collected data on distance travelled and activity profiles between January 1992 and June 1994 on adults living in Lodge group and Hook's group. Samples were collected between 0900 and 1100 hours and between 1400 and 1600 hours. On each day for which consortships were present, we took a sample on the consorting male that had been sampled least recently, and took a sample on the nearest non-consorting male immediately following to ensure that consort and non-consort samples were collected under similar conditions. Additional samples of non-consorting males were collected on days with no consortships, in which case the sampled male was the one for which non-consort samples had been taken least recently. We collected samples of non-consorting females for comparison with males, and determined sample order using a table of random numbers.

We collected two types of data simultaneously during 10-min focal animal samples (Altmann 1974). (1) We counted paces using a hand-held, mechanical counter. A pace was counted each time the male moved and planted his left foot, and paces were counted during all activities (Altmann & Samuels 1992). Pace counts were then used to calculate distance travelled during each sample (see Data Analysis). (2) We collected data on activity by means of instantaneous scan samples at 1-min intervals (point samples). Activity categories were as follows: *feed* (animal was in manual or oral contact with a food item, except that chewing was excluded; feed was recorded only as long as the food item was wholly or partly outside the animal's mouth), *move* (animal was locomoting and not simultaneously feeding), *social behaviour* (animal was grooming or being groomed by another individual, or engaged in any other agonistic or affiliative social interaction), *rest* (animal was sedentary and not engaged in feeding or in social interactions; included self-grooming) and *out-of-sight*.

We collected data on feeding bouts on consorting and non-consorting males in Hook's and Alto's groups between September 1987 and July 1991, as part of a larger study of male behaviour. Data were collected during 40-min focal animal samples between 0800 and 1600 hours, excluding 1200 hours. We determined sampling order using a table of random numbers, but modified it so that we sampled young or new immigrant males twice as often as older resident males. Data were collected using a hand-held interaction recorder, and beginning and end of feeding episodes were recorded continuously throughout the sample. A feeding bout began when the animal came in manual or oral contact with a food item, and ended when the animal ceased to reach for additional food items and the last item disappeared into the animal's mouth.

Data Analysis

All data were entered in Microsoft FoxPro™ for analysis. Pace rates (average number of paces per minute) were scaled to obtain hourly distance travelled, by assuming an average pace length of 1.11 m for males and 0.9 m for females. The average pace length for males was obtained by using the average pace length for adult females (J. Altmann & A. Samuels, unpublished data) and multiplying it by 1.23, the male:female ratio of linear body measurements (crown to rump length plus arm length; Altmann et al. 1993). We compared distance travelled in and out of consortships in two ways. First, we compared each consorting male with the male sampled immediately following him on that particular day, the 'matched' male. In this case we had 161 consort samples and 161 matched non-consort samples ($N=74$ consort and non-consort samples in Hook's group, $N=87$ in Lodge group). Second, we compared each male with himself in the two conditions, and for this analysis we restricted the data set to include only those males for whom we had a minimum of 5 samples in each condition (25.0 non-consort hours and 18.1 consort hours for 8 males in Hook's group; 24.6 non-consort hours and 21.6 consort hours for 7 males in Lodge group). By comparing consorting males both with themselves and with matched non-consorting males, we controlled for individual effects in one case, and for effects of the time and place of data collection in the other. In both cases we used the Wilcoxon signed-ranks test with two-tailed probabilities (Sokal & Rohlf 1981).

We examined feeding bout durations for males in and out of consortships by extracting samples of consortships from the larger 1987–1991 data set. For this analysis we used only samples of consortships that experienced no turnovers on the day the sample was taken. Turnovers occurred when the focal male either replaced or was replaced by another male as the female's consort partner some time during the day. Turnovers occurred for a variety of reasons, and we included only stable all-day consortships to minimize effects of variables that may be associated with turnovers, including aggression, exhaustion and changes in female fertility that would increase heterogeneity in fine-grained behavioural measures such as bout length. For each consort sample, we selected a matched non-consort sample on the same male, most taken within 10 days of the consort samples. The result was 41.7 h of consort samples and 40.6 h of matched non-consort samples on 18 males in Hook's and Alto's groups. We calculated the mean feeding bout length for each male in each condition by pooling all samples for a given male in a given condition. We then compared values for the 18 males during consortships with their non-consort values, using the Wilcoxon signed-ranks test with two-tailed probabilities.

We examined activity profiles in and out of consortships by comparing each male with himself, using the samples described above for comparisons of distance travelled. We calculated the proportion of time each male spent in the various activities during his consorting and non-consorting samples, and compared them using a Wilcoxon signed-ranks test with two-tailed probabilities.

RESULTS

Males travelled shorter distances per hour while consorting than they did while not consorting (Fig. 1). This was true both comparing each male to himself in the two conditions (T_S=17, P<0.01, N=15), and comparing each consorting male with his matched non-consorting male (t_S= −4.58, P<0.001, N=161; see Sokal & Rohlf 1981, page 448, for calculating the Wilcoxon test statistic with large sample sizes). This pattern was consistent across both Hook's and Lodge groups. In fact, travel distances during consortships were roughly 30% less than at other times (Lodge group, median=0.33 versus 0.47 km per hour; Hook's group, median=0.56 versus 0.87 km per hour), even though consorting males did not spend less time moving in either group (T_S=37, P>0.10, N=15). Males also spent significantly less time feeding while consorting than they did while not consorting (T_S=23, P<0.025, N=15). This difference was entirely due to males in Lodge group, however, all of whom reduced their feeding time during consortships, and was not consistent among males in Hook's group, four of whom spent more and four of whom spent less time feeding while in consortship (Lodge group, T_S=0, P=0.016, N=7; Hook's group, T_S=16, P>0.10, N=8; Fig. 2). Males in both groups spent more time socializing while consorting (T_S=0, P<0.005, N=15).

Non-consorting females travelled a median of 0.4 km per hour in Lodge group and 0.6 km per hour in Hook's group (Fig. 1). In both groups, non-consorting males travelled more than non-consorting females, but this difference was only significant in Hook's group (Mann–Whitney U-test, Hook's group: P<0.05; Lodge group: P>0.10). Consorting males travelled distances similar to those of non-consorting females in both groups (Mann–Whitney U-test, Hook's group: P>0.20; Lodge group: P>0.20).

Males had shorter feeding bouts during stable consortships than they did while not consorting (14 males had shorter bouts while consorting, 3 had longer, and one had bouts of the same length; T_S=34, P<0.05, N=17). This pattern was consistent in both Hook's and Alto's groups, so that feeding bouts were 15–20% shorter during consortships than they were while not consorting (Hook's group, median=41.1 versus 50.6 s; Alto's group, median=33.8 versus 40.2 s; Fig. 3).

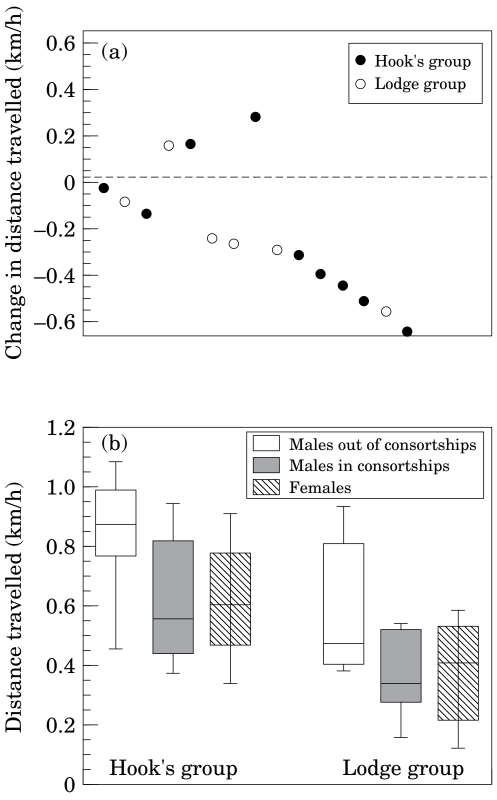

Figure 1. (a) Change in distance travelled by males during consortships relative to other times. Each dot represents the value for one male, values are ordered by absolute magnitude of change. Males in both groups travelled significantly shorter distances while consorting than while not consorting (Wilcoxon signed-ranks test, P<0.01, N=15). (b) Distributions of distance travelled hourly, in kilometres, by males out of and in consortships and by females. Males in consortships matched female travel distances. Boxes represent inter-quartile distances, solid horizontal lines indicate medians, and vertical lines indicate ranges. Note that the plot in part (b) is based on the same data set used for the within-male comparison in part (a).

DISCUSSION

At approximately double the body mass of their adult female counterparts, male baboons are faced with the task of obtaining approximately 60–80% more calories per day (based on energetic allometry) to support a level of activity comparable to that of females (Kleiber 1975; Demment 1983). Male baboons meet these greater energetic requirements by moving with impunity to the

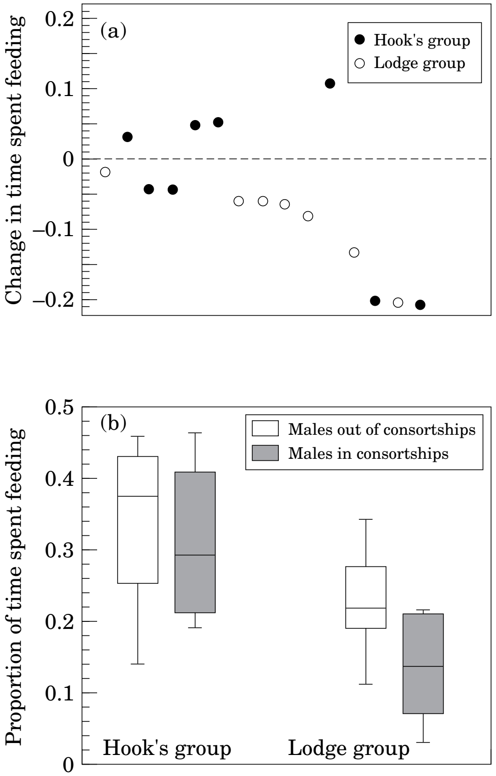

Figure 2. (a) Change in time spent feeding by males during consortships relative to other times. Each dot represents the value for one male, values are ordered by absolute magnitude of change. Males spent less time feeding while consorting than while not consorting, but this difference was due entirely to males in Lodge Group: in Hook's Group, 4 males spent more and 4 males spent less time feeding while in consortship. See text. (b) Distributions of proportion of time spent feeding by males out of and in consortships. Conventions as in Figure 1. Note that the plot in part (b) is based on the same data set used for the within-male comparison in part (a).

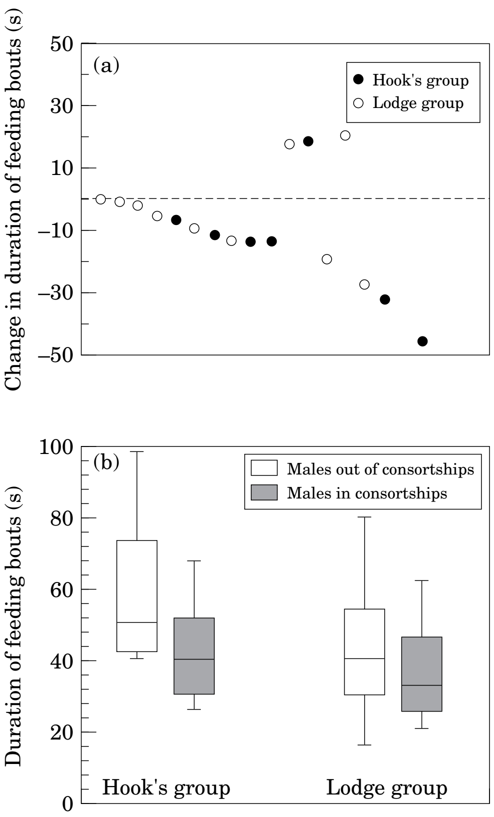

Figure 3. (a) Change in feeding bout durations for males during consortships relative to other times. Each dot represents the value for one male, values are ordered by absolute magnitude of change. Males in both groups had longer feeding bouts while not consorting than while in stable consortships (Wilcoxon signed-ranks test, $P<0.05$, $N=17$). (b) Distributions of feeding bout durations, in seconds, for males out of and in consortships. Conventions as in Figure 1. Note that the plot in part (b) is based on the same data set used for the within-male comparison in part (a).

highest quality food resources and feeding there uninterrupted by all but higher-ranking males. With their large body size and formidable canines, males are less constrained in foraging location than are females, who are more vulnerable to predators and who are encumbered by foraging interruptions and the need to monitor movements of dependent young (Altmann 1980; Whitten 1982). Although the relatively freewheeling foraging of males involves moving greater distances and thereby expending more energy, males can apparently obtain a higher rate of nutritional intake by consuming larger mouthfuls of probably more nutritious foods at greater bite rates. During consortships, we found that males gave up their independent foraging: in following their consort females (Saayman 1970; Hausfater 1975; Seyfarth 1978; Rasmussen 1986), they travelled shorter distances and had shorter feeding bouts and thus probably lower quality and rate of food intake. Males in rich habitats such as those in Lodge group and in Gombe National Park (Packer 1979) also spent less time feeding while in consortships than otherwise, and their energy consumption may have been compromised more dramatically as a result. Although time spent feeding was not lower during consortships either for Hook's group or for baboons at Mikumi (Rasmussen 1985), Rasmussen proposed that males fed less than the 'optimal' time during consortships, where optimal was defined as the mean proportion of time spent feeding by the three highest ranking adult males in the group. These relatively slight decreases in time spent feeding would be expected if energy consumption is compromised primarily through decreases in feeding efficiency rather than in absolute time available for feeding.

Although male baboons forage relatively independently when not mate guarding, they none the less live throughout the year in groups with females and young, and may thereby experience some foraging constraints relative to solitary males, even when not consorting (Slatkin & Hausfater 1976). In contrast, males of many other mate-guarding species live singly outside the breeding season, or in loose, all-male groups in which membership is unstable (red deer and other ungulates: Clutton-Brock et al. 1982; elephants: Moss & Poole 1983). Foraging within a stable and close-knit social group may limit the reserves that male baboons can accumulate against the costs entailed by mate guarding, but year-round membership in baboon groups provides the only access to reproductive females, who breed throughout the year in this species.

The fact that reproduction occurs throughout the year for baboons rather than being concentrated into a single breeding season may further limit the energetic reserves that males can accumulate prior to any mate-guarding period because males will usually have only a week or two, or even a few days, in which to recoup energetic losses from a previous consortship. Recovery of energy reserves and preparation for future mate-guarding episodes no doubt influences mate-guarding behaviour in many species. Among blackbirds, males increase their investment in mate-guarding behaviour when they are better nourished (Cuthill & MacDonald 1990), and among elephants, extreme loss of condition in a given year results in reduced mate guarding in the next year (Poole 1989). Although habitat quality and nutritional status are probably always important for mate guarders, however, we hypothesize that the temporal dispersion of reproduction in non-seasonal breeders puts a premium on minimizing the costs of mate guarding, on evaluating the costs of a current mate-guarding attempt against the ability to invest soon in another attempt, and on evaluating the female's fertility and therefore the potential reproductive risks of not guarding the reproductive female. In habitats with less abundant food resources and greater foraging demands, the constraint of highly temporally distributed reproduction will be exacerbated because energy losses cannot be recouped as rapidly. Males in richer habitats, in contrast, will be able to accrue more reserves over shorter periods. We predict that, all other factors being equal, these males will be more effective mate guarders, will be able to engage in longer mate-guarding episodes, and will guard mates that have lower potential reproductive value or that are less cooperative and perhaps therefore require more investment.

When reproduction occurs in isolated events spread throughout the year and is interspersed with short periods of recovery and accumulation of reserves, the difference in activities and energetic balance associated with any single mate-guarding episode and preparation/recovery period will of necessity be small, even if the total annual investment in mate guarding is as large as in a seasonally breeding species. Just as consistent individual differences in reproductive performance are easier to detect for males than for females, for whom short-term variance in reproductive success is less, so too, we propose, the cost of mate guarding has been easier to demonstrate in seasonally breeding species. As with the analogy to sex differences in reproductive success, however, cumulative differences may give a very different picture than that obtained in a short period, and the annual or lifetime investment in mate guarding for non-seasonal breeders like baboons may be similar to the seasonal cases that have been better studied, in which energetic costs are evident in dramatically reduced body condition after a single breeding season (Geist 1971; LeBeouf 1974; Clutton-Brock et al. 1982; Poole 1989). The study of these cumulative differences requires more refined behavioural measurements and studies that extend over longer periods of time. Travel distances and feeding-bout durations, evaluated in the present study, provide two such measurements; sensitive measures of food quality and intake rate are two other important ones.

We have shown that baboon males face constraints during mate guarding that interfere with normal foraging activity. Furthermore, we suggest that more sensitive behavioural measures than those generally used are required to evaluate the energetic costs of mate guarding for animals that breed throughout the year. Finally, we propose that food availability influences both the extent to which males compromise their energy intake while mate guarding, and the effectiveness with which they guard mates.

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