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Costs of cooperative behaviour in suricates (*Suricata suricatta*)

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Functional interpretations of helping behaviour suggest that it has evolved because helpers increase their direct or indirect fitness by helping. However, recent critiques have suggested that helping may be an unselected extension of normal parental behaviour, pointing to evidence that all mature individuals commonly respond to begging young (whether they are parents, relatives or non-relatives) as well as to the lack of evidence that cooperative activities have appreciable costs to helpers. Here we provide an example of one form of cooperative behaviour that is seldom performed by parents and has substantial energetic costs to helpers. In the cooperative mongoose, *Suricata suricatta*, non-breeding adults commonly babysit young pups at the natal burrow for a day at a time, foregoing feeding for 24 hours. Parents rarely contribute to babysitting, and babysitting has substantial energetic costs to helpers. Members of small groups compensate for the reduced number of participants by babysitting more frequently, and neither the proportion of time that babysitters are present nor the survival of litters vary with group size.

Keywords: cooperation; carnivores; breeding costs; guarding

1. INTRODUCTION

Over the past 20 years, cooperative breeding has been the focus of intensive research aimed at determining how individuals benefit by helping to rear the progeny of other animals (Brown 1987). Studies of communal breeding vertebrates have now reached a point where generalizations concerning the ecology and evolution of cooperative behaviour are beginning to emerge (Brown 1987; Emlen 1991, 1997; Smith 1990; Stacey & Koenig 1990). In many (though not in all) communal breeding species, adult survival is relatively high and breeding habitat is saturated. Under these conditions, young animals that disperse have little chance of breeding successfully, and may enhance both their survival and their chance of breeding by remaining in their natal group if this increases the chance that they will eventually breed in their natal territory. Where it is in the interests of potential reproductives to remain in their natal group, they may be able to gain 'indirect' benefits by helping close relatives to rear young, thus increasing their inclusive fitness (Hamilton 1964). In several cooperatively breeding birds and mammals, the breeding success of reproductives is positively correlated with the number of helpers (Emlen 1991; Rood 1990; Macdonald & Moehlman 1983) and experimental removal of helpers leads to a measurable decrease in the breeding success of reproductives (Brown *et al.* 1982; Emlen 1991).

Many studies of cooperative breeders have suggested that helping is an adaptive trait whose evolution and subsequent maintenance has been favoured by kin selection (Emlen 1991). However, recent critiques of adaptive interpretations of helping behaviour suggest that care of young by non-breeding juveniles and adults may represent an unselected, non-adaptive extension of parental behaviour, pointing out that (i) all group members commonly respond to begging young by feeding them; (ii) helpers often feed unrelated young as well as relatives; and (iii) there is little firm evidence that helping has substantial costs to helpers (du Plessis 1993; Jamieson 1989; Jamieson & Craig 1987). Evidence that would argue against this position would include demonstrations that forms of cooperative behaviour exist to which parents do not contribute; that helping has substantial costs to helpers; and that helping varies with the parents' need for assistance.

However, all three lines of evidence are uncommon. In most cooperative vertebrates, parents contribute more heavily than helpers to most forms of cooperative behaviour (Stacey & Koenig 1990); few studies have been able to measure the costs of helping under natural conditions though there is circumstantial evidence that these can be considerable (Reyer 1984); and relatively few studies have yet been in a position to investigate whether the contributions of helpers are adjusted to the needs of the brood. One exception is a recent study of white-winged choughs (*Corcorax melanorhamphos*) where all group members

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contribute to nest-building and incubation. Here, younger helpers lose body mass in proportion to the amount of incubation they perform and individuals vary their contributions in relation to group size, reducing time spent incubating in larger groups (Heinsohn & Cockburn 1994).

Here, we describe a form of cooperative behaviour in suricates (*Suricata suricatta*) to which breeding adults rarely contribute, and investigate its costs as well as the extent to which the contributions of helpers vary with group size. Suricates are diurnal, desert-adapted mongooses that live in packs of 3–20 adults and subadults, accompanied by their dependent young (Doolan *et al.* 1996*a*,*b*; Macdonald 1992). Packs occupy ranges of 2–10 km^2 in arid areas of southern Africa. Groups have an approximately equal sex ratio and commonly include several adult males, of which one is usually dominant over all others (Doolan & Macdonald 1996*b*). In most groups, a single dominant female breeds, but multiple females may breed when food is abundant, although dominant females produce more litters than subordinates, raising up to three litters of 3–7 pups per year (Clutton-Brock *et al.* 1998*a*; Doolan & Macdonald 1996*a*,*b*).

During the period for which the young remain at the natal burrow, one or more group members remain at the burrow, guarding the young against terrestrial and avian predators. In addition to their guarding functions, the presence of babysitters may reduce heat loss by the pups when both are underground. Babysitters typically remain at the burrow from dawn until dusk and rarely feed during this time, while the rest of the group leaves on its daily foraging excursion. However, in a minority of cases, groups return to the natal burrow during the course of the day and the guard may then change. Babysitters warn emerging pups of the approach of predators and guard the burrow against solitary suricates or neighbouring groups, and will chase away small predators, such as yellow mongooses (*Cynictis penicillata*).

2. METHODS

(a) *Study area*

Our study area used two sites in the South African Kalahari: one at Nossob in the Kalahari Gemsbok National Park (25°17′S, 20°32′E) and one on ranchland close to Van Zyl's Rus about 120 km to the south-east. Rainfall in both areas averaged around 250 mm yr^{-1} (Clutton-Brock *et al.* 1998). Rain fell mostly between December and March (Rooyen *et al.* 1990). Both areas consisted of a mixture of dry riverbeds, river terraces on either side, and sparsely vegetated sand dunes (Leistner *et al.* 1973; Rooyen *et al.* 1991). Except when predators approached or during the heat of the day (when they rested below ground), the animals spent most of the daytime foraging in the open and it was usually possible to keep all individuals in view.

Our research focused on a total of 28 different groups, ranging in size from 2–27 individuals. Groups were located and counted every two weeks throughout the study. In analyses of the relationship between group size and reproductive parameters, group size was the average number of adults and juveniles in the group, calculated per fortnightly period over the year. Between April 1993 and April 1997, we monitored 57 breeding attempts and were able to measure the distribution of babysitting for 26 of these litters. For most analyses, our sample size was the number of breeding attempts involving different breeding females: more than one breeding attempt from a given group was included only if the breeding female had changed or if a subordinate female bred. Exceptions included our analysis of weight lost by babysitters (where our sample size was the number of individuals sampled) and the analysis of changes in babysitting time with group size, where each point represented a different litter.

All suricates in our study groups could be recognized individually and were habituated to close observation (Clutton-Brock *et al.* 1998). In addition, members of eight groups were trained to stand on an electronic balance, making it possible to weigh them shortly after they emerged from the burrow in the morning and shortly before they entered it again in the evening. Breeding females were identified from overt signs of pregnancy and lactation. In most groups, either a single female bred or one bred more frequently than other females (Clutton-Brock *et al.* 1998). In social interactions, breeding females were typically dominant over other group members. Dominant males were identified from aggressive interactions with other group members and from their high frequency of anal marking, which was nearly an order of magnitude higher than that of other males (T. H. Clutton-Brock, unpublished data). All individuals were sexed during capture or by close observation. We classify animals as pups from 0–3 months, as juveniles from 3–12 months and as adults at 12 months and over. Few adults breed before they are two-years-old.

After pups were born, one adult group member typically remained at the breeding burrow when other members of the group left to forage (see above). Babysitters usually remained at the burrow from dawn to dusk but, on a minority of days, the group returned to the breeding burrow during the day and the babysitter exchanged places with another group member. After a litter was born, we initially visited the breeding burrow every morning and evening until the pups began to travel with the group, although in some cases we failed to monitor groups regularly and breeding attempts were only discovered several days after parturition occurred. At other times, several groups bred synchronously and we were not able to visit all breeding burrows each day.

If babysitters changed during the course of the day, we continued to visit the group twice a day and estimated each group member's contribution to babysitting by calculating the number of half-days on which it was with the pups. In groups where babysitters did not change during the course of the day, we calculated the number of days on which each animal was in attendance. Occasionally, a juvenile remained with an adult at the breeding burrow, and less commonly, two adults remained. In these cases, all attendant individuals were recorded as having contributed. To measure each individual's contribution to babysitting, we counted the number of half-days that each individual animal babysat for each litter, then expressed this as a proportion of the total number of half-days on which data were collected (including time when the group left no babysitter). Where groups were visited once a day, we performed the same calculations on full days. We then divided values for each individual by the mean contribution of all individuals over six-months-old, giving a measure of the relative contribution of different individuals. For each group, we calculated the average contribution made by individuals in different dominance–sex categories. Where we had data for more than one litter involving the same breeding female, average contributions of different dominance–age categories were calculated across the different litters and a single figure was entered into the final analysis.

In statistical comparisons of the effects of babysitting on weight loss, we compared weight changes in babysitters with the mean weight change for other adults in the same group on the same day. Where we had multiple measures for the same individual, we averaged these, and the sample size for these comparisons was the number of different babysitters sampled. In a small minority of cases when the babysitter was not observed to change, babysitters showed a marked increase in body weight during the day, indicating that they had left to feed. These cases were omitted in our estimates of the costs of babysitting.

With one exception, non-parametric tests were used (Siegel 1956). U indicates a Mann–Whitney U-test, r_s a Spearman rank order correlation coefficient, and T or z a Wilcoxon signed ranks test. In our analysis of the effects of group size and time spent babysitting versus weight loss, we use multiple regression (Sokal & Rolf 1969) and quote the relevant F ratio values. All p values quoted are two-tailed. Error bars in figures show inter-quartile ranges.

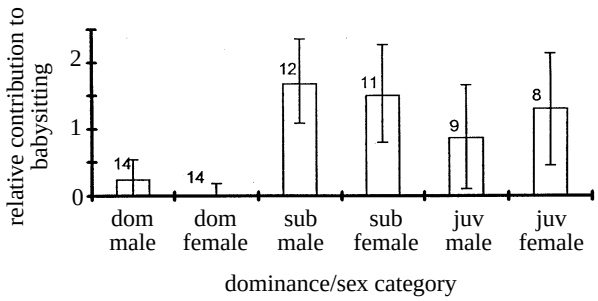

Figure 1. Relative contributions to babysitting by different group members. Sample size is the number of breeding attempts involving different breeding females and is shown above each column. As not all groups included all categories of animals, sample size varied between categories. Extending lines show inter-quartile ranges.

3. RESULTS

(a) *Group size and reproduction*

The sizes of 28 different groups that we observed between April 1993 and April 1997 ranged from 2–27 animals. The adult sex ratio was approximately equal. The average composition of 33 different groups whose members were counted in 1993 was 1.89 adult males, 1.90 females, and 1.03 young. The adult sex ratio did not differ between small and large groups (groups of no more than four individuals: 33 males, 32 females; groups of at least five individuals: 16 males, 16 females), nor did the ratio of adults to young vary between small and large groups (groups of no more than four individuals: 45 adults, 18 young; groups of at least five individuals: 49 adults, 21 young).

After females gave birth, their groups typically continued to use the natal burrow for at least four weeks. Pups first emerged from the burrow around 19 days after birth. In 19 cases, we were able to identify the date of birth precisely and record the number of days until the pups emerged (mean = 18.9 ± 4.11). Litter size at emergence averaged 4.1 ± 1.5 pups, with a range of 1–8 for a sample of 24 litters. Around seven days after emergence, the pups left the natal burrow and began to travel with the group, foraging in different areas each day (=6.9 d, $n=10$, range = 3–11).

Ten out of 57 litters (15.8%) died before emergence. In most cases, we were unable to determine the likely cause of litter failure. However, in two cases, litters were killed when a neighbouring group visited the natal burrow. In one of these cases, no babysitter was left at the burrow, while, in the other, the babysitter was displaced by the invading group. A total of 256 young emerged from 57 litters during the four years of our study, and we were able to monitor the survival of 238 young from 53 litters. A total of 90% of these pups survived to two weeks, 70% to eight weeks, 37% to six months and 18.5% to one year (Clutton-Brock *et al.* 1998*b*).

(b) *Division of labour*

Between birth and the time that pups began to travel with the group, a babysitter normally remained at the breeding burrow throughout the day. Across our sample of 26 litters, pups were left unguarded at the natal burrow on average for 12.9% ± 18.00 of the time, one babysitter was in attendance for 58.7% ± 23.32, two for 10% ± 8.37 and more than two for 2.87% ± 4.99. Babysitters usually changed on successive days. Out of a total number of 220 babysitting sequences, 204 involved a single day, 27 involved a run of two days by the same animal, seven a run of three days and five a run of four or more days.

Breeding females rarely contributed to babysitting, and spent significantly less time babysitting than subordinate females ($U=21$, $n=14,11$, $p<0.001$; see figure 1). Dominant males, too, spent less time babysitting than other group members ($U=7$, $n=11,12$, $p<0.001$; figure 1). Among subordinates, there were no significant differences in the frequency of babysitting between the sexes ($T=4$, $n=7$, $p>0.05$; see figure 1).

Four breeding attempts in our sample were by subordinate females. In none of these cases did the dominant female contribute to babysitting. For example, in a breeding attempt by the dominant female of one group, the dominant female was responsible for 2.5% of babysitting, two subordinate females for 50% and 45%, and the dominant male for 2.5%. When the same two subordinate females bred six weeks later, the dominant female did not contribute to babysitting, the dominant male contributed 53.3% and the two subordinates contributed 50% and 16.7% each. In another case where a subordinate female bred on her own, the dominant female did no babysitting. Finally, in two cases where a dominant and a subordinate bred synchronously, the dominant did no babysitting while the subordinate mothers contributed 32% and 27% of the babysitting, respectively.

Babysitting was widely but unevenly distributed across group members. Excluding breeding females and dominant males, in 13 out of 16 litters all adults contributed, in two other litters a single adult did not contribute and in one case two of six adults did not contribute. Of the group, one subordinate commonly spent substantially more time babysitting than any other. Overall, the most frequent babysitter was at the burrow for 40.0% ± 14.5 of the time and the second most frequent babysitter for 25% ± 9.1 ($n=35$), although the contribution of the top babysitter ranged from 16–88% of babysitting time between litters. Top babysitters were as likely to be males

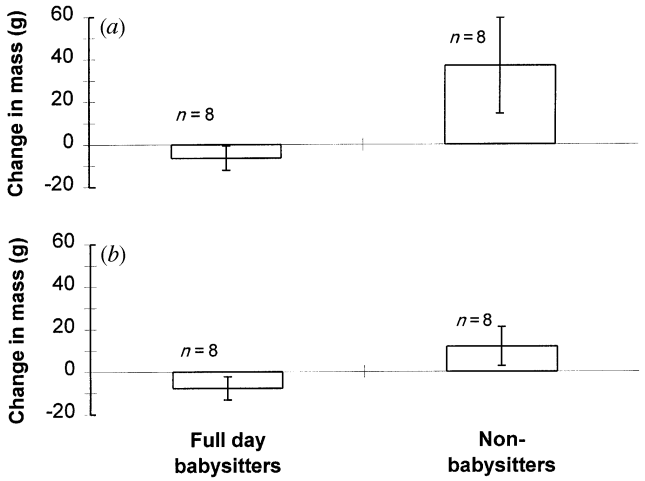

Figure 2. Daily weight gains and losses by babysitters and other group members over (*a*) 12-hour periods; and (*b*) 24-hour periods following the start of a full day's babysitting. Sample size was the number of different babysitters measured. Weight losses for non-babysitting were calculated by measuring the mean weight gain (or loss) by non-babysitting adults on the same day and calculating the mean of these estimates over the same sample of days.

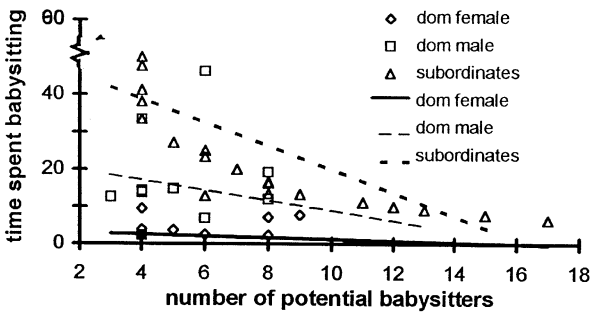

Figure 3. Time spent babysitting by dominant females, dominant males, and subordinates in breeding attempts involving groups of different sizes ($n=25$ litters). Cases where subordinate females bred were excluded from this sample. Points for subordinates show the mean value for all subordinates over one-year-old.

as females (12 versus 13 litters). They were commonly (but not invariably) sibs or previous offspring of the breeding female: for 20 litters where the relationship of the top babysitter to the breeding female was known, eight (40%) were offspring, six (30%) were siblings of the mother, and six (30%) were neither offspring nor siblings. The babysitters tended to be relatively heavy: in four of the six cases where we were able to compare the weight of the top babysitter with the average weights of other subordinates, the top babysitter was the heaviest individual.

(c) *Costs of babysitting*

Babysitting entailed substantial energetic costs. Over the 12 hours from the start of a full day's bout of babysitting, babysitters lost 6.4±5.7 g (1% of body weight) while other group members gained 36.2±22.5 g or 5.9% of body weight over the same period ($z=2.45$, $p<0.014$, $n=8$). Over the 24-hour period following the start of a full day spent babysitting, the babysitter lost 7.81±5.5 g on average (1.3% of body weight), while other group members gained 11.8±9.2 g (1.9% of body weight) ($z=2.45$, $p=0.014$, $n=8$; see figure 2).

Over complete breeding attempts, weight losses for frequent babysitters were large. In a sample of 24 litters, top babysitters averaged 25 g (3.8% of body weight) loss over the period of babysitting and second-ranked babysitters averaged 4.6 g (0.73% of body weight) compared with an average weight gain for the other non-lactating group members of 1.48 g (0.26% of body weight). In some cases, weight losses were substantially higher: weight losses of between 6% and 11% of body weight were recorded for top babysitters in one-fifth of the sample.

Where individuals babysat for two or more days in succession, weight loss increased rapidly. In 16 cases where the same individual babysat on two successive days and we were able to collect body weight data, the babysitter lost 7.6 g over the first 24-hour period and 19.1 g over the second ($z=2.64$, $p=0.008$).

In a sample of 12 litters for which data on weight change were available, we investigated relationships between average weight change for the top two babysitters and the proportion of babysitting that they contributed as well as the size of the group, using multiple regression. In this sample, average weight loss increased with the proportion of babysitting done and tended to decline with group size (babysitting contribution: F ratio$=6.72$, $p=0.029$; group size: F ratio$=3.67$, $p=0.088$).

(d) *Group size and babysitting*

In small groups, the number of individuals available to share babysitting duties was reduced but there was little evidence that the survival of pups during the period of babysitting changed with group size. Overall, 5 of the 19 litters produced by small groups (less than or equal to six individuals) failed to emerge, whereas 5 of the 38 litters produced by large groups (more than six individuals) failed to emerge (Fisher's exact test: $\chi^2=0.016$, $p=0.43$, $p=0.551$). The survival of pups between emergence and the time at which they left the natal burrow was not significantly related to group size ($rs=0.202$, $n=47$, $p=0.145$).

Both breeding adults and subordinates adjusted their contributions to babysitting to the number of potential helpers. Time spent babysitting by breeding females and by dominant males increased slightly in small groups: dominant males, $rs=-0.64$, $n=25$, $p<0.001$; dominant females, $rs=-0.36$, $n=25$, $p<0.08$; see figure 3). Time spent babysitting by individual subordinates increased to a greater extent ($rs=-0.96$, $n=25$, $p<0.001$; see figure 3) with the result that the proportion of babysitting contributed by subordinates increased as group size declined ($rs=-0.54$, $n=25$, $p<0.01$). Because of these increases, there was no tendency for pups to be left alone at the natal burrow for a higher proportion of time when group size was small ($rs=-0.15$, $n=25$, $p=0.46$).

Variation in group size also affected the distribution of babysitting among subordinates. Although the proportion of babysitting time contributed by the top babysitter did not vary significantly with group size ($rs=0.30$, $n=25$, $p=0.15$), standardized variance in babysitting time among subordinates declined with increasing group size ($rs=0.47$,

$n=25$, $p<0.05$) because fewer individuals made very small contributions to babysitting in small groups.

4. DISCUSSION

The low frequency of babysitting by breeding females and dominant males and the substantial energetic costs of babysitting suggest that babysitting is unlikely to be a non-adaptive extension of parental care. In most of the litters that we sampled, breeding females did not contribute to babysitting at all and dominant males did so rarely (figure 1). In most litters, the bulk of the babysitting was contributed by subordinates of over 12-months-old, including animals born in the group as well as immigrants. Non-breeders guard the breeding burrow in a variety of cooperative carnivores (Solomon *et al*. 1996), but guarding is by no means universal and rarely or never occurs in inappropriate circumstances. In this study, individuals rarely returned to the breeding burrow if another adult was already there and, when groups encountered litters born to members of other groups during the course of their daily foraging journeys, they never guarded them and sometimes chased away the babysitter and killed the pups.

Babysitting involved a protracted period without feeding and was normally associated with substantial loss in body weight. On average, individuals lost 1.3% of their initial body weight over a 24-hour period during babysitting while frequent babysitters showed an average weight loss of around 4% of body weight over the course of a breeding attempt and this ranged up to 11% in some cases. At least in females, it is likely that these losses were associated with fitness costs, for there was a pronounced weight threshold in the probability of breeding (T. H. Clutton-Brock, unpublished data). Recent studies of cooperative birds and fish have also shown that cooperative behaviour can reduce the growth, survival or breeding success of helpers (Taborsky 1984; Arnold 1990; Heinsohn & Cockburn 1994). The high costs of babysitting to subordinates suggest that any heritable tendency to babysit would be rapidly eroded by selection if it did not have substantial direct or indirect benefits to helpers. Although, for ethical reasons, we have not removed babysitters, virtually all studies of other vertebrates where parents or helpers guard show that the removal of guards leads to a substantial reduction in the survival of eggs or young (Clutton-Brock 1991).

Individuals also adjusted their contributions to babysitting in relation to the size of the group and the number of animals available to contribute. The same individuals rarely remained at the breeding burrow on two successive days, so that there was increased need for more group members to contribute in small groups. Though the relative contribution of the most frequent babysitter did not change with group size, fewer subordinates avoided babysitting altogether in small groups and standardized variance in babysitting time declined. In addition, dominant males and breeding females increased their contributions to babysitting in small groups, although these were never large (see figure 3). Similar relationships between group size and time spent incubating have been found in white-winged choughs (Heinsohn & Cockburn 1994): in large groups, individuals less than one-year-old rarely contributed to incubation while in small ones, they contributed as much as older individuals.

The study raised a number of questions about the reasons for the division of labour that we observed. The relatively small contributions made by breeding females and dominant males to babysitting resembles the situation in dwarf mongooses, *Helogale parvula*, where breeders of both sexes rarely guard pups at the burrow (Rasa 1977). In both species, dominant females probably contributed little to babysitting because of the unusually high costs of lactation in cooperative breeders (see Creel *et al*. 1991). Breeding female suricates typically conceive their next litter shortly after birth, and the need to guard the breeding female against wandering males may account for the dominant male's reluctance to remain at the natal burrow when the group leaves to forage.

The absence of a sex difference in babysitting frequency among subordinates appears to differ from the division of labour described in dwarf mongooses, *Helogale parvula*, and banded mongooses, *Mungos mungo*. In dwarf mongooses, subordinate females are principally responsible for guarding young at the burrow, though male helpers contribute more than females to vigilance and provisioning young (Rood 1978; Rasa 1985, 1987, 1989). In contrast, subordinate males play the principal role in guarding at the breeding burrow in banded mongooses (*Mungos mungo)* (Rood 1974); R. Woodroffe, personal communication), though another study has found no significant difference between the sexes (Ottaviani 1997). Why these differences exist is not yet clear and it is possible that they will prove to be an artefact of the small number of groups sampled in these studies. However, one possible explanation is that where subordinates of one sex are more likely to breed than those of the other, they are less willing to contribute to energetically expensive activities such as babysitting. In dwarf mongooses, subordinate males are more likely to breed successfully than subordinate females (Keane *et al*. 1994) while, in banded mongooses, the frequency of breeding by subordinate males is unknown, but multiple females commonly breed (Rood 1974); R. Woodroffe, personal communication). If this hypothesis is correct, there should be little or no difference in the probability of males and females breeding as subordinates in suricates.

Finally, our study raised the question as to how the division of labour was controlled. In many cases, it was clear which animal was going to babysit as soon as the group emerged, because one animal remained close to the burrow entrance and showed no interest in feeding. We rarely observed any aggression directed at babysitters when the rest of the group left the breeding burrow, and it seems unlikely that babysitting is enforced on subordinates by dominant group members. Whether babysitters gain direct or indirect benefits from babysitting is not yet clear.

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