Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*)

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Abstract

In most co-operative breeding species, some individuals contribute much more to helping behaviour than others. The most well-established explanation of such variation is based on kin selection and suggests that, in the absence of detectable differences in relatedness, individuals who suffer lower costs for a given level of help should contribute more. Differences in helping effort between dominance/sex categories were investigated in co-operatively breeding banded mongooses *Mungos mungo* in Uganda. The most conspicuous form of help in this species is provided by individuals who babysit offspring at the den while the rest of the pack goes off to forage. Across eight groups, the survival rate of pups increased with the average number of babysitters guarding them, consistent with the hypothesis that helpers benefit the brood that they guard. There was no difference between dominant males, subordinate males and breeding females in total contributions to babysitting. Subordinate males, however, contributed more to babysitting in the mornings, which were the longest and presumably the most energetically expensive sessions of the day. In six litters in one well-studied pack, dominant males and breeding females reduced their contribution to babysitting for the period that females were in oestrus. By contrast, subordinate males increased their contribution to become the main babysitters during this time. These results are consistent with the hypothesis that, where helping conflicts with breeding, individuals with little chance of direct reproduction can help at a lower fitness cost than those with a high probability of successful reproduction.

Key words: helping behaviour, co-operation, babysitting, social evolution, *Mungos mungo*

INTRODUCTION

Why do some individuals work harder than others in co-operatively breeding species? Variation in helping effort among group members is a conspicuous and universal feature of animal societies, yet relatively little is known about its evolutionary causes (Cant & Field, 2001). There are, however, several hypotheses, the most well established of which is based on kin selection (Hamilton, 1964; Grafen, 1984; but see Kokko, Johnstone & Clutton-Brock, 2001; Kokko, Johnstone & Wright, 2002 for models based on alternative explanations). Individuals will be selected to help at a level which maximizes their inclusive fitness pay-off $rB(h) - C(h)$, where r is the coefficient of relatedness between helper and recipient, $B(h)$ is the direct fitness benefit to the recipient as a function of the helper's effort h, and $C(h)$ is the direct fitness cost to the helper as a function of its own effort. Differences among group members in any of these three terms could account for observed differences in work rate among group members.

To date, most empirical tests in vertebrates have focused on the prediction that, where the costs and benefits of helping do not differ among group members, closely related helpers should work harder than their less closely related groupmates. While some studies have found the predicted positive correlation between helping effort and kinship, several others have not (see Clutton-Brock, Brotherton *et al.*, 2000 and references therein). This inconsistency across studies may arise because in many species the costs of helping differ substantially among group members (Boland, Heinsohn & Cockburn, 1997; Clutton-Brock, Gaynor *et al.*, 1998; Heinsohn & Legge, 1999; Cant & Field, 2001). For example, older, larger individuals may be better able to bear the energetic costs of helping than their younger groupmates (Heinsohn & Cockburn, 1994; Boland *et al.*, 1997; Clutton-Brock, Brotherton *et al.*, 2000). Alternatively, where helping and breeding are to some extent mutually exclusive activities within a group, individuals who have little chance of direct reproduction are liable to suffer lower fitness costs through helping than those with a high probability of breeding (Clutton-Brock, Gaynor *et al.*, 1998; Cant & Field, 2001).

This study examines the variation in the contributions of males and females, and of different dominance classes,

to a conspicuous and costly form of helping behaviour in banded mongooses *Mungos mungo*, and the possible evolutionary causes of such variation. Banded mongooses are small (*c.* 1.5 kg) diurnal herpestids, which live in groups (or 'packs') of around 18 individuals, and reproduce up to four times a year (Rood, 1974, 1975, 1983, 1986; Waser *et al.*, 1995; Cant, 2000; Cant, Otali & Mwanguhya, 2001; De Luca & Ginsberg, 2001). A breeding attempt usually involves several adult females who give birth together on the same day (Cant, 2000). Their pups are kept underground for 3–4 weeks, during which period one or more adults remain behind to guard them while the rest of the pack goes off to forage (Rood, 1974, 1975). This form of helping or 'babysitting' is characteristic of the social mongooses (Rood, 1986), and has been shown to have substantial energetic costs in suricates *Suricata suricatta* because babysitters rarely feed (Clutton-Brock, Gaynor *et al.*, 1998; Clutton-Brock, Brotherton *et al.*, 2000). Babysitting in banded mongooses spans the period when mating occurs, allowing the potential conflict between helping and breeding to be investigated. Specifically, three main questions were addressed. (1) Is the presence of babysitters associated with increased offspring survival? (2) Do subordinate males, with little chance of mating, contribute more than dominant males or breeding females? (3) Does babysitting effort depend on the reproductive status of females?

METHODS

The study was conducted on and around Mweya peninsula in Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E) between November 1995 and August 1997. The habitat is medium-height grassland, and annual precipitation is typically 800–900 mm. During the study information was collected on 341 mongooses living in 14 packs. Average home-range size was 69 ha (Cant *et al.*, 2001). Further details of the site and study population are given elsewhere (Cant, 2000; Cant *et al.*, 2001; De Luca & Ginsberg, 2001).

Mongooses were captured in baited live traps and anaesthetized by injection (for details see Cant, 2000; De Luca & Ginsberg, 2001). While they were under anaesthetic, adults were fitted with plastic colour-coded collars so that individuals could be identified. Younger animals were marked by shaving a symbol into the fur on the animal's rump using hair clippers. One or 2 adults in each pack were fitted with a radio-collar (Telonics Ltd, Mesa, AZ, U.S.A.). Individuals of known age were classed as adults if >1 year old, sub-adults if between 6 months and 12 months old, and pups if <6 months old. Packs were located by radio-telemetry and approached on foot until the animals were sighted.

The study was carried out under licence from Uganda National Council for Science and Technology and Uganda Wildlife Authority. The methods used (in particular, the trapping and immobilization procedure) were passed by the Research Division of Uganda Wildlife Authority.

Babysitting behaviour

Between June 1996 and August 1997, data were collected on babysitting for 20 breeding attempts in 8 packs. For *c.* 4 weeks after the females in a pack had given birth, 1 or more adults and sub-adults remained behind at the den when the rest of the pack left to forage. It was sometimes possible to determine the identity of babysitters by direct observation of entrances to the natal den, but usually the dens lay in dense thickets of *Capparis tormentosa* or deep within erosion gullies, making it impossible to observe movements directly. The identity of babysitters was therefore inferred by censusing the foraging pack and working out which individuals were missing. These absent pack-members were assumed to be babysitters if the rest of the pack was >50 m from the natal den, and if dispersal or death could be ruled out as explanations for their absence. On 18 occasions, it was possible to check this method using a second observer stationed at a den whose entrances were visible. On each occasion the inferred and actual babysitters were the same.

Usually, packs with pups <4 weeks old were visited once each morning and afternoon for at least 1 h to determine which individuals were babysitting. In addition, 1 highly habituated pack was followed all day on several occasions to examine changes in babysitters during the day. Sometimes, several packs gave birth around the same time and it was not possible to visit each pack every day.

Pup survival

For 13 litters in 8 packs, it was known how many females had given birth, and therefore it was possible to estimate the survival rate of young as the number of pups emerging divided by the estimated total litter size at birth. This total birth litter size was estimated from the age specific mean foetal litter sizes of all the females that had given birth (see Cant, 2000). These foetal litter sizes were based on a sample of 50 females from 7 age classes that were trapped 2–3 weeks after oestrus and for whom the number of foetuses was estimated by palpation, as described by Cant (2000). Where data on survival rates of several litters in the same pack were available, a single mean value was entered in the analysis. The number of packs varies in some of the analyses presented below; in each analysis the maximum number of packs for which data were available is used.

Contributions to babysitting

The individuals in each pack were separated into 3 classes: breeding females, dominant males and subordinate males (>6 months old). Subordinate or sub-adult females were not considered because, with only 3 exceptions, all females >9 months old were known to have been pregnant in each of the 20 litters which were used in the analysis. Males were classed as dominant if they had been observed mate-guarding females during oestrus when the data on babysitting were collected (Cant, 2000). In 1 pack, no data were available on mate-guarding. This pack comprised

2 adult males and 3 adult females, so both males were classed as dominant on the grounds that they would have access to females.

The analysis of relative contributions of individuals to babysitting follows that of Clutton-Brock, Gaynor *et al.* (1998). Each occasion on which babysitters were left at the den for >1 h was classed as a 'babysitting session'. The number of 'sessions' that each individual babysat for each litter was counted and expressed as a fraction of the total number of babysitting sessions on which data were collected, including times when the pack left no babysitter, but excluding times when the whole pack was found at the den. These values for each individual were divided by the median contribution of all individuals in the pack >6 months old to give a measure of the relative contribution of different individuals. An equivalent procedure was used to calculate relative contributions to babysitting for morning sessions only. Where data were available for >1 litter in the same pack, a median value for each dominance/sex category across litters within that pack was calculated and a single value entered in the analysis. Thus the sample size in these cases was the number of packs.

Babysitting and the reproductive status of females

Female packmates came into oestrus *c.* 10 days after parturition (Cant, 2000). 'Pack oestrus' was defined as the period from the first to the last observed mating or mate-guarding in the pack, and typically lasted 5–8 days. Detailed information was collected on babysitting during pack oestrus for 6 litters in 1 habituated pack (pack 1Bp) over 14 months. Statistical tests were performed on data from this pack using the number of breeding attempts as the sample size. Contributions to babysitting were calculated for pack oestrus and non-oestrus periods separately, so that the value for each individual was measured relative to the contributions of other individuals for that period, either pack oestrus or non-oestrus. To examine absolute changes in the frequency with which different classes of individuals babysat, a 'babysitting attendance rate' was calculated for each class. This was the total number of times individuals in a certain class babysat during the period (oestrus or non-oestrus), divided by the number of individuals in that class, divided by the total number of sessions on which data were collected. For each litter, this yielded a single figure for each sex/dominance category.

Data analysis

Means are quoted ± SE; medians are given with interquartile range (IQR). Non-parametric tests follow Siegel & Castellan (1988).

RESULTS

Group size during the study averaged 18 adults (range 5–44) plus two individuals <6 months old. Usually all pregnant females in a pack gave birth on the same day (Cant, 2000). The pack continued to use the natal den for an average of 7 days (range 3–19, $n = 9$ litters in five packs) before transferring pups to a different den. In the period before emergence, pups were moved between dens an average of 3.1 times (range 2–5, $n = 9$ litters in five packs).

Description of babysitting behaviour

Babysitters were left behind at the den during morning and afternoon foraging sessions. Usually, different individuals babysat for the morning and afternoon sessions: the same individual remained at the den on both occasions on 12.5% of days ($n = 56$ days; data from pack 1Bp only). On rare occasions the pack returned to the den more than once during the morning or afternoon, whereupon babysitters were usually exchanged. Babysitters were changed at least once on 28% of morning sessions ($n = 42$) and 20% of afternoon sessions ($n = 37$). The first babysitting session of the day was more than twice as long as any other (first morning session, median duration 4.5 h; other sessions, median duration 2 h; Mann–Whitney U-test: $U = 230$, $n_1 = 18$, $n_2 = 19$, $P < 0.001$; data from pack 1Bp only).

Across six packs, no babysitters were left behind on average for $11.2 \pm 11.4\%$ of babysitting sessions, one babysitter was present on $30.2 \pm 16.5\%$ of sessions, two on $21.5 \pm 8.2\%$, three on $19.6 \pm 9.4\%$, four on $10.5 \pm 10.1\%$, and five or more babysitters were present on $8.0 \pm 7.2\%$ of sessions. The whole pack was found at the breeding den on a median of 20.3% of afternoon sessions (IQR 6.2), but almost never in the morning (median 0.0%, IQR 6.2) (Wilcoxon signed ranks test: $t^+ = 21$, $n = 6$, $P < 0.05$). More babysitters stayed behind for afternoon sessions compared to morning sessions (morning sessions = 2.0 ± 0.7 babysitters/session, afternoons = 2.461 ± 0.6; paired t-test, $t_9 = -2.94$, $P < 0.05$).

Is presence of babysitters associated with increased offspring survival?

Across eight packs there was no correlation between pack size and number of babysitters (modal pack size *vs* mean number of babysitters: $n = 8$ packs, $r^2 = 0.39$, $F_{1,6} = 3.87$, NS). Mean pre-emergence survival rate of pups in these eight packs increased with mean number of babysitters for those litters ($n = 8$, $r^2 = 0.47$, $F_{1,6} = 7.28$, $P < 0.05$ (Fig. 1), but not pack size ($n = 8$, $r^2 = 0.18$, $F_{1,6} = 2.25$, NS).

Do subordinate males contribute more than other dominance/sex categories?

Across packs, there was no difference between males and females, or among breeding females, dominant males and subordinate males, in relative contribution to babysitting (Fig. 2a; Wilcoxon signed ranks test, males *vs* females,
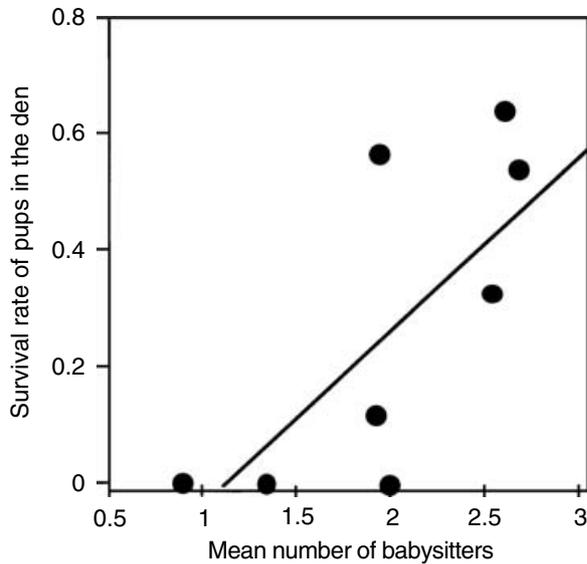
Fig. 1. Estimated survival rate of pups in the den *vs* mean number of babysitters in eight packs. Each point represents a pack. Numbers above points, the number of litters for that pack. The least-squares regression is shown $(\log((y + 1) * 1000) = 0.38 + 0.33x)$.

$t^+ = 28$, $n = 8$, NS; Friedman test, females *vs* dominant males *vs* subordinate males, $\chi^2 = 0.96$, d.f. $= 2$, NS). In the morning, however, males contributed more to babysitting than females (Wilcoxon signed ranks test, males *vs* females, $t^+ = 34$, $n = 8$, $P < 0.05$) and this difference was a result of the higher contribution of subordinate males (Fig. 2b; Friedman test, $\chi^2 = 6$, d.f. $= 2$, $P < 0.05$, post-hoc analysis; Siegel & Castellan, 1988: difference in ranks females *vs* sub males $= 9$; critical difference $= 8.96$, $P < 0.05$).

**Does babysitting effort depend on reproductive status of females?**

For six litters in one pack in which females came into oestrus while pups were in the den, the relative contributions of dominance/sex categories to babysitting differed according to the reproductive status of the females. In breeding females and dominant males, there was a significant (or, for males, almost significant) reduction in relative contribution to babysitting for the days when females were in oestrus (Wilcoxon signed ranks test, females, $t^+ = 21$, $n = 6$, $P < 0.05$; dominant males, $t^+ = 20$, $n = 6$, $P = 0.06$). By contrast, there was a significant increase in the relative contribution of subordinate males (Wilcoxon signed ranks test: $t^+ = 21$, $n = 6$, $P < 0.05$). These differences in *relative* contributions to babysitting arose because during pack oestrus, the absolute attendance rate of dominant males and breeding females dropped below the average for the whole period. The absolute attendance rate of subordinate males, by contrast, rose above this average during pack oestrus (Fig. 3). This increased attendance rate by subordinate males partially compensated for the drop
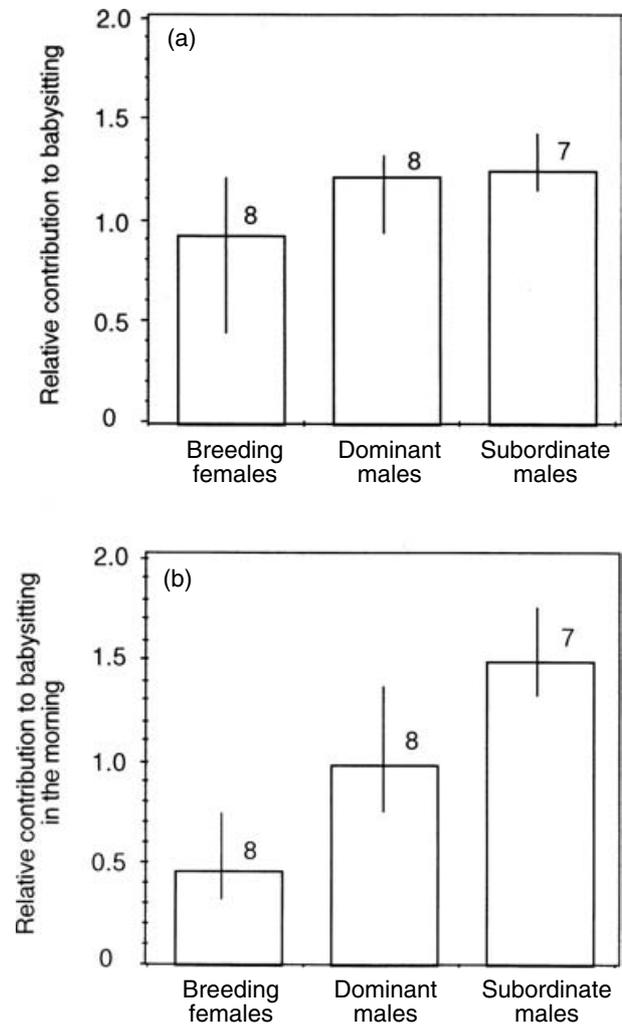
Fig. 2. Relative contribution to babysitting by individuals of different sex/dominance categories: (a) all babysitting sessions; (b) morning sessions only. Columns, medians, error bars are inter-quartile ranges; numbers above columns, number of packs. $n = 7$ for subordinate males because one pack had no individuals in this class. Subordinate females are not included as a class because, with only three exceptions, all females > 9 months old were pregnant in each of the litters used in the analysis.

in attendance by females and dominant males to some degree, so that there was no significant difference in the average attendance rate during oestrus and non-oestrus periods (Wilcoxon signed ranks test, $t^+ = 15$, $n = 6$, NS). Babysitting sessions during pack oestrus were longer than those in non-oestrus periods (oestrus, median duration $= 4.75$ h (IQR 0.7); non-oestrus, median $= 3.25$ h (IQR 0.7); Wilcoxon signed ranks test, $t^+ = 21$, $n = 6$, $P < 0.05$).

Detailed information on babysitting during pack oestrus was available for a single litter in one other habituated pack (pack 1D). One of two adult females in this pack gave birth in May 1997, and both females came into oestrus 8 days later. Before pack oestrus, the average attendance rate was 0.12 (attendances/individual/session). During the 9 days of pack oestrus, the average attendance
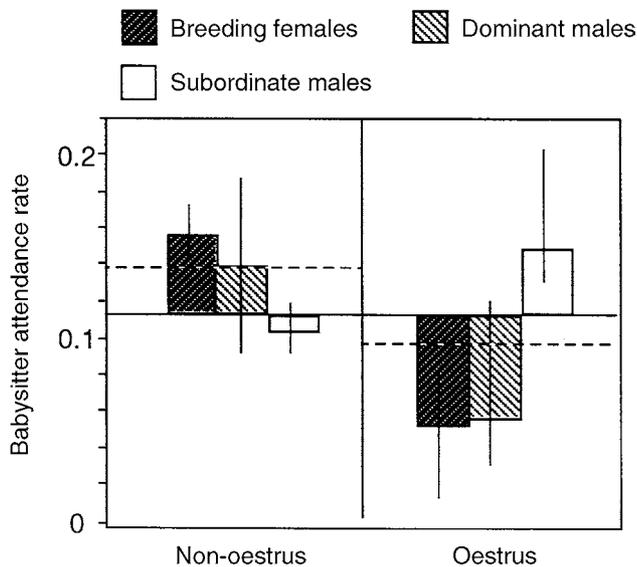
Fig. 3. Absolute babysitting attendance rates when females were in oestrus and when they were not. Columns ascend/descend from the median attendance rate across the whole babysitting period. Dashed horizontal lines, average attendance rate for non-oestrous periods (left hand side of the diagram) and oestrous periods (right hand side); columns, medians, error bars are inter-quartile ranges. Data shown are for six breeding attempts in one pack.

rate dropped by 68% to 0.038. Before the females entered oestrus, at least one babysitter was present at the den for all sessions (11/11), but over the oestrus period the den was left completely unguarded for 75% of sessions (9/12). One or more pups were alive in the den during this time, and a single pup was seen at the entrance to the den on the afternoon of day 8 of oestrus. By day 10, the pack had changed den and the litter had failed.

Top babysitters

In the most well-studied pack (pack 1Bp), 85% (±4.6) of individuals >6 months old babysat for at least one session per litter. However, the distribution of babysitting among pack members was highly uneven. In one breeding attempt, for example, one subordinate male babysat on 43% of sessions (15/35), when the average attendance rate of other males in the group was 6.7%. One male in pack 1Bp was the top babysitter for three breeding attempts in a row. In six breeding attempts, the top babysitter's contribution averaged 5.2 times the median contribution for the pack. In five out of six litters, the top two babysitters were subordinate males; in the other litter, one of the breeding females came second. Eight top babysitters (all subordinate males) ranged in age from 9 to 24 months (mean = 17.5 months). There was no difference in weight between top babysitters and other males of similar age around the time of babysitting (Wilcoxon signed ranks test, $t^+ = 28$, $n = 8$, NS). Animals were not trapped frequently enough to test whether top babysitters lost weight over the period of babysitting.

Of eight top babysitters (all subordinate males) in pack 1Bp, one became dominant within 6 months. Four were forcibly evicted from the pack along with nine other males in December 1996 (Cant *et al.*, 2001). In the new pack formed by these males, three of the four became dominant. Of the three other top babysitters, two were thrown out of the pack along with four other males in September 1997 (J. Gilchrist, pers. comm.). They subsequently dispersed away from the study area and their fate is unknown.

DISCUSSION

Banded mongooses that remained behind at the den while the rest of the pack went off to forage probably incurred some energetic costs. Some individuals babysat for protracted periods (up to 9 h), while others missed out on prime foraging opportunities for up to 5 days in a row. Previous work on suricates has shown that babysitting is associated with a substantial loss in body weight (Clutton-Brock, Gaynor *et al.*, 1998). In this study it was not possible to measure weight change of babysitters, but it seems reasonable to suppose that the foregoing of feeding opportunities will have similar, directly detectable costs in banded mongooses. Pre-emergence survivorship of pups increased with the average number of babysitters, but not with group size, which supports the hypothesis that individuals who babysit provide tangible benefits to the offspring that they guard. Babysitters have been seen to deter potential predators from approaching the den (M. A. Cant, F. Mwanhughya and E. Otali, pers. obs.), and, importantly, defend the offspring against raids by neighbouring mongoose groups (Cant *et al.*, 2001).

Overall contributions to babysitting did not differ between males and females, or dominants and subordinates. It could be argued, however, that the level of effort expended on helping might be higher for subordinate males than other dominance/sex categories. First, subordinate males contributed more than breeding females or dominant males to babysitting in the morning. These morning sessions are the longest of the day, and banded mongooses do the majority of their foraging in the morning. Breeding females were least likely to stay behind in the morning, which may reflect both their increased energetic requirements during lactation (Creel & Creel, 1991), and the importance of the morning foraging session. Second, in the most intensely studied pack, subordinate males became the principal babysitters when females were in oestrus: a time when babysitting sessions were longest and presumably the most energetically expensive. A finer-grained analysis, using the duration of babysitting sessions rather than simply their number, would help to reveal whether these differences in attendance patterns translate into differences in foraging intake. Additional data are also required to determine whether the changes in babysitting patterns observed during oestrus in one group are typical of others.

Energetic costs aside, however, the costs of babysitting during pack oestrus in terms of missed opportunities to

breed are probably much *lower* for subordinate males compared to dominant males. Oestrous females rarely stayed behind to guard the pups, and frequently stayed away for 6 h or more. They were closely and aggressively guarded all this time by dominant males, and most subordinate males had little chance of mating (Cant, 2000). Subordinate males, therefore, would forfeit little direct reproduction by remaining at the den to guard pups, whereas dominant males (who obtain more than 80% of observed matings; Cant, 2000) would stand to lose a substantial share of paternity. In obligate co-operative breeders such as banded mongooses, an individual's decision to help, and its optimum helping effort, may depend crucially on its reproductive potential within the group, with the hardest working individuals being those with the lowest chance of direct reproduction (for a model of this effect see Cant & Field, 2001). There is a clear connection here to the issue of reproductive skew (Vehrencamp, 1983; Reeve, 1991; Cant, 1998; Cant & Johnstone, 1999; Johnstone, 2000): where helping conflicts with breeding, one would expect high skew societies, in which only a few group members breed, to show greater variation in helping effort than low skew societies, in which the partitioning of direct reproduction is more equal. Similarly, in mixed sex groups like those of social mongooses, differences between males and females in helping effort may ultimately depend on sex differences in the level of reproductive skew. In support of this hypothesis, dwarf mongooses *Helogale parvula* show the opposite pattern to that observed in banded mongooses: female subordinates, who, unlike female *M. mungo*, have a lower chance of direct reproduction than male subordinates (Creel & Waser, 1994, 1997; Keane *et al.*, 1994), do the majority of babysitting (Rood, 1978; Rasa, 1987, 1989; see also Clutton-Brock, Gaynor *et al.*, 1998).

In common with observations of *S. suricatta* (Clutton-Brock, Gaynor *et al.*, 1998), there was no evidence that babysitters were coerced into providing help. Babysitters would often emerge from the den in the morning to bask and stretch with the rest of the pack, but then remain behind, without aggression, when the group moved off shortly thereafter. Rather, evidence suggests that babysitters that remain behind to guard young could gain substantial kin selected benefits. The identity of breeding females and dominant males is stable over several breeding attempts, so that young subordinate males are likely to be full or half siblings to many of the litter that they guard. Moreover, the positive relationship between the average number of babysitters and survival rate of pups, in conjunction with observations of active defence of the natal den by babysitters, indicates that babysitters do, in fact, benefit the reproductive success of the breeders they help.

Genetic relatedness *per se*, however, cannot explain why some subordinate males become 'superbabysitters', when their male littermates, who are presumably more or less equally related to the litter, contribute relatively little. Research on suricates indicates that individual differences in contributions to babysitting are not correlated with differences in relatedness to the brood (Clutton-Brock, Brotherton *et al.*, 2000). Rather, helping effort in this species is influenced by factors which affect the energetic costs of helping, namely the age and nutritional condition of helpers. In banded mongooses, there is little information on what factors are responsible for the substantial individual variation in helping effort that exists among male members of the same cohort. The propensity to babysit may to a large extent depend on an individual's energetic or nutritional state, as it does in suricates (Clutton-Brock, Brotherton *et al.*, 2000). Alternatively, babysitting may entail direct benefits to some subordinates. For example, subordinate males who are likely to become dominant in the future may gain from babysitting because this ensures that they will eventually inherit a large group ('group augmentation'; Kokko *et al.*, 2001). Ongoing studies, including feeding experiments, detailed weight measurements, and the collection of long-term data on the fate of babysitters, will help to address these possibilities.

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