

Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*

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Evolutionary explanations of cooperative breeding based on kin selection have predicted that the individual contributions made by different helpers to rearing young should be correlated with their degree of kinship to the litter or brood they are raising. In the cooperative mongoose or meerkat, *Suricata suricatta*, helpers babysit pups at the natal burrow for the first month of pup life and frequent babysitters suffer substantial weight losses over the period of babysitting. Large differences in contributions exist between helpers, which are correlated with their age, sex and weight but not with their kinship to the young they are raising. Provision of food to some group members raises the contributions of individuals to babysitting. We discuss the implications of these results for evolutionary explanations of cooperative behaviour.

Keywords: mammals; cooperation; helping behaviour

1. INTRODUCTION

Hamilton’s rule (Hamilton 1964, 1975) predicts that indirect benefits will favour the evolution of cooperation whenever $rb - c$ exceeds zero (where r is the relatedness of helpers to recipients, b is the benefits derived from help by the recipients and c is the cost of helping to the helper). While the widespread tendency for helpers to be closely related to breeders in cooperative vertebrate societies is consistent with Hamilton’s rule, more specific tests have been impeded by the difficulty of accurately measuring the costs of remaining and helping in the natal group (see Grafen 1984; Cockburn 1998). This has led a number of recent studies to test the related prediction that, where b and c vary little between individuals, differences in the level of contributions to rearing young between resident helpers should be correlated with their relatedness to breeders. Results so far are mixed: while some studies have produced evidence supporting an association between kinship and contributions to cooperative activities (Owens & Owens 1984; Reyer 1984; Curry 1988; Reeve 1992; Komdeur 1994a,b), others have found no consistent association between contributions to helping behaviour and variation in relatedness (du Plessis 1993; Piper 1994; Dunn *et al.* 1995; Delay *et al.* 1996; Magrath & Whillingham 1997).

Correlations between kinship and the level of contributions to cooperative behaviour might be absent for at least three reasons. First, where the costs of helping are very low, the net fitness benefits of adjusting contributions to the level of relatedness may be trivial (Grafen 1984; Cockburn 1998) so that discrimination between close and distant relatives is not favoured. Second, different helpers may be unable to tell close kin from distant kin or unrelated animals. And, third, underlying correlations between the level of contributions to cooperative activities

and kinship may be obscured by variation in the costs of helping to different helpers. Consequently, there is now a need to investigate the effects of kinship on contributions to cooperative behaviour in situations where helping is known to have appreciable costs and the influence of other factors is known and can be controlled for.

In this paper, we examine the relationship between contributions to babysitting by different helpers and the helpers’ relatedness to the pups they are caring for in free-ranging groups of meerkats (or suricates), *Suricata suricatta*, controlling for other factors likely to influence contributions to cooperative behaviour. Meerkats are desert-adapted, cooperative mongooses living in groups of three to 25 animals that typically include a dominant female that is responsible for more than 75% of all breeding attempts, a dominant male that fathers most of the offspring born in the group and a number of helpers of both sexes (Doolan & Macdonald. 1997a,b; Clutton-Brock *et al.* 1998a,b, 1999a,b). Dominant males and females are able to displace other individuals of the same sex from disputed sites and mark their environment (usually with anal gland secretion) four to five times as frequently as other group members. The dominant female also controls the presence of subordinate adult females in the group (Clutton-Brock *et al.* 1998b). During the first three weeks after the dominant female gives birth, one or two helpers remain at the natal burrow each day to ‘babysit’ the young when the rest of the group leaves to forage (Clutton-Brock *et al.* 1998a). Babysitters usually (though not invariably) remain at the burrow for a full day while the rest of the group is foraging and feed little or not at all during their period of babysitting. The energetic costs of babysitting are substantial and are reflected in changes in body weight: babysitters lose between 1 and 2% of body weight over the 24 h period while other group members gain around 2% (a net difference of 3–4%) and frequent babysitters lose up to 11% of body weight over the period of babysitting

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(Clutton-Brock *et al.* 1998a). Since there is a close relationship between body weight and the probability of animals breeding, weight losses as large as these may have a substantial effect on the individual's fitness.

Here, we investigate the relationship between kinship and babysitting frequency, and also examine the effects of the helper's sex, age, body weight, daily weight gain and group size on contributions to babysitting. In addition, to investigate the possibility that variation in nutrition might be an important cause of the large differences in contributions to helping behaviour that exist between individuals, we experimentally fed samples of helpers (matched with controls of the same age and sex) and investigated the extent to which feeding increased their contribution to babysitting.

2. METHODS

Our analyses were based on 56 breeding attempts by 15 different free-ranging groups of meerkats at two sites in the southern Kalahari between April 1993 and April 1998 (Clutton-Brock *et al.* 1998a, 1999c). All animals were habituated to observers and could be identified from individual characteristics or from transponders inserted soon after birth. Groups were visited daily during breeding attempts and, from the day of birth until the pups began to forage with the group, we recorded the identity of the babysitter each morning and evening. Each helper's relative contribution to babysitting was calculated as the proportion of half days when it remained at the breeding burrow during the babysitting period. In all comparisons, we excluded the principal breeding female and the principal breeding male in each group since dominant animals usually contributed little to babysitting (Clutton-Brock *et al.* 1998a). We also excluded all subordinates of less than six months for the same reason from simple comparisons (Clutton-Brock *et al.* 1998a). We subsequently repeated all simple comparisons restricting the sample of helpers to animals over 12 months and obtained the same results. Helpers and pups were weighed by inducing individuals to stand on a sand-filled tray on an electronic balance using small rewards (<0.5 g) of hard-boiled egg (Clutton-Brock *et al.* 1998a). Individuals were weighed at the start and end of each day, allowing us to measure each helper's daily weight gain for the 12-h period of activity.

Kin relationships between 114 helpers and the litters they were caring for were calculated from pedigrees derived from a parentage analysis (Marshall *et al.* 1998) based on 12 variable microsatellite loci used in combination with records of the mother of each litter and the identity of the likely father. A broader analysis of genetic relationships within groups confirms that our identification of mothers is always correct and that over 80% of pups are fathered by the resident, dominant male (Griffin 1999). Coefficients of 0.5 were assigned to full siblings; 0.25 to half siblings, aunts and uncles; 0.125 to cousins (Griffin 1999) and 0.00 to unrelated immigrants before they had bred.

Thirteen individuals in our sample were of unknown pedigree because they were born before the start of the study and kinship for these animals was estimated from an analysis of microsatellite band-sharing using the Kinship 1.2 Program (Marshall *et al.* 1998; K. F. Goodnight, personal communication), which established the most likely relationship between pairs of individuals (Griffin 1999). Most helpers were closely related to the pups that they helped to rear (average relatedness between helpers and pups calculated across eight groups was

0.24, s.e.=0.05; for male helpers it was 0.23, s.e.=0.02; for female helpers it was 0.27, s.e.=0.02) but 25% of litters were raised in groups that included at least one unrelated, immigrant helper as well as one or more related helpers.

To investigate the possibility that any effects of kinship on babysitting contributions were obscured by the effects of the helper's age, sex, weight and daily weight gain on helping behaviour, we constructed a generalized linear mixed model (GLMM) using the GENSTAT 5.3 statistical package. We used data from 31 breeding events in nine different groups, fitting the number of sessions that each helper babysat to a binomial distribution with the total number of sessions as the denominator (parents and dominant individuals were excluded from the analysis). To investigate the effects of age, we used age categories (juveniles three to six months; sub-adults six to 12 months; yearlings one to two years; and older adults greater than two years) because the exact ages of immigrants and individuals born before the start of the study were unknown. Weight was calculated as the mean of all morning weights for each helper recorded during the babysitting period. Weight change was calculated as the mean weight gain during morning foraging sessions, throughout the babysitting period, excluding days when the helper was babysitting. Preliminary analyses revealed that litter code needed to be included as a random term in the GLMM but not group identity (Schall 1991). We included all likely explanatory variables in the maximal regression model and dropped terms sequentially until the model only included terms whose elimination would significantly decrease the explanatory power of the model. The significance of terms was tested using the Wald statistic, which is distributed as χ^2 .

3. RESULTS

(a) *Babysitting contributions*

Contributions to babysitting varied widely between individual helpers: for 36 breeding attempts involving 11 groups, the most frequent babysitter was at the burrow for a median of 42% (inter-quartile range (IQR), 30–54%) of daytime during the period of babysitting while the least frequent babysitter was at the burrow for 8% (IQR, 0–22%) of the time.

(b) *Correlations between kinship and cooperative behaviour*

The large differences in the level of contributions to babysitting that existed among helpers showed no simple correlation with kinship. Across groups, the (mean) coefficient of relatedness to pups was no higher for top babysitters than for bottom babysitters (Wilcoxon test, $Z = 0.149$, $n = 20$, $p = 0.88$; figure 1a). There was no significant difference in percentage contributions to babysitting between helpers that were full siblings of the pups and all other babysitters (Wilcoxon test, $Z = 1.241$, $n = 18$ litters, $p = 0.21$; figure 1b) and unrelated immigrants did not differ significantly in the level of their contributions from related helpers (Wilcoxon test, $T = 15$, $n = 8$ litters, $p = 0.67$). Finally, within groups, there was no consistent correlation between percentage contributions to babysitting by different helpers and their coefficient of relatedness to pups: values of r_s for the rank correlation between babysitting contributions and the coefficient of relatedness calculated across helpers within breeding events were positive for 13 litters and negative for 16 litters (sign test, $p = 0.77$).

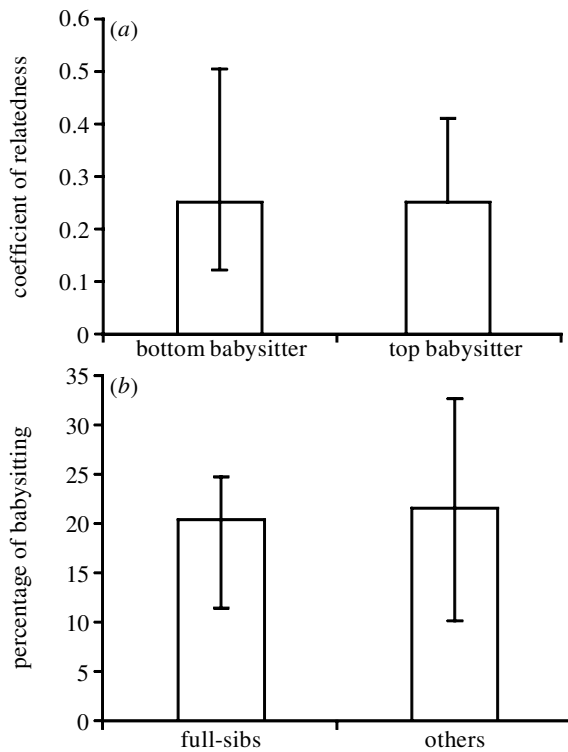


Figure 1. Effects of relatedness on contributions to babysitting in meerkats. (a) Coefficients of relatedness of the most frequent and least frequent babysitters (see §2) to the litters that they were rearing. (b) Percentage of babysitting sessions contributed by full siblings of the pups versus all other individuals (excluding parents and/or dominant animals). Median values and IQRs are shown.

Groups with pups at the burrow failed to leave a babysitter on guard (exposing the pups to attacks by neighbouring groups, snakes and other predators) for a median of 3.8% of daytime (IQR, 0–11.5%, range 0–39%, $n = 40$ litters). Across litters, there was no evidence of a relationship between the proportion of daytime that no babysitter remained with the pups and the mean coefficient of relatedness between helpers (excluding parents) and the pups they were caring for ($r_s = -0.052$, $n = 40$, $p < 0.5$).

(c) **Other factors affecting contributions to cooperative behaviour**

Our GLMM model of variation in contributions to babysitting examined the effects of the helper’s age, sex, kinship, average weight and morning weight gain as well as of litter size, which proved to have no effect on contributions and was excluded (table 1). Our model showed that the age and sex of individuals interacted to affect their contributions. Male and female sub-adults (six to 12 months) and yearlings (one to two years) contributed equally to babysitting but female juveniles and adults contributed more than males of the same age (figure 2). Among females, juveniles contributed less than sub-adults and yearlings while adults contributed the most (figure 2). In contrast, among males, both juveniles and adults contributed less than sub-adults and yearlings. The effects of age interacted with those of group size. Individuals babysat less in larger groups (where more helpers were available to contribute) but the reduction in contributions

Table 1. GLMM (Schall 1991) of factors affecting the proportion of days spent babysitting by helpers

(Interaction terms are denoted*. The directions of the effects of significant terms are discussed in the text. The significance of terms in the model were tested using the Wald statistic, which is distributed as χ^2 .)

	Wald statistic	d.f.	p
terms included in model			
age category	19.6	3	<0.001
group size	24.8	1	<0.001
age category*group size	32.5	3	<0.001
sex	0.43	1	0.53
age category*sex	21.1	1	<0.001
weight change	15.7	1	<0.001
weight	13.8	1	<0.001
terms excluded from model			
relatedness	1.13	1	
number of pups	0.00	1	0.99

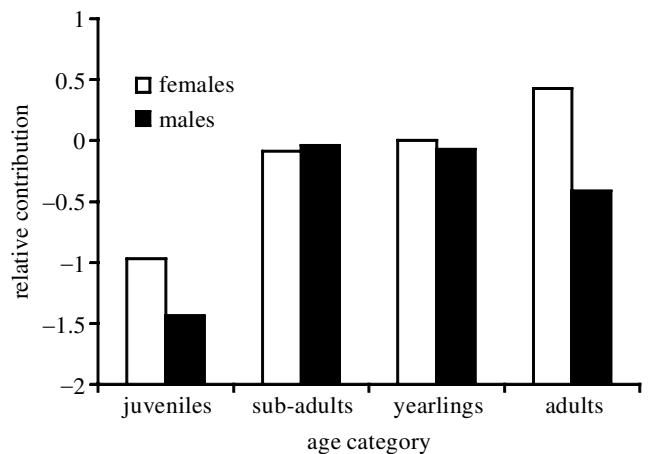


Figure 2. Relative contributions to babysitting by different age and sex categories of helpers. Histograms show the predicted values of contributions by different categories of animals in our GLMM model (table 1). Values are relative to the contribution of yearling females, which is set at zero. Juveniles, three to six months; sub-adults, six to 12 months; yearlings, 12–24 months; adults, greater than two years.

in large groups was most pronounced among sub-adults. Individual differences in weight and weight gain were also important. Heavier individuals of both sexes contributed more than lighter ones and, when this effect was controlled for, individuals that gained more weight when foraging, babysat more than those that gained less. There was no significant effect of relatedness and this was excluded from the final model (table 1).

(d) **Effects of nutrition on cooperative behaviour**

The strong relationship between contributions to babysitting and daily weight gain suggested that variation in nutrition had an important influence on cooperative behaviour. To determine whether or not this was the case, we paired one to six helpers (mean = 4.5) in six different groups with control animals of similar age and sex in the same group and fed one, randomly selected member of each pair with 25 g of hard-boiled hen’s egg each day for seven weeks following the birth of a litter. Over this

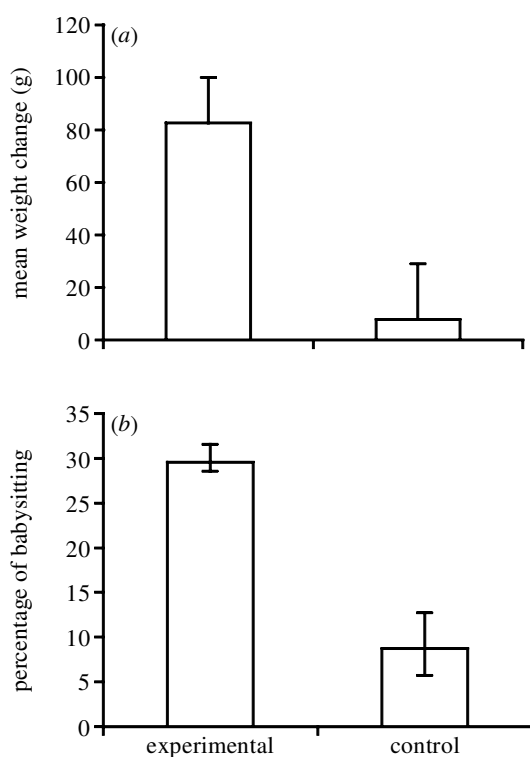


Figure 3. Effects of supplementary feeding on contributions to babysitting. Fifty per cent of helpers over six months old were fed daily with 25g of hard-boiled egg during the seven-week period of pup dependence. Controls were unfed members of the same group matched for age and sex. (a) Mean (\pm s.e.) weight change over the seven-week period of pup dependence. (b) Median (and IQR) contributions to babysitting by fed and unfed helpers.

period, fed helpers gained 82.5 ± 17.3 g while matched, unfed helpers gained 7.9 ± 21.1 g (paired t -test, $t = 5.5$, $n = 6$, $p = 0.0003$; figure 3a). Median contributions to babysitting by fed helpers, calculated as the percentage of the total number of babysitting bouts performed by all group members, were around three times higher (median = 30%; IQR 29–32%) than median contributions by unfed helpers (median = 9%; IQR 6–13%; Wilcoxon test, $T = 0$, $n = 6$, $p < 0.05$; figure 3b).

4. DISCUSSION

Our results provide no indication that the large differences in contributions to babysitting that exist among helpers are related to differences in their kinship to the litter they were caring for: there was no consistent correlation, within groups, between the contributions made by different helpers and their relatedness to breeders or pups and unrelated immigrants contributed as much as close relatives. In addition, there was still no association between the level of contributions to cooperative behaviour and kinship when controlling for the effects of litter and group size and the helper's age, sex and weight (table 1). Our results indicate, instead, that the large differences in levels of cooperative behaviour that exist among helpers are related to factors likely to affect the costs of helping, including the helper's age, weight and daily weight gain. Experimental feeding of some helpers showed that fed helpers increased the level of their contri-

butions. These results are similar to recent studies of white-winged choughs, *Corcorax melamporos*, which show that providing food for all group members raises contributions by younger animals (Boland *et al.* 1997).

The absence of correlations between kinship and the level of contributions to cooperative behaviour contrasts with the results of two previous studies of social mammals. In brown hyenas, *Hyaena brunnea*, Owens & Owens (1984) found an association between the frequency with which helpers brought food to cubs and their relatedness to the litter, while Reeve (1992) found that, in captive groups of naked mole-rats, *Heterocephalus glaber*, helpers closely related to the litter were most likely to remain active when the queen was removed. This apparent contrast could suggest that cooperative mammals vary in the effect of kinship on helping frequency. However, Owens & Owens' (1984) study was based on data derived from a single group of hyenas and their data were inadequate to support the conclusion that individual differences in helping behaviour were significantly related to kinship. In addition, Reeve's results could have arisen because the removal of the breeding female had less effect on the activity of younger, smaller (and, coincidentally, more closely related) helpers than on that of older and larger ones (see Sherman *et al.* 1991). Other attempts to relate variation in helping behaviour to kinship in naked mole-rats have found no obvious correlation (Jacobs & Jarvis 1996). Firm evidence of close associations between levels of helping behaviour and kinship in other social vertebrates is also scarce (Woolfenden & Fitzpatrick 1984; Brown 1987; Curry 1988; Ligon & Ligon 1988; Cockburn 1998) though helpers in Seychelles warblers, *Acrocephalus sechellensis*, contribute more heavily to feeding young when they are assisting their parents (Komdeur 1994a).

While the absence of consistent associations between proximity of kinship and relative contributions to cooperative behaviour provides no support for explanations of cooperation based on kin selection, it does not exclude the possibility that benefits to kin play an important role in the evolution and maintenance of cooperative behaviour. However, none of the three reasons proposed for an absence of association between contributions and kinship that we describe above (see §1) provides a satisfactory explanation. Our previous work (Clutton-Brock *et al.* 1998a) suggests that the energetic costs of babysitting are substantial; although resident helpers may conceivably be unable to differentiate between close and distant kin, this argument cannot satisfactorily explain why unrelated immigrants contribute as much as close relatives; and controlling for factors likely to affect the costs of helping (including the helper's age, weight and daily weight gain) fails to reveal any association between kinship and babysitting contributions. Future studies of cooperative breeding might usefully investigate whether the direct benefits that helpers gain from cooperation could be sufficient to maintain this behaviour. The widespread tendency for helpers to join close relatives in preference to distant relatives or non-kin (Emlen & Vehrencamp 1983; Emlen 1990, 1997) does not necessarily exclude this possibility, for helpers may commonly derive direct benefits by joining close relatives (including greater familiarity with the territory or may be more likely to be tolerated by close kin with which they have established social relationships).

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