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Counting the costs: the evolution of male-biased care in the cooperatively breeding banded mongoose

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In cooperatively breeding vertebrate societies, male and female helpers commonly vary in how much they invest in cooperative activities. Most explanations for this phenomenon centre on sex differences in the fitness benefits that helpers accrue through providing care, and few studies have explored how sex differences in the costs of helping are likely to influence how much care males and females provide. I investigated helper contributions in the banded mongoose, *Mungos mungo*, and asked whether differences in the way that helping trades off against male and female reproductive success can explain sex biases in helping effort. Contributions to the two main pup care activities were strongly male biased, and helping resulted in both sexes losing weight in the short term. This weight loss is unlikely to reduce the breeding success of males, as, although heavy males are more likely to gain access to oestrous females, any weight lost through helping can be regained before the next oestrous event. Furthermore, males less than 2 years old rarely gain access to oestrous females regardless of their body weight. Short-term reductions in body weight are likely to be more costly for females as the helping period coincides with conception and gestation of the next litter, and weight loss at this time is likely to reduce their probability of breeding successfully. These results suggest that male-biased care in this species has arisen because males and females differ in the way that helping trades off against their reproductive success.

Keywords: alloparental care; banded mongoose; cooperative breeding; fitness; helping; *Mungos mungo*; sex bias

In cooperatively breeding vertebrate societies, where individuals provide care to offspring that are not their own, male and female helpers commonly differ in the amount they invest in cooperative activities (Cockburn 1998). In most cooperative birds and some cooperative mammals, male helpers provide most of the offspring care (Stacey & Koenig 1990; Sanchez et al. 1999; Allaine et al. 2000), whereas in other cooperative birds and mammals, helper investment is predominantly female biased (e.g. Rood 1978; Koenig et al. 1983; Komdeur 1996; Clutton-Brock et al. 2002; Berg 2005). The widespread phenomenon of sex-biased helper investment is thought to arise because males and females differ in the benefits they accrue through providing care (Cockburn 1998; Clutton-Brock et al. 2002). For example, there is evidence from Florida scrub-jays, *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1984) and meerkats, *Suricata suricatta* (Woolfenden & Fitzpatrick 1984; Clutton-Brock et al. 2002) that help is provided predominantly by the philopatric sex, perhaps because helpers of the philopatric sex stand to benefit more from rearing additional group members. Sex-biased investment may also arise through sex differences in variance in reproductive success (Koenig et al. 1983), or parentage uncertainty (Charnov 1981), both of which influence the benefits that males and females can gain from helping (for a review of other hypotheses see Cockburn 1998).

When attempting to estimate the fitness benefits available to male and female helpers, however, it is important to consider whether the costs of providing care (in terms of lost reproductive opportunities) differ between the sexes. If helping trades off against the reproductive success of one sex more than the other, this could reduce the net benefits of providing care to that sex, resulting in sex-biased helping effort (Cant 2003). For example, if helping entails an energetic cost then it may pay the sex that has a higher probability of reproducing successfully to invest less in helping and conserve energy for direct reproduction

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(Heinsohn 2004). Similarly, if body mass is more important for successful reproduction in one sex than the other, perhaps because of the high cost of gestation and egg production in females (Clutton-Brock et al. 1989; Monaghan et al. 1998) or because of its role in competition for mates in males (Plavcan & Van Schaik 1997), then that sex would be expected to contribute less to cooperative care. Although a number of studies of cooperative breeders have shown that helping is energetically costly (reviewed in Russell et al. 2003; Heinsohn 2004), few have considered how energetic costs translate into reduced reproductive success, or whether this differs for male and female helpers. These trade-offs are likely to be particularly important in species with low reproductive skew, where helpers regularly breed, but may still play a role in high-skew societies if helping reduces the probability that an individual will attain the breeding role in the future. To date, however, the importance of reproductive costs in explaining sex biases in helping effort remains largely unexplored.

I investigated sex differences in helper investment in the banded mongoose, *Mungos mungo*, a cooperatively breeding carnivore with low reproductive skew. Banded mongooses live in stable groups of 8–40 individuals (Cant 2000), although groups can temporarily be as large as 70. Groups breed up to four times per year and during each breeding attempt multiple females come into oestrus in synchrony and mate with multiple males within the group (Cant 2000). After a 63-day average gestation period, 1–10 females give birth synchronously to a communal litter of up to 16 pups. All group members assist in rearing pups by ‘babysitting’ them at the natal den for the first 4 weeks of life (Cant 2003) and by provisioning pups with food items until they are able to forage independently (Gilchrist 2004; Hodge 2005). As oestrus occurs postpartum (10 days after birth on average), the period of pup care coincides with conception and gestation of the next litter. Both sexes regularly breed in their natal group, and body mass has a positive influence on reproductive success in both males and females (Cant 2000; Gilchrist et al. 2004). Females that are relatively heavy for their age at conception have a higher probability of conceiving (80%) than females that are relatively light (55%), and the growth and survival of a female’s offspring also increase with her weight at conception (Hodge 2003). In males, the heaviest individuals in the group are more likely to gain access to females during oestrus (Cant 2000).

Banded mongooses provide a good opportunity to investigate whether trade-offs between helping and reproduction can explain sex differences in care, as although body mass has a positive influence on reproductive success in both sexes, help-induced weight loss is less likely to reduce the breeding success of male banded mongooses for two reasons. First, while females begin breeding at around 1 year of age (minimum 10 months; Cant 2000), males rarely gain access to oestrous females until they are 2 years old, regardless of their body mass (Hodge 2003), so helping before the age of 2 will have little impact on their breeding success. Second, while females must maintain high body mass throughout gestation, males need do so only during oestrus, which lasts for 6 days on average (Cant 2000). If males can regain any mass lost through helping before the next oestrous event, then helping may have little impact on their reproductive success. I therefore predicted that, if helping results in short-term loss of body mass during the period of peak pup care, female banded mongooses will invest less in cooperative activities than males, because loss of body mass is more likely to reduce their reproductive success. Previous work on this species suggests that males do contribute more to babysitting than females (Gilchrist 2001; Cant 2003) but it is unclear whether this bias persists if contributions to other activities are considered. In this study I asked two specific questions. (1) Does helping result in loss of body mass in banded mongooses and, if so, can this be regained at the end of the breeding attempt? (2) How do males and females differ in their contributions to babysitting and pup feeding?

METHODS

Study Site and Data Collection

Between February 2000 and March 2002, data were collected from a population of 421 individually marked banded mongooses living in eight social groups in the Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E). Details of habitat and climate are given elsewhere (Cant 2000). All individuals in the study population were habituated to the presence of observers, allowing the collection of behavioural data from within a few metres. In five groups, individuals were trained to step on to a portable electronic balance for regular weighing. Animals were weighed in the evening, at the end of the day’s foraging session. Groups were visited approximately every 4 days to collect behavioural and life history data and, as a result, accurate ages (within 5 days) were known for the majority of the study population (87%). Individuals aged 0–3 months were classified as pups, those aged 3–6 months as infants, those aged 6–12 months as subadults, those aged 12–24 months as yearlings and those aged >24 months as adults. Individuals born before the start of the long-term study (March 1997) were aged from head width and tooth wear (Cant 2000). I refer to all individuals in the group that provided care as ‘helpers’, regardless of whether they bred in the current breeding attempt (following Jennions & Macdonald 1994; Cockburn 1998; Russell 2004). This is reasonable, as there is no evidence to suggest that potential parents preferentially care for their own offspring (Gilchrist 2004). However, in some analyses I distinguished between individuals that were unlikely to have bred in the current breeding attempt (‘nonparents’) and those that were (‘parents’).

To allow easy identification in the field, large animals that had ceased growing were fitted with colour-coded plastic collars (weighing about 1.5 g, which is less than 0.12% of the animals’ body weight; range 0.08–0.15%), and growing animals were given unique haircuts. Collars and haircuts were maintained by trapping individuals every 3–6 months, although fur could be trimmed with scissors without the need for capture in well-habituated groups. Individuals were captured in box traps (Tomahawk

Live Trap Co., Tomahawk, WI, U.S.A.) which were baited with small pieces of fish, and placed beneath dense bush to provide shade and protection. Traps were set at dawn and checked at regular intervals (maximum 2 h) until most group members had been captured. All traps were closed by 1600 hours. Trapped individuals were anaesthetized with an intramuscular injection of 1 mg/kg of ketamine (Vetalar: Veterinary Drug Co., York, U.K.) and 0.8 mg/kg of medetomidine (Domitor: Veterinary Drug Co., York, U.K.). After processing (typically 10 min) captured animals were injected with 0.8 mg/kg atipamezole (Antisedan: Veterinary Drug Co., York, U.K.) to reverse the effects of the medetomidine and placed in a covered trap to recover before being released at the trap site. This trap method was used successfully 1107 times to trap 392 individuals with no detectable adverse effects on the animals. Permission to conduct this research was given by the Ugandan Council for Science and Technology and trapping procedures and research methods were approved by the Ugandan Wildlife Authority.

Data Collection

All data were collected during the 'pup care period' which began when pups were born and ended when they were 3 months old and able to find much of their food independently. For the first month of life, pups remain at the natal den and are guarded by one or more helpers, termed 'babysitters', while the rest of the group forages (the 'babysitting period'). Throughout the babysitting period, groups were visited during the morning foraging session and any temporarily absent individuals were recorded as babysitting. This method is effective as banded mongooses have never been observed to leave the group on short-term prospecting forays. An individual was classified as babysitting only if the group was visited for more than 15 min, and the main group was more than 100 m away from the natal den. At approximately 27 days of age (range 18−38, $N = 19$ litters), pups begin to accompany the group on foraging trips. As they are initially incapable of finding their own food, they are provisioned with prey items, mainly burrowing invertebrates, by older group members (Hodge 2005). During this 'pup-feeding period' (which began when pups first foraged with the group and ended when they were independent at 3 months), I recorded when an adult fed a prey item to a pup ad libitum. Analyses of contributions to both babysitting and pup feeding were restricted to those breeding attempts in which more than 10 full mornings of data were collected.

Statistical Analysis

The majority of analyses required multivariate statistics, which were performed in Genstat 5.4.2 (Lawes Agricultural Trust, Rothamsted, Harpenden, U.K.). As most multivariate analyses involved repeated sampling of individuals, litters or groups, I used linear mixed models (LMMs) and generalized linear mixed models (GLMMs). These are similar to general(ized) linear models, but allow both fixed and random terms to be included. Normally distributed data were analysed with LMMs with an identity link function, and binomial and Poisson data were analysed with GLMMs with a logit and log link function, respectively. In all mixed models, variance components were estimated by using the restricted maximum likelihood (REML) method, and random terms were retained in the model unless variance components were zero. All potential explanatory terms were dropped sequentially until only those terms that explained significant variation remained. Once the minimal model had been established, each dropped term was then put back into the minimal model to obtain its level of nonsignificance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested, but results are presented only for those that were found to explain significant variation. All statistical tests were two tailed. Unless otherwise stated, means are quoted ± 1 SE.

Helping and Weight Loss

Helper contributions and weight changes

To investigate whether care entails an energetic cost, I tested whether the amount of care provided by an individual influenced its daily change in body mass during the breeding attempt. I calculated the change in body mass (g/day) of helpers throughout the babysitting and pup-feeding periods by taking the gradient of the regression line between an individual's age (in days) and evening weight during the period under consideration. I calculated changes in body mass both during the babysitting period over the first 30 days after pups were born and during the pup-feeding period over the first 30 days after pups began foraging with the group (as this is the period when pup feeding is most intense). Daily changes in body mass were calculated only for individuals that were weighed more than four times during the period under investigation, and were not calculated for pregnant or lactating females. Regressions between age and mass were linear during both the babysitting and pup-feeding periods.

The influence of helper contributions on daily changes in body mass was analysed with two LMMs. For the babysitting period, 118 daily changes in body mass from 43 individuals were fitted as the response variable, and the number of days the individual spent babysitting was fitted as the main fixed effect. For the pup-feeding period, 103 daily changes in body mass from 37 individuals were fitted as the response variable and the individual's contribution to pup feeding (feeds/h) was fitted as the main fixed effect. Contributions to both babysitting and pup feeding were categorized as 'low' (bottom third), 'medium' (middle third) and 'high' (upper third) and included as a categorical variable. Both models controlled for the potential confounding influences of mass at the start of the relevant helping period (g), sex, rainfall during the relevant helping period (mm), age (months), litter size at emergence, and group size (total group members > 3 months). Only individuals older than 6 months were included in these analyses. For the babysitting period, the number of days spent active during oestrus was also fitted as a covariate, as the oestrous period generally coincides with babysitting and may influence growth. Individual and litter identity were fitted to both models as a random term, but group identity was omitted as the variance component was zero.

Regaining weight after helping

To investigate changes in body mass across breeding attempts, I divided the pup care period into 2-week blocks, and compared the mass of individuals at the end of the 2-week block with their mean mass in the week before the litter was born. This provides a measure of how an individual's mass changed across the pup care period. To control for the possibility that an individual's mass changed across the pup care period for reasons other than helping (e.g. because of variation in rainfall, food availability, etc.), I looked at the difference in the change in mass between an individual that provided a lot of care (top helper) and one that provided little (bottom helper). All pairs were the same age (within 50 days) and sex and none were observed actively mate guarding during the oestrous periods of any of the litters investigated. To investigate whether helpers were likely to regain mass at the end of the breeding attempt, I used paired *t* tests to test whether top helpers were significantly lighter than bottom helpers during the peak pup care period (8 weeks after birth) and at the end of the breeding attempt when pups were less reliant on helpers (8–12 weeks after birth).

Sex Differences in Helper Investment

To investigate whether male and female banded mongooses differ in levels of helper investment, I began by looking at the overall influence of age and sex on contributions to babysitting and pup feeding. I ran two GLMMs on (1) 433 individual contributions to babysitting by 104 individuals over 22 breeding attempts in six groups and (2) 253 individual contributions to pup feeding by 81 individuals over 10 breeding attempts in three groups. For the babysitting analysis, the number of days that each individual babysat a given litter was fitted as the binomial response term, with the number of possible babysitting days as the binomial denominator. For the pup-feeding analysis, the average number of feeds given per 3-h period (rounded to the nearest whole number) for each individual was fitted as the response term in a GLMM with a Poisson error structure. The age category (infant, subadult, yearling, adult) and sex of the individual were fitted as the main fixed effects. The following terms were fitted as covariates: mass at the start of the pup care period (controlled for age); rainfall during the pup care period (mm); litter size at emergence; and group size (total group members > 3 months). The contribution of the helper to babysitting (total number of days spent babysitting the litter that was being fed) was also included as a potential explanatory term in the feeding analysis, to investigate whether contributions to the two helping activities were correlated. Individual and litter identity were fitted to both models as random terms, but group identity was omitted as the variance component was zero. As the aim of these analyses was to investigate specifically the influence of age and sex, I do not mention the significance of other terms included in the model, but details are provided in the legend for Fig. 3a, b in the Results.

I then looked in detail at whether the factors that influence helper contributions differ for male and female helpers by conducting the GLMMs described above for yearling and adult individuals separately. Analysing yearlings and adults separately allowed a comparison of the factors that influence helper contributions when only females are able to breed (yearlings) and when both sexes are able to breed (adults). For yearlings, analyses included the same terms as described above. For adults, parental status (whether a helper could be a parent to a pup in the litter) was included as an additional fixed effect. Females that were confirmed pregnant before the birth of the litter and males that were observed mate guarding during the oestrous period before the birth of the litter were considered to be potential parents. Parental status was not included for analysis of yearling helper contributions, as only females could be potential parents. Full details of sample sizes for these analyses are given in Tables 1 and 2 in the Results. I also conducted an additional analysis on females, to investigate the influence of current pregnancy status on contributions to pup feeding. 'Pregnant' refers to those females that were pregnant during the pup-feeding period, and 'nonpregnant' refers to those females that were not. This GLMM was conducted on 53 pup-feeding contributions by 17 females over 11 breeding attempts in three groups.

Helper feeding experiment

To investigate possible sex differences in the effect of helper hunger levels on contributions to pup feeding, I conducted a supplementary feeding experiment. On day 1, two observers conducted simultaneous 30-min focal watches on two individuals of the same age and sex. Any food items consumed or fed to a pup were recorded. The following day, one individual of the pair was selected randomly and fed with approximately 100 g of dried fish before the morning foraging session. Fifteen minutes later, focal watches were conducted on both individuals as before. I compared the proportion of food items found that were fed to pups on experimental and control days for fed and unfed individuals of both sexes.

RESULTS

Helping and Weight Loss

Helper contributions and weight changes

Individuals that invested heavily in babysitting lost body mass during the babysitting period compared to individuals that invested less (LMM: $\chi^2_2 = 33.79$, $P < 0.001$; Fig. 1), after I controlled for a significant negative influence of age ($\chi^2_1 = 6.36$, $P = 0.012$) and a negative influence of group size ($\chi^2_1 = 17.83$, $P < 0.001$). Similarly, individuals that invested heavily in pup feeding had significantly different rates of weight change from those

Table 1. Factors affecting contributions to babysitting and pup feeding in yearlings

	Babysitting (days/breeding attempt)			Pup feeding (feeds/3 h)		
Explanatory terms	Effect size±SE	χ^2	P	Effect size±SE	χ^2	P
Age (months)	0.11±0.023	**24.34**	<**0.001**	0.041±0.024	2.70	0.10
Sex						
Female	See Fig. 4	**16.81**	<**0.001**	0±0	**11.29**	**0.001**
Male	See Fig. 4			1.45±0.43		
Mass						
Heavy	See Fig. 4	**13.74**	<**0.001**	0±0	**5.46**	**0.019**
Light	See Fig. 4			−0.57±0.24		
Rainfall (mm)	−0.002±0.005	0.21	0.65	−0.002±0.002	0.41	0.52
Group size	−0.052±0.032	2.64	0.10	−0.017±0.027	0.41	0.52
Litter size	0.060±0.036	2.68	0.10	0.015±0.043	0.13	0.74
Babysitting contribution	N/A	N/A		0.066±0.035	3.57	0.059
Sex*mass	See Fig. 4	**5.51**	**0.019**	—	—	—
Constant	−3.88±0.05			−1.30±0.41		

Babysitting analysis was conducted on 159 babysitting contributions by 79 individuals over 20 breeding attempts in six groups. Pup-feeding analysis was conducted on 141 pup-feeding contributions by 53 individuals over 11 breeding attempts in three groups. Group, litter and individual identity were included as random terms. The term 'mass' is the residual of weight taken against age (residuals were calculated for males and females separately). Light animals are relatively light for their age and heavy animals are relatively heavy for their age. Significant terms are highlighted in bold.

that invested little ($\chi^2_2 = 10.19$, $P = 0.006$; Fig. 1). None of the other terms included had a significant influence on changes in body mass in either the babysitting or pup-feeding period.

Regaining weight after helping

Most weight loss occurred during the first 8 weeks of the pup care period (Fig. 2). Top helpers were significantly lighter than bottom helpers during the first 8 weeks of pup care (paired *t* test: $t_{26} = -6.01$, $P < 0.001$), but there was no significant difference by the end of the pup care period when pups were receiving less care ($t_{14} = 0.62$, $P = 0.55$).

Sex Differences in Helper Investment

General patterns of care

Contributions to the two main pup care activities were strongly male biased. With the exception of infants, males contributed more to babysitting than females across all age categories (GLMM: $\chi^2_1 = 27.13$, $P < 0.001$; Fig. 3a). Males also contributed more than females to pup feeding ($\chi^2_1 = 8.10$, $P = 0.004$; Fig. 3b) although this effect of sex was strongest in subadults and yearlings, with no difference between the investment levels of male and female adults (Fig. 3b). Yearling males invested more than any

Table 2. Factors affecting contributing to babysitting and pup feeding in adults

	Babysitting (days/breeding attempt)			Pup feeding (feeds/3 h)		
Explanatory terms	Effect size±SE	χ^2	P	Effect size±SE	χ^2	P
Age (months)	−0.011±0.007	2.32	0.13	−0.023±0.011	**4.15**	**0.042**
Sex						
Female	0±0	**11.14**	<**0.001**	0±0	1.37	0.24
Male	1.01±0.30			0.62±0.53		
Mass						
Heavy	0±0	1.32	0.25	0±0	0.26	0.61
Light	0.33±0.28			0.19±0.37		
Rainfall (mm)	−0.002±0.002	0.45	0.50	−0.01±0.005	3.66	0.056
Group size	−0.009±0.002	0.13	0.72	0.075±0.045	2.79	0.10
Litter size	−0.007±0.003	0.06	0.81	−0.004±0.091	0.00	0.96
Babysitting contribution	N/A	N/A		0.99±1.87	0.28	0.60
Parent						
No	0±0	**5.64**	**0.018**	0.44±0.48	0.83	0.36
Yes	0.67±0.28					
Constant	−4.054±0.34			−0.63±0.39		

Babysitting analysis was conducted on 293 babysitting contributions by 59 individuals over 21 breeding attempts in six groups. Pup-feeding analysis was conducted on 100 pup-feeding contributions by 26 individuals over 11 breeding attempts in three groups. Group, litter and individual identity were included as random terms. The term 'mass' is the residual of weight taken against age (residuals were calculated for males and females separately). Light animals are relatively light for their age and heavy animals are relatively heavy for their age. Significant terms are highlighted in bold.

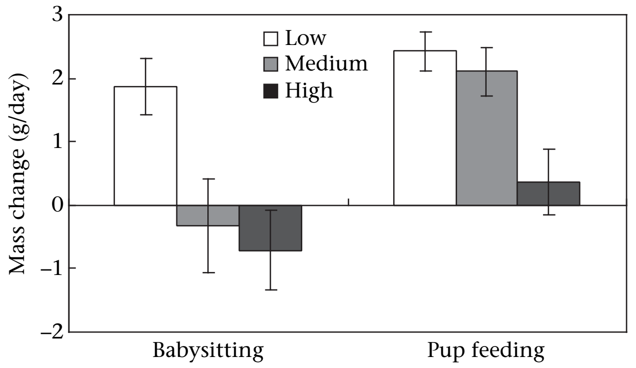

Figure 1. The effects of contributions to helping (low, medium, high) on rates of daily mass change during the babysitting and pup-feeding periods. Means ± SEs predicted from two linear mixed models are shown. Individual and litter identity were included as random terms.

other age or sex category to both babysitting and pup feeding (Fig. 3a, b).

Within age and sex classes, some individuals invested disproportionately more in helping than others. These ‘super-helpers’ contributed over five times as much as other group members. The mean ± SD number of days that individuals over 3 months old babysat per litter was 1.24 ± 2.34, and the mean number of times individuals fed pups/3 h ± SD was 0.26 ± 0.41. The top helper for each litter, however, babysat for 7.41 ± 3.98 days on average ($N = 22$ litters) and fed pups 1.36 ± 0.42 times per 3-h period ($N = 11$ litters). For all litters the top babysitter and pup feeder were male.

Helping effort in yearlings

After I controlled for the influence of age and sex (Table 1), contributions to babysitting by yearlings were strongly associated with their body mass (Table 1). However, mass affected contributions to babysitting differently in males and females: males that were relatively heavy contributed

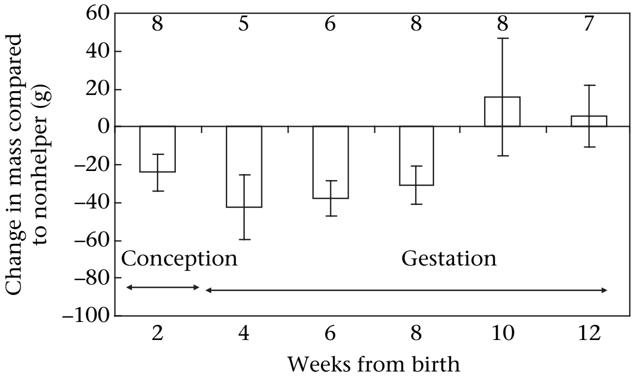

Figure 2. The change in body mass of the top helper in each litter in comparison to a nonhelper at different stages during the pup-feeding period. Sample sizes (number of pairs) are given for each 2-week period. Means ± SEs are shown. Arrows indicate the approximate timing of conception and gestation in relation to the pup care period.

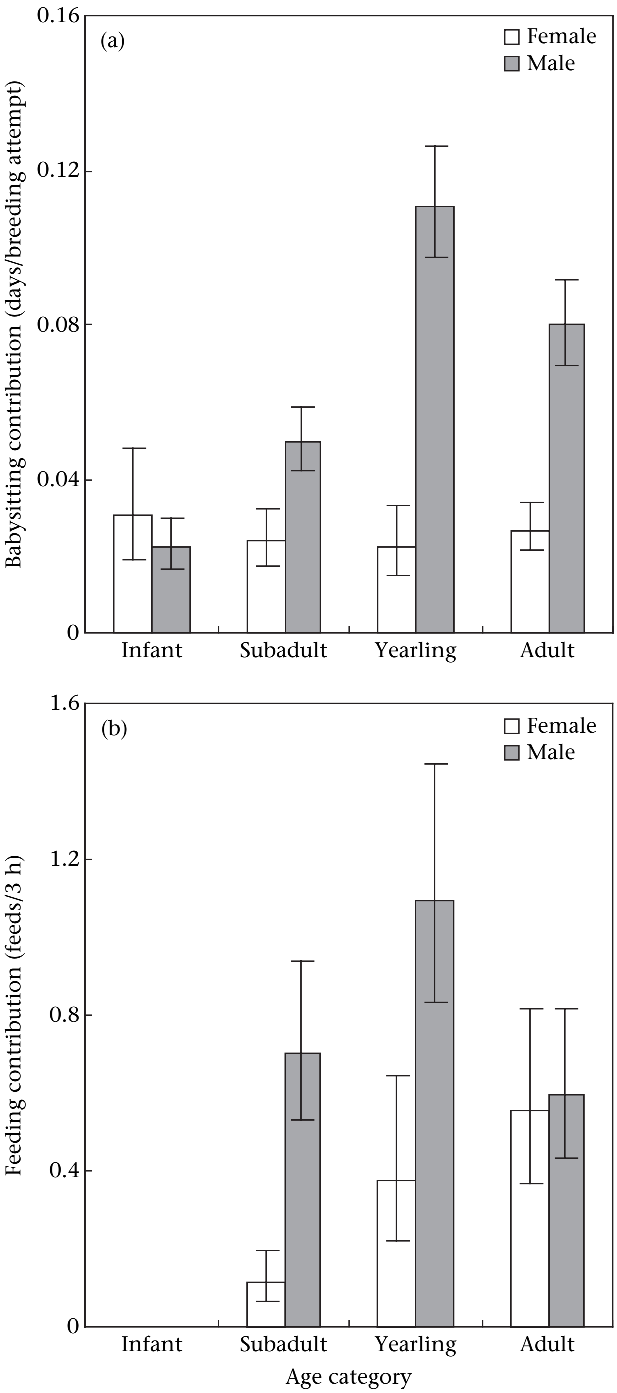

Figure 3. The influence of age and sex on the contributions made to (a) babysitting and (b) pup feeding. (a) Means ± SEs predicted from a generalized linear mixed model (GLMM) controlling for the significant negative influence of helper number (GLMM: $\chi^2_1 = 4.14$, $P = 0.042$). Litter size, rainfall and weight were included in the model, but had no significant influence on contributions to babysitting. (b) Means ± SEs predicted from a GLMM. Helper number, litter size, rainfall, weight and babysitting contribution were included in the model, but had no significant influence on contributions to pup feeding. Litter and individual identity were included as random terms in both analyses.

more to babysitting, whereas females that were relatively heavy contributed little (Table 1, Fig. 4). Heavy yearlings of both sexes also contributed more to pup feeding, but there was no significant interaction between age and mass (Table 1). None of the other terms included in either model had a significant influence on the babysitting and feeding contributions of yearling individuals (Table 1).

Helping effort in adults

Adult males contributed significantly more to babysitting than adult females (Table 2). After I controlled for this effect, adult contributions to babysitting were strongly influenced by an individual's likelihood of parentage. Males and females with a high likelihood of parentage contributed more to babysitting than nonbreeding helpers (Table 2). Sex had no influence on adult contributions to pup feeding, but both male and female helpers fed pups less as they aged (Table 2). Parental status had no significant influence on contributions to pup feeding overall (Table 2), but in females, pup-feeding effort was influenced by their current pregnancy status in conjunction with their likelihood of parentage (GLMM: $\chi^2_3 = 8.41$, $P = 0.038$). Mothers that were pregnant fed less than mothers that were not, and females that had no likelihood of parentage in the current litter contributed the least (Fig. 5). None of the other terms included in the models had any significant influence on the contributions of adult individuals to babysitting and pup feeding (Table 2).

Feeding experiment

Males that were experimentally fed increased the proportion of food items fed to pups significantly more than unfed controls (paired *t* test: $t_{10} = 2.93$, $P = 0.015$; Fig. 6). It was not possible to analyse the change in female provisioning rate statistically, because most females did not feed on both control and experimental days. Of eight experimentally fed females, six did not feed pups on either the control or experimental day, one increased her contribution to pup feeding following supplemental feeding, and the other decreased it.

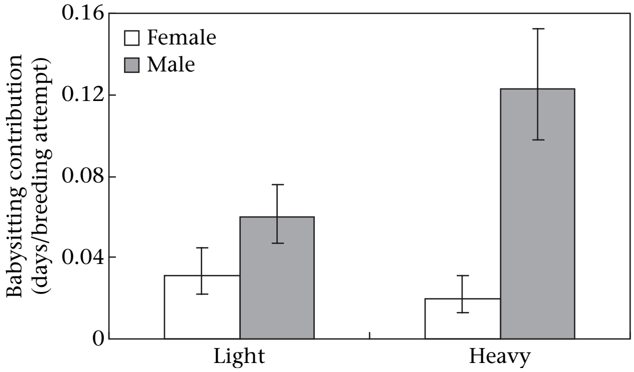

Figure 4. The influence of weight and sex on the contribution of young individuals (<1 year) to babysitting. Means ± SEs predicted from a generalized linear mixed model (GLMM) controlling for the significant influence of age are shown (GLMM: $\chi^2_1 = 23.98$, $P < 0.001$). Helper number, litter size and rainfall were included in the model, but had no significant influence on contributions to babysitting. Litter, group and individual identity were included as random terms.

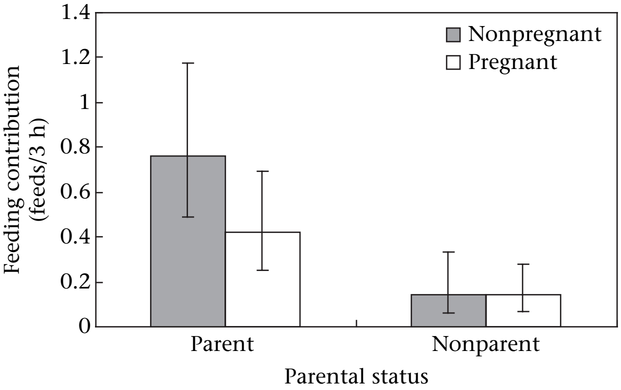

Figure 5. The influence of parental status and pregnancy on the contributions of females older than 1 year to pup feeding. Means ± SEs predicted from a generalized linear mixed model are shown. Helper number, rainfall, litter size, weight and babysitting contribution were included in the model but had no significant influence. Individual and litter identity were included as random terms.

DISCUSSION

My results indicate that in the banded mongoose, sex differences in the way that helping trades off against reproductive success can influence the amount that males and females invest in cooperative activities. Offspring care entails a short-term energetic cost, as individuals that contributed heavily to babysitting and pup feeding lost body mass relative to individuals that invested little. This change in mass occurred during the first 8 weeks of the pup care period, and as female banded mongooses conceive soon after they give birth, any weight loss at this time is likely to reduce both their likelihood of becoming pregnant (Gilchrist et al. 2004) and the growth of their offspring during gestation (Hodge 2003). Loss of body mass at this time is less likely to influence the breeding success of young males, as males rarely gain access to oestrous females until they are 2 years old, regardless of how heavy they are (Hodge 2003). Helping is therefore likely to reduce the reproductive success of females more than that of young males, which may explain why helper contributions in the banded mongoose were strongly male biased and why young males provided most of the care.

Although helping is unlikely to reduce the reproductive success of young males, loss of body mass before the oestrous period may still reduce the breeding success of adult males, as relatively heavy males are more likely to gain access to fertile females (Cant 2000). However, my results suggest that older males reduce the impact of helping by providing care only when it is unlikely to reduce their reproductive success. Older males reduced their contributions to cooperation during pup feeding, which may have allowed them to regain any mass lost before the next oestrous period. In addition, there is evidence that although older males invest heavily in babysitting, they

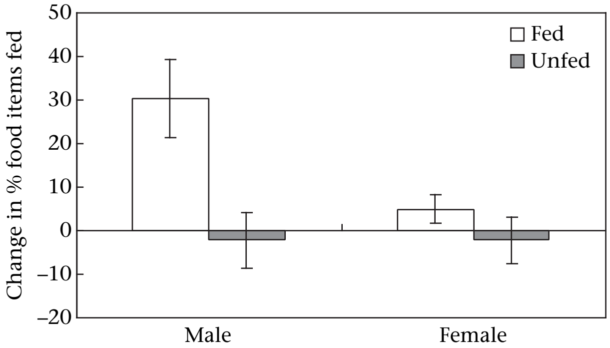

Figure 6. The change in the percentage of food items fed to pups between control and experimental days for fed and unfed males ($N = 11$ pairs) and females ($N = 9$ pairs). Means ± SEs are shown.

rarely babysit when females are in oestrus (Cant 2003), as this would reduce their opportunity to mate with fertile females. During this time subadult males with no possibility of successful reproduction are responsible for babysitting pups at the den (Cant 2003).

Although males are unlikely to breed before they are 2 years of age, the amount of care they provide when young may influence their future reproductive success. There is now evidence from several species that care provided early in life can have negative downstream effects over an individual's lifetime. For example, generous helpers show reduced survival in stripe-backed wrens, *Campylorhynchus nuchalis* (Rabenold 1990) and, in meerkats, individuals that provide a lot of care in the first 2 years of life are smaller in adulthood (Russell et al. 2003). The amount of care that male banded mongooses provide is unlikely to reduce their mass in the long term, however, as top helpers were able to regain much of the weight that they lost at the end of the pup care period. This suggests that individuals can compensate for any mass lost by foraging more intensively once pups are less dependent on care. Furthermore, even if males are not able to compensate fully within the same breeding attempt, the fact that helper contributions during the first 2 years of life are condition dependent is likely to minimize mass loss in the long term.

Differences in the likelihood of successful reproduction may explain why male and female banded mongooses responded differently to increases in food abundance and body condition. Males that were relatively heavy contributed more to babysitting, the most costly pup care activity, whereas relatively heavy females invested little. In addition, males increased their contribution to pup feeding in response to supplemental feeding whereas females did not. This may be because females can begin breeding in their first year, so are likely to benefit from investing any additional energy in reproduction rather than helping. These findings present a striking contrast to meerkats, where females that were fed as pups increased their helping rate, and females that were in good condition in their first year of life increased their helper contributions, but males did not (Clutton-Brock et al. 2002). This may be because meerkat males, unlike females, begin to conduct extraterritorial prospecting forays in their first year (Young et al. 2005), and may therefore benefit from conserving energy in preparation for the costs of prospecting and dispersal (Clutton-Brock et al. 2002). It appears, therefore, that in both banded mongooses and meerkats, sex differences in helping effort are influenced by the way that helping will trade-off against current or future reproductive success.

Can differences in philopatry explain male-biased care in the banded mongoose? While there is some evidence that banded mongoose females disperse more frequently than males (Hodge 2003), both sexes have the potential to become breeders in their natal group, and consequently both males and females are likely to gain similar benefits through group augmentation. Further work on dispersal is required to investigate fully the influence of philopatry on patterns of care in banded mongooses, but even if differences do exist, it seems unlikely that they could explain the extreme sex bias in care observed in this study. Instead, I suggest that male-biased care in the banded mongoose arises because helping reduces the reproductive success of females to a greater extent than that of males.

The extent to which sex-biased care may be influenced by differences in reproductive costs in other species is difficult to assess, as patterns are likely to be obvious only in the short term in species where reproductive skew is low. There is some evidence from low-skew joint-nesting birds that males contribute more than females to energetically costly overnight incubation, perhaps because this allows females to conserve energy for future egg production (Vehrencamp 2000). There is also some evidence from long-term studies in high-skew societies that the costs of care can generate sex differences in helping effort. For example, although nonbreeding female acorn woodpeckers, *Melanerpes formicivorus*, invest more in cooperative care than males, females reduce their investment earlier, perhaps because females disperse earlier than males and must conserve energy in preparation (Koenig et al. 1983). Female meerkats also reduce their contributions to cooperation as their likelihood of reproducing as a subordinate increases (Clutton-Brock et al. 2002). These results emphasize the need to understand fully how helping will influence the current and future reproductive success of male and female helpers if we are to gain a clear idea of the evolution of sex-biased care in cooperative animal societies.

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