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Who cares? Individual contributions to pup care by breeders vs non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*)

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Abstract Knowledge of the investment rules adopted by breeders and non-breeders, and the factors that affect them, is essential to understanding cooperative breeding as part of a life-history tactic. Although the factors that affect relative contributions to care of young have been studied in some cooperative bird species, there is little data on mammals, making coherent generalisations within mammals and across taxa difficult. In this study, we investigate individual contributions to pup escorting, a strong predictor of offspring provisioning, in the banded mongoose (*Mungos mungo*), a cooperatively breeding mammal in which reproductive skew is low. Contributions by those under a year old (which virtually never breed) increased with age and body weight but were generally low. Among older age classes (yearlings and adults), individuals that had not bred in the current litter generally contributed less to escorting than those that had bred (with the exception of yearling males). In addition, females that did not breed reduced their investment if they were heavy presumably because such females are more likely to breed in the following event and benefit from saving resources for this. The generally greater contributions by breeders in banded mongooses contrast with the recent findings in meerkats (*Suricata suricatta*), another obligatorily cooperative mongoose with similar group size but wherein reproductive skew is high. Our results suggest that relative contributions by breeders vs non-breeders are not dependent on group size but on the ratio of breeders to carers and the probability that non-breeders will breed in the near future.

Keywords Communal breeding · Contributions to care · Meerkats · Optimal investment · Reproductive skew

Introduction

In cooperative breeding species, group members contribute care to young that are not their offspring. Groups generally contain breeders and non-breeders within any one reproductive event. The reproductive role division within such groups is likely to affect the investment rules that govern contribution to care of young. Although investment rules of breeders and non-breeders have received some detailed attention in cooperative birds (Hatchwell 1999), we still know very little about investment rules in cooperative vertebrates in general (Heinsohn and Legge 1999; Heinsohn 2004) and in cooperative mammals in particular (Clutton-Brock et al. 2003, 2004; Russell 2004).

Breeders might be expected to show behavioural adaptations to their role as the reproductives in the group by reducing contributions to offspring rearing and maximising contributions to offspring production. This is certainly the case in the eusocial insects, and within vertebrates, the naked mole rat (*Heterocephalus glaber*) and meerkat (*Suricata suricatta*), where breeders contribute

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little to the rearing of their litter whilst non-breeders make substantial contributions (Lacey and Sherman 1991; Bourke 1999; Clutton-Brock et al. 2004). Notably, morphological differentiation of female breeders is also apparent in these groups (Wilson 1971; O'Riain et al. 2000; Russell et al. 2004).

Clutton-Brock et al. (2004) suggest that in obligate cooperative breeding vertebrate species (within which group sizes are typically large), breeders may be selected to invest less in the rearing of young relative to non-breeding helpers. This is less likely to be the case in more facultatively cooperative species where typically small group sizes constrain breeders from reducing their investment. In support of this, in obligate cooperative meerkats (*S. suricatta*), breeders (most notably females) generally contribute less than non-breeding helpers (Clutton-Brock et al. 2004). Although there is limited information on facultatively cooperative mammals, in facultative birds, breeders generally contribute more to offspring care than do non-breeding helpers (Hatchwell 1999). In addition, meerkat breeders reduce their contribution to a greater extent with increasing helper number and, unlike subordinates, do not increase their contribution with improved body condition or supplemental feeding (Clutton-Brock et al. 2004). Again, these results contrast with facultatively cooperative bird species in which breeders and non-breeders have more similar investment rules (Wright and Dingemanse 1999; MacColl and Hatchwell 2003). However, because contributions to care by breeders and non-breeders, as well as the factors that affect them, are poorly understood in societies of cooperative vertebrates (Cockburn 1998; Heinsohn and Legge 1999), and mammals in particular (Russell 2004), the validity of these generalisations is currently unclear.

The aim of this study was to determine the relative contributions to pup care, and the factors that affect them, by individual breeders vs non-breeders in the obligate cooperative breeding banded mongoose (*M. mungo*). Using the banded mongoose as a model system has at least three advantages for addressing these aims. First, very few studies have been conducted on the investment levels or rules of breeders and non-breeders in cooperatively breeding mammals or in obligate cooperative species in general (Clutton-Brock et al. 2004; Russell 2004). Second, virtually all previous studies that have considered the aims addressed have done so in 'high-skew' species wherein reproduction is monopolised largely by a dominant pair. In contrast, the banded mongoose has a 'low-skew' reproductive system, with most mature group members attempting to breed in each attempt (Cant 2000; Gilchrist et al. 2004). Third, the banded mongoose is closely related to the meerkat, a species in which reproductive skew is high but which otherwise lives in similarly sized groups and has similar life history. Consequently, the results of this study will add to our limited knowledge of the patterns of care and the factors that affect them in cooperative vertebrates, allow us to examine the hypothesis that obligate cooperative breeding is associated with lower investment in offspring provisioning by breeders than non-breeders and enable us to compare the pattern of offspring care in a low-skew cooperative breeding mongoose with that of a high-skew one, the meerkat.

The banded mongoose is a small (<2 kg) social mongoose of sub-Saharan Africa that lives, like meerkats, in relatively large groups for a cooperative vertebrate (range of group size 3–36 individuals, mean=14). Banded mongooses show low reproductive skew: 80% of females over 1 year old conceive, with up to 10 females giving birth simultaneously in the same den (Gilchrist et al. 2004). Similarly, multiple males in each group copulate with receptive females (Cant 2000). After birth, pups remain in a den for approximately 30 days, during which time they are guarded by group members and suckle milk from lactating female(s) (Rood 1974). From 1 month, pups join the group on foraging trips and are fed with invertebrates by both breeding and non-breeding group members until independence at 3 months of age. It is interesting to note that during this period of dependence, most pups form and maintain a stable one-to-one association with an older group member (termed escort; Gilchrist 2004). Escorts do not appear to preferentially care for their own pups (Gilchrist 2004). Escorts provision pups with food more than non-escorts, and escorted pups receive more food provisions that non-escorted pups (Gilchrist 2004; Hodge 2005). We therefore use escorting as an indicator of contribution to pup rearing.

First, we determine the effect of age and sex on individual contributions to pup escorting by individuals between independence (3 months) and adulthood (>2 years). Second, among individuals of breeding age (yearlings and adults), we investigate the influence of breeding status and increasing carer to pup ratios (an index of the availability of care) on individual contributions. Finally, we determine how individual body weight influences individual contributions.

Materials and methods

Study population and data collected

Fieldwork was carried out from March 1997 to February 2000 in an 8-km^2 area on and around Mweya peninsula, Queen Elizabeth National Park, southwest Uganda (0°12′ S, 27°54′ E). The vegetation of the study site was predominantly short and medium fire climax grassland with dense thickets of *Capparistomentosa* growing in association with

Azimatetracantha and *Euphorbiacandelabrum* (Lock 1977). The climate was equatorial, with little annual fluctuation in day length or temperature. Rainfall varied little between litters over the course of this study (mean daily rainfall=2.4 mm, range=0–5.8 mm).

Behavioural observations were collected on 10 groups of banded mongooses. Three of the groups had exclusive access to supplemental food from human garbage dumps (Gilchrist and Otali 2002; Otali and Gilchrist 2004). Individuals were wild, but habituated to close (<10 m) behavioural observation, and were located, trapped, anaesthetised, weighed and marked using the methods outlined elsewhere (Cant 2000; Cant et al. 2001). All procedures were licensed by the Uganda National Council for Science and Technology and the Uganda Wildlife Authority and followed the Guidelines of the Association for the Study of Animal Behaviour (ASAB 1991). There were no apparent ill effects to any of these procedures, and mongooses remained habituated after release.

Our aim was to examine individual contributions to pup escorting and the factors that affect them. Pups could be escorted from the first date that they travelled with a foraging group (approximately 27 days old) until independence at approximately 90 days old (Gilchrist 2001). A potential escort was defined as any independent group member that was over 90 days old at the birth of the emergent litter. The presence of pups and the identity of escorts and non-escorts were determined by visiting each group approximately twice daily, once in the morning and once in the afternoon, with each observation period lasting between 40 min and 3 h. On each visit, group members (>90 days old) were scored as in-association (1) or not (0) (Gilchrist 2004). A group member was scored as in-association when regularly observed to be within 30 cm of a particular pup during an observation period. The association score was a reliable summary of quantitative nearest-neighbour scan data (Gilchrist 2001). Association scores were compiled for every potential escort for the entire association period of an emergent litter: from the date of emergence to the last date that an escort–pup association was recorded for the litter.

We investigated the effects of the following variables on individual contributions to escorting: sex, age, carer to pup ratio, group size, breeding status, body weight, access to supplemental food, mean daily rainfall, contribution to babysitting the current litter and contribution to escorting the previous litter). Animals were classified as pups (0–90 days), infants (91–182 days), subadults (183–364 days), yearlings (365–730 days) and adults (greater than 730 days). The population has been observed continuously since 1995, with date of birth known for litters and all individuals uniquely marked (Cant 1998; Gilchrist 2001). Group size (number of individuals aged over 90 days) varied from 3 to 36 (mean=13.6), and the number of pups emerging from the communal den varied from 1 to 18 (mean=6.0). The availability of carers was estimated from the ratio of yearling and adult group members to pups (only 16% of escorting observations involved infants and subadults). The mean carer to pup ratio was 3.3:1 (range 0.8:1 to 16:1). Body weight of captured and anaesthetised animals was determined using an electronic top-pan balance (±1 g). Contribution to babysitting was calculated for each group member with 10 or more visits during the babysitting period for the emergent litter as: the proportion of visits the individual was a babysitter during the litter's babysitting period. Contribution to escorting the previous litter was calculated for each group member with 10 or more visits during that escorting period as: the proportion of visits in which the individual was in association during the previous litter's escorting period.

Whilst genetic data on maternity and paternity are currently unavailable, breeding status could be assigned reliably. Only those females that had been pregnant and had given birth at the time the emergent communal litter was born were potential mothers of pups in that litter. Pregnancy status was visually determined and confirmed by capture and palpation (Gilchrist et al. 2004). We refer to females that carried offspring to term in a current litter as 'breeders' and those that did not as 'non-breeders'. During female oestrus, some males mate-guard receptive females for 2 to 3 days (Cant 2000). Those males that mate-guard gain copulations, whilst those that do not mate-guard seldom do so (Cant 2000). Mate-guarding and non-mate-guarding males were reliably identified by observing oestrus groups for at least 1 h in the morning and afternoon. We refer to males that mate-guarded during a female's period of conception of a current litter as 'breeders' and those that did not as 'non-breeders'. It is important to note that we have found no evidence to suggest that individuals recognise their own offspring (Gilchrist 2004), and therefore simple cues, for example whether a female has given birth or whether a male has mate-guarded, are likely to be used by individuals as an indication of parentage (Davies et al. 1992; Haydock et al. 2001).

Statistical analysis

Statistical analyses were performed using GenStat 6. The factors affecting individual contributions to escorting (see below) were investigated using Iterated Reweighted Restricted Maximum Likelihood Models, a robust form of Generalized Linear Mixed Model (GLMM) with binomial error structure and logit link function. In each analysis, the number of observation periods that each individual was observed in association (as an escort) during pup rearing was fitted as the response term, and the total number of observation periods that each individual was observed was fitted as the binomial denominator. GLMM allows random terms to be fitted, with random terms accounting for repeated sampling across error terms (in this case, individuals, litters and groups) (Schall 1991). Random terms were dropped when identified as negative components of variation, indicating that they explained none of the variance in the model. Dispersion was estimated for all analyses.

Backward elimination was used in selecting fixed terms (including relevant interactions) for the minimal model (Sokal and Rohlf 1995). The minimal model included only those parameters that contributed significantly ($p<0.05$) to the explanatory power of the model. In GENSTAT, the significance of fixed terms are presented as Wald statistics, evaluated against the chi-square distribution (as is appropriate for large datasets, such as this one, e.g. Kruuk et al. 1999; Clutton-Brock et al. 2004). Results of these analyses do not generally differ qualitatively in comparison to using the more conservative F-distribution with denominator degrees of freedom equal to the number of units in the highest significant random stratum (Elston 1998). The sample size for each analysis is stated in the text (n=the total number of data points in an analysis). All means are presented as predicted means from the minimal models and are expressed as ±1 standard error.

Effect of age and sex

We tested the effect of age class (infant, subadult, yearling, adult) and sex on individual contribution to escorting. Overall, we obtained 485 escorting indices from 166 individuals during the rearing of 31 litters in 10 groups. Individual, litter and group identities were fitted as random terms to control for repeated measures of each (1–5 measures/individual, 4–31 measures/litter, 4–135 measures/group).

Effect of breeding status and carer to pup ratio

Further analyses were restricted to individuals of potential breeding age (i.e. over 1 year old). We tested the effect of the following variables on individual contribution to escorting: sex, age class, carer to pup ratio, group size, breeding status, access to supplemental food, rainfall, contribution to babysitting the current litter and contribution to escorting the previous litter. Overall, we obtained 371 escorting indices on 126 individuals during the rearing of 31 litters in 10 groups. Individual, litter and group identities were fitted as random terms to control for repeated measures of each (1–5 measures/individual, 3–23 measures/litter, 3–102 measures/group).

Effects of body weight

Body weight was obtained from captured (and anaesthetised) animals in a 2-week period before the birth of the current litter. We excluded weight data from pregnant females. For individuals over 1 year old, we obtained 146 weight measures for 71 individuals (1–6 measures/individual) before the rearing of 20 litters (1–18 measures/litter) in seven groups (1–94 measures/group). For subadults, we obtained 50 weight measures for 35 individuals (1–2 measures/individual), 11 litters (1–9 measures/litter) in four groups (1–41 measures/group). Body weight was corrected for age using residuals of regressions of age on weight, where individuals with negative residuals were categorised as light whilst those with positive residuals were categorised as heavy. Individual, litter and group identities were fitted as random terms to control for repeated measures. Body weight was then entered into the same model as for breeding status and carer to pup ratios above.

Results

Effect of age and sex

The proportion of observations upon which an individual escorted a pup varied significantly with the age class and sex of the individual (age class × sex interaction: χ^2=9.06, df=3, p=0.028, n=485). In both sexes, contributions to escorting increased substantially between the first year and the second year of life, with a decline thereafter in females (female age-class effect χ^2=30.3, df=3, p<0.001, n=201; male age-class effect χ^2=55.94, df=3, p<0.001, n=284; Fig. 1). Males made higher individual contributions to pup escorting than females in all age classes, but the difference was only significant within subadults and marginally not

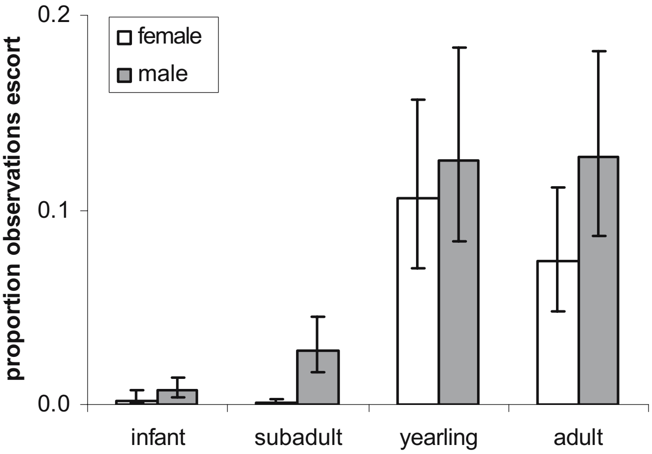

Fig. 1 Effect of age class and sex on individual contribution to pup escorting

significant within adults (sex effect: infant $\chi^2=1.08$, *df*=1, *p*=0.30, *n*=25, subadult $\chi^2=9.34$, *df*=1, *p*=0.002, *n*=90, yearling $\chi^2=0.31$, *df*=1, *p*=0.58, *n*=117, adult $\chi^2=3.59$, *df*=1, *p*=0.058, *n*=253).

Effect of breeding status and carer to pup ratio

Among individuals over 1 year of age, individual contributions to escorting pups was significantly affected by breeding status but dependent upon age-sex class (age–sex class × breeding status interaction: $\chi^2=10.49$, *df*=3, *p*=0.015, *n*=294, Fig. 2), and tended to be dependent upon the carer to pup ratio (breeding status × carer to pup ratio interaction: $\chi^2=3.28$, *df*=1, *p*=0.070, *n*=294).

Individual contributions to care were generally higher in males than females (age–sex class effect: non-breeders $\chi^2=11.1$, *df*=3, *p*=0.011, *n*=90; breeders $\chi^2=7.40$, *df*=1, *p*=0.060, *n*=204) and higher in breeders than non-breeders (breeding status effect: yearling females $\chi^2=1.02$, *df*=1, *p*=0.31, *n*=68; adult females $\chi^2=3.72$, *df*=1, *p*=0.054, *n*=80; adult males $\chi^2=4.87$, *df*=1, *p*=0.027, *n*=173) (Fig. 2). The exception was yearling non-breeding males, which tended to make higher individual contributions than yearling breeding males (yearling males $\chi^2=3.45$, *df*=1, *p*=0.063, *n*=49) (Fig. 2).

Whilst individual contributions to care decreased significantly with increasing carer to pup ratio in breeders ($\chi^2=7.00$, *df*=3, *p*=0.008, *n*=204; slope=−0.41±0.15), the effect was non-significant within non-breeders ($\chi^2=0.56$, *df*=1, *p*=0.45, *n*=90; slope=−0.10±0.13). In addition, whilst individual contribution to escorting decreased with carer to pup ratio overall ($\chi^2=6.73$, *df*=1, *p*=0.009, *n*=294), the effect of group size was non-significant (replacing carer to pup ratio with group size: $\chi^2=0.80$, *df*=1, *p*=0.37, *n*=294).

There was no significant effect of access to supplemental food or rainfall on an individual's contribution to escorting (all *p*>0.1, *n*=294). Additionally, an individual's escorting frequency was not significantly affected by its prior contribution to babysitting of the same litter or by its contribution to escorting the previous litter (*p*>0.1, *n*=294) (see Russell et al. 2003).

Effects of body weight

For subadults, heavy individuals tended to make higher contributions to escorting than light ones; but the effect was marginally non-signifiacnt ($\chi^2=3.62$, *df*=1, *p*=0.057, *n*=50).

After controlling for significant effects of carer to pup ratios (see above), contributions to escorting among those over 1 year old varied with the age-related body weight of individuals, but this effect tended to be dependent upon their sex and breeding status (three-way interaction sex × breeding status × weight category, $\chi^2=3.30$, *df*=1, *p*=0.069, *n*=87) (Fig. 3). Overall, among females, non-breeders that were heavy for their age contributed less than either non-breeders that were light or breeders (irrespective of breeder weight) (weight effect: non-breeding females $\chi^2=3.21$, *df*=1, *p*=0.073, *n*=9; breeding females $\chi^2=1.06$, *df*=1, *p*=0.30, *n*=19; breeding status effect: light females $\chi^2=0.02$, *df*=1, *p*=0.89, *n*=16; heavy females $\chi^2=14.67$, *df*=1, *p*<0.001, *n*=7). By contrast, overall among males, individuals that were heavy for their age contributed more than those that were light, irrespective of breeding status, (weight effect: non-breeding males $\chi^2=3.62$, *df*=1, *p*=0.057, *n*=30; breeding males $\chi^2=3.88$, *df*=1, *p*=0.049, *n*=33; breeding status effect: light males $\chi^2=0.14$, *df*=1, *p*=0.71, *n*=29; heavy males $\chi^2=0.76$, *df*=1, *p*=0.38, *n*=34). The age class effect was non-significant in this model ($\chi^2=1.94$, *df*=1, *p*=0.16, *n*=87).

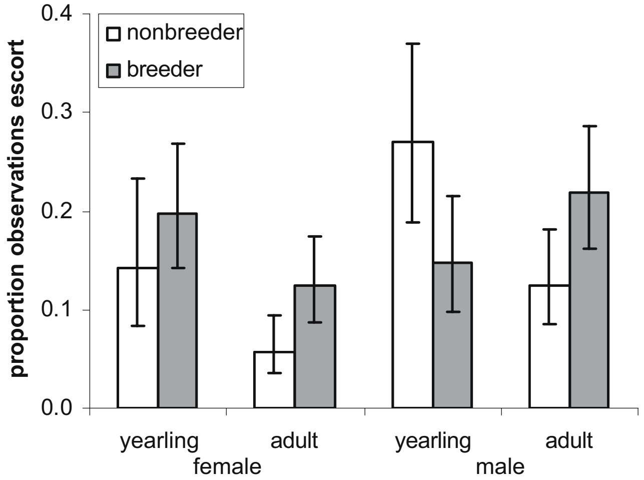

Fig. 2 Effect of sex, age class and breeding status on individual contribution to escorting

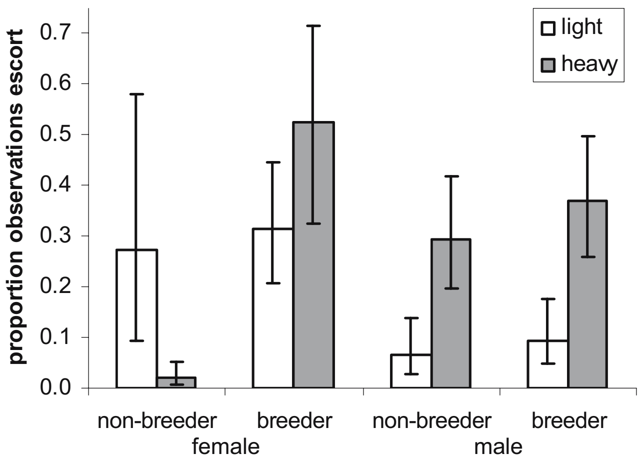

Fig. 3 Effect of sex, breeding status and relative weight (light or heavy) on individual contribution to escorting

Discussion

Currently, there is no general theory for understanding the variation in relative contributions to provisioning young between breeders and non-breeders (MacColl and Hatchwell 2003). Hatchwell (1999) showed that in cooperative birds, breeders reduce their investment in the presence of helpers when nestling starvation is rare, but they did not investigate whether or how this influenced relative contributions by breeders vs non-breeders. More recently, Clutton-Brock et al. (2004) hypothesised that, across cooperative vertebrates, non-breeders will make higher relative contributions to rearing young in obligate than facultative cooperative breeding species. In this respect, contributions might follow analogous patterns to cooperative insects, where breeders contribute relatively less with increasing group size (Bourke 1999).

Our results are not consistent with these ideas in their current form. Clutton-Brock et al. (2004) showed that in meerkat, an obligate cooperative breeder with large group sizes, breeders (particularly females) contribute less to rearing offspring than the same-sexed and similarly aged non-breeders. In contrast, in this study of the banded mongoose, another obligate cooperative breeding mongoose with large group sizes, adult breeders of both sexes contributed more (not less) to pup care than same-sexed adult non-breeders. In addition, within our study, we show that group size does not affect individual contributions to escorting. These results suggest that neither obligate cooperative breeding nor group size will be sufficient to account for the relative contributions to offspring rearing by non-breeders and breeders across cooperative vertebrates. In meerkats, increases in group size are correlated with increases in helper number and the carer to pup ratio due to high reproductive skew (Clutton-Brock et al. 2001, 2004). However, this is not necessarily the case in species with low reproductive skew. In the banded mongoose, increases in group size do not necessarily correspond to increases in carer number and the carer to pup ratio because of low reproductive skew. The important concept in predicting relative contributions to rearing young in cooperative vertebrates is not obligate vs facultative breeding or group size per se but availability of care. It is the availability of care in such social systems that may ultimately determine group reproductive success (Gilchrist 2006).

Clutton-Brock et al. 2004 also showed that for pup feeding, dominant (breeders) reduced contributions to care more markedly than subordinates (nonbreeders) as helper number increased. We present similar findings in this study—individual contribution to escorting decreased significantly with increasing carer to pup ratio for breeders but not non-breeders. This suggests that breeders are more sensitive to the availability of care.

Finally, in meerkats, high daily weight gain and/or supplemental feeding caused non-breeders to increase their level of care, with breeders exhibiting either no effect or a decrease in contribution (fed females) (Clutton-Brock et al. 2004). We found contrasting results in banded mongooses. Within females, relatively heavy non-breeders made substantially lower individual contributions to escorting. Within males, relatively heavy individuals made higher individual contributions to escorting (irrespective of breeding status).

Recently, Heinsohn and Legge (1999) and Heinsohn (2004) have highlighted the importance of viewing cooperative breeding within a life-history framework, where helpers attempt to increase their fitness directly and/or indirectly whilst waiting for an opportunity to breed. Within this framework, differences in individual contributions to care should reflect differences in the costs and benefits of providing care for each group member. Among non-breeders, it might be that the differences in the costs of care best explain differences in individual contributions (Heinsohn 2004). For example, in cooperative vertebrates, younger individuals are commonly inferior foragers to older individuals and, hence, will face greater relative energetic costs of contributing to rearing offspring. In line with this idea, a number of previous studies have found that young group members commonly contribute little to cooperation but can be induced to contribute more by providing supplementary food (Cockburn 1998; Heinsohn 2004). The results of our study are consistent with these suggestions; although young banded mongooses contributed relatively little care in comparison to other group members, they increased their contributions throughout their first year of life and contributed more when heavy.

In addition, costs of cooperating may be manifest as reduced chances of future reproduction although few studies have considered the costs of reproduction in this light (Russell et al. 2003). Nevertheless, this hypothesis makes the clear prediction that individuals should reduce investment in care when their probability of breeding in the near future is high (Cant and Field 2001). A number of our results are consistent with this prediction. First, non-breeding individuals reduced their level of care during adulthood (>2 years old) when their probability of breeding is higher (Hodge 2003). Age-related reductions in care by reproductively mature helpers have been documented previously but are generally provided as evidence of kinship effects because levels of helper relatedness to offspring generally decrease as helpers age (Brown 1987). However, age-related reductions in care may be more consistent with ideas of increasing costs rather than decreasing coefficients of kinship. Second, non-breeding females that were heavy for their age contributed substantially less than lighter non-breeding females. This is noteworthy because non-breeding females that are heavy for their age may be more likely to breed in the following reproductive event than females that are light for their age (Gilchrist et al. 2004). Third, in contrast to most cooperative mammals with high reproductive skew (Russell 2004), male banded mongooses contribute more than females to escorting, pup feeding and babysitting (Rood 1974; Cant 2003; Gilchrist 2004). Sex-biased contributions to care are often associated with sex-biased dispersal, with the philopatric sex making greater contributions (Cockburn 1998; Clutton-Brock et al. 2002). However, there is no evidence for sex-biased dispersal in our population (Cant et al. 2001; Gilchrist 2001). We explain the low female contribution relative to males by female-biased costs. This is because reproductive opportunities are common from an early age in low-skew species and because reproductive success is compromised by loss of condition more in female than male mammals (Gittleman and Thompson 1988; Clutton-Brock et al. 2006).

The results of our study suggest that relative contributions to rearing offspring by breeders and non-breeders are not only influenced by group size but also by reproductive skew. The striking difference between the social system of meerkats (Clutton-Brock et al. 2001) and banded mongooses (Cant 2000; De Luca and Ginsberg 2001; Gilchrist et al. 2004) is in their level of reproductive skew. Reproductive skew is likely to influence the relative contributions of breeders vs non-breeders for at least two reasons. First, reproductive skew will influence the availability of non-breeding carers, with high-skew species showing a greater ratio of carers to breeders and a greater potential for breeders to reduce their contributions. Second, the degree of reproductive skew will also influence the relative costs and benefits of non-breeders investing in care. In low-skew species, constraints on reproduction will be lower than they will be in high-skew species, and hence non-breeders will gain more from reducing investment and saving resources for future breeding. The generality of these results will require further testing of relative contributions by breeders and similarly aged, same-sexed non-breeders. Future studies which test the relative contributions of each in species which vary in their levels of reproductive skew might be particularly illuminating in elucidating the role of reproductive skew in governing patterns of contributions to offspring rearing in cooperative vertebrates.

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