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Food availability shapes patterns of helping effort in a cooperative mongoose

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In cooperatively breeding vertebrate societies, contributions to offspring care can vary greatly between group members. Kin selection theory predicts that cooperation will be favoured when directed towards relatives and when the cost to benefit ratio is low. The fitness costs of helping in turn depend on the impact of energetic investments in care on future reproductive success, which is likely to vary between helpers. For example, investments may impact more on a young helper, which needs to invest energy in growth and is an inexperienced forager. We investigated how a key predictor of cost, food availability (estimated using rainfall), influences helping behaviour in the banded mongoose, *Mungos mungo*. In this cooperative carnivore, a variable number of group members breed while almost all help to rear the communal litter. Nonbreeding females and juvenile males helped less when food was scarce, reflecting the potentially high costs of weight loss and reduced growth on survival and future reproductive success. In contrast, adult males maintained their investment in care as food supply decreased, probably because body condition has relatively little impact on male reproductive success in this species. Breeding females (with pups in the communal litter) also maintained their helping effort as food supply decreased. Although mothers invested highly in care, there was no evidence that they preferentially cared for their own pups, probably because synchronized birthing scrambles maternity cues. Patterns of care in the banded mongoose thus seem to reflect the benefits gained from helping and the long-term fitness costs to the helper.

One of the most striking features of animal societies is the degree to which individuals vary in their propensity to cooperate (Heinsohn & Legge 1999; Koenig & Dickinson 2004; Koenig 2006). This variation could be accounted for by Hamilton's (1964) rule, which states that cooperation occurs when $rb\text{-}c > 0$ (where r is the relatedness between helper and recipient, b is the fitness benefit to the recipient and c is the cost to the helper); hence cooperation can be favoured if it is directed towards kin. Accordingly, associations between kinship and cooperative behaviour have been found in many species (Emlen & Wrege 1988; Griffin et al. 2003; Covas et al. 2006; Langergraber et al. 2007; Kingma et al. 2011; Waibel et al. 2011). For example, both long-tailed tits, *Aegithalos caudatus*, and Seychelles warblers, *Acrocephalus sechellensis*, are more likely to help at nests containing kin than nonkin, and helpers increase their investment as kinship increases (Komdeur 1994; Russell & Hatchwell 2001). However, other studies have failed to find such relationships (Clutton-Brock et al. 2000; Langergraber et al. 2007; Riehl 2011) suggesting that kinship alone does not always predict investment in cooperation. Such inconsistencies could arise from differences in the capacity of the sensory system to detect relatedness accurately (Komdeur & Hatchwell 1999; Langergraber et al. 2007), through differences in the direct fitness benefits that can be gained from cooperation (Clutton-Brock et al. 2002), or through variation in the costs of providing help, which are likely to differ between helpers even when they are equally related to the recipients (Heinsohn & Legge 1999; Cant & Field 2001).

The costs of engaging in cooperative behaviour are often measured in short-term units, such as reduced food intake or body condition over a single breeding season (Tardif 1997; Heinsohn 2004). However, the c component of Hamilton's rule refers to lifetime fitness. To understand selection on cooperation, these short-term costs must be viewed in terms of their impact on lifetime reproductive success (Kacelnik & Cuthill 1990) and this may vary depending on the life history category of the helper (Bell 2010). For example, reduced food intake could impact upon

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juveniles to a greater extent than adults as juveniles are often less efficient foragers yet require energy for growth (Boland et al. 1997; Clutton-Brock et al. 2000). Similarly, individuals that are about to breed may experience greater costs investing in help than individuals that would not have to divert resources away from reproduction (Clutton-Brock et al. 2002; Cant & Field 2005). This contrast may be particularly strong among females, which bear the costs of gestation and lactation (Clutton-Brock et al. 1989), but may also be important among males if body condition is a key predictor of reproductive success (Solis et al. 2008). Helpers whose lifetime fitness is strongly reduced by the short-term costs of help (such as reduced calorific intake) would be expected to experience selective pressure to limit their investment in helping.

Banded mongooses, *Mungos mungo*, provide an excellent study system in which to investigate the impact of increasing short-term costs on patterns of helping behaviour. Banded mongooses are small (<2 kg) carnivores, common across sub-Saharan Africa and live in large stable groups (mean group size $= 29$ adults, range 5–40). They have a polygynandrous mating system and groups typically comprise a 'core' of breeding adults (two to five females and three to seven males), which breed regularly (Cant et al. 2010; Nichols et al. 2010), alongside younger individuals, which breed occasionally (Bell 2006). This contrasts with the single dominant breeding pair per group found among the majority of cooperatively breeding species (Russell 2004). Groups form when a cohort of males from one natal group joins a cohort of females from another natal group; hence group-founders are closely related within each sex but unrelated between the sexes (Nichols 2010). The offspring of the group-founders have close relatives of both sexes present in their natal group, but despite this they often breed in their natal group prior to, or instead of, dispersing (Gilchrist et al. 2004). Groups breed approximately four times per year (Bell 2010) with pregnant females usually giving birth to one to five pups each. Breeding is synchronized within but not between groups, with female group members often giving birth on the same night (Hodge et al. 2011). This extreme synchrony appears to arise because offspring suffer an increased risk of infanticide if their mother gives birth before other females, but suffer in competition with older littermates if their mother gives birth after them (Hodge et al. 2011). A possible consequence of this synchronous birth could be that mothers are unable to identify their own pups.

After the birth of the communal litter, pups are cared for by older group members until they can forage independently. Pup care is beneficial to pups (Hodge 2005) but costly to helpers, which lose weight while caring (Hodge 2007). Experimental manipulations based on supplemental feeding (Hodge 2007) and food deprivation (Bell 2010) show that the sexes respond differently to changes in the short-term costs of care. For example, males were found to maintain pup provisioning after food deprivation, while females reduced their provisioning rates (Bell 2010). This sex difference could be the result of differences in the impact of body condition on future reproductive capacity, with females suffering a greater cost of weight loss than males (Hodge 2007; Bell 2010). We extend this work by investigating whether group members modify their investment in pup care according to natural variation in food supply, which is strongly linked to variation in rainfall (Rood 1975; Dangerfield & Telford 1991; De Luca 1998).

On the basis of past work and our knowledge of the system we made a number of a priori predictions. First, we predicted that helpers whose future capacity to reproduce is strongly affected by body condition will reduce their investment in offspring care as rainfall decreases (that is, helping effort will be reduced as the c component of Hamilton's rule increases). However, no such reduction may be observed when body condition has little influence on future fitness. In the banded mongoose, female body condition influences a number of traits associated with fitness (age at first conception: Gilchrist et al. 2004; pup weight: Hodge et al. 2009; probability of being evicted from the group: Bell et al. 2011). Even short-term reductions in body weight may be costly for females as the helping period often coincides with conception and gestation of the next litter, and weight loss at this time is likely to reduce their probability of breeding successfully (Hodge 2007). In contrast, there is little evidence that male reproductive success or probability of eviction is related to body condition (Nichols et al. 2010; Bell et al. 2011). Instead, males appear to form an age-based dominance hierarchy, with subordinate males 'queuing' for a breeding position (Nichols et al. 2010). Subordinate males (which contribute highly to pup care) rarely gain access to oestrous females regardless of their body weight (Hodge 2007), so temporary weight loss is unlikely to have a large impact on the breeding success of these males. We therefore predicted that females will experience greater long-term costs of investing in help than males, and hence will reduce their contribution to help when rainfall is low. Males, however, may be less responsive to ecological factors influencing short-term weight loss.

Second, within females, we predicted that breeders will be less sensitive to changes in the cost of a given unit of care than helpers, because the r element of Hamilton's rule is greater for mothers than for nonmothers (Cant & Field 2005). In other words, because some of the pups will belong to a given mother, mothers have more to gain from helping and will therefore be prepared to pay a higher cost. Third, for breeders, fitness gains from helping are likely to be positively correlated with individual litter size (as average relatedness to the brood is likely to increase as the female's relative contribution to the litter increases). We therefore predicted that mothers that have contributed a large number of pups to the communal litter would be more resilient to reductions in rainfall than those that have contributed few pups. Finally, while breeders could potentially gain from directing help towards their pups, the high degree of birth synchrony found among banded mongooses could constrain the ability of females to identify their pups. We therefore tested the possibility that mothers preferentially help their own pups.

METHODS

Study Site and Behavioural Data Collection

Between 1998 and 2005, behavioural and genetic data were collected from six habituated groups of banded mongooses located in Queen Elizabeth National Park, Uganda, (0°12′S, 27°54′E). The climate is equatorial, with little seasonal fluctuation in temperature or daylength. Annual precipitation is typically 800–900 mm, with two dry periods in January–February and June–July (Cant 2000). Increasing rainfall increases the abundance of the small invertebrate prey that banded mongooses feed on (Rood 1975; De Luca 1998). Rainfall data, collected from Mweya Meteorological Station at the centre of the study site, was therefore used as an estimate of food availability. Groups were visited at least every 4 days to collect behavioural and life history data and, as a result, accurate ages (±3 days) are known for all individuals born within the study population. For individuals born outside of the study population or before the start of the long-term study (March 1997), age was estimated using tooth wear and head width (Cant 2000).

Groups were habituated to close observation on foot (<10 m) to allow the collection of behavioural data, and were located, trapped, anaesthetized and given individually identifiable markings using methods outlined elsewhere (Cant 2000; Nichols et al. 2010). On first capture, a small (ca. 2 mm) skin sample was taken from the tip of the tail for genetic analysis. To prevent infection, a sterile scalpel

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was used and the tail tip was treated with antibacterial lotion. All procedures were carried out under licence from Uganda National Council for Science and Technology and were approved by Uganda Wildlife Authority. No adverse effects of marking, trapping or anaesthesia were observed during the course of this study.

Helping behaviour takes two main forms: (1) babysitting, where one or more helpers remain at the natal burrow to guard pups while the rest of the group forages (pups aged up to 28 days) and (2) escorting, when pups are mature enough to forage with the group but are yet to develop skills for independent foraging (aged 28–90 days). During the babysitting period, pups are suckled by any lactating female, apparently without discrimination (Cant 2000), and pups are weaned onto solid food during the early part of the 'escorting' period. At this time, many pups form an exclusive bond with a single helper (termed an 'escort') with which it spends at least 70% of its time and receives most of its solid food (median 100%, Bell 2010). Both forms of pup care are likely to represent substantial energetic investments, with babysitters forgoing foraging for up to a full day (Cant 2003; Bell 2010) and pup–escort associations often remaining stable for the entire pup-feeding period (up to 9 weeks; Bell 2010). Individuals that contribute highly to either of these forms of help lose weight in comparison to those that contribute little to pup care (Hodge 2007). All individuals over the age of 6 months that remained in the group for the full babysitting or escorting periods were considered to be potential helpers.

Throughout the babysitting period, groups were visited during foraging sessions and any absent individuals were recorded as babysitting, providing that the group was visited for more than 15 min and the natal den was more than 100 m away. A distance of 100 m was chosen as this exceeds the maximum distance between banded mongooses during a foraging trip. We could therefore be certain that the individuals at the den were not part of the foraging session. This method has been verified by a previous study (Cant 2003) and is effective because banded mongooses have never been observed to leave the group on short-term prospecting forays (Hodge 2007). During the escorting period, the identity of escorts was established using scans. Adults that were within 30 cm of a particular pup for more than 50% of scans for an observation period were classed as escorts.

Among females, pregnancy could be identified ca. 40 days after conception by abdominal swelling. Females that were visibly pregnant before the birth of a litter were classed as 'breeders' and females that were not pregnant were classed as 'nonbreeders'. It is not easy to determine male breeding success as females mate multiply and matings often occur surreptitiously. Male reproductive success, however, is associated with age, with the oldest three males in each group mate guarding oestrous females and fathering the majority (ca. 85%) of pups (Nichols et al. 2010). As a consequence, males rarely gain access to oestrous females until they are at least 2 years old (Hodge 2007).

Maternity Analysis

Owing to birth synchrony and communal care, the parentage of pups cannot be determined behaviourally and genetic maternity assignment is required. DNA was extracted from skin samples using lysis with ProteinaseK, followed by a phenol–chloroform purification (Sambrook et al. 1989). Maternity analysis was based on 14 microsatellite loci (see Nichols et al. 2010 for details) and was conducted using the computer program Cervus, version 3.0 (Field Genetics, http://www.fieldgenetics.com), which uses a likelihood-based method to assign the most likely parents of an offspring at a specified confidence level. To maximize the accuracy of maternity assignment, analysis was restricted to the 69 litters for which all potential mothers were genotyped. A total of 391 maternities were assigned at a minimum of 90% confidence, including 329 assigned at a minimum of 95% confidence. Twelve pups remained unassigned, probably because of genotyping errors. Owing to the large number of potential fathers and incomplete sampling, it was possible to assign paternity at 90% confidence to a smaller number of pups (178 pups). Analysis involving genetic parentage assignment was therefore restricted to females.

Statistical Analysis

All statistical analyses were performed in the R statistical package 2.11.1 (R Development Core Team, Vienna, Austria). Data included repeat sampling from individuals, communal litters and groups. Generalized linear mixed models (GLMMs) were therefore used to control for pseudoreplication, with the random factors 'helper identity' and 'litter identity' nested within 'group identity'. Data were analysed in binomial GLMMs using logit link functions. Full models (including all second-order interactions) were fitted and then simplified by sequential removal of nonsignificant terms ($P > 0.05$), tested using ANOVA. Once the minimal model was achieved, each dropped term was retested by adding it to the final model.

To assess contributions to babysitting, GLMMs were fitted with the number of days each group member babysat fitted as the response variable with the total number of days the group was observed during the babysitting period as the binomial total. To assess contributions to escorting, GLMMs were fitted with escort status ($1 =$ individual was observed escorting, $0 =$ individual was not observed escorting) as the response variable. Each model investigated the impact of rainfall, along with other factors that may influence helping behaviour (including age and measures of likely reproductive success and available help). As investments in babysitting may affect subsequent investments in escorting, the proportion of time a helper spent babysitting the litter (during the same breeding attempt) was included as an explanatory variable in the analyses of escorting. Table 1 lists the predictor variables included in each model and full definitions of these variables are given in Table 2. Previous work on cooperative breeders has shown that helpers alter their contributions according to the needs of the offspring, which may partially depend on the amount of care provided by other group members (Heinsohn & Legge 1999). Banded mongoose litters require babysitting whatever the litter size, while each foraging pup only needs one escort (Bell et al. 2011). We therefore considered helper number to be the best measure of available help for babysitting analyses, and helpers per pup to be a better measure for escorting analyses. Including the alternative measure of available care did not alter the qualitative conclusions of the models.

For the analysis of babysitting, data were available for 53 females and 76 males in five groups over 25 litters, giving a total of 183 and 264 data points for females and males, respectively. For the analysis of escorting, data were available from 56 females and 72 males over 23 litters in six groups, giving a total of 168 and 232 data points for females and males, respectively. For the analysis of contributions to help by breeding females, babysitting data were available from 31 breeding females in five groups over 26 litters, giving a total of 96 data points, and escorting data were available from 40 females in six groups over 27 litters, giving 105 data points. Juvenile females rarely breed; hence it was not possible to consider juvenile and yearling females separately for the analysis of contributions to help by breeding females and these two age categories were combined.

To test whether breeders are able to direct care towards their own pups, a paired analysis was carried out. Thirty-one breeding females with at least one genetically assigned pup in the communal

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Table 1
Summary of generalized linear models fitted in this study

Explanatory terms	Effect size	SE	χ^2	*df*	*P*
Model 1. Variables affecting contributions to babysitting by males					
Constant	−3.64	0.31			
Helper number			1.40	1	0.24
Age category					
Juvenile	0.00	0.00			
Yearling	1.46	0.25			
Adult	1.74	0.24			
Rainfall	0.0057	0.0017			
Rainfall*Age category			9.95	2	0.007
Juvenile	0.00	0.00			
Yearling	−0.0049	0.0019			
Adult	−0.0051	0.0016			
Model 2. Variables affecting contributions to escorting by males					
Constant	−2.19	1.03			
Age category					
Juvenile	0.00	0.00			
Yearling	4.69	1.38			
Adult	2.88	1.07			
Rainfall	0.011	0.0056			
Helpers per pup	−0.29	0.12	5.57	1	0.004
Babysitting effort	4.18	1.46	5.57	1	0.018
Rainfall*Age category			8.43	2	0.015
Juvenile	0.00	0.00			
Yearling	−0.026	0.0095			
Adult	−0.014	0.0066			
Model 3. Variables affecting contributions to babysitting by females					
Constant	−3.53	0.31			
Helper number			0.14	1	0.71
Age category			6.69	2	0.035
Juvenile	0.00	0.00			
Yearling	0.34	0.19			
Adult	0.56	0.21			
Rainfall	0.0046	0.0022			
Breeding status	0.31	0.22			
Rainfall*Breeding status	−0.0047	0.0016	8.86	1	0.003
Model 4. Variables affecting contributions to escorting by females					
Constant	−7.20	2.76			
Babysitting effort			0.040	1	0.84
Age category			10.71	2	0.005
Juvenile	0.00	0.00			
Yearling	3.46	1.18			
Adult	3.07	1.17			
Rainfall	0.032	0.013			
Helpers per pup	−0.62	0.27	6.13	1	0.013
Breeding status	6.37	2.12			
Rainfall*Breeding status	−0.034	0.013	9.42	1	0.002
Model 5. Variables affecting contributions to babysitting by breeding females					
Constant	−2.84	0.19			
Rainfall			0.0008	1	0.97
Age category			1.92	1	0.17
Helper number			0.29	1	0.59
Number of pups			0.84	1	0.36
Rainfall*Number of pups			1.04	3	0.79
Model 6. Variables affecting contributions to escorting by breeding females					
Constant	0.20	−0.55			
Rainfall			0.64	1	0.43
Age category			0.012	1	0.91
Helpers per pup	−0.55	0.20	7.94	1	0.005
Babysitting effort			0.54	1	0.46
Number of pups			3.09	1	0.079
Rainfall*Number of pups			6.60	3	0.086

A summary of six general linear mixed models investigating contributions to pup care by males (Models 1 and 2), females (Models 3 and 4) and breeding females (Models 5 and 6). For each model, we show χ^2, *df* and *P* values associated with each term tested, along with the effect sizes (on a logit scale) and SE of terms included in the minimal model. All second-order interactions between explanatory variables were tested and are included in the table where interactions were significant (with the exception of the rainfall * number of pups interactions in models 5 and 6, which are presented out of interest despite not being significant; however these interactions are not included in the minimal model). Where interaction terms were significant, *P* values for interaction terms, rather than main effects, are presented. Where age categories are included in the minimal model, effect sizes for the reference category (juveniles) are always zero.

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Table 2
Definitions of predictor variables used in GLMMs

Explanatory factor	Definition
Helper sex	The sex of the helper
Age category	Individuals 6–12 months old were classed as juveniles, 12–24 months as yearlings and over 24 months as adults, following Hodge (2007) and Gilchrist & Russell (2007)
Rainfall	The total amount of rainfall during and for 14 days prior to the babysitting or escorting period (mm)
Helper number	The number of group members over 6 months old
Helpers per pup	The ratio of group members over 6 months old to pups in the communal litter
Babysitting effort	The proportion of days on which the helper was observed to babysit
Breeding status	Whether or not the female gave birth in the current breeding attempt (and hence is likely to have offspring in the communal litter)
Number of pups	The number of pups from the communal litter that were genetically assigned to a female

litter ($N = 13$ communal litters) were assigned a pair of pups, one of which they escorted and one of which they did not. To control for other factors, pups were matched for sex, were of a similar weight and were always from the same communal litter (controlling for group, carer number, litter size and rainfall). No pups were included in the analysis more than once.

RESULTS

The majority of individuals contributed to babysitting, with 77.1% of individuals being observed to babysit on at least one occasion per litter, while fewer than half (43.2%) of group members were observed escorting a pup. Both forms of care were male biased with males spending a mean ± SE of 14.2 ± 0.85% of days babysitting, compared to 8.3 ± 0.59% in females and 47.3% of males escorting a pup, compared to 37.1% of females. In all litters, the top babysitter was male and had no genetically assigned pups in the litter. Of the 11 top babysitters whose breeding success in the following litter had been assessed, 10 had no genetically assigned pups and one male fathered three pups.

Table 1 summarizes six GLMMs used to explore the effects of rainfall on helping behaviour. Among males, contributions to babysitting and escorting were influenced by an interaction between age and rainfall (Table 1: Models 1 and 2, Fig. 1), with juveniles (but not older males) decreasing their contribution to care with decreasing rainfall. Relationships involving rainfall were not significantly quadratic in any model. Males were significantly less likely to escort as the number of carers per pup increased and were significantly more likely to escort a pup if they contributed highly to babysitting during the same breeding attempt (Table 1: Model 2).

Among females, contributions to both babysitting and escorting were strongly influenced by an interaction between breeding status and rainfall (Table 1: Models 3 and 4, Fig. 2). Decreasing rainfall led to decreased contributions to pup care for nonbreeding females but did not reduce contributions among breeding females. When the analysis was restricted to reproductively mature females (over 1 year old), interactions between rainfall and breeding status remained significant (babysitting: $\chi^2_1 = 6.71$, $P = 0.010$; escorting: $\chi^2_1 = 6.64$, $P = 0.010$), implying that this effect is not simply due to juvenile females reducing their contributions to care when rainfall is low. Contributions to escorting were also influenced by age category and carer to pup ratio, with yearling and adult females helping at a higher rate than juveniles, and with contributions to escorting decreasing as the number of potential carers per pup increased (Table 1: Model 4). Among females, babysitting effort had no influence on subsequent contributions to escorting.

After we controlled for the significant influence of the number of helpers per pup, breeding females showed a tendency towards increased escorting effort with increasing reproductive success, although not significantly so (Table 1: Model 6). There was also a near-significant interaction between breeding success and rainfall, with females that had contributed fewer pups reducing their escorting effort when rainfall was low. Breeding females did not alter their contribution to babysitting according to the number of pups they contributed to the communal litter (Table 1: Model 5). Among breeding females, age category had no effect on helping behaviour and babysitting effort had no effect on the probability of escorting (Table 1: Models 5 and 6).

There was no evidence that breeding females were able to direct help towards their own pups. Of 31 pup–escort pairs, nine pups (29%) were offspring of the escort, while of the 31 matched pups that were not escorted by that particular helper, 10 (32%) were offspring of the escort (binomial test: $\chi^2_1 = 0.36$, $P = 0.55$). As some escorts were included in the analysis more than once (for separate communal litters), the analysis was repeated including each escort once only. Of the 16 remaining carers, four escorted pups and four matched unescorted pups were offspring of the escort.

DISCUSSION

We investigated the impact of rainfall, a key predictor of food availability, on patterns of pup care in the cooperatively breeding banded mongoose. We found contrasting patterns of care between the sexes. With the exception of juveniles, males invested highly in care regardless of rainfall. In contrast, females adjusted their investment in care according to both rainfall and breeding success, with breeding females investing highly in care and, unlike nonbreeding females, maintaining their investment when food was scarce.

Sex Differences in Helping Effort

Sex-specific patterns of pup care could result from sex differences in the way in which short-term costs of helping translate into long-term fitness effects. In the banded mongoose, both sexes lose weight through helping (Hodge 2007). While weight is largely regained within 10 weeks of the birth of the litter, such changes in body condition are likely to have a greater effect on female than on male reproductive success. Relatively heavy females begin to breed at a younger age (Gilchrist et al. 2004), produce heavier pups with higher survival chances (Hodge et al. 2009) and are less likely to be evicted from the group (Bell et al. 2011). Furthermore, as the period of pup care often coincides with the conception of the next litter, any weight loss at this time is likely to reduce both the likelihood of females becoming pregnant (Gilchrist et al. 2004) and the growth of their offspring during gestation (Hodge et al. 2009). In contrast, male reproductive success appears to be determined by an age-based dominance hierarchy (Nichols et al. 2010). Once age-based rank has been taken into account, weight has no influence on the amount of time males spend mate guarding oestrous females (Nichols et al. 2010), on the number of pups fathered per breeding attempt (Nichols

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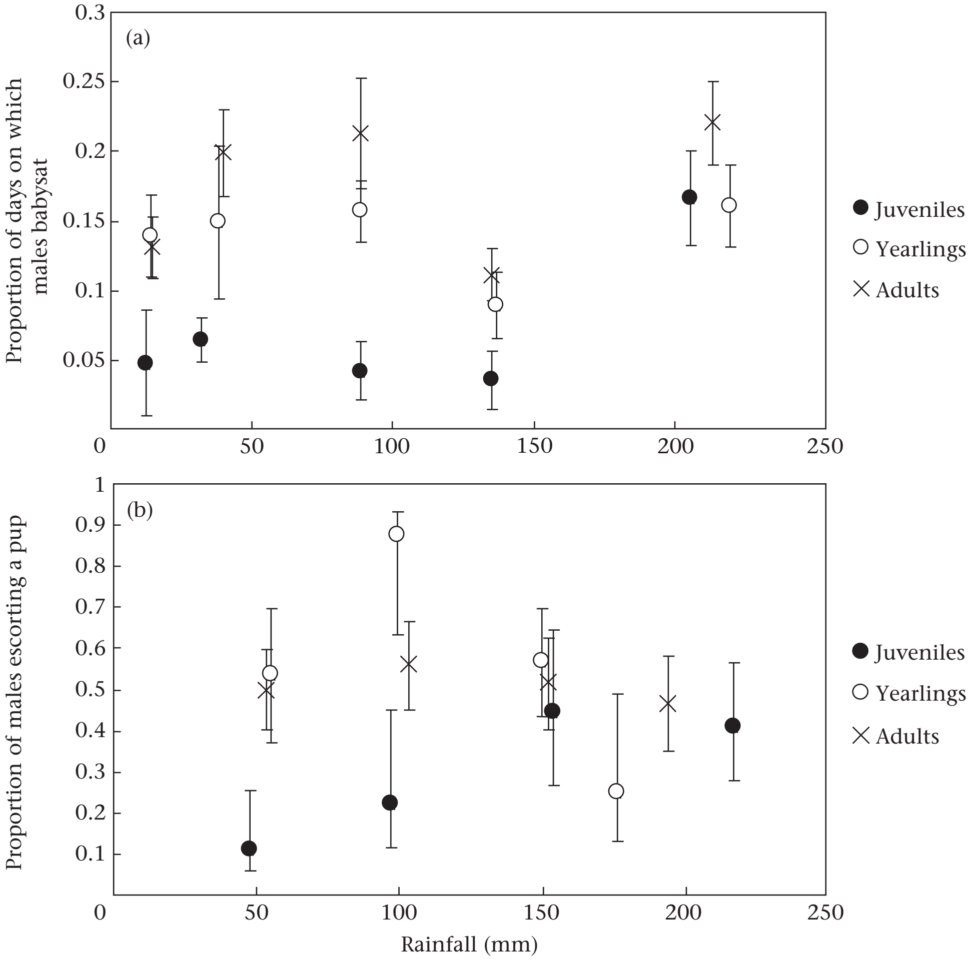

Figure 1. The effect of age category and rainfall on contributions by males to (a) babysitting and (b) escorting. In (a) means are calculated from raw data and are shown ±SE; in (b) the proportion of males escorting is shown ±80% binomial confidence limits.

et al. 2010) or on the probability that a male is evicted from the group (Bell 2010). Sex differences in the importance of body weight in determining reproductive success therefore provide a plausible evolutionary rationale for why contributions to pup care are male biased (Hodge 2007) and why the factors that influence contributions to care differ between the sexes.

Alternatively, sex differences in patterns of helping could be generated through differences in patterns of dispersal or relatedness. For example, where individuals benefit from living in a large group, the philopatric sex is likely to derive greater direct fitness benefits of raising recruits to their natal group than the dispersing sex (Kokko et al. 2001; Clutton-Brock et al. 2002). However, in the banded mongoose, both sexes disperse and both sexes have the potential to become breeders in their natal group; hence males and females may gain similar benefits from raising additional group members (Hodge 2007). Similarly, there appear to be no significant differences in genetic relatedness between male and female group members to pups (Nichols 2010), so sex biases in care are unlikely to be generated by differences in the indirect fitness benefits that can be gained from helping. One further possible explanation for male-biased helping in the banded mongoose is that males gain direct reproductive benefits from contributing highly to care; for example, top helpers could gain access to breeding females in the next reproductive event (Reyer 1980). However, 10 of the 11 top babysitters for which paternity data were available had no genetically assigned pups in the following breeding attempt, suggesting that male helpers do not gain matings through helping. This is likely to be because the individuals that provide the greatest contribution to pup care (generally subordinate males) rarely gain access to oestrous females as they are excluded by older mate-guards (Nichols et al. 2010).

Helping Effort in Males

As the long-term fitness costs of temporary weight loss are likely to be low for males, we might expect males to maintain their helping effort even when food is scarce. In accordance with this prediction, we found that yearling and adult males did not decrease their contribution to pup care as rainfall decreased. Conversely, juvenile males reduced their helping effort when rainfall and hence food supply was low, suggesting that young males may experience a long-term fitness cost of helping. Although male reproductive success does not appear to be related to body condition in the banded mongoose, breeding success does increase with age (Nichols et al. 2010); hence male helping effort should be balanced against future survivorship, which could be related to body condition or growth. However, the relationship between weight and survival is difficult to test as weight loss before death could indicate an underlying health condition, rather than being the cause of death. Nevertheless, when resources are scarce, the majority of juveniles appear to be below the threshold for which helping brings a net fitness benefit and they respond by reducing

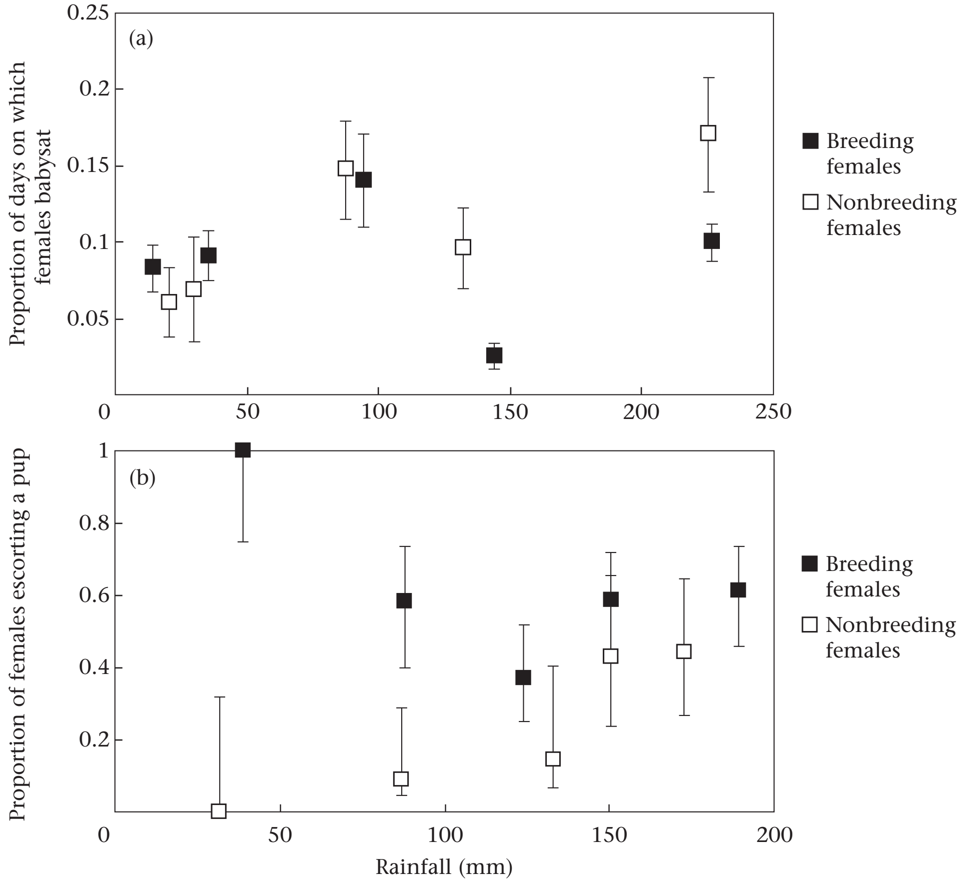

Figure 2. The effect of breeding status and rainfall on contributions by females to (a) babysitting and (b) escorting. In (a) means are calculated from raw data and are shown ±SE; in (b) the proportion of females escorting is shown ±80% binomial confidence limits. Juvenile females (that had not yet reached reproductive maturity) could not have bred and are therefore not included in the graphs.

their investment in care. Comparable relationships occur in other species; for example, juvenile meerkats, *Suricata suricatta*, contribute less to various cooperative activities (pup feeding, babysitting, digging, teaching and raised guarding) than older group members (Clutton-Brock et al. 2002; Thornton 2008), an effect that is at least partially dependent on low foraging success (Brotherton et al. 2001). A similar situation occurs in white-winged choughs, *Corcorax melanorhamphos*. This Australian passerine occupies a foraging niche that requires a long period of skill development and, as a consequence, juvenile birds acquire less food and help at lower rates than adults (Heinsohn 1991; Heinsohn & Cockburn 1994). Furthermore, when juveniles are given supplemental food, they increase their contribution in line with that of adults (Boland et al. 1997). This is comparable to the way in which juvenile banded mongooses increase their contribution to care when food is naturally abundant.

Helping Effort in Females

Among females, which experience a high long-term fitness cost of weight loss (Hodge 2007), we predicted that the helping effort of breeders would be less sensitive to reductions in food supply than the helping effort of nonbreeders because the *r* element of Hamilton's rule is likely to be greater for mothers than for nonmothers (Cant & Field 2001, 2005). In other words, individuals that stand to benefit highly from contributing to care are willing to withstand greater costs. Our results were consistent with this prediction; breeding females contributed highly to pup care despite the costs imposed by reduced rainfall, while nonbreeding females reduced their investment in help as rainfall decreased. Breeding females did not merely maintain their levels of pup care when rainfall was low, but instead appeared to increase their investment in care. This effect was particularly strong for escorting behaviour, possibly because breeding females require energy for lactation during the babysitting period so are unable to forgo a large number of foraging sessions at this time. Breeding females may increase their contribution to escorting during periods of low rainfall to compensate for the reduced level of care pups receive from nonbreeding females and juvenile males. This could result in breeders suffering disproportionately high costs of providing offspring care under bad environmental conditions. Compensatory care has been observed in other cooperative species, such as Arabian babblers, *Turdoides squamiceps* (Wright & Dingemanse 1999), carrion crows, *Corvus corone* (Baglione et al. 2010) and long-tailed tits (MacColl & Hatchwell 2003), in which parents and/or helpers adjust their chick-provisioning rate according to the level of help available from other group members.

Although, in banded mongooses, female breeders invest more in pup care than nonbreeders, this is not necessarily the case in other social species (Hatchwell 1999). In some species, such as meerkats (Brotherton et al. 2001) and naked mole-rats, *Heterocephalus glaber* (Bennett & Faulkes 2000), nonbreeding helpers provide a level of postnatal care equal to or greater than that provided by breeders, while in other species they contribute at lower levels, for example in long-tailed tits (MacColl & Hatchwell 2003), carrion crows (Canestrari et al. 2005, 2007) and laughing kookaburra, *Dacelo*

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novaeguineae (Legge 2000). Differences in the relative contributions to care by breeders and nonbreeders to some extent may occur because of functional differences between species. For example, the presence of lactation in mammals may result in differing patterns of help in comparison to those found among birds. Variation between species may also occur because of differences in group size (Clutton-Brock et al. 2004): breeders are able to reduce their investment in care as the number of nonbreeding helpers present within the group increases, a pattern that is observed among many cooperatively breeding species. Our results, combined with those of previous studies (Gilchrist & Russell 2007), suggest that it is not group size per se that is important, but the ratio of helpers to breeders, which varies with both group size and reproductive skew. Among high-skew species such as eusocial insects, mole-rats and meerkats, the ratio of helpers to breeders is high. Breeders therefore reduce their contributions to offspring care and maximize their reproductive output (Bourke 1999; Bennett & Faulkes 2000; Clutton-Brock et al. 2004). However, this is less likely to be the case among low-skew species as a larger proportion of group members breed, leaving few nonbreeders to care for offspring. Furthermore, helpers in low-skew societies may have a high probability of breeding in the near future so nonbreeders may receive greater fitness payoffs from reducing their investment in alloparental care and saving energy for future reproduction (Cant & Field 2005).

While female banded mongooses were less sensitive to the costs of helping if they gave birth to pups in the communal litter, there was little evidence that breeders altered their helping effort according to their reproductive success. This is somewhat surprising given the direct fitness benefits that could be gained by investing more in litters containing more of their own offspring, especially given that these relationships have been found in other species (Vehrencamp 1977; Stacey 1979; Rabenold et al. 1990; Davies et al. 1996). It is possible that female banded mongooses are unable to gauge their own litter size, or that variation in offspring survival to emergence negates the effect. A similar situation occurs in joint-nesting carrion crows, which appear unable to assess their contribution to the communal brood (Canestrari et al. 2005). Breeding female banded mongooses also failed to direct care towards their own pups and escorted their offspring in only 29% of cases. This is likely to be caused by the high degree of birth synchrony found within groups, with all pregnant females giving birth on the same night in the majority (64%) of litters (see Introduction; Hodge et al. 2011). A consequence of synchronous birth may be that information about the maternity of pups is scrambled, preventing mothers from identifying or directing care towards their own offspring and could also explain why females might have difficulty gauging their own litter size. This situation contrasts with that found in another cooperatively breeding carnivore with low reproductive skew among females: the African lion, *Panthera leo*. Lion cubs are often reared in a communal crèche and females contribute to care only if they have contributed to the communal litter. However, unlike the banded mongoose, female lions are able to identify and bias care towards their own offspring (Packer et al. 2001). In lions, infanticide may be prevented by the potentially lethal weaponry possessed by adult females (Packer et al. 2001) so that disguised maternity is not required, enabling females to benefit from directing care towards their own cubs.

Similar Patterns of Helping Effort for Two Forms of Care

Both babysitting and escorting are likely to represent a substantial energetic investment in pup care: babysitters forgo foraging for up to a day at a time while escorts give a proportion of their food to a pup for up to 9 weeks (Bell 2010). While it is difficult to estimate the relative costs of these two activities, it is possible that the longer-term nature of escorting may lead to reduced contributions from helpers that are more sensitive to the costs of weight loss. This could explain why almost all group members contributed to babysitting, while fewer than half escorted a pup. However, despite the potential differences between these two types of helping behaviour, the factors influencing patterns of babysitting and escorting and response to food availability remained largely the same. This may be because escorts are able to modify their daily investment in help by varying their pup-feeding rate according to their own body condition, in much the same way as individuals modify their investment in babysitting (Bell 2010). By adaptively altering their contributions, helpers may be able to minimize the long-term fitness implications of investing in care (Russell et al. 2003). Males that contributed highly to babysitting were significantly more likely to escort a pup than males that contributed little. Such correlations have been observed in other cooperative vertebrates such as meerkats (Clutton-Brock et al. 2003) and noisy miners, *Manorina melanocephala* (Arnold et al. 2005) and are likely to reflect individuals that are in good body condition, or are more efficient foragers, investing more in multiple forms of help.

Conclusions

Contributions to helping behaviour in wild banded mongooses seem to reflect the benefits gained from helping and the long-term fitness costs to the helper. The long-term fitness costs of helping are likely to differ between males and females (Hodge 2007) resulting in contrasting patterns of care between the sexes. With the exception of juveniles, males invested highly in pup care regardless of current food availability, while females appeared to adjust their investment according to both food availability and breeding success; breeding females contributed highly to care and, unlike nonbreeding females, maintained or increased their contribution when food was scarce. Helper contributions were therefore a flexible response, with individuals adaptively modifying their investment according to variation in the costs and benefits of providing care. However, the presence of a high degree of birth synchrony seems to scramble cues to maternity and hence prevents breeders from maximizing their fitness through identifying and directing care towards their own pups.

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