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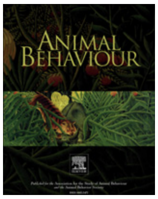

Food availability shapes patterns of helping effort in a cooperative mongoose

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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