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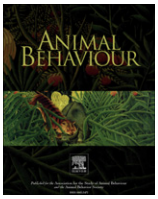

Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose

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Of key importance for understanding cooperative societies is the way in which reproductive opportunities are distributed among group members. Traditionally, skew has been thought of as a product of intrasexual competition. However, cooperatively breeding species often live in mixed-sex groups, so the behaviour of one sex has the potential to influence skew in the other. We addressed the importance of inter- and intrasexual conflict in determining reproductive skew through a study of paternity sharing in the cooperatively breeding banded mongoose, *Mungus mungo*. Unlike banded mongoose females, where reproductive skew is low, males exhibited high skew, with 85% of paternities being assigned to the three oldest males in each group. Individual males appeared unable to monopolize reproduction because females come into oestrus in synchrony and mate multiply. Instead, older males increased their success by mate guarding the oldest, most fecund females. Our findings therefore highlight the importance of mate choice in males and reveal the behavioural differences between the sexes that generate reproductive skew. They also emphasize the considerable influence that female behaviour can have on male reproductive skew.

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Cooperative breeding species show considerable variation in the way in which reproductive success is distributed among group members (Koenig & Dickinson 2004; Hager & Jones 2009). This variation, known as 'reproductive skew', is traditionally assumed to be a product of intrasexual competition, with members of the same sex competing between themselves for access to reproductive opportunities (Koenig & Haydock 2001; Cant & Reeve 2002; Koenig & Dickinson 2004). The degree of reproductive skew found within group members of a given sex is thought to depend on two critical factors: (1) the impact of subordinate breeding on the reproductive success of dominants, and (2) the extent to which dominant individuals are able to control subordinate breeding (Cant 2000; Russell 2004; Hodge 2009).

The relative importance of these two factors is likely to differ between the sexes. Among males, who produce large amounts of sperm, the limiting factor on reproductive success is generally the availability of breeding females (Clutton-Brock 2007). If subordinate males fertilize a proportion of these females, there will be fewer breeding opportunities available to dominant males, and, consequently, all subordinate breeding will have a negative impact on the fitness of dominants (Cant & Johnstone 1999). The reproductive success of dominant males in cooperatively breeding species is therefore likely to reflect the ability of males to control subordinate breeding.

In contrast to males, subordinate breeding among females does not necessarily have a negative impact upon the dominant animals' fitness. Females are physiologically more limited in the number of offspring they can produce, particularly among mammals, where investment through gestation and lactation is large. Where a cooperative group is capable of raising more offspring than one female can produce, subordinate breeding can lead to an increase in the total productivity of the group and dominant females may benefit from allowing related subordinates to breed (Cant & Johnstone 1999). Therefore, among female cooperative breeders, the ability of dominants to control subordinate breeding need only influence reproductive skew when subordinate breeding has a negative impact on the dominants' fitness. This may lead to lower levels of reproductive skew among female, but not male, group members when sufficient resources are available to support multiple female breeders.

While intrasexual competition is important in determining levels of reproductive skew, most cooperatively breeding

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vertebrates live in mixed-sex groups where the behaviour of one sex may influence skew in the other (Cant 2000; Koenig & Haydock 2001; Cant & Reeve 2002). Whereas dominant males are predicted to gain from monopolizing reproductive opportunities, the impact of high skew among males on female fitness is unclear. Multiple females may prefer to mate with particular males, for example males that will pass 'good genes' to offspring (Kirkpatrick & Ryan 1991). Under these circumstances, both females and dominant males will benefit from high reproductive skew among males. However, under other circumstances females may gain from a more equal distribution of paternity. For example, females may choose to mate with genetically compatible or unrelated males, resulting in there being no 'ideal' mate for all females (Foerster et al. 2003; Fossøy et al. 2007; Hoffman et al. 2007; Stapleton et al. 2007). Alternatively, females may mate promiscuously to disguise the paternity of their offspring. This could reduce the chances of their offspring being killed by infanticidal males (Hestermann et al. 2001; Wolff & Macdonald 2004), or maximize the amount of paternal care their offspring receive (Davies et al. 1996; Houston et al. 1997; Kohda et al. 2009).

In addition to being influenced by female mating behaviour, male reproductive success may also be influenced by male mating preferences. Male mate choice is predicted to occur when males are limited in their mating capacity (Schwagmeyer & Parker 1990) and when potential breeding partners differ in quality (Owens & Thompson 1994). Limited male mating capacity can arise when males have access to a restricted number of potential breeding partners, or when males experience high costs of breeding, for example if males transfer nutrients to females during copulation (Gwynne 1981; Forsberg 1987) or invest a lot in parental care (Gwynne 1991). Male mate choice may be particularly common in cooperatively breeding species, where males have access to a small number of potential breeding partners and where reproductive success often differs greatly between females (Clutton-Brock 2007).

We addressed the importance of intrasexual and intersexual competition in determining reproductive skew through a study of paternity sharing in the cooperatively breeding banded mongoose, *Mungus mungo*. Banded mongooses are small (<2 kg) mammals, common across sub-Saharan Africa, which live in large stable groups of up to 75 individuals (median 24). Groups typically comprise a 'core' of two to five breeding females and 4–12 breeding males, who participate in every breeding attempt (Cant et al. 2010), alongside younger individuals (up to 15 females and 25 males), who breed occasionally, and a variable number of pups and juveniles (Bell 2006). The majority of adult group members are under 3 years old, but some adults are much older, with a small fraction reaching 10 years or more (M. Cant & S. Hodge, personal observations). The most common cause of death is predation but a small number of individuals die as a result of disease, road traffic accidents or injuries sustained during fights with other groups. Unusually for cooperative breeding species, individuals of both sexes breed in their natal group, leading to a situation in which incest may be common (Gilchrist et al. 2004). Within each group, female reproduction is synchronized. Thus, all females over the age of 9 months enter oestrus within a few days of each other and those that conceive usually give birth on the same night in an underground den (Gilchrist 2006a). The oldest females come into oestrus first, followed by younger females a few days later (Cant 2000). Although females may benefit from breeding in groups, per capita reproductive success is reduced when large numbers of females breed together. Older, larger females respond to these reproductive costs by evicting smaller, younger females from the group en masse (Cant et al. 2010). Lactating females appear to suckle pups in the communal litter indiscriminately (Rood 1975, 1986), although this cannot be certain until parentage is assigned genetically. Most group members participate in rearing pups, including those who are unlikely to be parents (Hodge 2007). Together, the process of conception, birth and subsequent communal care is known as a 'breeding attempt'.

Male banded mongooses adopt one of two mating strategies. Some males guard oestrous females, following them closely and aggressively discouraging other males from approaching. Males typically guard the same female for 2–3 days before moving on to a second female. Other males trail guarded females, waiting for any opportunities to mate, a behaviour known as 'pestering'. Cant (2000) investigated male mating success in banded mongooses and found that although only 26% of males guarded females during oestrus, these males obtained the great majority (84%) of matings. A male's ability to guard receptive females from the advances of other males is therefore likely to have a large influence on his reproductive success. However, it is not possible for a single male to monopolize all breeding opportunities within a group because males cannot simultaneously guard more than one female. Males are therefore limited in the number of females they can breed with in a given breeding attempt but do have the opportunity to select which oestrous female to guard. The quality of potential female breeding partners varies; for example, heavier females produce heavier, more competitive pups (Hodge et al. 2009). Dominant males may therefore be able to increase their reproductive success by choosing to guard the most successful females in the group. However, male banded mongooses are unable to force copulations (Cant 2000) so female mating preferences may also influence male reproductive success. Females appear to take any opportunity to escape their guard and mate with additional males, and some have been seen to mate with up to five males during a single oestrous period (Cant 2000). This suggests that females may benefit from mating promiscuously, resulting in conflict between males and females over the optimal level of reproductive skew among males.

Cant's (2000) investigation into mating patterns in the banded mongoose showed that a small number of males monopolize the majority of matings. However, matings with nonguarding males were surreptitious, often occurring in dense undergrowth. It is therefore likely that the true number of matings obtained by nonguarding males was underestimated. Additionally, owing to a lack of genetic data, it was not possible to establish how mating success translated into reproductive success. In the current study, we used genetic paternity assignment, along with behavioural and ecological data, to investigate patterns of reproductive success found among male banded mongooses. We first investigated the factors that influence the number of pups that males sire within breeding attempts. We then looked in detail at the tactics males could use to enhance their reproductive success, looking specifically at mate-guarding behaviour and whether males can use mate choice to increase their reproductive success. We hypothesized that a male's reproductive success will be related to his competitive ability as a mate-guard, with older, larger males fathering more pups. We also predicted that males will achieve high reproductive success by preferentially guarding the most fecund females in the group.

METHODS

Study Site and Life History Data Collection

Our study was based on a population of banded mongooses in Queen Elizabeth National Park, Uganda (0° 12′S; 27° 54′E, for details of habitat see Cant 2000). 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 small invertebrate prey that banded mongooses feed on, so is in

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