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

turn likely to influence body condition. Rainfall was recorded on a daily basis by Mweya meteorological station.

Between 1998 and 2004, data were collected from a total of 658 banded mongoose individuals living in six social groups. All individuals in the study population were habituated to close observation on foot (<20 m), allowing the collection of behavioural data. In addition, the majority of individuals were trained to step on to a portable electronic balance for regular weighing. Groups were visited approximately every 4 days to collect behavioural and life history data and, as a result, accurate ages (±2 days) were known for the majority of the study population (92%). Where accurate ages were not known, ages were estimated using tooth wear (Cant 2000). During pack oestrus, continuous 20 min focal watches were conducted on all females to establish the presence and identity of any mate-guarding and pestering males. Mate guarding occurred when one male followed closely behind a particular female for an entire morning or afternoon foraging session. Guarding males aggressively discouraged other males from approaching the guarded female by snapping, lunging and pouncing towards approaching males. Pestering occurred when a nonguarding male shadowed a mate-guard and his female during a foraging session. Pestering males were often the recipients of aggression from guarding males. Guarding and pestering were conspicuous, easily recognized behaviours that could be scored subjectively, rather than by using objective measures such as nearest-neighbour distance (Cant 2000). Investment in guarding and pestering was measured as the proportion of observation sessions a male was seen displaying the behaviour.

To allow easy identification in the field, animals that had ceased growing were fitted with colour-coded plastic collars and growing animals were given unique haircuts. One or two adults in each group were fitted with radiocollars (Telonics Ltd, Mesa, Arizona, U.S.A.) with a 20 cm whip antenna. Collars and haircuts were maintained by trapping individuals every 3–6 months. Individuals were captured in baited live traps (Tomahawk Inc., Tomahawk, Wisconsin, U.S.A.) and were anaesthetized with an intramuscular injection of 1 mg/kg of ketamine and 0.8 mg/kg of medetomodine (described in Cant 2000). Particularly small individuals and those between 3 and 6 months old were given two-thirds of these doses. Individuals under 3 months of age were not anaesthetized. On first capture, all anaesthetized animals were tattooed with a unique code for permanent identification and a 2 mm skin sample for genetic analysis was taken from the tip of the tail using a sterile scalpel. Removal of the tail tip caused little or no bleeding. The end of the tail was treated with antibacterial lotion after sample collection. This process took approximately 10 min per animal, after which they were injected with 0.8 mg/kg of atapamezol and placed in a covered trap to recover before being released.

Ranked Age and Male Competitive Ability

In this paper, we use ranked age as an estimate of male competitive ability. Ranked age appears to be important during eviction events. These events represent direct and serious acts of aggression between group members, and are associated with conflict over reproductive opportunities (Cant et al. 2010). In almost all cases, older individuals evict younger individuals from the group (Cant et al. 2001; Gilchrist 2006b), implying that age is important in determining competitive ability. We used ranked age in analyses, rather than absolute age, because ranked age accounts for the ages of competing males.

Ethical Note

The trapping and anaesthetizing procedure was used over 2000 times during this study, and skin samples were taken from 750

individuals. In no case did any animal become sick or die as a result of these procedures. In well-habituated groups, individuals could be trapped in the presence of researchers, so traps were monitored constantly. For less habituated groups, it was not possible to trap all individuals with researchers present, so traps were left in a shady place and were checked at half-hourly intervals. Animals were released at the trap site within 3 h of being trapped. To minimize risk to pups, females were not trapped or anaesthetized in the latter stages of pregnancy (6 or more weeks postoestrus), nor were adults 'babysitting' pups at the natal den. Radiocollars weighed 27 g, and were fitted to adults weighing a minimum of 1350 g, so represented a maximum of 2% (mean 1.9%) of the animal's body weight. Plastic collars weighed 6 g and were fitted to adults over 1000 g, so represented a maximum of 0.6% (mean 0.4%) of the animal's body weight. To prevent any potential damage caused by collars, particular care was taken to ensure that all collars were loose-fitting, and radiocollars were regularly transferred between individuals. No adverse effects of collars were observed during the course of this study. As this research was conducted as part of a long-term study, collars were not removed after the data were collected, and all individuals in the study population continue to be monitored. This research was carried out under licence from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority.

Genetic Analysis

Tail-tip samples were incubated on a rotating wheel in 330 μl of lysis solution (10 mM Tris HCl (pH 8.0), 1 mM EDTA, 1% SDS, 50 μg/ml of proteinaseK), first at 55 °C for 2 h and then at 37 °C overnight. DNA was purified from the digested tissue sample using an equal phenol:chloroform purification followed by an ethanol and ammonium acetate DNA precipitation (Sambrook et al. 1989). Genotyping was conducted using a panel of 14 microsatellite loci, isolated from a variety of carnivore species (Table 1). PCRs were carried out in 11 μl reaction volumes, using approximately 20 ng of genomic DNA, 0.2 μM each of forward and reverse primers, 10 mM Tris, pH8, 50 mM KCl, 0.01% Tween 20, 0.01% gelatine, 0.01% non-idet P40, 0.025 units of Taq polymerase, 1.5–2.52 mM magnesium chloride and 0.01 uCi (α33P)-dCTP. The following PCR conditions were used with each primer pair: an initial denaturing step of 94 °C for 4 min, followed by 35 cycles of 94 °C denaturization for 45 s, 50–60 °C annealing for 30 s and 72 °C extension for 30 s, followed by a final elongation of 5 min at 72 °C. PCR products were resolved

Table 1
Details of microsatellites used in this study, including literature sources and polymorphism characteristics for 750 banded mongooses

Locus	Species isolated from	Source	Number of alleles	Polymorphic information content
Ss11-12	Meerkat	Waldick et al. 2003	9	0.626
Ss7-1	Meerkat	Griffin et al. 2001	5	0.594
Ss10-4	Meerkat	Griffin et al. 2001	4	0.412
Ss13-8	Meerkat	Griffin et al. 2001	7	0.336
Mm5-1	Banded mongoose	Waldick et al. 2003	3	0.381
Mm10-7	Banded mongoose	Waldick et al. 2003	3	0.330
TGN	Banded mongoose	Waldick et al. 2003	5	0.281
A248	Banded mongoose	Waldick et al. 2003	3	0.230
M53	Banded mongoose	Waldick et al. 2003	3	0.304
A226	Banded mongoose	Waldick et al. 2003	2	0.181
AHT130	Domestic dog	Griffin et al. 2001	3	0.491
Hj35	Small Indian mongoose	Thulin et al. 2002	6	0.688
Ag6	Antarctic fur seal	Hoffman et al. 2008	5	0.472
Ag8	Antarctic fur seal	Hoffman et al. 2008	3	0.568

by electrophoresis on standard 6% polyacrylamide gels and were visualized using a phosphorimager. Bands were scored manually.

Genotyping errors are problematic to studies involving parentage assignments, with error rates as low as 1% causing problems with parentage assignments (Hoffman & Amos 2005). We estimated error rates by re-genotyping a subset of 48 extracted samples (6.4% of all genotyped individuals) at all loci following Hoffman & Amos (2005). The error rate was found to be low, with a mean ± SE of 0.59 ± 0.17% of alleles incorrectly genotyped across loci. This error rate was taken into account by Cervus (see below) when assigning parentage.

Parentage Analysis

Parentage analysis was conducted using the computer package Cervus 3.0 (Marshall et al. 1998). The Cervus package uses a likelihood-based method to assign the most likely parents of an offspring at a specified level of confidence. Using Cervus, we sought to identify both the mother and father of each pup. Potential mothers of a communal litter were identified by their obviously distended bellies during the latter stages of pregnancy (usually confirmed by gently palpating the abdomen of the female or by observing sudden weight drop following birth). Potential fathers were identified as males in the group who were over 10 months of age at the time of conception. Males from outside the group were not considered potential fathers because extragroup matings are rare (Jordan et al. 2010). On average each pup had five potential mothers (range 1–10) and 12 potential fathers (range 4–21).

High levels of relatedness between group members can obviously reduce the power of the parentage analysis, especially where one or more candidates were not genotyped. To maximize the accuracy of maternity assignment, analysis was restricted to the 69 litters where all candidate mothers were genotyped. For paternity analysis, the larger number of candidate fathers meant that the requirement for all candidates to be sampled had to be relaxed. In practice, on average, 77% of candidate fathers were genotyped (range 35–100%).

Cervus simultaneously conducts maternity analysis (assigning the mother of the pup without taking potential fathers into account), paternity analysis (assigning the father of the pup without taking potential mothers into account) and parent pair analysis (assigning a parent pair to the pup while taking the genotype of potential mothers and fathers into account). As all potential mothers but not all potential fathers were sampled, we considered paternities assigned as part of a parent pair to be more reliable than paternities assigned without a corresponding maternity. We therefore included paternities in the analysis only if they were assigned as part of a parent pair. In total, 397 pups were included in the parent pair analysis, with 62 possible mothers and 110 possible fathers from nine banded mongoose groups. Of these 397 pups, 131 pups were assigned a parent pair at 95% confidence and a further 47 pups were assigned a parent pair at 90% confidence. Another 187 pups were assigned a most-likely parent pair at less than 90% confidence and 32 pups were unassigned.

Complete sampling of mothers, but not fathers, resulted in many pups being assigned a mother at a high confidence level, but not a father. As all potential mothers were sampled, we considered maternities assigned without a corresponding paternity to be reliable. In the Cervus maternity analysis, mothers were assigned to 329 pups at 95% confidence and 62 pups at 90% confidence, with 12 pups unassigned, probably owing to genotyping errors. The difference in the number of pups included in maternity analysis (403 pups) and parent pair analysis (397 pups) was due to six pups having no candidate fathers sampled.

Statistical Analysis

All statistical analyses were performed in the R statistical package 2.7.2 (R Development Core Team, Vienna, Austria). For the majority of analyses, the complexity of the data required the use of multifactorial statistics such as linear models. Data included repeat sampling from individuals, breeding attempts and groups so, to avoid the effects of pseudoreplication, linear mixed models were used. Mixed models allow random factors to be fitted, taking into account the variation explained by repeated sampling. If removing a random term from a model did not cause a significant decrease in the explanatory power of the model (tested by conducting an analysis of variance (ANOVA) between models), the random factor was removed from the linear mixed model and a linear model was used instead. Linear models were qualitatively similar to the equivalent linear mixed models, after random terms had been removed. Normally distributed data were analysed in a general linear model (GLM) or general linear mixed model (GLMM) with an identity link function. Data with a binomial or Poisson distribution were analysed using a logit link function and a log link function, respectively. Where Poisson-distributed data were used, over-dispersion was tested for.

Initially a maximal model with all potential explanatory factors, including random and mixed effects and second-order interactions, was fitted. Full models were simplified by removing terms sequentially starting from the least influential (highest P value or t value closest to zero). If removing this term caused a significant ($P < 0.05$) decrease in the explanatory power of the model, tested using ANOVA, the term was reinstated; otherwise it was removed. Nonsignificant random terms were removed first, followed by interaction terms and then fixed effects. Each dropped term was then added back into the minimal model to check that significant terms had not been wrongly excluded. Second-order interactions between fixed effects were included in the results only if they explained significant variance.

Model 1. Determinants of male reproductive success
To explore the factors that determine male reproductive success, the number of pups each male fathered in a breeding attempt was fitted as the response term in a GLM with binomial error structure. The number of paternity-assigned pups in the breeding attempt was fitted as the binomial total to represent the maximum number of pups that could be assigned to a male. Terms that could reflect male competitive ability were included in the model as explanatory factors. These were: male age rank, guarding investment, pestering investment and male weight. Definitions of all explanatory factors can be found in Table 2. The identity of the male, group and breeding attempt did not explain significant variance ($P > 0.05$), so were not included in the model as random factors. Data were available from 90 males from five groups in 44 breeding attempts, giving a total of 375 data points.

How guarding behaviour translates into reproductive success
Males could achieve high reproductive success through investing a greater proportion of their time in mate guarding, through guarding a larger number of females and/or through guarding older, more successful females. To explore these possibilities, we fitted four further models. Definitions of the explanatory factors included in these models can be found in Table 2.

Model 2. Investment in guarding.
To investigate whether older males enjoy greater reproductive success through increased investment in guarding, we fitted a GLMM with the number of observation sessions males were seen guarding as the response variable and the total number of sessions the group was observed

Table 2
Definitions of all explanatory factors included in Models 1–6

Explanatory factors	Definition
Male age rank	The ranked age of each adult male (over 10 months old) present in the group during oestrus, with rank 1 being the oldest
Guard age rank	The ranked age of each guarding male (male showing mate-guarding behaviour) present in the group during oestrus, with rank 1 being the oldest
Guarding investment	The proportion of observation sessions a male displayed guarding behaviour during group oestrus
Pestering investment	The proportion of observation sessions a male displayed pestering behaviour during group oestrus
Male weight	The mean weight (g) of a male, in the 40 days surrounding the conception of the litter
Female age	The age (years) of a female at the birth of a communal litter
Female weight	The mean weight (g) of a female, in the 12 days prior to the conception of a litter
Rainfall	The total amount of rainfall (mm) during pregnancy and lactation (60 days prior to the birth of the communal litter to 28 days after the birth of the litter). Increasing rainfall increases the abundance of small invertebrate prey that banded mongooses feed on, so is in turn likely to influence body condition
Mean litter success	The mean number of emergent pups per breeding female. This variable controls for factors such as predation that can cause reductions in communal litter size before pups emerge from the den

during oestrus as the binomial total. Male age rank was fitted as the potential explanatory factor. Male identity and breeding attempt explained significant variance ($P < 0.001$), so were fitted as non-nested random terms; however, the identity of the group did not explain significant variance ($P > 0.05$) and was not included. Data were available from 79 males across 14 breeding attempts from four banded mongoose groups, giving a total of 196 data points.

Model 3. Number of guarded females. To investigate whether older mate-guards are able to guard more females than younger mate-guards, the total number of females that each male guarded during oestrus was fitted as the explanatory variable in a GLM with Poisson error. Guard age rank was fitted as the explanatory factor. The identity of the male, group and breeding attempt did not explain significant variance ($P > 0.05$), so were not included in the model as random factors. This model included data from 42 guarding males in five groups for 16 breeding attempts, giving a total of 83 data points.

Model 4. Age of guarded females. To explore the possibility that males select older females to guard, a GLM with normal error structure was constructed. The mean age of guarded females was included as the response variable and guard age rank was fitted as the explanatory factor. Both the response and explanatory variables were log transformed to ensure normality. The identity of the male, group and breeding attempt did not explain significant variance ($P > 0.05$), so were not included as random factors. Data were available from 42 guarding males in five groups for 16 breeding attempts, giving a total of 83 data points.

Model 5. Success of guarded females. To investigate whether males choose to guard more successful females, the number of pups genetically assigned to the first female the male chose to guard was fitted as an explanatory variable in a GLMM with Poisson error structure. Guard age rank was included as an explanatory factor. The identity of the breeding attempt explained significant variance ($P < 0.01$), so was included in the model as a random factor; however, the identity of the male and group did not explain

significant variance ($P > 0.05$), so were not included as random factors. Data were available from 42 guarding males in five groups for 16 breeding attempts, giving a total of 83 data points.

Model 6. Female age and litter size. To investigate the relationship between female age and reproductive success, the litter size of each breeding female in each breeding attempt was fitted as the response variable in a GLM with Poisson distribution. Litter size was measured as the number of emergent pups genetically assigned to each female who gave birth in the breeding attempt. Emergent pups are those reaching 28 days old, when they first emerge from their natal den. Female age was fitted as an explanatory variable in the GLM, along with female weight, rainfall and mean litter success. Definitions of these explanatory factors can be found in Table 2. Only litters that had produced emergent pups and where at least 80% of emergent pups had been genotyped were used in this model to obtain good estimates of reproductive success. The identity of the female, breeding attempt and group did not explain significant variance ($P > 0.05$), so were not included in the model. Data were available from 41 females in six groups over 29 breeding attempts, giving a total of 110 data points.

RESULTS

Determinants of Male Reproductive Success

On average, males sired a mean ± SE of 0.33 ± 0.04 (range 0–7) pups per breeding attempt. However, the distribution of reproductive success was highly variable within groups. The ranked age of each male (with rank 1 being the oldest) had a highly significant effect on the number of pups each male sired (Model 1, GLM: $\chi_1^2 = 126.15$, $P < 0.001$; Fig. 1), with males of age rank 1, 2 and 3 fathering 85% of the 124 pups with fathers of known age rank. Males of rank 1, 2 and 3 had over nine times greater reproductive success than males of ranks 4 and above (mean ± SE = 0.74 ± 0.10 in comparison to 0.082 ± 0.022 pups per male per breeding attempt, respectively). Having fitted age rank, we found that none of the other predictor variables fitted to the model were significant (Table 3).

How Guarding Behaviour Translates into Male Reproductive Success

A mean ± SE of 46 ± 5% genotyped adult males in each group showed guarding behaviour during oestrus. Approximately half of these guarding males (52%) also showed pestering behaviour. A mean ± SE of 26 ± 4% of males did not guard and showed only
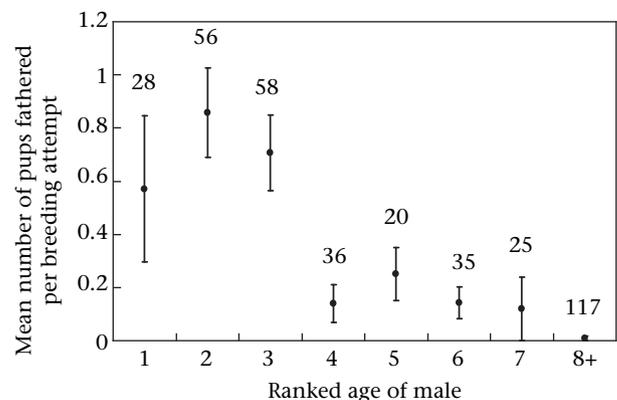

Figure 1. The effect of a male's age rank on reproductive success (the number of pups fathered per male per successful breeding attempt). The graph shows means calculated from raw data ± SE. Numbers above the bars indicate sample sizes.

Table 3
Summary of general linear models fitted in this study

	Term	Effect	SE	df	χ^2	P
Model 1	**Constant**	−0.05	0.21			
	Male age rank	−0.47	0.06	1	126.15	**<0.001**
	(Male age rank)^2			1	0.03	0.86
	Guarding investment			1	2.91	0.09
	Pestering investment			1	2.52	0.11
	Male weight			1	0.29	0.59
Model 2	**Constant**	−0.90	0.37			
	Male age rank	−0.27	0.04	1	38.85	**<0.001**
Model 3	**Constant**	0.71	0.15			
	Guard age rank	−0.08	0.04	1	4.01	**<0.05**
	(Guard age rank)^2			1	0.41	0.52
Model 4	**Constant**	1.59	0.09			
	Guard age rank	−0.58	0.07	1	14.24	**<0.001**
Model 5	**Constant**	0.60	0.22			
	Guard age rank	−0.16	0.05	1	12.81	**<0.001**
	(Guard age rank)^2			1	1.18	0.27
Model 6	**Constant**	1.13	0.24			
	Female age	0.08	0.04	1		**<0.05**
	Mean litter success	1.46	0.39	1	21.43	**<0.001**
	Female weight			1	0.15	0.70
	Rainfall			1	0.65	0.42

Model 1: determinants of male reproductive success; Model 2: investment in guarding; Model 3: number of guarded females; Model 4: age of guarded females; Model 5: success of guarded females; Model 6: female age and litter size. The table shows the effect size and associated SE calculated from the minimal models, along with the χ^2 value, degrees of freedom and P value associated with removing the term from the model. Factors remaining in minimal models are presented in bold, along with their associated P values.

pestering behaviour, and a further $28 \pm 4\%$ showed no sexual behaviour during oestrus. Male age rank was found to influence guarding behaviour significantly (Model 2, GLMM: $\chi^2_1 = 38.85$, $P < 0.001$; Fig. 2), with the oldest males in the group investing more time in mate guarding than the younger males.

Among males who displayed mate-guarding behaviour, there was a marginally significant tendency for older males to guard a greater number of females than younger males (Model 3, GLM: $\chi^2_1 = 4.01$, $P < 0.05$; Fig. 3a). Older males also guarded older females (Model 4, GLM: $\chi^2_1 = 14.24$, $P < 0.001$; Fig. 3b) and more successful females (Model 5, GLMM: $\chi^2_1 = 12.81$, $P < 0.001$; Fig. 3c) than younger males. Older females produced significantly larger litters of emergent pups than younger females (Model 6, GLM: $\chi^2_1 = 4.43$, $P<0.05$; Fig. 4) when the effect of mean litter success (Model 6, GLM: $\chi^2_1 = 21.43$, $P < 0.001$) was controlled for. The
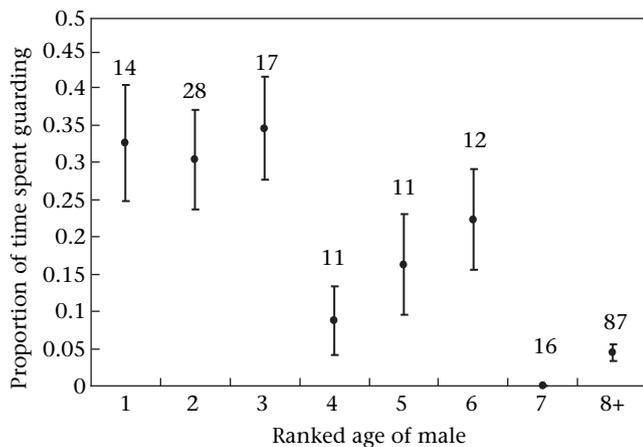
Figure 2. The effect of age rank on the proportion of time males spent mate guarding during oestrus. The graph shows means calculated from raw data $\pm$ SE. Numbers above the points indicate sample sizes.
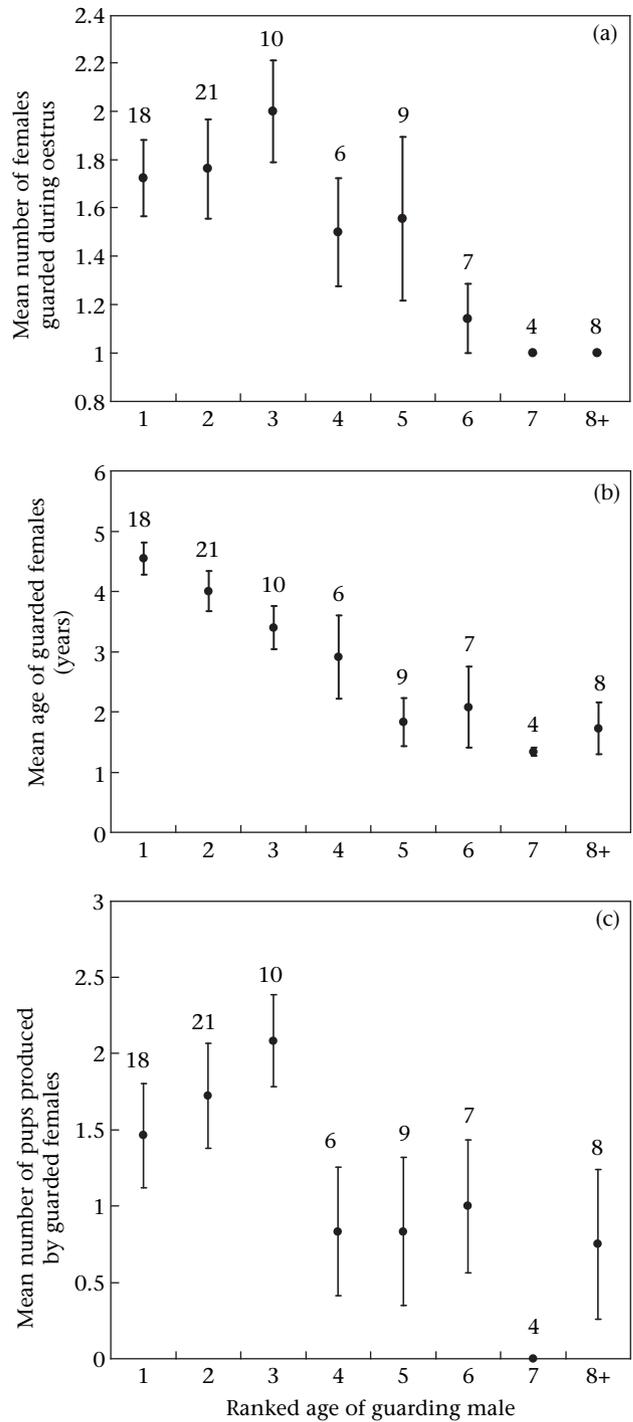
Figure 3. The effect of the age rank of the guarding male on (a) the number of females guarded, (b) the mean age of the guarded females and (c) the number of pups produced by the guarded females. The graphs show means calculated from raw data $\pm$ SE. Numbers above the points indicate sample sizes.

relationship between female age and litter size explains why the older males, who guarded older, more fecund females, had higher reproductive success.

Multiple Mating

Most maternal siblings tended also to have the same father, 77% of litters containing only full siblings. This percentage varied little
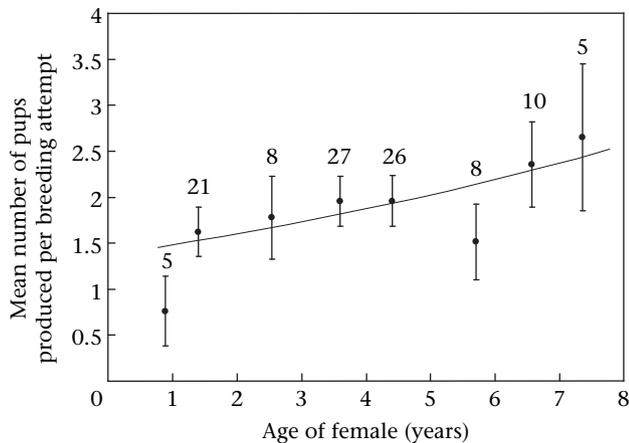
Figure 4. The effect of female age on the number of emergent pups produced. The graph shows predicted means ± SE from a GLM controlling for mean litter success (the mean number of pups per female giving birth). The solid line shows the linear regression predicted by the GLM. Numbers above the points indicate sample sizes.

with a female's litter size [71% (12 of 17 litters), 89% (eight of nine litters) and 75% (three of four litters) for litter sizes two, three and four pups, respectively]. No litters were assigned more than two fathers. In all seven litters containing pups fathered by two different males, manual inspection of genotypes revealed that in every case the nonpaternal male could be excluded. In other words, multiple paternity was unlikely to be an artefact of low-confidence assignments between closely related candidate males.

DISCUSSION

Here we examined realized male reproductive success in the cooperatively breeding banded mongoose. We found that age rank was the best predictor of male success and that this appeared to be mediated by older males both guarding more females and guarding older females. In turn, the older females produced more offspring. However, synchronized oestrus and female promiscuity prevented a single dominant male from completely monopolizing reproduction.

Distribution of Paternity

Older males (age rank 1, 2 and 3) had nine times the reproductive success of younger ranking males and fathered 85% of all pups. This confirms previous behavioural observations suggesting that increased relative age, size and weight are associated with greater investment in mate guarding and greater mating success (Cant 2000). By implication, there is an age-based dominance hierarchy, with subordinate males 'queuing' for a breeding position. Similar patterns appear common among males of other cooperatively breeding mammals. For example, dominant male dwarf mongooses, *Helogale parvula,* father 75% of pups (Keane et al. 1994), and dominant male meerkats, *Suricata suricatta,* father between 72% and 87% of all pups born (depending on study population) and have on average 12 times as many pups as subordinate males (Griffin et al. 2003).

High reproductive skew in male banded mongooses contrasts with low skew seen among females, where over 70% of adult female group members breed (Cant et al. 2010). Differences in the distribution of breeding opportunities between the sexes are likely to arise because of inherent differences between males and females in the way in which conflict over reproduction can be resolved (Cant & Johnstone 1999). While males will benefit from excluding other males from breeding, because in doing so they can increase their own success, the benefits to females of a similar strategy are unclear. When the cost of producing young is high, as in many mammalian species, females are physiologically restricted in the number of offspring they can produce. If a cooperative group is capable of raising more offspring than one female can produce, cobreeding can lead to an increase in the total productivity of the group. Dominant females may therefore benefit from allowing related females to breed, instead of attempting to monopolize reproductive opportunities (Cant & Johnstone 1999). This may lead to low levels of reproductive skew among female, but not male, breeders in the banded mongoose.

Mate Choice and Reproductive Success

Our results appear to support previous behavioural observations that mating success correlates strongly with guarding investment (Cant 2000), but there is an interesting difference. We found that once age rank was included in the model, the amount of time males spent guarding and pestering did not significantly influence their success. In other words, we appear able to reject a model where time spent guarding is the proximate determinant of success and older males are successful simply by guarding more than younger males. Instead, it seems that guarding is not random, and successful males not only guard more females than younger males, but also manage to guard older females who produce more pups and heavier pups (Hodge et al. 2009). Similar patterns are seen in other species. For example, male chimpanzees, *Pan troglodytes,* prefer to mate with older females, who are more likely to conceive than younger females, experience lower levels of neonatal mortality and have already demonstrated their ability to bear and raise offspring (Muller et al. 2006). Similarly, male hyaenas, *Crocuta crocuta* (Szykman et al. 2001), pigeons, *Columba livia* (Burley & Moran 1979) and Mormon crickets, *Anabrus simplex* (Gwynne 1981) also show preferences for females who are likely to have higher reproductive success.

Male mate choice may be especially common among cooperatively breeding species (Clutton-Brock 2007). In many cooperative breeders, males are limited in the number of potential breeding partners available to them, and reproductive skew among females is generally high (Koenig & Dickinson 2004). Males therefore stand to benefit from selecting the most successful females as breeding partners. However, in many cooperative breeders there is just one female per group who breeds on a regular basis, resulting in males having little choice of potential breeding partner. Although reproductive skew is usually high in females of species that breed cooperatively, banded mongooses are unusual in that reproductive success is shared by most adult females in the group, but females differ in their quality as breeders (Hodge et al. 2009). Banded mongooses therefore provide a good opportunity to demonstrate the importance of male mate choice in cooperatively breeding species, with older males outcompeting younger males for access to the best breeding females.

Female Control Over Paternity

In many other cooperatively breeding mammals, reproductive success is monopolized by a single male (Keane et al. 1994; Bennett & Faulkes 2000; Spong et al. 2008), whereas in banded mongooses, reproductive success is shared, on average, more or less equally between the three oldest males. One explanation for this difference is that females synchronize their oestrous periods to just a few days, so that multiple females are fertile simultaneously and cannot be successfully guarded by a single male. A similar situation is found in feral cats, *Felis catus* (Say et al. 2001), where the ability of dominant males to monopolize reproduction declines as the degree of synchrony of oestrus between females increases. However, we

cannot be certain whether female banded mongooses synchronize their oestrus primarily to reduce infanticide by other females, in which case the reduced skew in male success would be a passive by-product, or instead whether females actually benefit by spreading paternity across several males.

Young males (age rank 4 and above) fathered 15% of pups, probably because of promiscuous mating by females. Cant (2000) observed that 13 of 24 oestrous females, in addition to mating with their guard, also mated with nonguarding males (pesterers), usually surreptitiously in dense undergrowth, implying the real frequency might be even higher. Despite this, only 23% of litters (seven of 30 with two or more pups assigned) contained pups fathered by two different males, suggesting that these surreptitious matings are rather unsuccessful. Indeed, while females were seen mating with up to five different males (Cant 2000), we never assigned more than two fathers to a litter. None the less, it is worth asking why females should solicit matings from non mate-guarding males. One possibility is that females may gain genetic benefits, along similar lines to those proposed as explanations for extrapair paternity in birds (Johnsen et al. 2000; Foerster et al. 2003; Garvin et al. 2006; Stapleton et al. 2007). Thus, female banded mongooses may be trying to increase the fitness of their offspring by mating with more genetically compatible or less related males, possibly exploiting sperm competition (Jennions & Petrie 2000; Amos et al. 2001; Tregenza & Weddell 2002). Inbreeding avoidance through multiple mating could be particularly important in banded mongooses where potential mates may include both nonrelatives and closely related individuals (H. Nichols, unpublished data). Another possibility is that females may wish to mate multiply to increase paternal investment, as has been shown in dunnocks, *Prunella modularis* (Davies et al. 1996; Houston et al. 1997) and cichlids, *Julidochromis transcriptus* (Kohda et al. 2009). Male banded mongooses invest highly in pup care (Hodge 2007), and males who are likely to have contributed to the communal litter increase their investment (Gilchrist & Russell 2007). Female banded mongooses may therefore choose to mate multiply to maximize help from males in rearing their pups. Alternatively, females may mate with pestering males simply to reduce lost foraging time as a result of harassment.

Conclusions

Our findings demonstrate that, while multiple males do gain breeding success within banded mongoose groups, the oldest three males in the group father the vast majority of pups. This degree of reproductive skew is very different to the low degree of skew found among banded mongoose females (Cant 2000), and is likely to reflect the greater negative impact of subordinate breeding on dominant male reproductive success than on dominant female reproductive success (Cant et al. 2010). High reproductive skew among males appears to arise because older, more successful males select older, higher quality females to guard. However, a single male is unable to monopolize reproduction within groups completely, as females typically come into oestrus in synchrony, making it impossible for one male to guard all females within the group. Females also repeatedly evade their mate-guard and mate with other males within the group, allowing nonguarding males a share in paternity. These findings highlight differences between the sexes in the way in which intrasexual conflict can generate reproductive skew, and also brings to light the considerable influence that female behaviour can have on patterns of male reproductive skew.

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