Behavioral Ecology
doi:10.1093/beheco/ars008
Advance Access publication 7 February 2012

Original Article

Resource limitation moderates the adaptive suppression of subordinate breeding in a cooperatively breeding mongoose

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Social animal species show considerable variation in the way in which reproduction is distributed among group members. Recent attempts to explain this variation have proposed that differences in reproductive skew are attributable to differences in the net benefits group members receive from suppressing each other's breeding attempts. Despite receiving relatively little theoretical and empirical attention, the availability of resources required for successful breeding may have an important influence in determining the costs and benefits of suppressing reproduction and thus influence reproductive skew within social groups. Here, we test this possibility using a long-term study of female reproductive success in the banded mongoose *Mungos mungo*. We find that females experience greater costs of co-breeding when resources are in short supply and that older, more dominant females respond to this cost by suppressing subordinate breeding. This results in differing patterns of reproductive success for females of different competitive abilities, with the oldest, most dominant females breeding regardless of resource availability and younger, subordinate females breeding only when resources are abundant. Our findings highlight the role of resource limitation in determining the distribution of reproductive opportunities within social groups. *Key words:* cooperative breeding, dominance, rainfall, reproductive conflict, resource availability, suppression. *[Behav Ecol 23:635–642 (2012)]*

INTRODUCTION

Cooperative vertebrate societies show considerable inequality in the distribution of reproductive success among group members (Koenig and Dickinson 2004; Hager and Jones 2009). This variation, known as "reproductive skew," can range from the virtual monopolization of reproduction by just one breeding pair (e.g., among naked mole-rats *Heterocephalus glaber* [Bennett and Faulkes 2000], meerkats *Suricata suricatta* [Griffin et al. 2003; Hodge et al. 2008], and pied babblers *Turdoides bicolor* [Nelson-Flower et al. 2011]) to more egalitarian societies where the majority of group members breed (such as acorn woodpeckers *Melanerpes formicivorus* [Koenig et al. 1995] and African lions *Panthera leo* [Packer et al. 2001]). Several recent attempts to explain variation in reproductive skew have highlighted the role of contrasts in the costs and benefits of suppressing the breeding attempts of competing group members (Russell 2004; Hodge 2009; Clutton-Brock et al. 2010).

The suppression of breeding attempts can take many forms, ranging from interference with mating (Setchell and Wickings 2006; Nichols et al. 2010), infanticide (Mumme et al. 1983; Clutton-Brock et al. 2010), harassment (Curry and Grant 1989), and evicting rivals from the social group (Cant et al. 2010; Clutton-Brock et al. 2010), to the physiological suppression of reproduction through socially induced stress (Young et al. 2006). The costs to dominants of suppressing subordinates, although often overlooked, are not trivial (Rubenstein and Shen 2009). For example, mate guarding increases energy expenditure and reduces foraging efficiency (Saeki et al. 2005; Ancona et al. 2010), while eviction may be both energetically costly and stressful, potentially reducing the evictor's reproductive success (Bell et al. 2011). Other possible costs of expelling individuals from the group include a reduction in group size (Kokko et al. 2001) and, where group members are relatives, a potential reduction in the indirect fitness of the evictor (Gilchrist 2006). Similarly, infanticide could bear a considerable cost if the risk of inadvertently killing one's own offspring is high (Vehrencamp 1977; Monnin and Ratnieks 2001) or if other breeders have weaponry capable of causing severe injury (Packer et al. 2001). Wherever these costs accrue, selection should act on dominant individuals to suppress subordinate reproduction only when it benefits them to do so, implying that reproductive skew will covary with the costs and benefits of suppression (Clutton-Brock et al. 2010; Bell et al. 2011; Raihani and Clutton-Brock 2011).

The availability of resources required for breeding is likely to be a key factor in determining the costs and benefits of suppression (Hodge 2009). When the available resources restrict a group's maximum reproductive output to that which can be attained by a single individual, co-breeding will always be costly (Cant and Johnstone 1999). Here, individuals with the ability to monopolize the group's reproductive output should attempt to do so. In contrast, when resources are more abundant, the benefits gained by suppressing subordinate breeding will be reduced and reproduction should be shared more

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Received 27 May 2011; revised 8 November 2011; accepted 14 January 2012.

equitably (Cant and Johnstone 1999; Cant 2006). In this way, resource-mediated variation in the costs of co-breeding is likely to lead to variation in reproductive skew.

Although it is widely accepted that the availability of resources can influence the costs and benefits of subordinate dispersal, an idea known as the ecological constraints hypothesis (Hatchwell and Komdeur 2000; Ekman et al. 2004), the role of resource availability in determining reproductive skew within social groups has received considerably less attention, particularly among mammals (Russell 2004; Hodge 2009). Here, we investigate the impact of resource limitation on patterns of reproductive suppression in the banded mongoose (*Mungos mungo*). Banded mongooses are small (<2 kg) co-operatively breeding mammals, common across sub-Saharan Africa, which live in large stable groups (mean group size = 24). This species provides an excellent model for investigating the costs and benefits of female reproductive suppression because the level of reproductive monopoly varies widely over time (Cant et al. 2010), with up to 12 females co-breeding. Groups contain a "core" of 1–5 breeding females (Cant et al. 2010) and 3–12 breeding males that participate in every breeding attempt, alongside younger individuals (up to 15 females and 25 males) who breed occasionally, and a variable number of pups and juveniles (Bell 2006). The oldest 3 males guard the most fecund females and together father ~85% of all pups (Nichols et al. 2010). Groups defend territories year round and breed 2–4 times per year (Cant 2000). Within groups, reproduction is synchronized; females come into estrus within 10 days of each other and give birth, usually on the same night, in an underground den (Hodge et al. 2011). Pups emerge from the natal den after 3–4 weeks, and the majority of group members help in pup rearing, including those which are not parents (Hodge 2007; Nichols et al. 2010).

Conflicts over reproductive opportunities occur between female group members, the most conspicuous of which takes the form of eviction. During a subset of breeding attempts, older, more dominant females aggressively expel subordinate females from the group (Cant et al. 2010; Bell et al. 2011). Evicted females generally abort their pregnancy and return to their group but may disperse permanently (Cant et al. 2010). This form of reproductive suppression is costly for dominant females as evictions generally coincide with both gestation of the current litter and the care of dependent pups from the previous litter. The disruption and stress caused by an eviction can result in reduced weight, growth, and survival of the evictor's pups (Bell et al. 2011), implying that dominant females should only evict subordinates when it benefits them to do so. In addition, the availability of invertebrate prey varies greatly over time, being strongly linked to variation in rainfall (Rood 1975; Dangerfield and Telford 1991; De Luca 1998). This variation in resource abundance is likely to influence the costs and benefits of reproductive suppression and hence influence reproductive skew. To investigate the relationship between reproductive skew and resource availability, we test the predictions that 1) the costs of co-breeding are dependent on resource availability and 2) the oldest, most competitive females respond to this cost by suppressing the breeding attempts of subordinates.

MATERIALS AND METHODS

Study site and life history data collection

This study was conducted between November 1995 and December 2005 on a human-habituated population of over 1000 banded mongooses living in 10 social groups in Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E). Daily rainfall was recorded by Mweya metrological station. Annual precipitation is typically 700–800 mm, with 2 dry periods in January–February and June–July. Groups were visited approximately every 2 days, allowing accurate aging for all individuals born within the study population. Individuals are classified according to age as pups (0–90 days), subadults (91–600 days), and adults (>600 days). Females were considered to be breeding if they were identified as pregnant prior to the birth of a communal litter. Pregnancy can be identified ~40 days after conception by abdominal swelling (Cant 2000; Gilchrist 2006). Birth dates were inferred from sudden changes in body shape. Eviction events were defined as cases when females left their group for at least 1 day as a consequence of aggression from older females (Cant et al. 2010).

Pups were trained to step onto a portable electronic balance in return for a small reward of milk (<1 ml), allowing weighing without anaesthetization. For consistency, all weights were taken in the morning before foraging began. To distinguish between the effects of age and weight, weight data were controlled for age by regressing weight on age. Residual weights from these regressions were then used as variables in subsequent analyses. Best fits were achieved using quadratic regressions.

Trapping and anaesthetization

For field identification, adults were fitted with color-coded plastic collars (weighing 6 g, maximum 0.6% body weight) and subadults were given unique haircuts. Groups were located using 2 radio collars (weighing 27 g, maximum 2% body weight) fitted to adults. Collars and haircuts were maintained through periodic recapture and anesthesia. Animals were captured using baited live traps (Tomahawk inc.) and were anaesthetized with an intramuscular injection of 1 mg/kg of ketamine and 0.8 mg/kg of medetomodine. These doses were modified according to size, with particularly small individuals and those between 3 and 6 months old receiving two-thirds of the dose. On first capture, all individuals were tattooed with a unique code on their inner thigh for permanent identification, and a small (2 mm) skin sample was taken from the tip of the tail for genetic analysis. Tail tips were removed using a sterile scalpel, a process that resulted in little or no bleeding. The end of the tail was treated with antibacterial lotion after sample collection to prevent infection. This process took approximately 10 min per individual, after which they were injected with 0.8 mg/kg of atipamezole and were placed in a covered trap to recover before being released. Animals were released at the site of capture within 3 h of trapping. Females were not trapped or anaesthetized in the latter stages of pregnancy nor were adults "babysitting" pups at the natal den. This research was carried out under license from Uganda National Council for Science and Technology, and all procedures were approved by Uganda Wildlife Authority, and no adverse effects of collars, trapping, or anaesthetization were observed.

Age and rank

In almost all eviction events, older females expel younger females from the group (Cant et al. 2001, 2010; Gilchrist 2006; Bell et al. 2011), implying an age-based dominance hierarchy. We therefore used ranked age as a measure of competitive ability, with rank one females being the oldest. As banded mongoose pups are reared in large communal litters (Hodge et al. 2009), groups frequently contain cohorts of same-aged individuals. Where several females were the same age, they were given the same ranking. Groups were composed of a cohort of up to 4 females of the highest rank (rank 1), alongside one or more cohorts of younger lower ranking females (the lowest having a rank of 9). Eviction events generally involved several aggressors (usually the oldest 3–5 females in a group) forcibly expelling members of younger cohorts.

Genetic analysis

Skin samples were incubated in 330 µl of lysis solution (10 mM Tris–HCl [pH 8.0], 1 mM ethylenediaminetetraacetic acid, 1% sodium dodecyl sulfate, and 50 µg/ml of proteinase K), 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 (for details, see Table 1). Polymerase chain reactions (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, pH 8, 50 mM KCl, 0.01% Tween 20, 0.01% gelatin, 0.01% nonidet P40, 0.025 units of *Taq* polymerase, between 1.5 and 2.52 mM magnesium chloride, and 0.01 uCi (α33P)-dCTP. PCR conditions were as follows: an initial denaturing step of 94 °C for 4 min, followed by 35 cycles of 94 °C denaturation 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 by electrophoresis on standard 6% polyacrylamide gels, visualized using a phosphorimager and were scored manually.

Genotyping errors are problematic to studies involving parentage assignments, with error rates as low as 1% resulting in the failure to assign the correct parents (Hoffman and Amos 2005). We estimated error rates by regenotyping a subset of 48 extracted samples (6.4% of all genotyped individuals) at all loci following Hoffman and Amos (2005). Several samples from each polyacrylamide gel were regenotyped to ensure that errors did not result from misaligning alleles between gels. The error rate was found to be low, with a mean of 0.59 ± 0.17% (standard error, SE) of alleles incorrectly genotyped across loci, and there was no evidence that alleles had been misaligned between gels. This error rate was taken into account by Cervus when assigning parentage.

Maternity analysis

Due to birth synchrony, neither maternity nor paternity can be determined by observation alone and so genetic parentage assignment is required. Maternity analysis was conducted using the computer program Cervus, version 3.0 (Marshall et al. 1998), 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 in the face of close relatives, analysis was restricted to the 69 litters where all potential mothers were genotyped, yielding 391 maternities assigned at 90% confidence, including 329 assigned at >95% confidence. Twelve pups remained unassigned, probably due to genotyping errors.

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, breeding attempts, and groups. General(ized) linear mixed models (GLMMs) were therefore used to control for pseudoreplication. Where included, “female identity” and “breeding attempt” were nested within “group identity.” Data with normal and binomial distributions were analyzed in GLMMs using identity link and logit link functions, respectively. Full mixed models (including the second-order interactions) were fitted and then simplified by sequential removal of nonsignificant terms ($P > 0.05$), tested using analysis of variance. Once the minimal model was achieved, each dropped term was retested by adding back into the final model. P values for nonsignificant terms are presented in the results but were not included in the minimal model. Table 2 summarizes 4 GLMMs used to explore aspects of female breeding success in the banded mongoose. Full definitions of predictor variables are given in Table 3.

RESULTS

Does rainfall during pregnancy affect measures of pup fitness?

Model 1 examines factors that influence pup emergence weight and reveals a significant positive influence of rainfall both during pregnancy (effect size = 0.17, $\chi^2_1 = 5.23$, $P = 0.022$) and during lactation (effect size = 0.23, SE = 0.094, $\chi^2_1 = 5.34$, $P = 0.021$), suggesting an impact of resource availability. Pups with high-ranking mothers were heavier than pups with low-ranking mothers, but the effect was not significant ($\chi^2_1 = 2.85$, $P = 0.091$), while the mother’s age had no influence on pup weight ($\chi^2_1 = 0.81$, $P = 0.37$). When restricting the analysis to the 111 pups produced by 17 high-ranking females (rank 1–3) in 6 groups over 29 breeding attempts, the

Table 1

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

Locus	Species isolated from	Reference	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

Table 2
Details of the GLMMs constructed to analyze female reproductive success

Model	Type	Response variable	Predictor variables	Sample sizes
1. Does rainfall during pregnancy affect measures of pup fitness?	Normal	Pup weight at emergence (grams)	1. Rainfall during pregnancy 2. Rainfall during lactation 3. Mother's age 4. Mother's ranked age (relative to other breeding females)	168 pups 37 mothers 36 breeding attempts 8 groups
2. Is there a cost of co-breeding?	Binomial	Pup survival to 90 days: 1 = pup survived 0 = pup died	1. Pup weight at emergence 2. Number of breeding females 3. Mother's age 4. Mother's ranked age (relative to other breeding females)	258 pups 40 mothers 50 breeding attempts 8 groups
3. Do high-ranking females suppress subordinate reproduction when resources become limiting?	Binomial	Female breeding success: 1 = female gave birth 0 = female did not give birth	1. Rainfall surrounding conception 2. Natal origin of female 3. Female's age 4. Female's ranked age (relative to other female group members)	389 potential births 85 females 90 breeding attempts 9 groups
4. Do high-ranking females use eviction to suppress subordinate breeding?	Binomial	Eviction during pregnancy: 1 = eviction took place 0 = eviction did not take place	1. Rainfall surrounding conception 2. Number of female group members	97 breeding attempts 10 groups

effect of rainfall during pregnancy and lactation had a significant, positive effect on pup weight (GLMM: effect size = 0.21, SE = 0.072, $\chi^2_1 = 7.17$, $P = 0.0074$), indicating that the impact of resource availability is not restricted to low-ranking females. When breeding attempts involving evictions were excluded from the data set (leaving 107 pups from 23 breeding attempts in 6 groups), the effect of mother's rank on pup weight remained nonsignificant (GLMM: $\chi^2_1 = 3.02$, $P = 0.082$), suggesting that the failure to find a significant difference between the weights of pups born to dominant and subordinate females was not due to dominant females having to expend energy to evict pregnant subordinates.

Is there a cost of co-breeding?

On average, 47 ± 3.1% (SE) of emergent pups survived to nutritional independence at 90 days old. Pup survival was predicted by an interaction between pup weight and the number of females breeding (Model 2: $\chi^2_1 = 4.11$, $P = 0.043$; Figure 1). Breeding female number had little effect on the survival of heavy pups but the survival of light pups declined with increasing number of breeding females. Females who produce light pups, for example when there is little rainfall during pregnancy, therefore have lower success when more females breed. Mother's age (Model 2: $\chi^2_1 = 0.060$, $P = 0.44$) and rank (Model 2: $\chi^2_1 = 0.0095$, $P = 0.92$) had no effect on pup survival.

Do high-ranking females suppress subordinate reproduction when resources become limiting?

A mean of 68 ± 2.8% (SE) of adult females bred (gave birth) in each breeding attempt. Model 3 explores predictors of the likelihood of breeding and finds a significant interaction between ranked age and rainfall ($\chi^2_1 = 7.93$, $P = 0.0049$; Figure 2). Rainfall had little effect on the breeding success of high-ranking females but low-ranking females bred mainly when rainfall was high. Female age ($\chi^2_1 = 0.0054$, $P = 0.94$) and natal origin ($\chi^2_1 = 0.65$, $P = 0.42$) had no effect on breeding success once rank and rainfall had been taken into account. When the 7 breeding attempts involving eviction were excluded from the analysis (leaving 82 breeding attempts involving 83 females in 9 groups totaling 339 potential births), the interaction between rainfall and ranked age became nonsignificant ($\chi^2_1 = 0.26$, $P = 0.61$), as did the impact of rainfall ($\chi^2_1 = 0.19$, $P = 0.66$) and ranked age ($\chi^2_1 = 1.45$, $P = 0.23$), implying that the failure of low-ranking females to breed is due to dominant control (eviction) rather than subordinates refraining from breeding when conditions are poor.

Do high-ranking females use eviction to suppress subordinate breeding?

Evictions occurred in 8 (8.25%) of the 97 breeding attempts for which data were available. In total, 52 females were evicted, of which 20 are known to have aborted their litter. One evicted female died as a result of injuries sustained during the eviction and 13 permanently dispersed from the study population. Eleven evicted females failed to abort their litters and gave birth alongside the dominant females after returning to their group. Model 4 investigated the likelihood of eviction occurring found a significant interaction between the number of adult females in a group and rainfall ($\chi^2_1 = 5.65$, $P = 0.017$; Figure 3). In larger groups, evictions were significantly more likely to occur as rainfall declined, but evictions were unlikely to occur in smaller groups, regardless of rainfall.

DISCUSSION

Here, we explore the impact of resource availability on the distribution of reproduction among banded mongoose group members. We show that the costs experienced by female banded mongooses when co-breeding depend on resource availability. Females produce increasingly heavy pups as rainfall (a strong predictor of invertebrate prey abundance) increases. Heavy pups survive well to nutritional independence but light pups are less likely to survive, especially when a large number of

Table 3
Definitions of predictor variables used in GLMMs 1–4

Explanatory factor	Definition
Female's/ mother's age	The age of the female/pup's mother (days)
Female's/ mother's ranked age	The ranked age of each female/mother present in the group during a breeding attempt, relative to other female group members/breeding females (rank one being the oldest)
Pup weight at emergence	The weight of a pup (grams) taken the first time, the pup was weighed after emerging from the natal den. Weights were controlled for age, as described in the text.
Rainfall surrounding conception	The total amount of rainfall (mm) over the 60 days surrounding the conception of the communal litter
Rainfall during pregnancy	The total amount of rainfall (mm) over the 60 days prior to the birth of the litter, when females are pregnant
Rainfall during lactation	The total amount of rainfall (mm) over the 28 days after the birth of the litter, when pups remain in the natal den
Natal origin	Whether or not the female was in her natal group (the group she was born into) during the breeding attempt. Many cooperatively breeding species avoid breeding in their natal group as a means of avoiding close inbreeding.
Number of breeding females	The number of females that gave birth in a particular breeding attempt
Number of female group members	Number of females over 9 months old present within a group during a breeding attempt

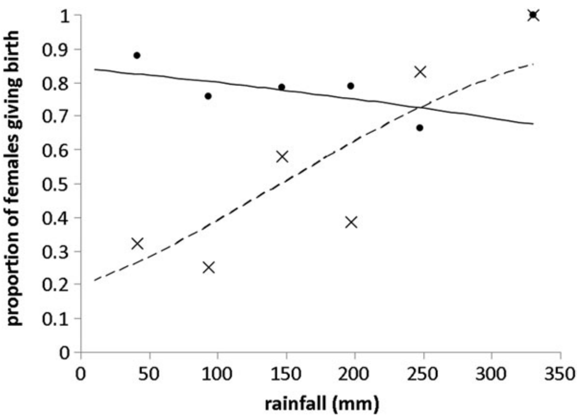

Figure 2
The effect of rainfall on the proportion of high- and low-ranking females breeding. The graph shows the regression and predicted means from GLMM 3 for rank 1 females (solid line and points) and rank 5 females (dotted line and crosses).

females breed. This is likely to be a result of increased competition between pups in large litters, where heavy pups are able to outcompete their smaller littermates for access to helpers (Hodge et al. 2009). Pups that spend more time in close proximity to a helper receive more food, grow faster, and are less likely to be depredated than pups that receive little help (helpers carry the nearest pup to safety when a predator approaches, Hodge 2005). Thus, when resources are scarce, dominant females (who are producing relatively small pups) will benefit from suppressing the breeding attempts of others, thereby reducing competition between pups for helpers and increasing their own pups' survival.

Resource-mediated variation in the cost of co-breeding results in variation in patterns of female reproduction, with high-ranking females breeding regardless of resource availability and low-ranking females breeding only when resources are abundant. This relationship could arise through subordinates exercising restraint in response to poor environmental conditions, as appears to happen in female house mice *Mus musculus domesticus* when nest sites are limiting (Hurst 1987) and in subordinate female chimpanzees *Pan troglodytes schweinfurthii* (Emery Thompson et al. 2007) and spotted hyenas *Crocuta crocuta* (Holecamp et al. 1996) who receive less or poorer

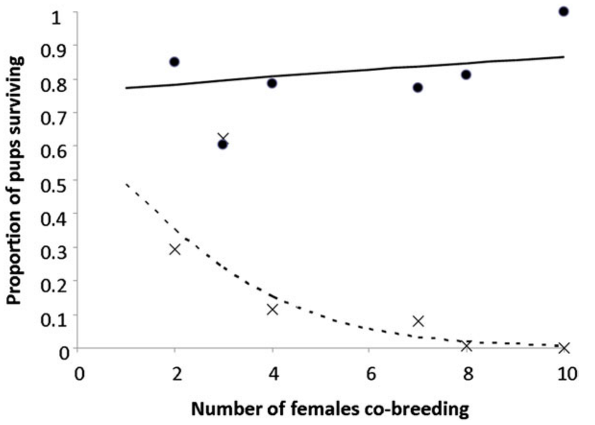

Figure 1
The effect of the number of females breeding on the survival of heavy and light pups. The graph shows the regression and predicted means from GLMM 2 for pups 50 g heavier than the mean (solid line and points) and pups 50 g lighter than the mean (dotted line and crosses).

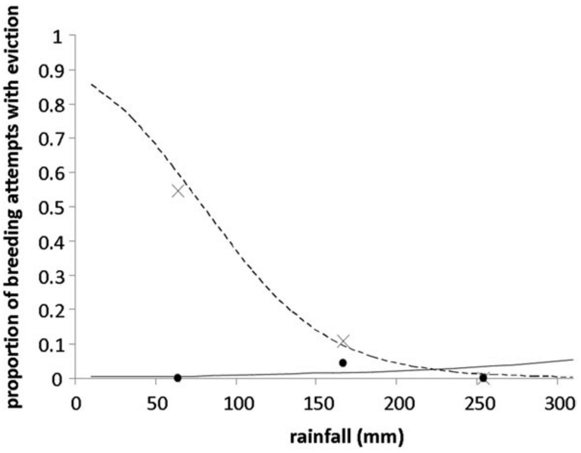

Figure 3
The effect of rainfall on the proportion of breeding attempts during which an eviction occurs. The graph shows the regression and predicted means from GLMM 4 for small groups (5 adult female group members: solid line and points) and large groups (10 adult female group members: dotted line and crosses).

quality food than their dominant counterparts. Refraining from breeding may be an adaptive strategy for subordinates if their offspring are inferior competitors and are likely to die when conditions are poor (Stockley and Bro-Jorgensen 2011). Although it is not currently possible to exclude this hypothesis, there are several lines of evidence that suggest that subordinate breeding failure in the banded mongoose is instead the result of dominant control. Firstly, banded mongoose females are able to suppress the breeding attempts of subordinates through temporarily or permanently evicting them from the group (Cant et al. 2010). We show that evictions become more likely as rainfall (and hence resource abundance) decreases, especially within large groups where conflict over breeding opportunities is likely to be high (Cant et al. 2010). Evictions are associated with increased abortion probability in banded mongooses (Cant et al. 2010) and with reduced conception rates and increased abortion rates in meerkats, probably due to increased stress (Young et al. 2006). By implication, dominant female banded mongooses use eviction as a means of reproductive control. Furthermore, when cases of eviction were excluded from the analysis of breeding success, there was no indication that low-ranking females failed to breed when rainfall was low, implying that subordinates are capable of breeding in poor conditions.

Although eviction is used as a means of reproductive suppression in the banded mongoose, a number of pregnant evictees were readmitted to their group and bred alongside dominants. The readmission of pregnant subordinates could be due to changes in resource abundance or could represent limitations in the ability of dominant females to control subordinate breeding despite the costs that are likely to be imposed by breeding in large groups. For example, it is possible that dominant females are unable to discriminate between pregnant and nonpregnant subordinates (Cant et al. 2010) or that dominants fail to induce abortion in older larger subordinates (Clutton-Brock et al. 2001).

Our results appear broadly in line with observations on other cooperatively breeding species, where reproductive skew is related to the net benefits, dominants receive by suppressing subordinate breeding. For example, dominant female meerkats produce lighter pups when breeding alongside subordinate females and respond to this cost during pregnancy by suppressing subordinate breeding attempts (Clutton-Brock et al. 2010). Similar relationships are seen in communal-nesting groove-billed anis *Crotophaga sulcirostris* (Vehrencamp 1977), greater anis *Crotophaga major* (Riehl 2011), and acorn woodpeckers *M. formicivorus* (Mumme et al. 1983), where females remove the eggs of co-breeders from joint nests prior to laying their own eggs. The net benefits of evicting subordinates from the group are likely to be higher in larger groups, as the cost of increased reproductive competition exceeds the benefit of having additional helpers present in the group. Consequently, intolerance of other breeders often increases with group size, examples being banded mongooses (Cant et al. 2010), marmosets *Callithrix kuhlii* (Schaffner and French 1997), and meerkats (Kutsukake and Clutton-Brock 2008; Clutton-Brock et al. 2010).

Although the role of resource availability in influencing reproductive roles within mammalian groups has been relatively little studied, it may be an important determinant of reproductive skew seen in many societies (Hodge 2009). For example, subordinate female meerkats are less likely to breed in seasons with low rainfall (Clutton-Brock et al. 2001), and low-ranking female spotted hyenas show reduced reproductive success when food resources are limiting, while the breeding success of high-ranking females is unaffected (Holecamp et al. 1996). Similarly, subordinate female Damaraland mole-rats *Fukomys damarensis* show a marked upregulation of their pituitary sensitivities to gonadotrophin releasing hormone (the suppression of which is thought to underpin anovulation) during the wet period relative to the dry (Young et al. 2010).

Rainfall and food supply prior to the breeding season have also been found to influence breeding roles in a number of avian cooperative breeders (such as white-throated bee-eaters *Merops bullockoides* [Emlen 1982], azure-winged magpies *Cyanopica cyanus* [Canario et al. 2004], and superb starlings *Lamprotornis superbus* [Rubenstein 2007]) and in some avian species, resource-related variation in subordinate breeding success has been linked to reproductive suppression. For example, in dry years but not in wet El Niño years, subordinate pairs of Galapagos mockingbirds *Nesomimus parvulus* have reduced breeding success in comparison to the dominant pairs they share a territory with, probably due to suppression by dominants (Curry and Grant 1989). In the Seychelles warbler *Acrocephalus sechellensis*, co-breeding only reduces dominant female reproductive success in poor-quality territories (Komdeur 2005). Here, there is no adaptive suppression of subordinate breeding but instead dominant females reduce competition from subordinates by laying more eggs of the dispersing sex, males (Komdeur 2005). The relationships between food availability, within-group conflict, and reproductive skew have been demonstrated experimentally in burying beetles *Nicrophorus vespilloides*. In this species, conflict between breeding females increases as food availability declines. Dominant females exclude subordinate females from the food supply, resulting in dominants having greater reproductive success than subordinates. However, when supplementary food is provided, subordinate reproductive success increases in line with that of the dominant (Eggert et al. 2008).

Theoretical models addressing the partitioning of reproductive opportunities between group members have provided an important insight into the factors that are likely to influence reproductive skew (Magrath et al. 2004; Hager and Jones 2009), and some models appear to be relatively successful at predicting quantitative differences in skew across species (Nonacs and Hager 2011). However, testing models of reproductive skew empirically has proved problematic, partly due to the difficulties of ensuring that the assumptions of the model have been met (Hodge et al. 2009). For example, the majority of models assume that subordinate reproduction is always costly to dominant females, such that subordinates are only allowed to reproduce in exchange for help or subordination ("transactional models," e.g., Vehrencamp 1983; Johnstone and Cant 1999) or when dominants are unable to prevent them from doing so ("compromise models," e.g., Cant 1998; Reeve et al. 1998). However, subordinate reproduction is not always costly to dominant females. Offspring production is associated with substantial energetic costs, particularly among mammals where investment in gestation and lactation are generally large. These costs are likely to be an accelerating function of litter size, that is, it becomes increasingly costly to add each subsequent offspring to a litter or brood (Cant and Johnstone 1999). Contributing additional offspring to a communal litter could therefore be relatively expensive for a dominant female (who has already contributed offspring to the litter) but cheap for a subordinate, who has not already contributed (Cant and Johnstone 1999; Cant 2006). Consequently, dominant females may not suffer a cost by allowing subordinates to breed when sufficient resources are available to support a large communal litter but may instead gain indirect fitness from allowing related subordinates to breed. However, when litter size exceeds that for which there are adequate resources to support, competition between offspring for limited resources increases and the reproductive success of dominant females is reduced. In this case, the costs of suppressing subordinate reproduction are outweighed by the benefits, and reproductive monopolization is likely to occur. Patterns of reproductive skew within species can therefore be generated through the net benefits that females can receive by suppressing the breeding attempts of others, without the need for reproductive concessions or limitations in dominant control (Clutton-Brock et al. 2010).

Although developed primarily for monogamous bird species, models of parental investment strategy might provide additional insight into patterns of reproductive skew in cooperative and communal breeders. Parents of many noncooperative species produce litters or broods containing offspring with variable competitive abilities (Mock and Forbes 1995). These competitive differences may serve to maximize parental fitness in an unpredictable environment by ensuring that parents always rear the maximum number of offspring that resources will allow (Lack 1947). When conditions are favorable, all offspring may survive but when resources are scarce, stronger "core" offspring can outcompete their weaker "marginal" siblings, leading to brood reduction (first laid out in the "core and marginal model" [Mock and Forbes 1995] and supported empirically by long-term studies in red-winged blackbirds *Agelaius phoeniceus* [Forbes and Glassey 2000; Forbes 2010]). Among cooperatively breeding species, competitive asymmetries between females may lead to core and marginal offspring being spread between parents, with the preferential rearing of core offspring generating variation in reproductive skew according to resource availability. One obvious difference between the biparental species that the "core and marginal" model was developed for and the banded mongoose is the method of brood reduction. In the banded mongoose, brood reduction occurs during gestation as a result of aggression between females (Cant et al. 2010). This contrasts with many biparental birds, in which brood size is reduced after hatching through siblicide or competition for food (Fujioka 1985; Bryant and Tatner 1990; Forbes and Glassey 2000). These differences in the timing of brood reduction could result from differences in the time at which parents are able to assess the availability of resources for offspring rearing. In the banded mongoose, rainfall during gestation (or a correlated variable) may provide an indicator of future food availability, allowing dominant females to reduce the size of the communal litter prior to litter birth. In addition, even if infanticide was otherwise the most efficient means of achieving brood reduction in the banded mongoose, the synchrony of birth by multiple females means that any infanticidal female risks killing her own offspring. Indeed, it seems reasonable to suppose that synchronous breeding represents an evolved strategy of subordinates that specifically aims to counter the threat of infanticide (Hodge et al. 2011).

FUNDING

Biotechnology and Biological Sciences Research Council; Natural Environment Research Council.

We thank the Ugandan Wildlife Authority and the Uganda National Council for Science and Technology for giving permission to carry out research in Uganda as part of a long-term study supported by Michael Cant, Tim Clutton-Brock, and Marta Manser. For help in the field, we thank Francis Mwanguhya, Solomon Kyabulima, Jason Gilchrist, and Neil Jordan. Thanks also go to Bill Amos and for commenting on the manuscript.

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