

# Adaptive Suppression of Subordinate Reproduction in Cooperative Mammals

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**ABSTRACT:** Attempts to account for observed variation in the degree of reproductive skew among cooperative breeders have usually assumed that subordinate breeding has fitness costs to dominant females. They argue that dominant females concede reproductive opportunities to subordinates to retain them in the group or to dissuade them from challenging for the dominant position or that subordinate females breed where dominants are incapable of controlling them. However, an alternative possibility is that suppressing subordinate reproduction has substantive costs to the fitness of dominant females and that variation in these costs generates differences in the net benefits of suppression to dominants which are responsible for variation in the frequency of subordinate breeding that is not a consequence of either reproductive concessions or limitations in dominant control. Here, we show that, in wild Kalahari meerkats (*Suricata suricatta*), the frequency with which dominants evict subordinates or kill their pups varies with the costs and benefits to dominants of suppressing subordinate breeding, including the dominants' reproductive status, the size of their group, and the relatedness of subordinates. We review evidence from other studies that the suppression of reproduction by subordinates varies with the likely costs of subordinate breeding to dominants.

**Keywords:** reproduction, suppression, cooperation, mammals, reproductive skew.

## Introduction

In most vertebrates that breed cooperatively, one dominant female in each group virtually monopolizes reproduction, generating high levels of reproductive skew (Magrath et al. 2004). For example, in birds, a single breeding female is usually the mother of all surviving offspring in

her group in white-winged choughs (*Corcorax melanorhamphos*; Heinsohn 1991), Arabian babblers (*Turdoides squamiceps*; Zahavi 1974), and long-tailed tits (*Aegithalos caudatus*; Hatchwell et al. 2001). In mammals, too, one dominant female virtually monopolizes reproduction in marmosets and tamarins (French 1997), wild dogs (*Lycaon pictus*; Creel and Creel 2001), Kalahari meerkats (*Suricata suricatta*; Griffin et al. 2003; Clutton-Brock et al. 2006; Hodge et al. 2008), and naked mole rats (*Heterocephalus glaber*; Faulkes and Abbott 1997). However, subordinates breed occasionally in many cooperative species (Russell 2004; Clutton-Brock et al. 2008), while, in communal breeders, including acorn woodpeckers (*Melanerpes formicivorus*; Koenig and Mumme 1987), groove-billed anis (*Crotophaga sulcirostris*; Vehrencamp 1977), banded mongooses (*Mungos mungo*; Cant 2000), African lions (*Panthera leo*; Bertram 1975), and several species of rodent (Hayes 2000), multiple females regularly reproduce.

Evolutionary explanations for variation in reproductive skew, both across and within species, assume that breeding by subordinates reduces the fitness of dominant females (but see Cant and Johnstone 1999). They suggest that dominant females concede reproductive opportunities to subordinates to either retain them in the group or discourage them from challenging (Vehrencamp 1983; Reeve 2000) or that subordinates breed where dominants are unable to prevent them from doing so (Cant 1998; Reeve et al. 1998), although some combine elements of both arguments (Magrath et al. 2004). Explanations of the first kind are usually referred to as "concessionary" or "transactional" models, while those of the second kind are referred to as "limited-control" or "constraint" models (Keller and Reeve 1994; Clutton-Brock 1998; Johnstone 2000; Magrath et al. 2004). Several empirical studies of cooperative vertebrates have now attempted to test these theoretical models. While some have produced results consistent with the predictions of transactional models, a larger number have concluded that the distribution of sub-

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ordinate breeding is consistent with predictions based on limited-control models of reproductive suppression and that subordinates commonly breed in situations where the capacity of dominants to prevent them from doing so is reduced (Clutton-Brock et al. 2001*b*; Haydock and Koenig 2003; Magrath et al. 2004; Crespi 2009).

To date, few studies have investigated whether contrasts in the costs and benefits of suppressing subordinate reproduction to dominants play an important role in generating variation in reproductive skew (Hodge 2009). This is surprising, as the costs and benefits to dominants of suppressing subordinate reproduction are likely to vary widely. As a result, variation in reproductive skew may sometimes be a consequence of differences in the costs and benefits of suppressing subordinate reproduction to dominants, without the need to invoke reproductive transactions or limitations in dominant control. For example, dominants might be expected to evict or suppress subordinates at times when they themselves are breeding rather than when they are not. Dominants may also gain more from suppressing subordinates when group size is large and further increases in the number of resident helpers are likely to reduce the fitness of offspring born to dominants, as a result of increased competition for resources between group members. Dominants may also be more tolerant of the breeding attempts of closely related females (whose reproductive success will contribute to indirect components of their inclusive fitness) than of the breeding attempts of distant relatives or unrelated females (Hamilton 1964). This explanation of variation in reproductive skew differs from the usual predictions of transactional models since no transactions or exchanges are involved and the frequency with which subordinates breed would not necessarily be expected to affect the probability that they would either leave the group or challenge the dominant female. In addition, it differs from the usual predictions of limited-control models since it suggests that dominants only attempt to prevent subordinates from breeding when this threatens their own fitness, so that variation in skew need not be related to contrasts in the capacity of dominants to control subordinates.

In this article, we use our long-term study of Kalahari meerkats (*S. suricatta*) to investigate whether dominant females suppress subordinate reproduction when the net fitness benefits to be gained from doing so are high. Kalahari meerkats are desert-adapted, cooperative mongooses that live in groups of 3–50 across the drier regions of southern Africa (Clutton-Brock et al. 1998, 1999). Each group contains one female who is behaviorally dominant to other group members and whose offspring are typically fathered by the most dominant male in the group (Griffin et al. 2003; Young et al. 2007; Hodge et al. 2008; Spong et al. 2008). Dominant females attempt to breed 2–4 times

per year (mean  $\pm$  SE =  $3.10 \pm 0.19$  observed pregnancies per year), and groups contain several sexually mature subordinate females who also attempt to breed but at lower rates (mean  $\pm$  SE =  $1.20 \pm 0.19$  observed pregnancies per year). Subordinate females have usually been born within the group (as females do not immigrate into established groups) and so are typically daughters, sisters, granddaughters, or nieces of the dominant female. Older subordinate females are the target of frequent aggression from the dominant female in their group, being periodically evicted from their group for several weeks at a time (Clutton-Brock et al. 1998). These temporary evictions appear to result in the stress-related suppression of subordinate reproduction, both disrupting conception and increasing rates of abortion (Young et al. 2006, 2008). Compared to dominant females, pregnant subordinates lose a high proportion of their litters before term (33% vs. 18%; Clutton-Brock et al. 2008), and, if their litters survive to term, their newborn pups are often killed by the dominant female or, less frequently, other females in the group (Clutton-Brock et al. 1998; Young and Clutton-Brock 2006). Pups born to dominants may also be killed by other females (Young and Clutton-Brock 2006), but subordinates consistently lose a higher proportion of litters than do dominants (71% vs. 13%, respectively). Pups remain at the natal burrow for their first 3 weeks of life and are guarded by all group members (Clutton-Brock et al. 2000). Subsequently, they begin to forage with the group and are provisioned by all group members until they are around 3 months of age and able to find food independently (Clutton-Brock et al. 2001*a*). In small groups, where the ratio of helpers to pups is relatively low, foraging pups regularly compete for access to helpers (Hodge et al. 2007, 2009), and helpers do not appear to discriminate between pups born to the dominant female and those born to other subordinates, readily feeding unrelated pups introduced experimentally (Clutton-Brock et al. 2001*c*).

Since subordinate females are almost always closely related to dominant females, evicting them or suppressing their breeding attempts will have appreciable costs to the indirect fitness of dominants, which are likely to be offset by substantial benefits to their direct fitness. To investigate whether this is the case, we first test the prediction that simultaneous breeding by subordinate females lowers the direct fitness of dominants. To do this, we compare the weight of pups born to dominants when subordinates breed at the same time and when subordinates do not. Any reductions in weight arising from competition are expected to compromise offspring fitness, as early-life growth among meerkats has positive downstream effects on survival and reproductive success (Russell et al. 2007). We then synthesize and extend previous analyses to investigate whether dominant females modify the frequency

with which they evict subordinates or kill their offspring in relation to variation in the costs of subordinate breeding to dominants. Specifically, we test whether the frequencies of eviction and reproductive suppression increase (1) when dominant females are breeding compared to times when they are not; (2) when group size is relatively large, as additional helpers will not be needed to care for the dominant female's pups, and their presence may increase competition for resources; and (3) in subordinate females that are more distantly related to the dominant female than other subordinates in the same group, so that their breeding success contributes relatively little to the dominant females' inclusive fitness.

## Methods

### *Study Site*

Data were collected from a wild population of meerkats at the Kuruman River Reserve, South Africa (26°58'S, 21°49'E), between October 1993 and May 2005. Descriptions of habitat, climate, and study population have been published elsewhere (Clutton-Brock et al. 1998). All animals in the study population could be individually identified by small dye marks on their fur and were habituated to close observation (from <1 m). Most were trained to step onto a portable electronic weighing balance before the morning foraging session, allowing regular measures of body mass to be collected without the need for capture. Pregnancy, which lasts for 70 days, could be detected from approximately the third week after conception, due to a swelling of the abdomen and associated weight gain. Births and abortions were identified from a sudden change in body shape and dramatic weight loss. We visited groups daily when parturition approached, so most birth and abortion dates were known to within 1 day. Individuals were classified as pups until they were 3 months of age and could forage independently.

### *Assessment of Relatedness*

As females were monitored during pregnancy, maternity was known for >99% of individuals born in the population, but genetic analysis was necessary to assign paternity. Descriptions of tissue sampling, DNA extraction, and genotyping methodologies are provided in detail by Spong et al. (2008). Paternity was assigned using the Cervus program (Marshall et al. 1998). Candidate males included all adult immigrant males within the group and all extragroup adult males seen in the vicinity of the group within 2 weeks of conception (Spong et al. 2008). To reduce false assignments, we excluded males who were offspring of the mother, as previous genetic work has shown zero incidence

of incestuous matings within groups (Griffin et al. 2003). Using this parentage information, we divided subordinate females into four categories, depending on their relatedness to the dominant female: sisters of the dominant female, who shared the same mother and father ( $r = 0.5$ ); daughters of the dominant female ( $r = 0.5$ ); granddaughters of the dominant female ( $r = 0.25$ ); and nieces of the dominant female ( $r = 0.25$ ).

### *Statistical Analysis*

Statistical analyses were conducted using Genstat, version 10 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Where multifactorial analyses involved repeated sampling of individuals, litters, or groups, linear mixed models (LMMs) and generalized linear mixed models (GLMMs) were used. These are similar to general(ized) linear models but allow both fixed and random terms to be included. All models involving binomially distributed data were analyzed using a logit link function. In all mixed models, random terms were retained, unless the variance component was found to be zero (and hence their removal did not influence the findings reported). In each model, all potential explanatory terms were entered and dropped sequentially until only those terms that explained significant variation remained. In all cases, repeating the analysis by successive inclusion of significant terms to build a minimal model from scratch yielded an identical final model. Each dropped term was then put back into the minimal model to obtain its level of nonsignificance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested, but results are presented only if found to explain significant variation. All statistical tests were two tailed. Unless otherwise stated, means are quoted  $\pm 1$  SE.

### *Does Subordinate Breeding Affect the Weight at Independence of Pups Born to the Dominant Female?*

To investigate whether dominant females suffer a cost when subordinates breed, we compared the weight of the dominant female's pups at independence (3 months) in litters where dominants bred alone and litters where a subordinate female gave birth within 30 days of the dominant. Pup weight at independence (g) was fitted as the response term in an LMM, and the breeding status of the dominant (alone, synchronously with subordinate) was fitted as the main term of interest. Group identity and litter identity were included as random terms. This analysis was conducted on 509 pups born to 29 dominant females in 159 litters (147 alone, 12 synchronously with subordinate) in 15 groups. To assess whether the costs that dominant females suffered were influenced by whether the subordinate breeder was a sister or a daughter, we took

all litters where subordinates bred and fitted the weight of the dominant female's pup into an LMM. The relatedness category of the subordinate breeder (sister, daughter) was fitted as the main term of interest, and the weight of the pup at emergence (controlled for age) was included as a covariate. Litter, group, and dominant female identity were included as random terms. This analysis used a data set of 44 pups born in 12 litters in seven groups to eight dominant females.

*Does the Frequency of Reproductive Suppression Vary with the Breeding Status of Dominant Females, the Size of Groups, or the Proximity of Kinship between Dominants and Subordinates?*

*Eviction.* We define eviction as situations where females are forced to spend an extended period of time outside their group as a result of aggression from the dominant (Young et al. 2006; Clutton-Brock et al. 2008). To investigate whether females were evicted during the dominant female's pregnancy, we took all adult females present in the group during each week and fitted whether they were evicted (1 = yes; 0 = no) as the response term in a binomial GLMM. The week from the dominant's date of giving birth was fitted as the main term of interest. This analysis used a data set of 6,770 eviction opportunities involving 263 females during 197 dominant-female pregnancies by 32 dominants in 16 groups. To investigate the factors that influenced whether a particular subordinate female was evicted during the dominant female's pregnancy, we identified all adult females present in groups during each pregnancy undergone by a dominant female and fitted whether each subordinate female was evicted from the group during that pregnancy as the binomial response term in a GLMM (1 = yes; 0 = no). This analysis used a data set of 645 potential evictions by 29 dominant females during 191 breeding attempts in 16 groups involving 231 subordinate females. Litter identity, group identity, dominant-female identity, and subordinate-female identity were included as random terms in both models. This second analysis is similar to that conducted by Young et al. (2006), but we extend this earlier work by using a larger data set, which allows us to assess whether different categories of related females (sisters, daughters, granddaughters, and nieces of the dominant female) differ in their likelihood of eviction.

*Abortion.* A female was deemed to have aborted if substantial weight loss occurred when the female had been visibly pregnant for less than 4 weeks and therefore was unlikely to have carried to full term (Young et al. 2006; Clutton-Brock et al. 2008). To investigate the factors that influenced whether females that conceived carried their

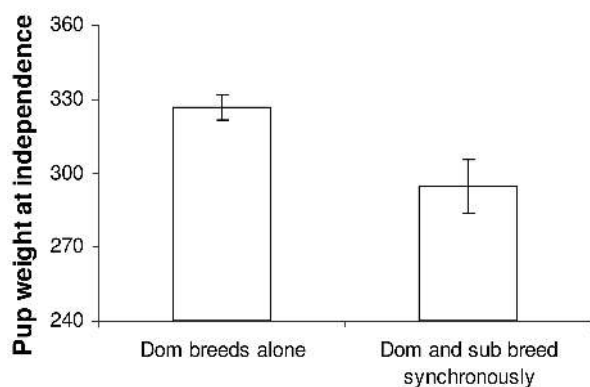
pregnancy to full term, we fitted whether each pregnant female carried to term or aborted (1 = yes; 0 = no) as the response term in a binomial GLMM. This analysis used a data set of 269 conceptions in 14 groups by 149 subordinate females. Group identity, dominant-female identity, and subordinate-female identity were included as random terms. This analysis is similar to that conducted by Clutton-Brock et al. (2008), but our analysis focuses on subordinates only.

*Infanticide.* Infanticide in meerkats usually occurs below ground, and direct observations are therefore rare (Young and Clutton-Brock 2006). Those direct observations that did occur ( $n = 12$ ) were within 4 days of the litter's birth and involved a pregnant female killing and eating pups born to another female within the group. To investigate whether the pregnancy status of other females in the group (and if pregnant, their relatedness to the mother) influenced the likelihood of infanticide, we fitted whether litters born to subordinate females failed in the first 4 days after birth as the binomial response term (1 = yes; 0 = no) in a GLMM, with 1 as the binomial denominator. We fitted a categorical variable incorporating the pregnancy status of other females as the main term of interest. "None pregnant" refers to situations when there were no other females pregnant in the group; if one other female was pregnant, they were categorized according to the relatedness of the pregnant female to the litter mother (none pregnant:  $n = 43$ ; sister pregnant:  $n = 23$ ; daughter pregnant:  $n = 7$ ; other pregnant:  $n = 7$ ). We first used this full data set to test the significance of the pregnancy status of other females on litter survival (following Young and Clutton-Brock 2006). To then assess the influence of the relatedness of any pregnant female to a parturient subordinate on the survival of her litter, we restricted this data set to those litters for which one other female was pregnant when the litter was born. Litters that were born when more than one female was pregnant (and hence more than one female was potentially infanticidal) were excluded from the analysis, as it would not have been possible to attribute the infanticide to any one female. The full model used a litter-survival data set of 81 litters born to 63 subordinate females in 16 groups, and the reduced model consisted of 37 litters born to 34 subordinate females in 12 groups at a time when one other female was pregnant. Group and female identity were included as random terms in both analyses.

## Results

*Does Subordinate Breeding Affect the Weight at Independence of Pups Born to the Dominant Female?*

As predicted, the offspring of dominant females are lighter at nutritional independence (3 months) when subordi-



**Figure 1:** Weight of dominant (*dom*) female's pups at independence (3 months), when the dominant female breeds alone or within 30 days of a subordinate (*sub*) female.

nates breed within 30 days than when no subordinate pups are present (LMM:  $\chi_1^2 = 4.86$ ,  $P = .029$ ; fig. 1; table 1). In litters where subordinate females bred, there was no evidence that whether the competing female was a sister or daughter had any influence on the weight of the dominant female's pups at independence (LMM:  $\chi_1^2 = 0.01$ ,  $P = .94$ ).

*Does the Frequency of Reproductive Suppression Vary with the Breeding Status of Dominant Females, the Size of Groups, or the Proximity of Kinship between Dominants and Subordinates?*

The probability that dominants will temporarily evict subordinate females from the group is strongly influenced by their own breeding status. Dominant females rarely evict subordinate females unless they are pregnant themselves: 92% (179/192) of observed evictions occurred when the dominant female was pregnant. The frequency of subordinate eviction also increases as the dominant's parturition approaches (GLMM:  $\chi_8^2 = 1,238.7$ ,  $P < .001$ ; fig. 2A). Pregnant dominants are also more likely to evict older

subordinates (GLMM:  $\chi_1^2 = 56.88$ ,  $P < .001$ ; fig. 2B; table 2), who are more likely to breed than younger ones. Dominants in large groups are also more likely to evict subordinates than are those living in small ones ( $\chi_1^2 = 4.64$ ,  $P = .031$ ; fig. 2C). Finally, dominants are more likely to evict nieces and grandoffspring ( $r = 0.25$ ) than offspring or sisters ( $r = 0.5$ ;  $\chi_1^2 = 9.15$ ,  $P = .027$ ; fig. 2D).

Subordinates are no more likely to abort their litters if dominants are pregnant than if dominants are not breeding (GLMM:  $\chi_1^2 = 1.24$ ,  $P = .27$ ; table 3), and subordinates distantly related to dominants were no more likely to lose their litters than were closer relatives ( $\chi_3^2 = 1.82$ ,  $P = .61$ ). However, abortion rates in subordinates rise in large groups, where the net benefits of additional recruits to dominants are likely to be low ( $\chi_1^2 = 4.35$ ,  $P = .040$ ).

If subordinate females do carry their litters to term, the probability that the litter will fail in the first 4 days post-parturition is substantially higher if other females in the group are pregnant at the time of birth (GLMM:  $\chi_3^2 = 14.32$ ,  $P = .002$ ; fig. 3; table 4). However, when the other females are pregnant, there is no indication that the frequency of infanticide is modified by the degree of relatedness ( $\chi_2^2 = 0.02$ ,  $P = .99$ ; fig. 3). There is also a marginally nonsignificant tendency for litter failure to increase in larger groups ( $\chi_1^2 = 3.65$ ,  $P = .056$ ; table 4).

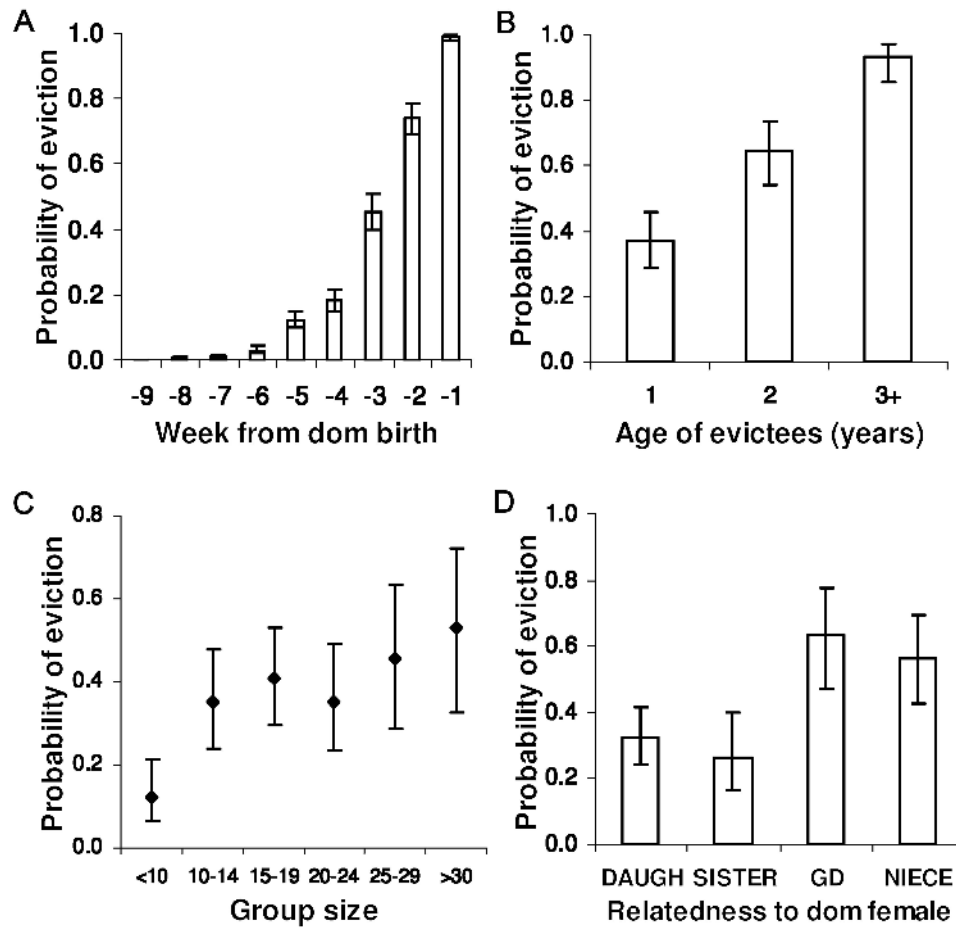
## Discussion

Dominant female meerkats suffer a cost when subordinates breed, producing pups that are lighter at independence than when dominants breed alone. This reduction in pup weight is likely to have important consequences for the fitness of dominant females, as low pup weight at 3 months is associated with reduced survival to adulthood and lower future breeding success (Russell et al. 2007). The reduction in the fitness of the dominant's pups when subordinates breed probably explains why dominant females regularly suppress the reproductive attempts of subordinates (Clutton-Brock et al. 1998; Young and Clutton-Brock 2006; Young et al. 2006). However, since dominants are

**Table 1:** Linear mixed model of factors affecting the weight of the dominant female's pups at 3 months (g)

Explanatory terms	Estimate $\pm$ SE	Wald statistic ( $\chi^2$ )	df	<i>P</i>
Dominant breeding status:				
Subordinate also breeds	.00 $\pm$ .00	4.86	1	<b>.029</b>
Alone	25.65 $\pm$ 11.64			
Pup weight at emergence (controlled for age)	20.59 $\pm$ 1.96	110.83	1	<b>&lt;.001</b>
Rainfall between 30 and 90 days	.070 $\pm$ .047	1.69	1	.20
Group size (mean individuals >3 months between 30 and 90 days)	.95 $\pm$ .93	.03	1	.86
Constant	302.40 $\pm$ 11.07			

Note: Significant terms are in bold. Litter identity ( $1,324.5 \pm 177.8$ ), dominant-female identity ( $123.4 \pm 103.2$ ), and group identity ( $-95.9 \pm 52.3$ ) were included as random terms. Analysis was conducted on 509 pups born to 29 dominant females in 159 litters (12 synchronous, 147 singular) in 15 groups.



**Figure 2:** A, Probability that subordinate females will be evicted during the period of the dominant (*dom*) female's gestation; B, probability that subordinate females of different ages will be evicted; C, probability that subordinate females will be evicted by dominants in groups of different sizes; D, probability that dominant females will evict subordinate females of different categories of relatedness. DAUGH = daughter; GD = granddaughter.

**Table 2:** Generalized linear mixed model of the factors affecting whether a subordinate female is evicted during the dominant female's pregnancy

Explanatory terms	Estimate $\pm$ SE	Wald statistic ( $\chi^2$ )	df	<i>P</i>
Subordinate age (months)	.17 $\pm$ .022	56.88	1	<b>&lt;.001</b>
Season	See text	27.89	3	<b>&lt;.001</b>
Number of adult females when dominant gave birth	-.20 $\pm$ .086	5.38	1	<b>.020</b>
Relatedness	See figure 3	9.15	3	<b>.027</b>
Group size ( $\log_{10}$ ; individuals 3 months at dominant birth)	3.13 $\pm$ 1.45	4.64	1	<b>.031</b>
Rainfall (mm) during dominant female gestation	.0044 $\pm$ .0041	1.17	1	.28
Subordinate-female weight <sup>a</sup>	.06 $\pm$ .14	.19	1	.66
Dominant female age at conception (months)	-.0054 $\pm$ .011	.22	1	.64
Constant	-1.74 $\pm$ .65			

Note: Significant terms are in bold. Dominant-female identity (0.19  $\pm$  0.52), subordinate-female identity (0.00  $\pm$  0.00), litter identity (2.52  $\pm$  0.57), and group identity (0.80  $\pm$  0.69) were included as random terms. Analysis used a data set of 645 potential evictions by 29 dominant females during 191 breeding attempts in 16 groups involving 231 subordinate females.

<sup>a</sup> Residuals of the subordinate female's mean nonpregnant weight during the dominant female's gestation were taken against their age in an asymptotic regression.

**Table 3:** Generalized linear mixed model of the factors affecting the probability of abortion in subordinate females

Explanatory terms	Estimate $\pm$ SE	Wald statistic ( $\chi^2$ )	df	<i>P</i>
Group size (individuals >3 months at conception)	.040 $\pm$ .019	4.35	1	<b>.040</b>
Rainfall (mm) in 2 months around conception	-.0058 $\pm$ .0034	2.89	1	.090
Pregnancy status of dominant female:				
Not pregnant	.00 $\pm$ .00	1.24	1	.27
Pregnant	-.29 $\pm$ .26			
Relatedness		1.82	3	.61
Subordinate-female weight at conception <sup>a</sup>	-.058 $\pm$ .17	.12	1	.73
Subordinate age (months) at conception	-.0012 $\pm$ .016	.01	1	.94
Constant	-.57 $\pm$ .21			

Note: Significant terms are in bold. Subordinate-female identity ( $0.00 \pm 0.00$ ), group identity ( $0.00 \pm 0.00$ ), and dominant-female identity ( $0.20 \pm 0.20$ ) were included as random terms. Analysis used a data set of 269 conceptions in 14 groups by 149 subordinate females.

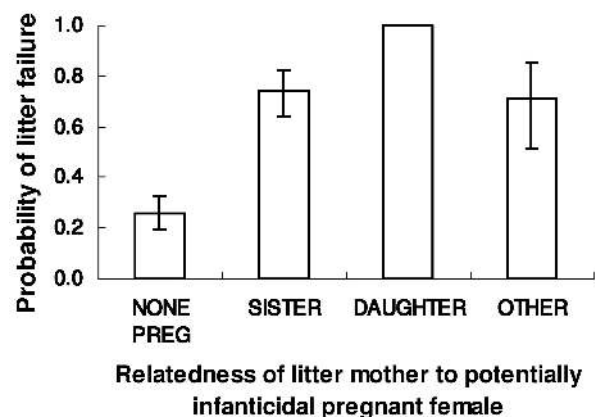
<sup>a</sup> Residuals were taken against female age in an asymptotic regression.

closely related to subordinates, suppressing the breeding attempts of subordinates or evicting them from the group involves losses to the indirect component of the dominant's fitness. As predicted, our results show that dominant females modify the degree to which they suppress subordinates in relation to the net benefits they are likely to gain from preventing them from breeding; they are more likely to kill pups born to subordinates when they are pregnant themselves and to evict subordinates when they are about to give birth themselves. Dominant females are also more likely to evict subordinates from the group when group size is large, and both the likelihood of abortion and the likelihood of infanticide also increase in large groups, where the benefits of additional recruits are low. Dominant females are also less likely to evict subordinates to whom they are closely related, although there was no evidence that relatedness influenced subordinate litter loss through infanticide.

The frequency of subordinate breeding and the degree of reproductive skew in other cooperative breeders also appears to be related to the net benefits to dominants of preventing subordinate reproduction. In several cooperative vertebrates, hostility to competing females and interference in their breeding attempts increases when dominants are reproductively active (Vehrencamp 1977; Mumme et al. 1983; Ebensperger 1998; Creel and Creel 2001), and there is some evidence that intolerance toward other breeding females can increase with group size: for example, in captive common marmosets, breeding females are more intolerant of female immigrants in larger groups than in small groups (Schaffner and French 1997). In addition, detailed studies of several primate societies show that females selectively direct aggression at more distantly related females and their offspring (Chapais 2006).

Variation in the net benefits of suppression to dominant females may also help to account for interspecific differences in the extent to which dominants suppress subor-

dinates and the observed degree of reproductive skew. In banded mongooses (*Mungos mungo*), where dominant females tolerate reproduction by subordinates and multiple females commonly breed in synchrony, the pups of dominant females show higher survival rates if one or more subordinate females breed at the same time (Cant et al. 2010). In African lions *Panthera leo*, females gain advantages from breeding at the same time as other females, as their offspring are jointly defended from infanticidal males (Packer et al. 2001). In addition, the costs of suppression in lions may be unusually high since females possess dangerous weapons, and even minor conflicts may be lethal (Packer et al. 2001). Suppression of subordinate reproduction by dominants and high levels of reproductive skew



**Figure 3:** Probability that subordinate litters failed within the first 4 days of birth when females of different categories of relatedness were pregnant or when no other females were pregnant (*NONE PREG*). *OTHER* = situations when the subordinate female was the granddaughter or niece of another pregnant female in the group. Means and standard errors are predictions from a generalized linear mixed model controlling for repeated measures among groups and females.

**Table 4:** Generalized linear mixed model of the factors affecting the probability that subordinate female litters fail in the first 4 days postbirth

Explanatory terms	Estimate $\pm$ SE	Wald statistic ( $\chi^2$ )	df	<i>P</i>
Pregnancy status and relatedness of other pregnant females	See figure 3	14.32	3	<b>.002</b>
Group size	.073 $\pm$ .038	3.65	1	.056
Rainfall during gestation (mm)	.0026 $\pm$ .0046	.31	1	.58
Subordinate-female age at conception (months)	.0092 $\pm$ .027	.00	1	.98
Subordinate-female weight at conception <sup>a</sup>	-.22 $\pm$ .35	.41	1	.52
Constant	1.04 $\pm$ .48			

Note: Significant terms are in bold. Subordinate-female identity ( $0.14 \pm 0.77$ ) and group identity ( $0.00 \pm 0.00$ ) were included as random terms. Analysis used a data set of 81 litters born to 63 subordinate females in 16 groups.

<sup>a</sup> Residuals were taken against female age in an asymptotic regression.

are also often found in species that have evolved in arid or semiarid conditions, where competition for resources is likely to be intense and reproduction by subordinates is likely to be particularly costly to dominants (Clutton-Brock et al. 2006).

Together with these studies, our results suggest that variation in the extent to which dominants suppress subordinate reproduction, both across and within species, can be a consequence principally of variation in the net benefits that dominants gain from suppressing reproduction by subordinates. This perspective differs from the traditional approach to studying reproductive skew, in that it does not make it necessary to invoke a threat of departure or challenge by subordinates or a lapse in dominant control to explain why dominants may tolerate subordinate reproduction. Where dominants are commonly closely related to their subordinates, they should, instead, be expected to suppress subordinate reproduction only if they would otherwise suffer net fitness costs when subordinates breed.

If variation in the extent to which dominants tolerate the presence or breeding attempts of subordinates is primarily related to the relative costs and benefits of suppressing them to the dominant's own fitness, subordinates that reproduce would not necessarily be expected either to be more likely to remain in the group or to forgo attempts to challenge and replace the dominant female in their group. As we have described in previous papers, there is little evidence that breeding reduces the probability that subordinates will disperse or will challenge the dominant female either in meerkats or in other cooperative breeders (Clutton-Brock 1998; Clutton-Brock et al. 2001*b*). Future attempts to develop and test models of reproductive skew need to investigate how variation in the net benefits of suppression to dominants interacts with selection for reproductive restraint among subordinates to affect the observed degree of reproductive skew.

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### Literature Cited

- Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. *Journal of Zoology* 177:463–482.
- Cant, M. A. 1998. A model for the evolution of reproductive skew without reproductive suppression. *Animal Behaviour* 55:163–169.
- . 2000. Social control of reproduction in banded mongooses. *Animal Behaviour* 59:147–158.
- Cant, M. A., and R. A. Johnstone. 1999. Costly young and reproductive skew in animal societies. *Behavioral Ecology* 10:178–184.
- Cant, M. A., S. J. Hodge, J. S. Gilchrist, M. B. V. Bell, and H. J. Nichols. 2010. Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proceedings of the Royal Society B: Biological Sciences* 277:2219–2226.
- Chapais, B. 2006. Kinship, competence, and cooperation in primates. Pages 47–64 in P. M. Kappeler and C. van Schaik, eds. *Cooperation in primates and humans: mechanisms and evolution*. Springer, Berlin.
- Clutton-Brock, T. H. 1998. Reproductive skew, concessions and limited control. *Trends in Ecology & Evolution* 13:288–292.
- Clutton-Brock, T. H., P. N. M. Brotherton, R. Smith, G. M. McIlrath, R. Kansky, D. Gaynor, M. J. O'Riain, and J. D. Skinner. 1998. Infanticide and expulsion of females in a cooperative mammal. *Proceedings of the Royal Society B: Biological Sciences* 265:2291–2295.
- Clutton-Brock, T. H., A. Maccoll, P. Chadwick, D. Gaynor, R. Kansky, and J. D. Skinner. 1999. Reproduction and survival of suricates



- (*Suricata suricatta*) in the southern Kalahari. *African Journal of Ecology* 37:69–80.
- Clutton-Brock, T. H., P. N. M. Brotherton, M. J. O’Riain, A. S. Griffin, D. Gaynor, L. Sharpe, R. Kansky, M. B. Manser, and G. M. McIlrath. 2000. Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proceedings of the Royal Society B: Biological Sciences* 267:301–305.
- Clutton-Brock, T. H., P. N. M. Brotherton, M. J. O’Riain, A. S. Griffin, D. Gaynor, R. Kansky, L. Sharpe, and G. M. McIlrath. 2001a. Contributions to cooperative rearing in meerkats. *Animal Behaviour* 61:705–710.
- Clutton-Brock, T. H., P. N. M. Brotherton, A. F. Russell, M. J. O’Riain, D. Gaynor, R. Kansky, A. Griffin, et al. 2001b. Cooperation, control, and concession in meerkat groups. *Science* 291:478–481.
- Clutton-Brock, T. H., A. F. Russell, L. L. Sharpe, P. N. M. Brotherton, G. M. McIlrath, S. White, and E. Z. Cameron. 2001c. Effects of helpers on juvenile development and survival in meerkats. *Science* 293:2446–2449.
- Clutton-Brock, T. H., S. J. Hodge, G. Spong, A. F. Russell, N. R. Jordan, N. C. Bennett, and M. B. Manser. 2006. Intrasexual competition and sexual selection in cooperative meerkats. *Nature* 444:1065–1068.
- Clutton-Brock, T. H., S. J. Hodge, and T. P. Flower. 2008. Group size and subordinate reproduction in Kalahari meerkats. *Animal Behaviour* 76:680–700.
- Creel, S., and N. M. Creel. 2001. *The African wild dog: behavior, ecology and conservation*. Princeton University Press, Princeton, NJ.
- Crespi, B. J. 2009. Social conflict resolution, life history, and the reconstruction of skew. Pages 480–507 in R. Hager and C. B. Jones, eds. *Reproductive skew in vertebrates: proximate and ultimate causes*. Cambridge University Press, Cambridge.
- Ebensperger, L. A. 1998. Strategies and counter strategies to infanticide in mammals. *Biological Reviews of the Cambridge Philosophical Society* 73:321–346.
- Faulkes, C. G., and D. H. Abbott. 1997. The physiology of reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. Pages 302–334 in N. G. Solomon and J. A. French, eds. *Cooperative breeding in mammals*. Cambridge University Press, Cambridge.
- French, J. A. 1997. Proximate regulation of singular breeding in callitrichid primates. Pages 34–75 in N. G. Solomon and J. A. French, eds. *Cooperative breeding in mammals*. Cambridge University Press, Cambridge.
- Griffin, A. S., J. M. Pemberton, P. N. M. Brotherton, G. McIlrath, D. Gaynor, R. Kansky, J. O’Riain, and T. H. Clutton-Brock. 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology* 14:472–480.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. I, II. *Journal of Theoretical Biology* 7:1–52.
- Hatchwell, B. J., C. Anderson, D. J. Ross, M. K. Fowlie, and P. G. Blackwell. 2001. Social organization of cooperatively breeding long-tailed tits: kinship and spatial dynamics. *Journal of Animal Ecology* 70:820–830.
- Haydock, J., and W. D. Koenig. 2003. Patterns of reproductive skew in the polygynandrous acorn woodpecker. *American Naturalist* 162:277–289.
- Hayes, L. D. 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour* 59:677–688.
- Heinsohn, R. G. 1991. Evolution of obligate cooperative breeding in white-winged choughs: a statistical approach. *Proceedings of the International Ornithological Congress* 20:1309–1361.
- Hodge, S. J. 2009. Understanding variation in reproductive skew: directions for future empirical research. Pages 439–466 in R. Hager and C. B. Jones, eds. *Reproductive skew in vertebrates: proximate and ultimate causes*. Cambridge University Press, Cambridge.
- Hodge, S. J., T. P. Flower, and T. H. Clutton-Brock. 2007. Offspring competition and helper associations in cooperative meerkats. *Animal Behaviour* 74:957–964.
- Hodge, S. J., A. Manica, T. P. Flower, and T. H. Clutton-Brock. 2008. Determinants of reproductive success in dominant female meerkats. *Journal of Animal Ecology* 77:92–102.
- Hodge, S. J., A. Thornton, T. P. Flower, and T. H. Clutton-Brock. 2009. Food limitation increases aggression in juvenile meerkats. *Behavioral Ecology* 20:930–935.
- Johnstone, R. A. 2000. Models of reproductive skew: a review and synthesis (invited article). *Ethology* 106:5–26.
- Keller, L., and H. K. Reeve. 1994. Partitioning of reproduction in animal societies. *Trends in Ecology & Evolution* 9:98–103.
- Koenig, W. D., and R. L. Mumme. 1987. *Population ecology of the cooperatively breeding acorn woodpecker*. Princeton University Press, Princeton, NJ.
- Magrath, R. D., R. A. Johnstone, and R. G. Heinsohn. 2004. Reproductive skew. Pages 157–176 in W. D. Koenig and J. L. Dickinson, eds. *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge.
- Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7:639–655.
- Mumme, R. L., W. D. Koenig, and F. A. Pitelka. 1983. Reproductive competition in the communal acorn woodpecker: sisters destroy each other’s eggs. *Nature* 306:583–584.
- Packer, C., A. E. Pusey, and L. E. Eberly. 2001. Egalitarianism in female African lions. *Science* 293:690–693.
- Reeve, H. K. 2000. A transactional theory of within-group conflict. *American Naturalist* 155:365–382.
- Reeve, H. K., S. T. Emlen, and L. Keller. 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? *Behavioral Ecology* 9:267–278.
- Russell, A. F. 2004. Mammals: comparisons and contrasts. Pages 210–227 in W. D. Koenig and J. L. Dickinson, eds. *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press, Cambridge.
- Russell, A. F., A. J. Young, G. Spong, N. R. Jordan, and T. H. Clutton-Brock. 2007. Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society B: Biological Sciences* 274:513–524.
- Schaffner, C. M., and J. A. French. 1997. Group size and aggression: “recruitment incentives” in a cooperatively breeding primate. *Animal Behaviour* 54:171–180.
- Spong, G., S. J. Hodge, A. J. Young, and T. H. Clutton-Brock. 2008. Factors affecting the reproductive success of dominant male meerkats. *Molecular Ecology* 17:2287–2299.
- Vehrencamp, S. L. 1977. Relative fecundity and parental effort in the communally nesting anis, *Crotophaga sulcirostris*. *Science* 197:403–405.
- . 1983. A model for the evolution of despotic versus egalitarian societies. *Animal Behaviour* 31:667–682.
- Young, A. J., and T. H. Clutton-Brock. 2006. Infanticide by subor-

- dinates influences reproductive sharing in cooperatively breeding meerkats. *Biology Letters* 2:385–387.
- Young, A. J., A. A. Carlson, S. L. Monfort, A. F. Russell, N. C. Bennett, and T. Clutton-Brock. 2006. Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the USA* 103: 12005–12010.
- Young, A. J., G. Spong, and T. H. Clutton-Brock. 2007. Subordinate males prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society B: Biological Sciences* 274:1603–1609.
- Young, A. J., S. L. Montfort, and T. H. Clutton-Brock. 2008. Physiological suppression in subordinate female meerkats: a role for restraint due to the threat of dominant interference. *Hormones and Behavior* 53:131–139.
- Zahavi, A. 1974. Communal nesting by the Arabian babbler: a case of individual selection. *Ibis* 116:84–87.

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Subadult meerkats play-fighting. When their mother dies, sisters compete intensely for the breeding position, and losers are evicted from the group. Photograph by Russell Venn.