

# Determinants of reproductive success in dominant female meerkats

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## Summary

1. In cooperative societies with high reproductive skew, selection on females is likely to operate principally through variation in the probability of acquiring dominant status and variation in reproductive success while dominant. Despite this, few studies of cooperative societies have investigated the factors that influence which females become dominant, and/or their reproductive output while in the dominant position.
2. Here we use long-term data from a wild meerkat population to describe variation in the breeding success of dominant female meerkats *Suricata suricatta* and investigate its causes.
3. Female meerkats compete intensely for breeding positions, and the probability of acquiring the breeding role depends upon a female's age in relation to competitors and her weight, both at the time of dominance acquisition and early in life.
4. Once dominant, individual differences in breeding success depend principally on the duration of dominance tenure. Females remain for longer in the dominant position if they are heavier than their competitors at the start of dominance, and if the number of adult female competitors at the start is low.
5. Female breeding success is also affected by variation in fecundity and pup survival, both of which increase with group size. After controlling for these effects, female body weight has a positive influence on breeding rate and litter size, while the number of adult female competitors reduces litter survival.
6. These findings suggest that selection for body weight and competitive ability will be high in female meerkats, which may moderate their investment in cooperative activities. We suggest that similar consequences of competition may occur among females in other cooperative societies where the benefits of attaining dominance status are high.

**Key-words:** dominance, eusocial, lifetime reproductive success, queen, variance.

## Introduction

In cooperatively breeding vertebrates, reproduction is usually monopolized by a small number of dominant individuals, with all group members helping to rear their young (Solomon & French 1997; Koenig & Dickinson 2004). While a number of studies have investigated the fitness benefits that subordinates may gain from helping (for reviews see Cockburn 1998; Dickinson & Hatchwell 2004; Russell 2004; Komdeur 2006), relatively few have examined the factors that influence which individuals are able to attain the dominant breeding position, the primary route to gaining fitness. In addition, the factors that influence the dominant's reproductive success over the course of their tenure are poorly understood

(Clutton-Brock *et al.* 2006). This lack of information on the factors that determine dominance acquisition and dominant breeding success is unfortunate, as selection in cooperative societies is likely to operate primarily through variation in the reproductive success of dominant breeders. As a result, selection may strongly favour strategies that increase an individual's likelihood of attaining dominant status, as well as their breeding success while dominant, which could moderate or constrain selection for helping if the two trade-off against each other.

In this paper, we examine dominance acquisition and the determinants of reproductive success in dominant female meerkats *Suricata suricatta*. In these cooperative mongooses, reproduction is largely monopolized by a single female in each group who is behaviourally dominant to all other same sex group members and produces one to four litters of pups

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per year (Doolan & Macdonald 1997). Groups contain up to 50 subordinate group members (15 on average) of even sex ratio, who help to rear the dominant female's pups (Clutton-Brock *et al.* 1998). Subordinate females breed occasionally, but their reproductive success is low, producing only 0.4 ( $\pm 0.2$ ) independent pups per female per year on average ( $\pm$  SD), compared with 5.5 ( $\pm 3.1$ ) for dominant females. The low breeding success of subordinates is due in part to inbreeding avoidance, as subordinate females commonly lack access to unrelated breeding partners (O'Riain *et al.* 2000), and also because dominants suppress subordinate reproduction through stress-induced suppression (Young *et al.* 2006) and infanticide (Clutton-Brock *et al.* 1998; Young & Clutton-Brock 2006).

Female meerkats attain the dominant position in two ways. They can become dominant in their natal group (because the current dominant has died or been displaced) or they can disperse and found a new group, usually with a coalition of related females. Using data from our long-term meerkat study, we first examine the factors that influence which females acquire dominance when a vacancy arises. A previous comparison of dominance acquisition processes between males and females suggest that age and body weight are important (Clutton-Brock *et al.* 2006); we extend this work to look at the influence of early body weight and mother's dominance status. Second, we partition variance in the reproductive success of dominant females into the three main fitness components (breeding tenure, fecundity and offspring survival), allowing us to identify which component has the strongest influence on reproductive success (Clutton-Brock 1988). Finally, we investigate the factors that influence each of the above fitness components across a female's tenure, examining the effects of the dominant female's phenotype (age and weight) and aspects of her social environment (group size and competitor number) while controlling for external ecological variables (rainfall and season).

## Materials and methods

### STUDY SITE AND STUDY POPULATION

Data were collected from a wild population of meerkats inhabiting a 50 km<sup>2</sup> area of ranchland in the South African Kalahari (26°58'S, 21°49'E) between January 1994 and May 2005. Details of climate and habitat at the study site have been described in detail elsewhere (Russell *et al.* 2002). The study population during this period totalled over 1000 individuals, living in 17 social groups, all of whom were habituated to close observation (< 2 m). All individuals were marked with subcutaneous transponder chips, and could be recognized in the field by unique dye marks on their fur, which were applied without the need for capture. Study groups were visited approximately once every 3 days, and during these visits changes in group composition and other life-history data (e.g. changes in dominance status and births) were recorded. The ages of most individuals in the population (> 98%) were therefore known exactly. In addition, > 95% of study animals were trained to step on to an electronic balance, allowing the weights of most group members to be recorded each morning prior to foraging. Group members older than 1 year (who

therefore had the potential to breed) are referred to as 'adults', and all subordinate individuals over the age of 3 months as 'helpers'. Individuals were classified as pups until they were 3 months of age.

Each group contained one female who was behaviourally dominant to all other same sex group members and was usually the oldest and heaviest female in the group (Griffin *et al.* 2003). Over the course of this study we were able to observe 40 dominant females in 17 groups, although samples sizes vary between analyses depending on the type of data available for each female. Following a change in dominance, or after formation of a new group, the identity of the new dominant could be determined through behavioural observations of dominance assertion; these include slamming females with their hip, rubbing females with their chin or, in extreme cases, by attacking and biting. Adult females respond to these dominance assertion behaviours by retaliating, or by assuming a characteristic submissive posture and emitting a peeping vocalization (Kutsukake & Clutton-Brock 2006). Females were recorded as having assumed the dominant breeding position if all other adult females responded submissively to dominance assertion behaviours for at least 1 week.

Pregnancy in meerkats lasts for approximately 70 days and could be identified at about 30 days by swelling of the abdomen and an increase in body mass (Clutton-Brock *et al.* 1998). Birth dates could be accurately determined by a sudden change in the female's weight and body shape. As there were rarely behavioural signs of oestrus, conception dates were estimated by backdating 70 days from birth. Pups remain in an underground burrow for the first few weeks of life, emerging for the first time at about 3 weeks of age, and begin foraging with the group about 1 week later (Brotherton *et al.* 2001; Hodge, Flower & Clutton-Brock 2007). Offspring that emerge from the natal burrow are referred to as 'emergent pups' and those that survive to 3 months of age as 'independent pups' (because by this age they have become independent foragers).

All research protocols were approved by the University of Pretoria Ethics committee and conform to the Association for the Study of Animal Behaviour guidelines for the use of animals in research.

### STATISTICAL ANALYSIS

Statistical analyses were conducted using Genstat 6.2 (Lawes Agricultural Trust, Rothamsted, Harpenden, Herts, 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 and Generalized Linear Models, but allow both fixed and random terms to be included. Normally distributed data (confirmed by an Anderson-Darling normality test) were analysed using an identity link function and data with a binomial distribution were analysed using a logit link function. In all mixed models, variance components were estimated using the Restricted Maximum Likelihood (REML) method, and random terms were retained in the model 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 their level of nonsignificance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested, but results are only presented if found to explain significant variation. All statistical tests were two-tailed. Unless otherwise stated, means are quoted  $\pm 1$  SE.

#### ACQUISITION OF DOMINANCE STATUS

To estimate the proportion of female pups that attain the dominant position during their lifetime, the percentage of females that emerged before 1 May 2001 that became dominant before 1 May 2005 was calculated. Females born before this date were chosen, as these females had the potential to reach 4 years of age by 1 May 2005 (when observations for this study ceased). This is likely to provide a good indication of whether they attained dominance in their lifetime, as 96% (26 of 27) females whose date of birth was known that attained dominance in our study did so by the time they reached 4 years of age. As 57% of females born during this period dispersed away from the study population, it was also necessary to estimate the proportion of dispersing females that were likely to have attained the dominant position. To do this, it was assumed that females dispersing away from the study site achieved similar dominance success to those that dispersed within our study population.

To investigate the factors that influenced which female attained dominance when a vacancy arose, the age of the successful female in relation to other females in the group was recorded. If the oldest female did not become dominant, or if the oldest competing females were of the same age, the average nonpregnant weight of competing females in the 3 months before the dominance change was compared, as well as their weight when they reached independence at 90–97 days. To investigate whether mother's dominance status influenced a female's probability of becoming dominant, whether or not females who had the opportunity to reach 4 years of age (i.e. those born before 1 May 2001) became dominant was included as the binomial response term in a GLMM (1 = Yes, 0 = No) with 1 as the binomial denominator. The dominance status of the female's mother at conception and the female's mean weight at independence (between 90 and 97 days) were fitted as the variates of interest. Repeated measures within litters, groups and mothers were controlled by including them as random terms. This GLMM analysis was restricted to 143 females who survived to 1 year of age, and for whom weight data at independence were available.

#### VARIATION IN BREEDING SUCCESS AMONG DOMINANT FEMALES

To assess variance in the breeding success of dominant females, the total number of independent pups produced by 27 dominant females whose entire tenure was observed was calculated. For those females that produced at least one emergent pup during their tenure, the contribution of dominance tenure ( $L$ , in months), fecundity ( $F$ , the number of pups that emerged from the natal burrow per year) and offspring survival ( $S$ , proportion of emergent pups that survived to 3 months) to the variance in breeding success was calculated using the method described by Brown (1988). This approach decomposes the variance in dominant breeding success into the individual contributions of  $L$ ,  $F$  and  $S$ , as well as the contribution of the products of these three components ( $L \times F$ ,  $F \times S$ ,  $L \times S$  and  $L \times F \times S$ ). The relative contribution of the product of two components (say  $L \times F$ ) is the effect over and above the effect of the individual components considered independently. Contributions can be positive or negative, depending on how variables covary with each other (a negative component arises when one variable cancels the effect of another). Bootstrapping was used to estimate 95% confidence limits. To calculate the contribution of individuals that did not breed to the total variance in dominant breeding success (DBS), we used the method outlined by Brown (1988). This compares the

proportion of variance accounted for by those females who produced at least one emergent pup ( $P \times \text{Variance in DBS}$  where  $P = n_{\text{breeders}}/n_{\text{total}}$ ) with the proportion accounted for by those dominants who failed to breed ( $P \times 1 - P \times \text{mean DBS}^2$ ).

#### DURATION OF DOMINANCE TENURE

Dominance tenure was measured from the date on which an individual acquired dominance to the date that dominance ended. To investigate the factors that influence the tenure of dominant females, the tenures of 26 females (in months) were log transformed and fitted as the normally distributed response term in a GLM. The influence of whether or not the dominant was the oldest individual in the group, the age at which the female attained dominance (in months), whether or not the female attained dominance in her natal group, the number of competitors (subordinate females older than 1 year) and group size (total individuals older than 3 months) at the time of the dominance change were investigated. For a restricted data set of 15 dominance tenures where there was more than one adult female in the group and where weight data were available for both females, the difference in the mean non-breeding weights of the new dominant and her largest competitor in the 2 months around the dominance change was included as a covariate.

#### DOMINANT FEMALE FECUNDITY

Dominant female fecundity (measured as the number of pups produced that emerged per year) is a product of three reproductive components: (1) the rate at which females give birth; (2) the probability that litters survive to emergence; and (3) the number of pups produced per litter. To investigate the factors that influence all three traits, two separate analyses were conducted. First, the factors that influence the overall values of each component for dominant females during their tenure were investigated. Using these values 'per tenure' is important as these provide an overall measure of breeding success while dominant, and it is these values that are used to breakdown components of variance in breeding success. However, as the use of mean values may mask the effects of highly variable terms (such as group size, weight and rainfall), a second, more detailed analysis was conducted, which investigated the factors that influenced each component 'per breeding attempt'. These 'per breeding attempt' analyses are similar to those conducted by Russell *et al.* (2003a), which investigated breeding success in both dominant and subordinate females. We extend this earlier work by investigating the influence of rainfall, season, competitor number and dominance tenure.

#### BREEDING FREQUENCY

For 25 dominant females in 15 groups who held their tenure for at least 1 year, the number of times each female gave birth per year during her period of tenure was calculated and fitted as the normally distributed response term in a GLM. The factors that influence breeding frequency were also investigated in more detail, by dividing each female's tenure into 3-month windows, and fitting whether or not she gave birth during each window as the binomial response term (1 = Yes, 0 = No) in a GLMM. This second analysis is necessary to confirm any correlation between group size and breeding frequency, as, in the 'per tenure' analysis, a correlation between group size and mean breeding rate could simply arise because the average group size increases when dominant females breed at high rates (rather than because large groups allow dominant females to breed more

often). All birth windows began on the same date each year (1 January, 1 April, 1 July and 1 October) and females were only included if their dominance tenure began before the window start date and lasted for at least 3 months. This yielded a data set of 263 potential births by 26 dominant females in 15 groups. The potential explanatory terms tested for both analyses are listed in Table 2. The term 'Season' divides each year into 3-month blocks (January–March, April–June, July–September, October–December) and in this analysis refers to the month in which the birth window began. For all other analyses 'Season' refers to the month in which the litter was born.

#### LITTER SURVIVAL

Although newborn litters remain in an underground burrow for the first few weeks of life, the survival of the litter can be determined by whether or not the group continue to leave a babysitter (Young & Clutton-Brock 2006). A litter was deemed to have survived if at least one pup emerged from the natal burrow. To investigate the survival of litters to emergence 'per tenure', the number of surviving litters produced by 26 dominant females was fitted as the binomial response variable in a GLM, with the total number of litters produced by that female as the binomial denominator. This approach allows the factors that influence the proportion of a female's litters that survive to be investigated, while simultaneously accounting for the number of litters produced (Wilson & Hardy 2002). The factors that influence litter survival 'per breeding attempt' were then investigated in more detail by fitting whether or not each litter survived until emergence from the natal burrow as the binomial response term (1 = Yes, 0 = No) in a GLMM with 1 as the binomial denominator. The 'per breeding attempt' analysis used a data set of 232 litters born to 36 dominant females in 17 groups. The potential explanatory terms tested in both analyses are given in Table 3.

#### LITTER SIZE

To investigate dominant female litter size 'per tenure', the mean number of emergent pups 22 dominant females produced per litter during their tenure was calculated. This was fitted as the normally distributed response term in a GLM. The factors that influenced litter size 'per breeding attempt' were then investigated in more detail, by fitting the number of emergent pups produced per litter as the normally distributed response term in a LMM. This analysis used a data set comprising 143 litters produced by 28 dominant females in 14 groups. The potential explanatory terms tested in both analyses are given in Table 4.

#### PUP SURVIVAL TO INDEPENDENCE (3 MONTHS)

To investigate offspring survival 'per tenure', the number of emergent offspring born to 27 dominant females that survived to 3 months were fitted as the binomial response term in a GLM with the number of emergent pups as the denominator. The factors that influence the survival of dominant female pups 'per breeding attempt' were then investigated in detail by fitting the number of pups that survived to independence per litter as the binomial response term in a GLMM with the number of emergent pups as the binomial denominator. This 'per breeding attempt' analysis used a data set of 202 litters born to 35 dominant females in 17 groups. The potential explanatory terms tested for both analyses are listed in Table 5.

## Results

### ACQUISITION OF DOMINANCE STATUS

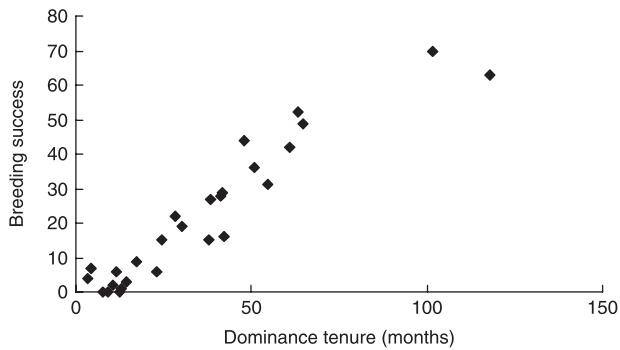
On average, female meerkats acquired dominance status aged  $27.4 \pm 9.2$  months (mean  $\pm$  SD), but this was highly variable, ranging from 13.9 to 53.6. Females attained the dominant position by two routes; they either acquired the dominant position in their natal group (41%, 12 of 29 females), or they dispersed and founded a new group, usually in conjunction with several other females (59%, 17 of 29 females). Only 22 (8%) of the 264 female pups born in our study site between January 1994 and May 2001, attained dominant status within our study population. Of 58 females born in our study population who could be followed after they dispersed, 14 (24%) became dominant. If it is assumed that 24% of the 94 females who dispersed out of our study site achieved the same success, the likely overall proportion of females that attain dominance in their lifetime is raised to 17% ( $22 + (0.24 \times 94)/264$ ).

When dominance vacancies arose, the relative age of competing females exerted an important influence on their probability of acquiring dominant status. Following the death of the dominant female, the oldest female subordinate inherited her position in 100% of cases ( $n = 14$ ), and when several related females established a new breeding group, the oldest acquired dominant status in nine of 11 cases (82%). Where there was no difference in age between the oldest females present, or where a younger female became dominant, the females that attained dominant status were significantly heavier than those that did not, both at the time of dominance acquisition (successful: mean  $\pm$  SE =  $699 \pm 17$  g, unsuccessful:  $665 \pm 19$  g; paired  $t$ -test:  $t_{13} = 2.60$ ,  $P = 0.023$ ) and at 3 months of age (successful: mean  $\pm$  SE =  $397 \pm 16$  g, unsuccessful:  $338 \pm 20$  g; paired  $t$ -test:  $t_7 = 2.80$ ,  $P = 0.027$ ).

The acquisition of dominance was also associated with the dominance status of a female's mother. Of 137 females known to have dominant mothers who survived to 1 year, 23 (17%) acquired dominant status in our study population, whereas of 31 females born to subordinate mothers, only one individual (3%) did so (Fisher's exact test:  $P = 0.042$ ). This effect appeared to be driven by differences in weight between dominant and subordinate young, as when the weight of the pup at independence was controlled in a GLMM ( $\chi^2_1 = 10.54$ ,  $P < 0.001$ ) the influence of mother's dominance status had no significant effect ( $\chi^2_1 = 0.82$ ,  $P = 0.37$ ).

### VARIATION IN BREEDING SUCCESS AMONG DOMINANT FEMALES

Of 27 females who held dominant positions for at least 3 months, one female did not produce any emergent pups. The mean number of independent offspring produced by the remaining 26 females was 22.9 (range = 0–72) with a standardized variance of 0.79. Including the one female who did not breed raised variance in breeding success to 0.86, of which more than 99% was contributed by females who bred. Partitioning variance in breeding success for those dominant



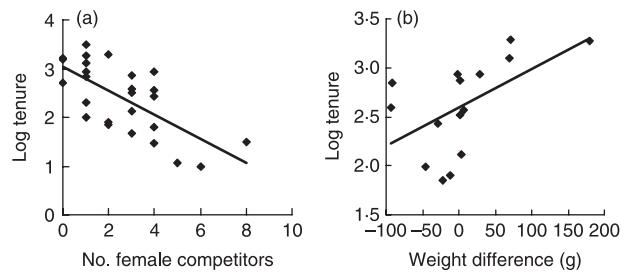
**Fig. 1.** Breeding success (total pups reared to 3 months while dominant) of dominant females in relation to their dominance tenure ( $n = 27$ ).

females that bred into the three fitness components (dominance tenure, fecundity (emergent pups produced per year) and pup survival) revealed that dominance tenure explained the largest proportion of variation (55%; Fig. 1, Table 1). Fecundity and pup survival explained 18% and 16% of variation, respectively. The products of components had relatively little effect on the variance in dominant female breeding success, with the exception of tenure by survival, which contributed a further 21% over and above the individual components.

#### DURATION OF DOMINANCE TENURE

Dominant females retained their position for 21.9 ( $\pm 26.2$ ) months on average ( $\pm$  SD), ranging from 10 days to over 8 years. A female's dominance tenure typically ended in her death (71%; 17 of 24 cases). In 29% (seven of 24) of cases, however, dominant females were displaced by another female in the group. In four of these cases displacement occurred within 2 months of taking over dominance and the remaining three cases occurred when the female had been dominant for about 1 year; twice after the dominant female had become temporarily separated from the group, and once when the dominant female was sick. Five of the seven displaced females left the group within 6 months of losing dominance.

Dominant female tenure length declined significantly as the number of adult females in the group at the time of dominance acquisition increased (GLM:  $F_{1,25} = 20.89$ ,  $P < 0.001$ ; Fig. 2a), but there was no significant influence of group size



**Fig. 2.** The influence of (a) the number of competitors at the start of the dominance period ( $n = 26$ ) and (b) the difference in body weight between the dominant female and her heaviest same sex competitor ( $n = 15$ ) on dominance tenure.

( $F_{1,25} = 2.79$ ,  $P = 0.11$ ), whether the dominant female was the oldest female in the group at the time of the dominance change ( $F_{1,25} = 0.20$ ,  $P = 0.88$ ) or the absolute age of the dominant female when she attained dominance ( $F_{1,25} = 0.04$ ,  $P = 0.85$ ). Whether or not the female attained dominance in her natal group also had no influence on the length of tenure ( $F_{1,25} = 0.12$ ,  $P = 0.73$ ). Where the difference in weight between the dominant female and her largest competitor was known, weight difference had a significant positive influence on the length of dominance tenure ( $F_{1,14} = 5.58$ ,  $P = 0.034$ ; Fig. 2b).

#### DOMINANT FEMALE FECUNDITY

##### Breeding frequency

Dominant females gave birth a mean ( $\pm$  SD) of 2.58 ( $\pm 0.56$ ) times per year (range = 1–4). The mean frequency with which dominant females gave birth during their tenure, ranged from 0.32 to 3.66 and increased with the average group size during their tenure (Table 2). A more detailed analysis of the probability that dominant females gave birth in a 3-month period, confirmed the positive influence of group size (Table 2; Fig. 3a) and also revealed a significant positive influence of female body weight on their likelihood of breeding (Table 2, Fig. 3b). A female's probability of breeding was also strongly influenced by time of year, with females less likely to give birth between April and June than at other times of year (January–March =  $0.87 \pm 0.04$ , April–June =  $0.15 \pm 0.04$ , July–September =  $0.68 \pm 0.05$ , October–December =  $0.94 \pm 0.03$ ; Table 2).

**Table 1.** Percentage contribution of different fitness components to individual variation in the breeding success of dominant females (total pups surviving to 3 months)

	Dominance tenure		Fecundity (emergent pups per year)		Survival (proportion of emergent pups that survived to 3 months)	
	%	95% CI	%	95% CI	%	95% CI
Tenure	<b>55.3</b>	25.3, 104.1				
Fecundity	<b>9.3</b>	–51.7, 15.8	<b>17.8</b>	7.5, 34.5		
Survival	<b>20.9</b>	0.9, 40.6	<b>8.4</b>	–5.9, 23.5	<b>16.0</b>	8.2, 25.7
Three-way contribution	<b>–9.9</b>					

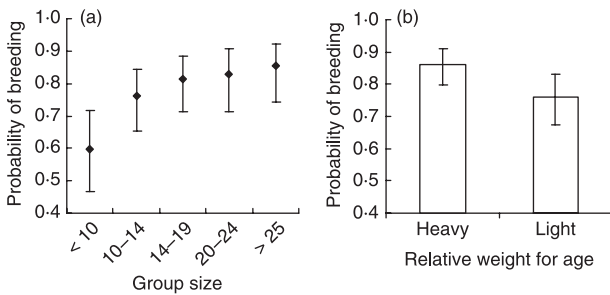
**Table 2.** Factors affecting dominant female birth rate

Model term	Estimate $\pm$ SE	Statistic*	d.f.	P
<b>Births per year during a female's tenure (GLM)</b>				
Mean group size	0.043 $\pm$ 0.016	7.04	1	0.015
Mean non-breeding weight (g)	0.0030 $\pm$ 0.0018	2.67	1	0.12
Tenure length (months)	0.0037 $\pm$ 0.0039	0.88	1	0.36
<b>Natal group</b>				
Natal	0 $\pm$ 0	0.47	1	0.50
Non-natal	0.16 $\pm$ 0.23			
Rainfall year <sup>-1</sup> (mm)	0.00080 $\pm$ 0.00012	0.32	1	0.58
Age at start of tenure (months)	-0.0025 $\pm$ 0.12	0.04	1	0.84
Mean number of adult females	-0.002 $\pm$ 0.11	0.0	1	0.99
Constant	2.027 $\pm$ 0.28			
<b>Probability of breeding per 3-month period (GLMM)</b>				
Season	See text	31.51	3	< 0.001
Mean non-breeding weight during window† (g)	0.52 $\pm$ 0.25	4.41	1	0.036
Group size at start of window	0.062 $\pm$ 0.031	3.83	1	0.050
Number of adult females at start of window	0.035 $\pm$ 0.069	0.97	1	0.32
Total rainfall during window (mm)	0.0023 $\pm$ 0.0081	0.08	1	0.78
Tenure at window start (months)	0.0023 $\pm$ 0.0082	0.08	1	0.78
Age at window start (months)	0.000089 $\pm$ 0.0086	0.00	1	0.99
Group identity (random term)	0.00 $\pm$ 0.00			
Window identity (random term)	2.94 $\pm$ 1.13			
Female identity (random term)	0.00 $\pm$ 0.00			
Constant	2.33 $\pm$ 0.68			

Births per year during a female tenure was analysed using a GLM with normal errors and an identity link. The probability of breeding per three month period was analysed in a GLMM with a binomial error structure and a logit link.

\*F statistics are provided for GLM analyses and Wald statistics ( $\chi^2$ ) are provided for GLMM analyses.

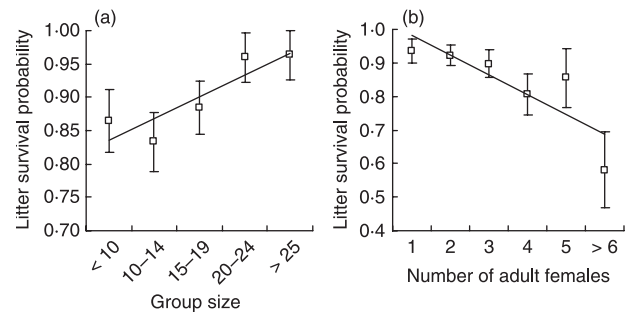
†Residuals were taken against female age in an asymptotic regression.



**Fig. 3.** The influence of (a) group size and (b) dominant female weight on the probability that the dominant female will give birth in a 3-month period. Both graphs show predicted values from a GLMM controlling for the influence of season, and repeated measures within group, female and birth window.

#### LITTER SURVIVAL

Of 264 litters born to dominant mothers, 31 (11%) failed to emerge from the natal burrow. The average proportion of dominant female litters that survived between birth and emergence across the course of their tenure varied from 0.5 to 1 across females and increased with the age of the female when she attained dominance (Table 3). There was also a trend for litter survival to decline as rainfall declined (Table 3). A more detailed analysis of the probability that individual litters survived to emergence per breeding attempt revealed that survival increased with group size (Fig. 4a;



**Fig. 4.** The proportion of litters that survived from birth to emergence plotted on (a) group size and (b) the number of adult females in the group, after group size effects were controlled in a GLMM.

Table 3), but after group size effects were controlled, declined as the number of subordinate female adults in the group increased (Fig. 4b; Table 3).

#### LITTER SIZE

Dominant females produced between one and seven pups per breeding attempt (mean  $\pm$  SD = 3.93  $\pm$  1.20). Across 22 dominant females, the mean litter size across their tenure varied from three to five and increased with the average non-breeding weight of the female during her tenure (Table 4). Within each breeding attempt, litter size was also found to increase with female body weight (Fig. 5; Table 4). After

**Table 3.** Factors affecting dominant female litter survival

Model term	Average effect	Statistic*	d.f.	P
Proportion litters surviving per tenure (GLM)				
Age at start of tenure (months)	0.059 ± 0.023	8.58	1	0.009
Rainfall year <sup>-1</sup> (mm)	-0.0058 ± 0.0030	3.86	1	0.07
Mean group size	0.033 ± 0.032	1.09	1	0.31
Mean non-breeding weight (g)	0.0038 ± 0.0038	1.01	1	0.33
Mean number of adult females	0.052 ± 0.10	0.27	1	0.61
Natal group				
Natal	0 ± 0	0.04	1	0.85
Non-natal	-0.068 ± 0.36			
Tenure length (months)	0.00084 ± 0.0054	0.02	1	0.88
Constant	-0.024 ± 0.58			
Probability of litter survival per breeding attempt (GLMM)				
Mean group size 30 days post-birth	1.15 ± 0.048	10.19	1	0.001
Mean number of adult females 30 days post-birth	-0.24 ± 0.11	5.07	1	0.024
Season	See text	5.72	3	0.13
Age at conception (months)	0.015 ± 0.011	1.87	1	0.17
Weight at conception (g)†	0.099 ± 0.24	0.17	1	0.68
Tenure at birth (months)	0.0043 ± 0.010	0.18	1	0.70
Rainfall 30 days post-birth (mm)	-0.0013 ± 0.0040	0.11	1	0.74
Group identity (random term)	0.10 ± 0.28			
Female identity (random term)	0.00 ± 0.00			
Constant	1.74 ± 0.25			

The proportion of litters surviving per tenure was analysed using a GLM with a binomial error structure and a logit link function. The probability of litter survival per breeding attempt was analysed using a GLMM with a binomial error structure and a logit link function.

\*F statistics are provided for GLM analyses and Wald statistics ( $\chi^2$ ) are provided for GLMM analyses.

†Residuals were taken against female age in an asymptotic regression.

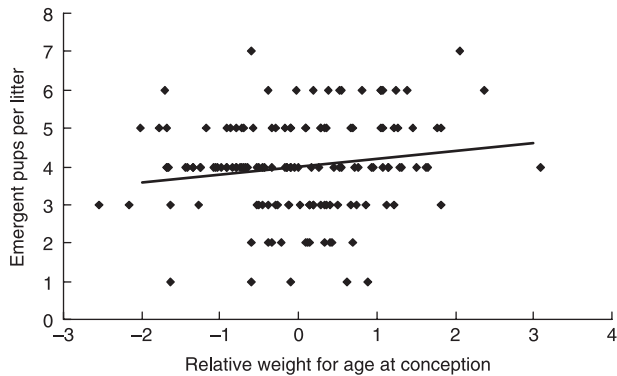
**Table 4.** Factors affecting dominant female litter size

Model term	Average effect	Statistic*	d.f.	P
Mean litter size per tenure (GLM)				
Mean non-breeding weight (g)	0.0057 ± 0.0018	10.71	1	0.004
Rainfall year <sup>-1</sup> (mm)	-0.0020 ± 0.0014	2.20	1	0.15
Tenure length (months)	-0.0042 ± 0.0037	1.25	1	0.28
Natal group				
Natal	0 ± 0	0.25	1	0.62
Non-natal	-0.11 ± 0.22			
Age at start of tenure (months)	0.0017 ± 0.010	0.21	1	0.66
Mean group size	0.0044 ± 0.018	0.06	1	0.80
Mean number of adult females	-0.019 ± 0.053	0.13	1	0.73
Constant	-0.26 ± 1.30			
Litter size per breeding attempt (LMM)				
Season	See text	15.47	3	0.001
Weight at conception (g)†	0.23 ± 0.11	4.51	1	0.034
Tenure at birth (months)	-0.010 ± 0.0052	3.69	1	0.06
Mean group size during gestation	-0.024 ± 0.015	2.46	1	0.12
Mean number of adult females during gestation	-0.035 ± 0.067	2.24	1	0.14
Age at conception (months)	-0.0068 ± 0.0052	1.68	1	0.20
Total rainfall during gestation (mm)	-0.00090 ± 0.0023	0.16	1	0.69
Group identity (random term)	0.50 ± 0.14			
Female identity (random term)	0.11 ± 0.17			
Constant	4.33 ± 0.21			

Mean litter size per tenure was analysed in a GLM with normal error structure and an identity link function. Litter size per breeding attempt was analysed in a LMM with a normal error structure and an identity link function.

\*F statistics are provided for GLM analyses and Wald statistics ( $\chi^2$ ) are provided for GLMM analyses.

†Residuals were taken against female age in an asymptotic regression.



**Fig. 5.** The size of litters born to dominant females in relation to their age-controlled weight at conception ( $n = 143$  litters). Graph shows raw data, alongside the fitted line generated from a LMM controlling for the influence of season and repeated measures within groups and females.

controlling for this effect, there was a marginally nonsignificant trend for litter size to decline as the length of time that the female had been in the dominant position when she gave birth increased (Table 4). Litter size was also influenced by when the litter was born within the breeding season: litters born early (July–September) were significantly smaller than those born later (January–March =  $4.33 \pm 0.21$ , April–June =  $4.25 \pm 0.56$ , July–September =  $3.37 \pm 0.21$ , October–December =  $4.15 \pm 0.57$ ; Table 4).

#### PUP SURVIVAL TO INDEPENDENCE (3 MONTHS)

On average ( $\pm$  SD)  $75 \pm 25\%$  of emergent pups born to dominant females survived to independence. Across dominant females, the proportion of emergent pups that survived to independence ranged from 0 to 100% and increased with tenure duration (Table 5). There was also a nonsignificant trend for pup survival to increase with mean group size (Table 5). A more detailed analysis of pup survival to independence per breeding attempt revealed an interaction between the effects of litter size and group size: in large groups ( $> 10$  helpers), there was a significant tendency for pup survival to increase with litter size, while in small groups ( $< 10$  helpers) survival declined with litter size (Table 5, Fig. 6).

#### Discussion

Only a small proportion (17%) of female meerkats became dominant during their lifetime, but those that did had the potential to produce over 70 pups during their tenure, a figure far higher than in many other mammals with a similar longevity (Clutton-Brock 1988). Our analyses demonstrate that a female's ability to attain and maintain the dominant position is strongly influenced by the number and age of other females in the group; females are unlikely to become dominant if there are older females present, and are less likely

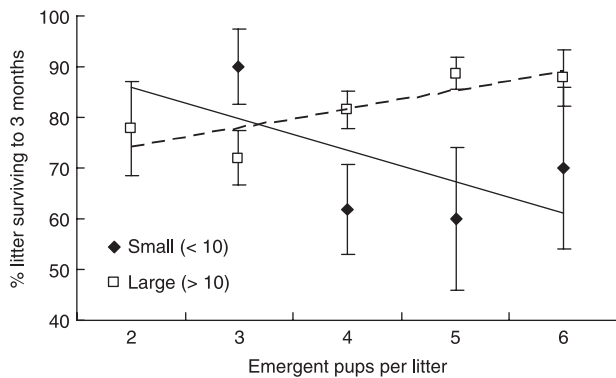
**Table 5.** Factors affecting dominant female pup survival

Model term	Average effect	Statistic*	d.f.	<i>P</i>
<b>Proportion emergent pups surviving per tenure (GLM)</b>				
Tenure length (months)	$0.013 \pm 0.0055$	5.95	1	0.023
Mean group size	$0.049 \pm 0.026$	3.68	1	0.07
Mean non-breeding weight (g)	$0.0039 \pm 0.026$	1.21	1	0.29
Mean number of adult females	$0.074 \pm 0.080$	0.94	1	0.34
Age at start of tenure (months)	$-0.0052 \pm 0.016$	0.10	1	0.75
Rainfall year <sup>-1</sup> (mm)	$0.00064 \pm 0.0026$	0.06	1	0.81
Natal group				
Natal	$0 \pm 0$	0.03	1	0.86
Non-natal	$-0.055 \pm 0.32$			
Constant	$0.80 \pm 0.31$			
<b>Proportion emergent pups surviving per litter (GLMM)</b>				
Litter size $\times$ group size	Fig. 6	4.43	1	0.035
Litter size at emergence	Fig. 6	2.69	1	0.10
Total rainfall 60 days post-emergence (mm)	$0.0033 \pm 0.0022$	2.13	1	0.14
Mean group size 60 days post-emergence	Fig. 6	1.87	1	0.17
Tenure (months)	$0.0080 \pm 0.0077$	1.08	1	0.30
Age at conception (months)	$0.0059 \pm 0.0075$	0.62	1	0.43
Season	See text	1.64	3	0.65
Weight at conception (g)†	$0.013 \pm 0.17$	0.01	1	0.94
Mean number of subordinate adult females 60 days post-emergence	$-0.0014 \pm 0.060$	0.00	1	0.98
Group identity (random term)	$0.00 \pm 0.00$			
Female identity (random term)	$0.55 \pm 0.34$			
Constant	$1.17 \pm 0.24$			

The proportion of pups surviving per tenure was analysed using a GLM with a binomial error structure and a logit link. The proportion of emergent pups surviving per litter was analysed using a GLMM with a binomial error structure and a logit link.

\*F statistics are provided for GLM analyses and Wald statistics ( $\chi^2$ ) are provided for GLMM analyses.

†Residuals were taken against female age in an asymptotic regression.



**Fig. 6.** The percentage of emergent pups that survived to 3 months against litter size in small (< 10 helpers) and large (> 10 helpers) groups. Graph shows raw data alongside the fitted line generated from a GLMM controlling for repeated measures within groups and females.

to keep the dominant position if the number of other females is high. When these effects are controlled, relatively heavy females are more likely to become dominant, and also hold the dominant position for longer. Dominant female birth rate and litter size also increase with body weight, but litter survival declines as the number of adult females in the group increase, presumably as a result of infanticide by subordinates (Young & Clutton-Brock 2006). We suggest that the limited number of breeding opportunities among female meerkats, together with the high potential breeding success of dominant breeders, will generate strong selection for females to increase their body weight relative to competitors and control the number of potential competitors within the group.

The need to control potential competitors may explain the unusual patterns of aggression observed in meerkat societies. Dominant females are commonly the most aggressive individuals (Clutton-Brock *et al.* 2005) and they target this aggression towards adult females (Clutton-Brock *et al.* 2006). At its most extreme, this aggression results in the eviction of subordinate females from the group, which could serve to temporarily remove potentially infanticidal females (Clutton-Brock *et al.* 1998; Young & Clutton-Brock 2006), to suppress their reproduction (Young *et al.* 2006), and also to encourage their permanent dispersal (Young 2003). Aggression between females is common in social insects with high reproductive skew (for reviews see Reeve & Ratnieks 1993; Choe & Crespi 1997), and has also been reported in some other high skew birds and mammals, including naked mole rats *Heterocephalus glaber* (Sherman, Jarvis & Alexander 1991), Damaraland mole rats *Cryptomys damarensis* (Cooney & Bennett, 2000) and brown jays *Cyanocorax morio* (Williams, 2004).

Several studies of noncooperative mammals and birds have attempted to partition the breeding success of females throughout their lifetime, and in most cases, the survival of offspring was found to make the largest contribution to variation in female breeding success (Clutton-Brock 1988). Less information is available in cooperative species on the

components of variance in dominant breeding success. Two notable exceptions, are the Florida scrub jay *Aphelocoma coerulescens* and the long-tailed tit *Aegithalos caudatus* in which offspring survival was also found to make the largest contribution to variation in breeding success (Fitzpatrick & Woolfenden 1988; Maccoll & Hatchwell 2004). In contrast, we show that the reproductive output of dominant female meerkats depends principally on the time they spend in the dominant position, with offspring survival and fecundity explaining a smaller proportion of variation. This difference is likely to arise, in part, because variation in the breeding tenure of female meerkats is higher than in both Florida scrub jays and long-tailed tits, and, in part, because dominant female meerkats invariably have a large number of helpers (15 on average) to assist in rearing young, which is likely to reduce variance in offspring survival. The importance of dominance tenure to meerkat breeding success will strengthen selection for aggression and body weight among female meerkats, as newly dominant females who are larger than their competitors, and who encourage the permanent dispersal of competitors through eviction, are likely to hold their position for longer.

As with previous work on this species (Russell *et al.* 2003a), we found a positive influence of helpers on the breeding success of dominant female meerkats. Females living in larger groups bred at higher rates, both when comparing across a female's tenure and in a 3-month period. Our 'per breeding attempt' analyses also indicate that litter survival is higher in larger groups and that larger groups raise larger litters successfully. Positive effects of group size on the reproductive output of dominant breeders have been demonstrated in numerous other studies (Emlen & Wrege 1991; Komdeur 1994; Innes & Johnston 1996; McGowan, Hatchwell & Woodburn 2003; Brouwer, Heg & Taborsky 2005; Hodge 2005; but see Magrath & Yezzerinac 1997; Cockburn 1998). This apparent positive influence of helpers on the reproductive output of dominant breeders may explain why the reproductive output of meerkats and other cooperative species is unusually high. In these species, offspring do not rely on parental investment from their mother, which may allow litter sizes to increase and interbirth intervals to fall, allowing more offspring to be reared over the course of their tenure.

Although our results suggest that weight and an ability to control subordinate females have an important influence on whether a female attains and maintains the dominant position, there is clearly a strong stochastic element. Unlike dominants, subordinate female meerkats do not evict other subordinates and therefore have little control over the number of adult subordinate competitors in the group. As a consequence, small females could attain the dominant position if they happened to be the oldest female in their group when a vacancy arose. Nevertheless, as females will be unable to predict when a dominance vacancy will arise, selection should favour those who maintain high body weight throughout their lives. This may explain why weight at nutritional independence is a strong predictor of whether females become dominant, as females who are heavy at independence are also likely to be

heavy into adulthood (Russell *et al.* 2007). In particular, female meerkats should maintain higher body weight than their same sex littermates, as females rarely compete for dominance with individuals from other groups, and it is individuals of the same age that represent the biggest threat. This raises the possibility that females may benefit from attempting to 'outgrow' female littermates during development. While, to our knowledge, this has never been investigated in high skew cooperative vertebrate, there is evidence that some species of coral reef fish regulate their growth according to the weight of other group members (Wong 2007).

The importance of maintaining body weight for both the acquisition of dominance, and breeding success while dominant, may have important consequences for the amount that individuals invest in cooperative activities. Helping to rear offspring results in weight loss in meerkats (Russell *et al.* 2003b) and, as a consequence, helping may be more costly for older females who have a higher chance of becoming dominant. This may explain why subordinate female meerkats reduce their investment in costly cooperative activities as they age (Clutton-Brock *et al.* 2002). Although few vertebrate studies have investigated the traits that allow individuals to become dominant, there is evidence that cooperative investment and future reproductive success trade-off against each other in *Polistes* wasps (Cant & Field 2001) and banded mongooses *Mungos mungo* (Hodge 2007), as well as in male meerkats (Young, Carlson & Clutton-Brock 2005). We suggest that selection to attain dominance could have an important impact on the amount that individuals invest in cooperative activities in other cooperative species, particularly those where the benefits of attaining dominance are high, and where larger individuals are more likely to attain and maintain the dominant position.

Our results emphasize the important influence that competition for breeding opportunities can have on the selection pressures operating in females in high skew cooperative societies. Recent work suggests variance in breeding success can be higher in females than in males (Hauber & Lacey 2005), which could generate more intense competition among females, and reverse the usual pattern of sexual selection (Clutton-Brock *et al.* 2006). As increases in group size are likely both to increase reproductive skew and lower the proportion of females that can acquire the dominant position, the strength of female competition is likely to be higher in species that form large cooperative groups. Selection for competitive ability among females may therefore be higher in mammals, which form relatively large breeding groups, than in most cooperatively breeding birds, where breeding groups are usually smaller (Russell 2004). This could have important consequences for the amount that individuals invest in cooperative activities, and also has the potential to influence other aspects of their life history, such as rates of senescence (as it may pay females to live longer if this increases their chance of attaining dominance). We suggest that further work on the determinants of reproductive success in species of varying group size will prove fruitful.

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