Behav Ecol Sociobiol (2006) 59: 541–548
DOI 10.1007/s00265-005-0079-7

ORIGINAL ARTICLE

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# Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats *Suricata suricatta*

Received: 21 March 2005 / Revised: 21 June 2005 / Accepted: 1 September 2005 / Published online: 27 October 2005

**Abstract** In many cooperatively breeding species, dominant females suppress reproduction in subordinates. Although it is commonly assumed that aggression from dominant females plays a role in reproductive suppression, little is known about the distribution of aggressive interactions. Here, we investigate the distribution of aggressive and submissive interactions among female meerkats (*Suricata suricatta*). In this species, dominant females produce more than 80% of the litters, but older subordinates occasionally breed. Dominant females commonly kill the pups of subordinates and usually evict older female subordinates from the group 1–3 weeks before the birth of the dominant female's litter. The aggression frequency of the dominant female toward subordinates and the submission frequency that each subordinate female showed to the dominant female increased as the age of the subordinate female increased and as the birth of the dominant female's pups approached. Moreover, as birth approached, both of these behaviors intensified more quickly between the dominant female and older subordinates than between the dominant female and younger subordinates. The aggression frequency of the dominant female toward each subordinate female predicted whether that subordinate female was evicted from the group; the submission frequency by each subordinate female predicted the timing of their eviction during the pregnancy period of the dominant female. These results support the idea that conflict between dominant and subordinate females increases with the age of subordinates and, since older subordinate females are most likely to reproduce, suggest that dominant females may less easily control reproductive attempts by older subordinate females.

**Keywords** Cooperative breeding · Meerkats · Aggression · Reproductive suppression · Reproductive conflict · Eviction

Communicated by S. Alberts

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## Introduction

In cooperatively breeding vertebrates, reproduction is usually monopolized by a dominant pair. Subordinate individuals rarely reproduce and instead help rear the offspring produced by the dominant pair (Stacey and Koenig 1990; Solomon and French 1997; Koenig and Dickinson 2004). Subordinate females suffer impaired fertility due to interferences by the dominant female, resulting in reproductive suppression (Creel and Creel 1991; Creel and Waser 1997; Faulkes and Abbott 1997; Moehlman and Hofer 1997; Schoech et al. 2004; Russell 2004). Incest avoidance may also partly contribute to the low level of fertility of subordinate females because the group is usually composed of related individuals (Koenig and Haydock 2004; O'Riain et al. 2000). However, incest avoidance alone may be insufficient to explain the low fertility in subordinate females because they occasionally have contact with unrelated males (Burland et al. 2004).

Despite these constraints on the reproduction of subordinate females, it has been reported that subordinate females of cooperatively breeding vertebrates do occasionally reproduce (Creel and Waser 1991; Creel and MacDonald 1995; Clutton-Brock et al. 2001; Creel and Creel 2002; French 1997). Two models from the reproductive skew theory give different explanations for the occurrence of subordinate reproduction. The concession model (Vehrencamp 1983a,b; Keller and Reeve 1994; Clutton-Brock 1998) assumes that the dominant female can control the reproduction of subordinates and that the presence of the subordinate increases the fitness benefits of the dominant individual. This model predicts that the dominant individual offers subordinates staying incentives by allowing them to reproduce. In contrast, the limited control model (Reeve et al. 1998; Cant 1998; Clutton-Brock 1998) assumes that the dominant individual cannot completely control the reproduction of subordinates and predicts that reproduction by subordinates is a result of failure of reproductive monopolization by the dominant individual.

It is commonly suggested that aggression from dominant females plays an important role in suppressing and interfering with subordinate reproduction (Creel et al. 1992; Bennett and Faulkes 2000; Creel and Creel 2002). The frequency of within-group aggression is generally low in cooperatively breeding vertebrates during periods when group membership is stable (Rasa 1987; Stacey and Koenig 1990; Solomon and French 1997; Schaffner and Caine 2000; Bennett and Faulkes 2000), but frequent aggression between females within groups occurs when a dominant dies or leaves the group (Lazaro-Perea et al. 2000; O'Riain et al. 2000; Zack and Rabenold 1989) or when unrelated males immigrate (Cooney and Bennett 2000). At present, it is not clear whether the distribution of aggression reflects the distribution of reproductive conflict and whether the dominant female attacks subordinate females who are most likely to reproduce. Additionally, it is unknown whether increased aggression is a precursor of eviction in species in which the dominant individual ejects subordinates by aggression.

In this study, we investigated whether reproductive conflict between dominant and subordinate females in meerkats (*Suricata suricatta*) is reflected in aggression or submission, and whether these interactions change according to both the risk posed by each subordinate female and the reproductive state of the dominant female. Aggression by the dominant female in this species is manifested during pregnancy (Clutton-Brock et al. 1998). Although dominant females produce more than 80% of the litters, subordinate females, old and heavy ones in particular, occasionally reproduce (Doolan and MacDonald 1997a,b; O'Riain et al. 2000; Clutton-Brock et al. 2001; Griffin et al. 2004). Several lines of evidence indicate the presence of permanent reproductive conflict among females. Subordinate females are physiologically capable of breeding when they have a chance to do so; although estrogen levels are lower in subordinates than in dominant females, exogenous injection of gonadotropin-releasing hormone induces comparable concentrations of circulating luteinizing hormone in dominant and subordinate females (O'Riain et al. 2000; Clutton-Brock et al. 2001; Carlson et al. 2004). Second, infanticide is common, and both dominant and subordinate females kill each other's new pups (Doolan and MacDonald 1997b; Clutton-Brock et al. 1998). In the later period of the dominant female's pregnancy, subordinate females more than 9 months old are often expelled from the group (Doolan and MacDonald 1996, 1997a,b; Clutton-Brock et al. 1998, 2001). By evicting subordinate females, the dominant female can prevent them from potentially killing her pups (Clutton-Brock et al. 1998). Eviction is costly for expelled females: They experience weight loss and decreased fertility (Young 2003). Subordinate females who are evicted are allowed to return to the group after the dominant female has given birth (Clutton-Brock et al. 1998). Clutton-Brock et al. (2001) and Young (2003) found that older females or nonoffspring of the dominant female (i.e., sisters) are more likely to be evicted from a group. Young (2003) further reported that older females are likely to be evicted earlier than younger females. These results suggest that reproductive conflict is particularly intense between older subordinate females and the dominant female in meerkats.

Our analysis addressed three main questions. First, which group members does the dominant female attack during the breeding period? In particular, are older subordinate females that are likely to reproduce attacked more frequently than are younger or immature females? Second, does aggression frequency increase in the later stage of the dominant female's pregnancy, when she commonly evicts the older subordinate females, and does it predict the probability and timing of eviction? Third, does submission frequency reflect the risk of being attacked and evicted from a group? If so, do the subordinate females that are most likely to reproduce show submissive behavior most frequently? Do they increase their submission frequency as the pups' birth approaches? Does submission frequency predict the probability and timing of eviction?

## Methods

### Study animals and field site

This study was conducted in Kalahari, South Africa, close to Vanzylsrus (26°58′ S, 21°49′ E), between September and December 2003. The study site consisted of the dry riverbeds of the Kuruman River, herbaceous flats, and vegetated dunes. The ecological conditions and climate of this region are described elsewhere (Clutton-Brock et al. 1999a,b; Russell et al. 2002). The study population consisted of 198 individuals living in 13 social groups. One individual meerkat in each group was fitted with a radio collar, thereby allowing groups to be located on any predetermined date. All individuals were habituated to close observation (i.e., from <1 m) and could be identified by a unique pattern of dyeing mark on the fur. The ages of most individuals were known to within a few days because they had been observed since birth. Groups were visited at least once every 3 days to collect demographic and behavioral data. Most individuals were habituated to a weighing balance, which allowed weight data to be collected regularly.

### Observation methods

N.K. conducted continuous focal observations (Altmann 1974) of the dominant female in nine groups that varied in size from 9 to 36 individuals at the beginning of the observation period (median=19). Morning focal observations began when the group appeared from the sleeping burrow and continued after the group left the burrow to forage until they became inactive at midday. Evening focal observations began when the group was located and ended when the dominant female entered the evening sleeping burrow. Observations ceased when the pups were born, but the research team checked whether the evicted subordinate females returned to the group after the birth of the pups. On average, each focal session lasted 3 h and 33 min; sessions lasting <1 h were excluded. A mean of 22 focal observations were conducted on each group (range=7–33, total observation hours=608 h).

During observations, we recorded all social interactions involving the focal dominant female, that is, all aggression received and performed, all submission received, and the identity of the interacting partner. Aggressive behavior was classified as follows: 'charge' (running directly at the subordinate), 'hip-slam' (slamming its hip against the side of a subordinate), 'chin mark' (rubbing its chin on a subordinate), 'hit' (swatting a subordinate with one paw), 'chase', and physical contact by 'biting'. Submissive behavior included high-pitched vocalizations that typically lasted more than a few seconds and groveling movements or assuming a crouching posture in the presence of the dominant female. Submission was sometimes intense and included the subordinate female persistently following and grooming the dominant female. We labeled these types of submission 'intensive' submission. During each focal observation, we recorded all individuals that came within a 1-m radius of the dominant female; hereafter, these are referred to as 'encounters'.

## Statistical analysis

We used separate generalized linear mixed models (GLMMs; Schall 1991) to examine the predictors of each response variable: the aggression frequency of the dominant female against each subordinate female, the submission frequency of each subordinate female to the dominant female, and 'intensive' submission by each subordinate female. Mixed models allow both fixed and random terms to be fitted to a model. Random terms take into consideration repeated sampling; we included the group, the identity of the litter, and the identity of each subordinate female as random terms. Aggression was excluded when it was a result of competition over a food item because such interactions may not reflect reproductive conflict. To analyze aggression, we set the number of times that a dominant female attacked each subordinate female as a dependent term with a Poisson distribution. Similarly, we used the number of times that each subordinate female spontaneously submitted to the dominant female as a dependent term to investigate the factors affecting submission. We did not include submission as a variable when it occurred soon after aggression by the dominant female because, in such a case, it was a response to the immediate aggression. However, including this type of submission in the analysis did not qualitatively change the results.

In all models, we used the same set of predictor variables, which are known to have important effects on meerkat behavior or presumed to reflect, in combination, the risk posed by different subordinate females and the vulnerability of the dominant female (Clutton-Brock et al. 1998, 2001; Young 2003):

*The age of each subordinate female*: calculated in days, all of which were known accurately.

*The weight of each subordinate female*: calculated by averaging all morning weights of each female during the observation period. Since age and weight are correlated, we calculated an average weight for each age class and subtracted this from the actual weight of each subordinate female. These 'residual' weight values were used in the model.

*Whether or not the subordinate female was an offspring of the dominant female*: since the number of nonoffspring was low (5 of 87 females) with few repeated observations, the support for this analysis is weak, and this result should be considered suggestive rather than definitive.

*The number of days before the dominant female gave birth*.

*The number of helpers on the day of observation*: during the study period, the youngest individuals were more than 6 months old. Previous studies have shown that individuals older than 6 months contribute to pup care more often than do individuals of less than 6 months and that their contribution level is comparable with that of adult subordinates (Clutton-Brock et al. 2001, 2002; Russell et al. 2003). Thus, in this study, we consider all group members to be helpers.

Since there was large variation among subordinate females in the number of encounters during focal observations (0–97 encounters; mean±SE=14.3±0.2 per focal observation session; individual mean±SE=4.4±0.2 encounters per hour), we did not use interaction frequency per hour as a dependent term. Instead, we controlled for the amount of time that each subordinate female encountered the dominant female by including it as a covariate.

Only those subordinate females that encountered the dominant female at least three times in an observation session were included. During this study season, only two subordinate females were confirmed to be pregnant when they were in the group and were evicted in an early stage of the dominant female's pregnancy. Because of the small number of pregnant subordinate females, and few repeated observations, we abandoned our investigation of whether the pregnancy of subordinate females affected social interactions. Following Crawley (2002), we included all likely independent terms and possible interactions in the maximal model and excluded terms sequentially until the model included only those terms whose elimination would significantly decrease the Akaike's Information Criterion (AIC) of the model (i.e., a decrease of 2 units of AIC).

For each subordinate female, we analyzed the effect of the frequencies of aggression and submission on eviction.

**Table 1** Factors affecting aggression frequency by the dominant female

| | *b* (SE) | *t* | *df* | *P* |
|---|---|---|---|---|
| Age of subordinate females | 0.006 (0.0009) | 6.51 | 50 | <0.0001* |
| Number of days until birth of pups | −0.016 (0.007) | 2.24 | 781 | 0.025* |
| Weight | −0.001 (0.002) | −0.76 | 49 | 0.45 |
| Offspring or not (0=offspring, 1=nonoffspring) | 3.76 (5.74) | 0.66 | 37 | 0.52 |
| Number of helpers | −0.03 (0.02) | −1.29 | 781 | 0.2 |
| Age* (days) | – | −4.32 | 781 | <0.0001* |

Analysis was conducted on 87 females in 47 litters and nine groups. Repeated measures within individuals (*N*=2–19), litters (*N*=2–84), and groups (*N*=10–309) were controlled

Factors with * are ones that remained in the final model

We calculated the means for the aggression frequency and/or submission for each subordinate female by averaging the aggression and/or submission frequency (divided by the number of times that each subordinate female was in proximity to the dominant female) during one focal observation, and then set those mean frequencies as explanatory terms in the GLMMs. Whether or not a given subordinate female was evicted from the group was fitted as a binomial response term in the model (Clutton-Brock et al. 2001), and the timing of the eviction (the number of days until the birth of the pups) was fitted as a Poisson response term. Furthermore, we investigated whether expelled subordinate females left the group permanently or returned to the group within 1 month after the birth of the pups. We examined the influence of aggression and submission frequencies on whether the subordinate females returned by setting them as binominal response terms in the GLMMs. In those models, we set group and litter identities as random terms.

## Results

### Aggression frequency

On average, dominant females attacked subordinate females in 3.0% (SE=0.4%) of their encounters and 0.08 times (SE=0.01) per hour. Aggression frequency received increased with the age of subordinate females (Table 1; Fig. 1). In addition, the aggression frequency increased as the birth of the dominant female's pups neared (Table 1). Those two factors interacted, and as the birth of their pups approached, dominant females attacked older subordinate females relatively more frequently than they did younger female subordinates (Table 1).

When we restricted the analysis to potentially reproductive subordinate females by excluding subordinate females too young to reproduce (i.e., younger than 9 months), the model revealed an influence of the age of the subordinate female ($b$±SE=0.006±0.002, $df$=36, $t$=4.10, $P$=0.0002) and an interaction between the age of the subordinate female and days until birth ($b$±SE=−0.0001±0.00003, $df$=476, $t$=−2.61, $P$=0.009), while the main effect of days until birth disappeared ($b$±SE=0.012±0.013, $df$=476, $t$=0.95, $P$=0.34).

### Submission by subordinate females

The mean frequency of submission by subordinate females was 19.1% (SE=1.3%) of their encounters and 0.39 times (SE=0.04) per hour. Submission frequency was affected both by the age of the submissive individual and the days

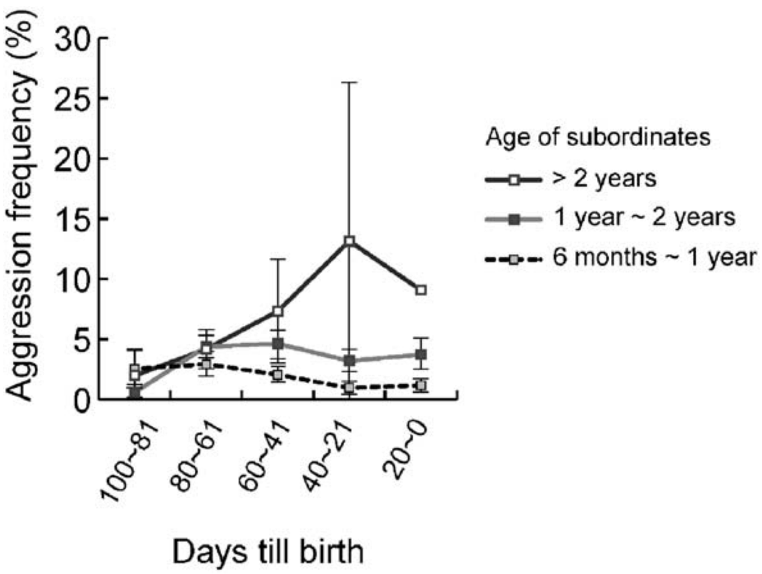

**Fig. 1** Changes in the aggression frequency of dominant females (the number of times dominant females behaved aggressively toward each subordinate female divided by the number of times each subordinate female was in proximity to the dominant female) in each age class, determined by the number of days until the birth of pups. Data were pooled across nine dominant females and their interactions with 87 subordinate females. Individual mean±SE is shown

**Table 2** Factors affecting frequencies of (a) submission and (b) intense submission by the subordinate female

| | *b* (SE) | *t* | *df* | *P* |
|---|---|---|---|---|
| (a) | | | | |
| The age of subordinate females | 0.003 (0.0004) | 7.79 | 50 | <0.0001* |
| Number of days until birth of pups | −0.016 (0.0032) | 18.07 | 765 | <0.0001* |
| Weight | −0.002 (0.001) | −1.78 | 49 | 0.08 |
| Offspring or not (0=offspring, 1=nonoffspring) | −0.28 (0.34) | −0.82 | 37 | 0.42 |
| Number of helpers | −0.01 (0.01) | −1.27 | 764 | 0.2 |
| Age* (days) | | −2.63 | 765 | 0.001* |
| (b) | | | | |
| The age of subordinate females | 0.006 (0.0009) | 6.51 | 50 | <0.0001* |
| Number of days until birth of pups | 0.006 (0.006) | 0.96 | 765 | 0.34 |
| Weight | −0.003 (0.002) | −1.4 | 49 | 0.17 |
| Offspring or not (0=offspring, 1=nonoffspring) | −0.82 (0.55) | −1.48 | 37 | 0.15 |
| Number of helpers | 0.06 (0.04) | 1.47 | 765 | 0.14 |
| Age* (days) | | −3.57 | 765 | 0.0004* |

Factors with * are ones that remained in the final model

until the birth of the dominant female's pups (Table 2a). Frequency of submission increased with the age of subordinate females and as the birth of the dominant female's pups approached (Table 1). These two effects interacted, and the relative difference in the submission rates between younger and older subordinates increased as parturition date approached. Because the independent terms affecting submission frequency were identical to those affecting the aggression frequency by the dominant female, these results indicate that submission reflects the risk of aggression by the dominant female (Fig. 2).

When we restricted the analysis to potentially reproductive subordinate females by excluding the subordinate females too young to reproduce, the age of subordinate females (*b*±SE=0.003±0.001, *df*=36, *t*=3.94, *P*=0.0004) and days until birth (*b*±SE=−0.022±0.006, *df*=476, *t*=−3.79, *P*=0.0002) still affected submission frequency. The interaction between these two variables was not significant in the final model (*b*±SE=0±0, *df*=476, *t*=−0.83, *P*=0.40).

The frequency of 'intense' submission was affected only by the age of subordinate females (Table 2b).

### Relationship to eviction

During the study period, 51 of 87 (58.7%) subordinate females were evicted from their groups. The proportion of females evicted varied among groups, from 21 to 85% (mean=64.9%). The mean frequency of aggression received was higher in subordinate females that were evicted than in those that were not (*b*±SE=24.9±11.6, *df*=75, *t*=2.15, *P*=0.035). Submission frequency was unrelated to the probability of eviction (*b*±SE=0.93±1.10, *df*=75, *t*=0.85, *P*=0.40).

The timing of eviction was not related to the mean frequency of aggression received by each subordinate female (*b*±SE=0.27±0.49, *df*=43, *t*=0.56, *P*=0.58) but was associated with submission frequency (*b*±SE=−0.53±0.23, *df*=43 *t*=−2.28, *P*=0.028). Subordinate females that submitted frequently were evicted earlier than were females who submitted less frequently. Ten of 51 subordinate females that were evicted from the group returned after the dominant female gave birth. Neither aggression frequency (*b*±SE=−3.11±4.44, *df*=43, *t*=−0.70, *P*=0.49) nor submis-

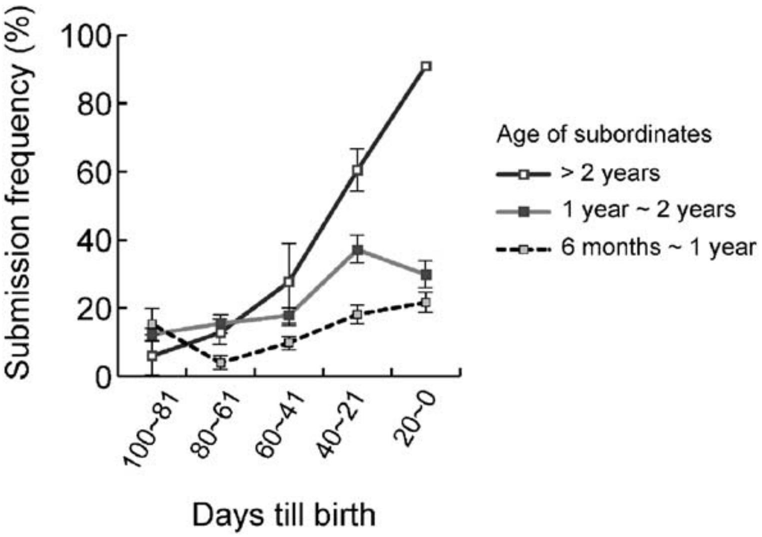

**Fig. 2** Changes in the submission frequency of each subordinate (the number of times subordinate females behaved submissively toward the dominant female divided by the number of times that each subordinate female was in proximity to the dominant female) in each age class, determined by the number of days until the birth of the dominant female's pups. Data were pooled across nine dominant females and their interactions with 87 subordinate females. Individual mean±SE is shown

sion frequency (b±SE=1.77±1.37, df=43, t=1.29, P=0.20) was related to the return of the subordinate females to the group after the birth of the dominant female's pups.

## Discussion

The aggression frequency of the dominant female toward subordinate females increased with the age of the subordinates. In addition, as parturition approached, aggressive behavior toward older subordinate females increased at a higher rate than did aggression toward younger subordinates. Because older subordinate females are more likely to reproduce and are more likely to be evicted at an earlier stage of the dominant female's pregnancy (Clutton-Brock et al. 2001; Young 2003), these results suggest that eviction and aggression reflect reproductive conflict between females. Because aggression frequency affects eviction timing, increased aggression may be a precursor to eviction and may function to interfere with the reproduction and fertility of subordinate females (O'Riain et al. 2000; Clutton-Brock et al. 2001).

Few studies have investigated the distribution of aggression in individually identified groups of cooperatively breeding mammals. The distribution of aggression by dominant females in meerkats was similar to that of a primate species of the family Callitrichidae, in which targeted aggression among females results in the eviction of subordinate females from the family group (French 1997). Naked mole rats also show a superficially similar pattern of aggression to that of meerkats: The dominant female attacks ('shoves') older, less related, and larger females (Bennett and Faulkes 2000; van der Westhuizen et al. 2002). However, another study showed that the shoving rate of the dominant female against pups was more frequent than that against adults (Stankowich and Sherman 2002). This suggests that shoving behavior in naked mole rats has multiple functions (Bennett and Faulkes 2000), and the link between reproductive conflict and aggression is unclear. In other social carnivores, the aggression rate by a dominant female decreases or does not change during the breeding period compared with that during the nonbreeding period (wild dog: Creel and Creel 2002; dwarf mongooses: Creel et al. 1992). This contrasts with our finding in meerkats that aggression frequency increases as the birth of the dominant female's pups approaches. Another interesting pattern of aggression in other species of carnivores is that aggression by subordinates is often frequent. In dwarf mongooses, for example, aggressive behavior is frequently seen between individuals of similar rank (Creel et al. 1992). Although our study did not survey aggression by subordinates, severe aggression among subordinates was rarely observed during the breeding season (personal observation). These comparisons suggest that patterns of aggression and whether aggression manifests reproductive conflict between dominant and subordinate females vary with species, even among carnivores.

The factors that influenced the submission frequency of subordinate females were identical to those of the aggression frequency, and the age of subordinate females strongly influenced the frequency of the behavior. Older subordinate females submitted more frequently than did younger ones, and intense submission with persistent following and grooming was performed by older females. Submission frequency increased as the birth of the dominant female's pups approached, and at a higher rate for older subordinate females than for younger ones. The similarity of the factors that explain submission and aggression suggests that subordinate females submit in response to aggression from the dominant female and to risk of eviction. This idea was further supported by the finding that more submissive subordinate females were evicted earlier than were less submissive ones.

Our results suggest that the patterns of aggression and submission in meerkats reflect reproductive conflict between females. Since previous studies in meerkats and other cooperatively breeding species focused on the eviction itself, not on how subordinate females are evicted over time, the strategies that the dominant female uses to accomplish the eviction and the social interactions between females have remained unknown. This study has shown that aggression increases gradually during the dominant female's pregnancy and that eviction is a consequence of accumulated aggression by the dominant female. Had we not considered these social interactions, we may have underestimated the intensity of reproductive conflict and social cost on subordinate females in this cooperatively breeding society. Thus, this study emphasizes the importance of analyzing social interactions to understand within-group reproductive conflict in cooperatively breeding species. Additionally, this study provides general implications for understanding reproductive skew among females in social vertebrates. The concession model proposes that a dominant individual will allow subordinates to reproduce within a group despite the fact that the dominant female can inhibit the reproductive attempts by the subordinates. Previous studies in meerkats have clarified intense reproductive conflicts among females (see "Introduction") and have suggested that dominant females may less easily control reproductive attempts by older subordinate females (Clutton-Brock et al. 2001). This study shows that aggression in meerkats is a characteristic of the relationship between the dominant female and subordinate females during the breeding season and provides supporting evidence for the limited control model, but not for the concession model.

**Acknowledgements** We would like to thank English, S., Moyes, K., Fry, Z., Ballantyne, F., Baker, M., Flower, T., King, A., Ross-Gillespie, A., Walker, C., Skinner, K., Hill, M., Golabek, K., Johnson, H., Minting, P., Thornton, A., Turbe, A., Spong, G., van der Vyver, M., Scantlebury, M., Ridley, M., Raihani, N., and Hollen, L., for support over the course of this study. We especially thank Jordan, N., Sharpe, L.L., Russell, A., Hodge, S., Young, A., Manica, A., and Matsumura, S., for supporting for this study and the discussions. Hodge, S., and Young, A., gave many useful comments on the manuscript. This study was supported by JSPS Research Fellowships.

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