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Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats

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In cooperative animal societies, dominant females typically show higher breeding success than subordinates, and are commonly believed to control the extent of reproductive sharing. However, studies of social insect societies reveal that subordinates too can interfere with the breeding attempts of others, with important implications for the distribution of fitness within colonies. Here, we show that subordinate females in a high-skew vertebrate (the meerkat, *Suricata suricatta*), also exert a substantial influence over the reproductive attempts of others. In meerkat societies, pregnant dominants are known to kill subordinate litters, but we show that pregnant subordinates also kill pups; not only those of other subordinates but the dominant's as well. Litters born to females of any rank were half as likely to survive their first 4 days if a subordinate was pregnant. However, dominant females were more likely than subordinates to give birth when no other females were pregnant, and so lost fewer litters to infanticide than subordinates. This is probably due in part to dominants employing counter-tactics to reduce the incidence of subordinate pregnancy. We discuss the broad implications of subordinates having a degree of control over reproductive sharing for future attempts to understand the distribution of reproduction in animal societies.

Keywords: reproductive skew; cooperative breeding; subordinate control

1. INTRODUCTION

In many animal societies, a single dominant female enjoys substantially higher breeding success than her subordinates (Keller & Reeve 1994; Magrath *et al.* 2004). In these 'high-skew' societies, dominants are commonly assumed to control the distribution of reproduction, with subordinates having little or no capacity to interfere with the breeding attempts of others (Keller & Reeve 1994). However, studies of high-skew insect societies reveal that subordinate females too can influence the reproductive success of other group members, by killing the eggs and larvae of other subordinates and manipulating both the dominant's share and the sex ratio of her brood (Bourke & Franks 1995). Under these circumstances, tactical power struggles among many group members, each with a degree of control, will determine the

distribution of fitness within social groups (Reeve & Jeanne 2003). The possibility that subordinate females in high-skew vertebrate societies may also interfere with the reproductive attempts of other group members (both dominants and subordinates) remains largely unexplored. Here, we investigate the extent to which subordinate females can disrupt the breeding attempts of other group members in the high-skew societies of meerkats (*Suricata suricatta*).

Meerkats are social mongooses that live in groups of 3–50 individuals, in which dominant females are responsible for the majority of reproduction (over 80% of pups that survive to independence: Clutton-Brock *et al.* 2001). The low reproductive rates of subordinate females can be attributed partly to their low conception rates (due commonly to a lack of access to unrelated breeding partners) and partly to the loss of a proportion of their litters to infanticide by dominants (Clutton-Brock *et al.* 2001). If the dominant female is pregnant when a subordinate gives birth, she typically kills the subordinate's litter, thereby maximizing the cooperative care available to her own pups (Clutton-Brock *et al.* 2001). By the same logic, pregnant subordinate females should also benefit from eliminating litters born to other females, but the extent of subordinate infanticide has yet to be investigated. We first describe direct observations of infanticide by female meerkats and then, using survival data for 248 litters from 16 groups, investigate whether the presence of pregnant subordinates affects the survival of litters born to: (i) dominants and (ii) other subordinates.

2. MATERIAL AND METHODS

We studied 16 groups of individually identifiable, habituated meerkats in the South African Kalahari desert between 1995 and 2003 (Clutton-Brock *et al.* 2001). Groups were visited at least once every 3 days to collect behavioural, life history and body weight data. The dominant female in each group was behaviourally dominant to, and typically older and heavier than, all other females in the group (Clutton-Brock *et al.* 1998, 2001). Pregnancy, which lasts for 70 days, could be detected from the third week after conception, due to a swelling of the abdomen and nipples and concomitant weight gain (Clutton-Brock *et al.* 2001). Births were identified from a sudden change in body shape and dramatic weight loss. A female's pregnancy state on a given day could therefore be back-calculated from subsequent monitoring. New-born litters remained underground for three weeks, but their survival could be monitored daily by recording whether the group continued to leave babysitters during foraging trips (Clutton-Brock *et al.* 2001).

We investigated whether the presence of pregnant subordinates when a litter was born affected its survival chances, using two generalized linear models (GLM; one for subordinate litters and one for dominant litters), each with a binomial response term (1=some pups survive, 0=all die). All observed cases of within-group infanticide occurred within 4 days of the litter's birth and were associated with the loss of the entire litter ($n=13$), and so to minimize the influence of other sources of mortality (e.g. predation) on our survival estimates, we considered survival of the litter to 4 days of age. While alternative sources of mortality may still influence our survival estimates, they are unlikely to account for any consistent variation associated with the pregnancy state of subordinate females, particularly as a series additional variables were controlled in our analyses. In addition to the primary term of interest (the pregnancy state of other females on the day the litter was born), we fitted the age and weight of the mother at conception (her weight averaged over the 5 day period around conception), season (January–March, April–June, July–September, October–December), maximum daily temperature and group size at birth, and the previous month's rainfall as covariates in both models. A small proportion of litters was excluded from the analyses as we could not be certain whether they had survived, as they were born within a week of another (12.1%, 34 of 282). The analysis of subordinate litter survival used a sample of 120 litters born to 66

subordinates in 16 groups, while the analysis of dominant litter survival used 128 litters, born to 21 dominants in 12 groups. For both analyses, similar mixed effects models revealed no significant repeatability of mother or group identity ($p > 0.1$), and inclusion of both as random effects yielded qualitatively similar results to the GLMs presented. Statistical analyses were conducted using GenStat (Rothamsted, UK).

3. RESULTS

As pups spent their first three weeks in the breeding burrow, infanticide could only be observed if pups were brought to the surface in the process. On 13 occasions (different litters), females brought one or more live pups, recently born to another group member, to the surface, killed them and (usually) ate them. In every case, the entire litter failed that day. The killer was known to be pregnant in 12 (92.3%) of these cases. In seven of the 13 cases the dominant female killed a subordinate's pups, but on four occasions a subordinate female killed another subordinate's pups, and on two occasions a subordinate female killed the dominant's pups. In a further 10 cases of possible infanticide, females dragged dead pups to the surface and ate them, and here too, females of each rank combination ate each other's pups. Males were never seen killing pups born in their own groups.

Of 248 litters monitored, 106 failed prior to emergence (three weeks of age) and the majority of these failed during their first 4 days (90.6%; 96 litters). Analyses of litter survival strongly suggest that infanticide by pregnant subordinates can account for a substantial proportion of the early litter failure suffered by both dominant and subordinate mothers. Litters born to dominant females were significantly less likely to survive their first 4 days if one or more subordinate females were pregnant when the litter was born (GLM: $F_{1,125} = 28.91$, $p < 0.001$, figure 1), controlling for group size (GLM: $F_{1,125} = 4.08$, $p = 0.043$). Similarly, litters born to subordinate females were significantly less likely to survive if another female (whatever her rank) was pregnant when the litter was born (GLM: $F_{3,115} = 8.62$, $p < 0.001$, figure 2), controlling for group size (GLM: $F_{1,115} = 6.70$, $p = 0.01$). None of the other covariates had significant effects in either analysis. While females of both ranks lost a substantial proportion of their litters if other females were pregnant when the litter was born (figures 1 and 2), dominant females were significantly more likely to give birth at times when no other females were pregnant (97 of 128 litters) than subordinate females were (29 of 120 litters: $\chi^2 = 66.02$, $p < 0.001$). Accordingly, dominant females lost a significantly smaller proportion of their litters overall than subordinates did (16 of 128 and 79 of 120 litters, respectively: $\chi^2 = 88.3$, $p < 0.001$).

4. DISCUSSION

Previous work has shown that when dominant female meerkats are pregnant, they kill litters born to subordinates (Clutton-Brock *et al.* 2001). Our findings strongly suggest that subordinate females also exert a substantial influence over the reproductive attempts of other group members. Pregnant
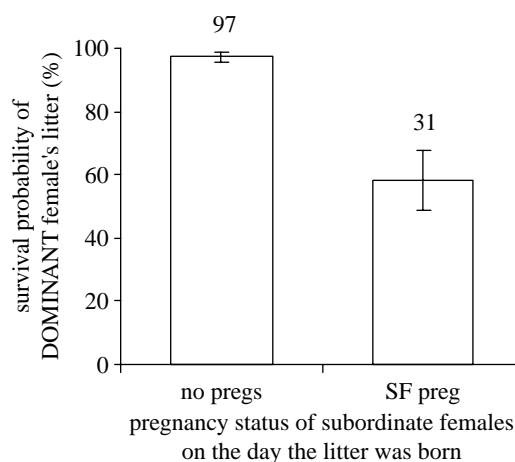

Figure 1. Dominant female litters were less likely to survive (mean ± s.e.) if one or more subordinate females (SF) were pregnant when the litter was born (n = litters).

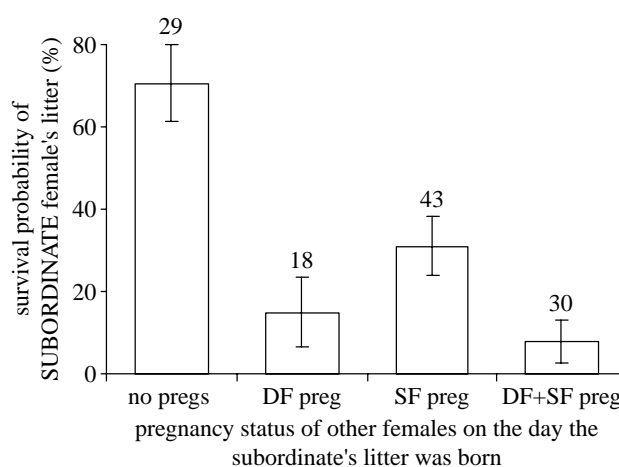Figure 2. Subordinate female litters were less likely to survive (mean ± s.e.) if another female (either dominant (DF) or subordinate (SF)) was pregnant when the litter was born (n = litters).

subordinates killed pups born to both dominant and subordinate mothers, and their presence when a litter was born was associated with a substantial reduction in litter survival (roughly halved). Indeed, infanticide by subordinates may be the primary cause of early litter failure among dominants, as 13 of the 16 such losses occurred when subordinates were pregnant. Like dominants, pregnant subordinates should benefit from eliminating the litters of competitors, as this will maximize the helper-to-pup ratio for the rearing of their own litters (Clutton-Brock *et al.* 2001).

In species where subordinates can interfere with the breeding attempts of others, dominants might be expected to evolve counter-strategies to prevent this. In meerkat societies, the dominant female typically drives her subordinate females from the group for the last three weeks of her pregnancy, during which time the evictees are less likely to conceive and suffer elevated rates of abortion (Young 2003). This unusual tactic may explain why subordinate females were less likely to be pregnant when the dominant gave birth than when other subordinates gave birth, and hence why dominants seem to lose a smaller proportion of their litters to infanticide than subordinates. Though

evictees typically remain on the group's territory, their temporary expulsion from the group may reduce the risk of infanticide further by limiting their access to the dominant's newborn litter (Clutton-Brock *et al.* 1998).

The infanticidal power struggles of female meerkats have strong parallels with the mutual egg-tossing behaviour of co-breeding females in some communally nesting low-skew birds (e.g. Vehrencamp 1977; Mumme *et al.* 1983). In these species, as in meerkats, females destroy eggs laid before their own in an attempt to gain a reproductive advantage. However, in contrast to meerkats, the inability of any one female to reduce consistently the risk of egg destruction by her co-breeders means that no single female can largely monopolize reproduction (Vehrencamp 1977; Mumme *et al.* 1983). These comparisons suggest that, where multiple parties can interfere with the breeding attempts of others, the extent of reproductive sharing may depend on the degree to which competitive asymmetries give any one individual an advantage in the power struggle. Attempts to apply existing theory on the role of competitive asymmetries in conflict resolution (e.g. Maynard Smith & Parker 1976) to the specific problem of reproductive sharing in social groups might therefore prove rewarding.

To our knowledge, our study provides the first evidence that subordinate females in high-skew vertebrate societies are able to kill the young of other group members. The lack of similar evidence to date may be due, at least in part, to the lack of studies that have directly investigated the possibility of infanticide by subordinates, coupled with the difficulty of both detecting infanticide and identifying its perpetrators. The patterns of infanticide among females in our study and those of low-skew vertebrates, suggest that females are most likely to kill offspring when attempting to breed themselves (e.g. Vehrencamp 1977; Mumme *et al.* 1983; Hoogland 1995). If infanticide by subordinates does occur more widely among high-skew vertebrates, it might therefore be expected to occur in those species where subordinates do still breed, albeit at low rates.

The findings of our study, coupled with evidence from social insects (Bourke & Franks 1995), suggest that even in societies where a single dominant female largely monopolizes reproduction, subordinates may retain the capacity to disrupt the breeding attempts of others. This has two broad implications for attempts to understand variation in reproductive sharing in animal societies. First, approaches that consider reproductive skew as arising from a tactical power struggle among multiple parties, each with a degree of control (e.g. Reeve & Jeanne 2003), may be more broadly applicable than those that restrict the capacity for control to dominants alone. Second, evidence that subordinates can directly interfere with the breeding attempts of dominants suggests that theoretical approaches to reproductive sharing based on the need to pacify disruptive subordinates (e.g. Reeve & Keller 1997) may often be more appropriate than those based on the need to retain subordinates who would otherwise leave (e.g. Keller & Reeve 1994).

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