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Group size and the suppression of subordinate reproduction in Kalahari meerkats

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In animal societies, contrasts in reproductive skew among females are caused by variation in the frequency of reproduction by subordinates. However, despite widespread interest in the extent and causes of reproductive skew, few empirical studies have investigated the factors affecting the frequency of successful reproduction by subordinates. We tested the prediction that the extent to which dominants restrict the reproductive success of subordinates should increase as group size rises and the marginal benefits of additional helpers falls. In a long-term study of wild meerkats, *Suricata suricatta*, we found that dominants were more likely to evict subordinates in large groups than small ones, and that the frequency of breeding by subordinate females declined with group size, largely as a result of increases in abortion rate. The breeding frequency of subordinate females was also influenced by their age and weight, which probably reflects the capability of subordinates to breed and their ability to resist the attempts of dominants to suppress them. These findings highlight the importance of investigating variation in the benefits to dominants of controlling subordinate reproduction as well as variation in the benefits of breeding to subordinate females when attempting to understand variation in subordinate breeding success.

Keywords: breeding success; cooperative breeding; fitness; meerkat; reproductive skew; *Suricata suricatta*

Among vertebrates that breed cooperatively, the number of females contributing to reproduction in each group varies widely (Keller & Reeve 1994; Emlen 1996, 1999; Magrath et al. 2004). In some species, a single female is responsible for almost all breeding attempts in the group and subordinates rarely or never breed, as in naked mole rats, *Heterocephalus glaber* (Faulkes & Abbott 1997); in others, subordinates breed but do so less frequently or are less successful than dominants, as in Florida scrub jays, *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1984), meerkats, *Suricata suricatta* (Clutton-Brock et al. 2001a, 2006), spotted hyaenas, *Crocuta crocuta* (Hofer & East 2003) and dwarf mongooses, *Helogale parvula* (Creel & Waser 1994); and in a few, most females breed at intervals and differences in breeding success between group members are small, as in lions, *Panthera leo* (Packer et al. 2001).

Two main theoretical explanations for variation in the frequency of breeding by subordinate females (and the resulting differences in reproductive skew) have been proposed. First 'limited control' or 'tug-of-war' models suggest that differences in the proportion of females breeding are a consequence of variation in the capacity of dominant females to control reproduction by subordinates (e.g. Reeve et al. 1998; Johnstone 2000; Reeve & Shen 2006). Alternatively, 'concession' models assume that dominants have full control of subordinate reproduction but make reproductive concessions to subordinates in return for assistance with rearing their young and that differences in the frequency of subordinate breeding reflect variation in the magnitude of reproductive concessions needed to induce subordinates to comply (e.g. Vehrencamp 1979, 1983; Reeve & Ratnieks 1993; Reeve 2000).

Empirical research in a number of vertebrate societies has shown that dominants do not always have full control of subordinate reproduction (Clutton-Brock 1998; Haydock & Koenig 2002; Kutsukake & Nunn 2006). For

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example, in meerkats, where, on average, a single female is responsible for over 80% of breeding attempts in their group (Clutton-Brock et al. 1999; Griffin et al. 2003), the assumptions of concession models do not apply as subordinate females do not leave their natal group voluntarily, so that dominants do not need to provide reproductive concessions to retain them. There is also no indication that subordinates that have bred are less likely to leave the group or challenge the dominant, whereas there is good evidence to suggest that subordinates breed more frequently when dominant control is weak (Clutton-Brock et al. 2001a).

Where dominants do not have complete control over subordinate reproduction, the outcome of reproductive tugs of war are likely to depend partly on the resource-holding power or RHP (Parker 1974) of the contestants and partly on how much dominants and subordinates are prepared to invest in winning contests (Maynard Smith & Parker 1976). Relative investment by dominants and subordinates in winning should largely depend on the benefits of breeding to subordinates as well as the benefits to dominants of preventing them from doing so. A number of studies have already shown that the frequency with which subordinates breed depends on factors likely to affect their ability to rear healthy offspring (Hoogland & Foltz 1982; Wasser & Barash 1983). In meerkats, for example, older subordinates and those that are relatively heavy for their age are more likely to breed than younger or lighter ones and, when these age effects are controlled, subordinates living in groups that include unrelated males are more likely to breed than those living in groups consisting of relatives (Clutton-Brock et al. 2001a). In contrast, few studies have yet investigated whether the frequency of subordinate reproduction is affected by variation in the benefits dominants are likely to gain from suppressing subordinates (Hodge, in press).

Meerkats are cooperative mongooses, living in groups of 2–50 individuals ($\bar{X} \pm \mathrm{SD} = 16.7 \pm 8.6$) in the arid regions of southern Africa (Doolan & Macdonald 1997). Groups typically consist of a dominant female, a number of subordinate females (who are usually close relatives of the dominant female), a number of natal subordinate males (who are usually offspring of the dominant pair), and one or more immigrant males, of which one is dominant to other males in the group (Griffin et al. 2003; Spong et al. 2008). The dominant female produces up to four litters of pups per year (Clutton-Brock et al. 1999) who are cared for by all group members (Clutton-Brock et al. 2000, 2001b; Brotherton et al. 2001; Hodge et al. 2007). Subordinate individuals reach sexual maturity at around 1 year and both sexes disperse into another group at around 2 years of age. However, unlike males, females may inherit the dominant breeding position in their natal group, and may also breed as subordinates, although they do so at low rates in comparison to dominants. This is partly because they often lack access to unrelated breeding partners (O'Riain et al. 2000), and partly because dominant females suppress subordinate breeding attempts by evicting them from the group or killing their offspring (Clutton-Brock et al. 1998; Young & Clutton-Brock 2006; Young et al. 2006). As in many cooperative breeders (Clutton-Brock et al. 1982; Van Schaik et al. 1983; Hoogland 1985a), the breeding success of dominant female meerkats increases with the number of animals in their groups (Russell et al. 2003; Hodge et al. 2008), but declines in larger groups, probably as a consequence of increases in both resource competition and reproductive interference between group members (Clutton-Brock et al. 1998; Young & Clutton-Brock 2006). Dominant females living in large groups might therefore be expected to be less tolerant of both the presence of subordinate females and their attempts to breed than those living in small groups.

In this paper, we used our 14-year data set to investigate the effects of variation in group size on (1) the effects of group size on the probability that subordinate female meerkats will be evicted from the group by the dominant female and (2) the frequency with which they attempt to breed and their success in rearing litters. We examined the effects of group size on five separate components of subordinate reproductive success: the frequency of (observed) pregnancies; the survival of litters to term; litter size; the survival of litters to emergence from the natal burrow (around 3 weeks after birth); and the survival of pups from emergence to nutritional independence at 3 months. In each analysis, we used multifactorial statistical models to control for a range of environmental and social parameters known to affect the frequency of reproduction (Clutton-Brock et al. 2001a; Russell et al. 2002, 2003; Hodge et al. 2008) and compared the effects of group size on the breeding success of subordinates with the effects on the breeding success of dominants. We also investigated the influence of the number of adult females in the group on subordinate breeding success to assess whether it is group size per se or a difference in the number of competitors that has the greatest influence on subordinate reproduction.

METHODS

Study Site and Study Population

All data were collected from a wild population of meerkats inhabiting an area of ranchland in the South African Kalahari close to Van Zyls Rus (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 (Clutton-Brock et al. 1998; Russell et al. 2002). During this period, at any one point in time, our study population consisted of 200–300 individually recognizable individuals living in 10–15 social groups, most of whom were habituated to observation from less than 2 m. Over the entire period of the study, we monitored the breeding success of more than 300 adult females belonging to 23 different groups. All individuals 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 every 3 days throughout the study period and during these visits changes in group composition (i.e. births, deaths and evictions) and pregnancy status (births, conceptions, abortions) were recorded. As a consequence of this intensive monitoring the ages of most individuals in the population