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The causes of physiological suppression among female meerkats: A role for subordinate restraint due to the threat of infanticide?

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Abstract

In many animal societies, subordinates exhibit down-regulated reproductive endocrine axes relative to those of dominants, but whether this 'physiological suppression' arises from active interference by dominants or subordinate self-restraint is a matter of debate. Here we investigate the roles that these processes play in precipitating physiological suppression among subordinate female meerkats, *Suricata suricatta*. We show that, while subordinate females are known to suffer stress-related physiological suppression during periodic temporary evictions by the dominant female, their low estrogen levels while within their groups cannot be readily attributed to chronic stress, as their fecal glucocorticoid metabolite levels during this time are comparable to those of dominants. The low estrogen levels of subordinate females also cannot be explained simply by self-restraint due to factors that could reduce their payoff from maintaining their fertility regardless of the presence of the dominant female (young age, a lack of unrelated mates, poor body condition and limited breeding experience), as substantial rank-related differences in fecal total-estrogen metabolite levels remain when such factors are controlled. We suggest that this residual difference in estrogen levels may reflect a degree of subordinate restraint due in part to the dominant female's ability to kill their young. Accordingly, subordinate female estrogen levels vary in association with temporal variation in the likelihood of infanticide by the dominant. Attempts to identify the causes of physiological suppression should be cautious if rejecting any role for dominant interference in favor of subordinate restraint, as the dominant's capacity to interfere may often be the reason why subordinates exercise restraint.

Keywords: Reproductive suppression; Reproductive skew; Infanticide; Social stress; Cooperative breeding; Dominant control; Dominance; Cooperation; Conflict; Eusociality

Introduction

In many animal societies, subordinate females breed at markedly lower rates than dominants and show down-regulation at one or more levels of the reproductive endocrine axis relative to dominants, a condition termed 'physiological suppression' (e.g. Schoech et al., 2004; Young, in press). While many studies have now reported evidence of physiological suppression among subordinates, the extent to which this arises from active interference by dominants (dominants actively and forcibly down-regulating the reproductive physiology of subordinates), restraint by subordinates (subordinates down-regulating their own reproductive physiology as, given their circumstances, they stand to benefit from doing so) or a combination of the two, remains a key area of debate (e.g. Abbott et al., 1997; Creel, 2001; Young et al., 2006; see Young, in press).

Early studies of physiological suppression suggested that it could be the result of active interference by dominants; dominants might forcibly down-regulate the reproductive axes of subordinates by subjecting them to chronic 'stress' (commonly reflected as chronic elevation of circulating glucocorticoid levels; GCs), through frequent attacks (Keverne et al., 1982). This is an attractive hypothesis as chronic stress is known to compromise fertility in a variety of taxa (Pottinger, 1999), and studies of some social vertebrates have supported the prediction that subordinates should show elevated GC levels (reviewed in von Holst, 1998). However, a number of studies focusing on cooperatively breeding species in particular, where physiological suppression is at its most apparent, have revealed that subordinates commonly show

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average GC levels equal to or actually lower than those of dominants (reviewed in Creel, 2001; Goymann and Wingfield, 2004), and two experimental studies found no evidence of a role for social stress in subordinate infertility (Abbott et al., 1997; Faulkes and Abbott, 1997). These findings suggest that, while stress-related suppression may certainly play a key role in precipitating physiological suppression in some cooperative vertebrates (e.g. Young et al., 2006), social stress *alone* cannot readily account for physiological suppression across all vertebrate societies (Abbott et al., 1997; Creel, 2001).

Evidence that physiological suppression often occurs in the absence of chronic stress has led to the suggestion it may commonly arise instead from subordinates exercising physiological restraint: down-regulating their own reproductive physiology so as to maximize their fitness (Snowdon, 1996; Abbott et al., 1997; Creel, 2001). While many studies have invoked a role for subordinate restraint in precipitating physiological suppression, comparatively few have identified the ultimate cause(s) of that restraint. In theory, physiological restraint should be favored by any factors that reduce a subordinate's expected fitness payoff from maintaining their fertility (reviewed in Young, in press). Such factors can be usefully divided into two broad classes. The first comprises factors that could reduce a subordinate's expected payoff from maintaining their fertility regardless of the presence of the dominant. Such factors include a lack of access to unrelated breeding partners, which subordinates commonly experience having delayed dispersal from their natal groups, and in response to which they often exhibit physiological suppression (e.g. Cooney and Bennett, 2000; O'Riain et al., 2000). Other factors in this class include young age, poor body condition and having little or no breeding experience (Wasser and Barash, 1983; Snowdon, 1996; Carlson et al., 2004), all of which may tend to affect subordinates more acutely than dominants, as they tend to be younger, lighter and less experienced (e.g. Creel and Creel, 1991; Clutton-Brock et al., 2001).

The second class of factors that may contribute to selection for subordinate restraint are those that arise directly from the presence and/or likely actions of the dominant. Evidence that physiological suppression in some species cannot be readily attributed to chronic stress imposed by the dominant, yet is nevertheless lifted when the dominant and subordinate are separated (e.g. common marmosets, *Callithrix jacchus*, Abbott et al., 1997; and naked mole-rats, *Heterocephalus glaber*, Faulkes and Abbott, 1997), suggests that subordinates may indeed exercise restraint due, at least in part, to the presence and/or likely actions of their dominant. Perhaps the most likely adaptive explanation for such restraint is that the dominant has the capacity to disrupt and/or punish the subordinate's attempts to breed (e.g. with mate guarding, Komdeur et al., 1999; pregnancy disruption, Young et al., 2006; or infanticide, Digby, 2000; see Johnstone and Cant, 1999; Hamilton, 2004 for relevant theory), thereby reducing the subordinate's expected payoff from maintaining their fertility in the dominant's presence. However, evidence linking the extent of subordinate restraint to the likelihood of such disruptive action *per se* remains elusive.

To advance our understanding of the ultimate causes of physiological suppression, further studies should seek to establish the relative importance of active interference by dominants and subordinate restraint, and to tease apart the factors that contribute to any restraint detected. In this study, we address both of these aims by investigating the causes of physiological suppression among subordinate female meerkats (*Suricata suricatta*). Meerkats are social mongooses that live in cooperative groups of up to 50 individuals. One female in each group is behaviorally dominant to, and typically older and heavier than, all other females (Clutton-Brock et al., 2001). This 'dominant female' shows markedly higher mean estrogen concentrations than subordinate females and conceives at substantially higher rates, producing >80% of the pups that survive their first month of life (Clutton-Brock et al., 2001; Carlson et al., 2004). The lower mean estrogen levels of subordinates are thought to underpin at least in part their relative infertility, perhaps reflecting weaker or less frequent ovarian cycles. Identifying the causes of this disparity in mean estrogen levels is the goal of this study.

Recent work on meerkat societies strongly suggests that stress does plays a key role in the suppression of subordinate female reproduction: during periodic temporary evictions from the group by the dominant female, subordinate females suffer stress-related suppression of their pituitary sensitivity to gonadotrophin releasing hormone (GnRH) and associated reproductive failure (Young et al., 2006). However, the stress experienced during these temporary evictions alone cannot readily explain the generally low estrogen levels of subordinate females, as they are also low during the long periods that subordinates spend within their groups (when their pituitary sensitivity to GnRH is comparable to that of dominants; O'Riain et al., 2000; temporary evictions occur no more than once every 3 months and last an average of 3 weeks; Young et al., 2006). Whether the low estrogen levels of subordinate females could be due instead to chronic stress arising from ongoing harassment while within their groups is not yet clear. Previous work does suggest however that subordinate females exercise a degree of physiological restraint while within their groups, showing lower estrogen levels and conceiving at lower rates both when lacking access to unrelated males and when in poor body condition (Clutton-Brock et al., 2001; Carlson et al., 2004). Whether subordinates also exercise restraint due in part to the likelihood that the dominant will disrupt their breeding attempts has yet to be investigated. This could well be the case though, as dominant females become infanticidal when pregnant, such that subordinate litters born at this time have only a 15% chance of survival, compared to 70% at other times (Young and Clutton-Brock, 2006). Here we investigate the extent to which the low estrogen levels of subordinate females within their groups can be attributed to stress-related suppression imposed by the dominant or to restraint by subordinates, and seek to tease apart the factors that contribute to any restraint detected. To achieve this, we investigate the potential roles played by three sets of processes in turn.

Stress-related suppression of subordinate females while within their groups

We test the prediction that, if this is the case, subordinate females within their groups (away from evicted periods) should