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.

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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...
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 subordi

te’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 play 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...
show significantly higher GC levels than dominant females. Importantly, we allow for the possibility that dominants only subject to chronic stress the subset of subordinates who might otherwise attempt to breed (see Young et al., 2006; Young, in press), by testing for statistical interactions between dominance status and factors that predict a subordinate’s likelihood of attempting to breed (older age, better body condition and having unrelated males within the group; Clutton-Brock et al., 2001) in our analyses of the factors affecting female GC levels.

Subordinate restraint due to factors that may act regardless of the dominant’s presence

We test the prediction that, if this is the case, the estrogen levels of females should be negatively associated with factors that may reduce their expected payoff from maintaining their fertility regardless of the presence of the dominant (specifically young age, a lack of access to unrelated breeding partners, poor body condition and a lack of prior breeding experience). If a significant difference in the estrogen levels of dominants and subordinates persists when all of these factors are controlled, it would suggest that these factors alone cannot account entirely for the physiological suppression of subordinates.

Subordinate restraint due to the likelihood of infanticide by the dominant

We test the prediction that, if this is the case, subordinate females may modulate their estrogen levels to avoid conceiving at times when the dominant female is likely to be pregnant (and hence infanticidal) when their own litter is eventually born. As any temporal pattern in subordinate’s estrogen levels might alternatively arise from correlated variation in the physiological stress they experience, we also test whether subordinate GC levels vary across the same set of contexts.

Methods

The study was conducted on ranchland in the South African Kalahari desert between 1999 and 2003 (for details of the study site, population and climate, see Clutton-Brock et al., 1999). The study population comprised 10 meerkat groups that had previously been habituated to close observation, allowing the collection of detailed behavioral, weight and endocrine data. Animals were marked with subcutaneous transponder chips and distinguished by placing small spots of hair dye on their coats. Study groups were visited at least once every 3 days to collect measures from 181 fecal samples collected from 14 dominant females and 41 unrelated males within the group; Clutton-Brock et al., 2001) in our analyses of the factors affecting female GC levels.

Hormone sample collection and assay methods

Measures of a female’s estrogen and GC levels were obtained non-invasively by measuring the hormone metabolite concentrations in their feces. Fecal samples were collected whenever animals defecated, were immediately placed on ice and then were frozen on return to camp. To control for circadian variation in hormone concentrations, a two-level factor was fitted in each of our analyses reflecting sample collection time (AM for morning sessions, 06:00–12:00; PM for afternoon sessions, 15:00–20:00). Steroid–hormone metabolites were extracted from the samples using standard methodologies (Monfort et al., 1997). Briefly, fecal samples were dried using a Savant Instruments SpeedVac Rotary Evaporator (Forma Scientific, Ohio), pulverized and thoroughly mixed. 0.18–0.19 g of fecal powder was then combined with 6 ml of 100% ethanol, vortexed (10 s) and then boiled (20 min) to extract the metabolites. After centrifugation (50 g, 15 min), the supernatant was decanted into a tube and dried completely under a stream of compressed air; during evaporation, the vessel walls were rinsed twice with ethanol (4 ml). The residue was then redissolved in 1 ml methanol (the tubes were vortexed (1 min), placed in an ultrasonic glass cleaner (30 s) and then vortexed again (15 s). A portion of the extract was then diluted 1:50 in PBS buffer (pH 7.0) and frozen (~20 °C) for subsequent radioimmunoassay (RIA).

The concentrations of estrogen metabolites in fecal extracts were determined using a double antibody 125I RIA for Total Estrogens (ICN Biomedicals Inc., Costa Mesa, California, USA), which had been previously validated for the monitoring of estrogens in meerkat fecal samples (Moss et al., 2001). The antiserum cross-reacts 100% with both estradiol-17b and estrone, 9.0% with estradiol, 7.0% with estradiol-17a, 2.5% with equilin and 0.01% with all other steroids tested. Assays were conducted according to the instructions provided with the kit except that all reagent volumes were halved. Fecal extracts (1:800 dilution) were assayed (250 l) in duplicate. Intra-assay coefficients of variation for two separate internal controls were 1.7% and 15.3%. The concentrations of GC metabolites in fecal extracts were determined using a double-antibody 125I RIA for corticosterone (ICN Biomedicals Inc., Costa Mesa, California, USA), which had been previously validated for the monitoring of GCs in meerkat fecal samples (Young et al., 2006). The antiserum cross-reacts 100% with corticosterone, 0.34% with deoxycorticosterone, 0.10% with testosterone, 0.05% with cortisol, 0.03% with aldosterone, 0.02% with progesterone and <0.01% with all other steroids tested. Assays were conducted according to the instructions provided with the kit except that all reagent volumes were halved. Fecal extracts (1:50 dilution) were assayed (50 l) in duplicate. Intra-assay sensitivity was 2.5 ng/mg. Intra-assay coefficients of variation were <10% and inter-assay coefficients of variation for two separate internal controls were 9.0% and 7.7%.

Statistical analyses

All statistical analyses were conducted using GenStat (Lawes Agricultural Trust, Rothamsted, UK). All analyses made use of General Linear Mixed Models (GLMMs), which are similar to General Linear Models except they allow for both fixed terms and random terms to be defined (Crawley, 2002). Random terms allow the analysis to take account of repeated measures; in this case Group and Individual were fitted as random terms in all analyses to account for repeated measures taken at these levels. All fixed terms were initially entered into the model and then sequentially dropped until only those fixed terms whose elimination would have reduced the explanatory power of the model significantly remained (thereby yielding the ‘minimal model’). In each case, a forward stepwise procedure yielded the same minimal model, confirming its structure. All two-way interactions were tested, but only those that were statistically significant are presented in the tables. The statistical significance of each term was derived by dropping it from the minimal model (if it was part of the minimal model) or adding it to the minimal model and then dropping it (if it was not part of the minimal model). All statistical tests are two-tailed.

Stress-related suppression of subordinate females while within their groups

To investigate whether the low estrogen levels of subordinate females could be due to chronic stress imposed by the dominant, we tested whether subordinate females within their groups show higher average fecal GC metabolite concentrations than dominant females, using a GLMM. We used GC metabolite measures from 181 fecal samples collected from 14 dominant females and 41
subordinate females from 10 groups. All samples were from females of breeding age (older than 9 months, Young et al., 2006) who were within their groups (neither evicted nor within 2 weeks of return from eviction) and not pregnant when sampled (as GC levels typically vary with pregnancy stage; Johnson and Everitt, 1999). A natural logarithm transformation was used to normalize the GC data for analysis. To control for factors that might confound a comparison of dominant and subordinate GC levels, and to allow for the possibility that dominants target only a subset of subordinates who might otherwise attempt to breed (Young, in press), the following terms were fitted to the model in addition to dominance status: female age (in days, log-transformed), body condition (the residuals of body weight on age) and breeding experience (nulliparous, primiparous or multiparous), whether the female had unrelated males within her group (immigrants since she was born), whether it was the peak conceptive season (June–January inclusive, Young et al., 2006), group size (excluding pups), number of female group members of breeding age, whether the female was lactating and the time of sample collection (AM or PM).

Subordinate restraint due to factors that may act regardless of the dominant’s presence

We used a GLMM to investigate whether the difference in estrogen levels between dominant and subordinate females could be explained by subordinate restraint in response to factors that may act independent of the presence and/or actions of the dominant (young age, poor body condition, limited breeding experience and a lack of unrelated males within the group). We used total-estrogen metabolite measures from 143 fecal samples collected from 13 dominant females and 41 subordinate females from 10 groups. As for the GC analysis, all samples were from females of breeding age who were within their group (neither evicted nor within 2 weeks of return from eviction) and not pregnant at the time of sampling. A natural logarithm transformation was used to normalize the total-estrogen data for analysis. The following fixed terms were fitted to the model in addition to dominance status: the potential reasons for restraint (female age (in days, log-transformed), body condition (residuals of body weight on age), breeding experience (nulliparous, primiparous or multiparous) and whether she had unrelated males within her group (immigrants since she was born)); seasonal and group characteristics (whether it was the peak conceptive season (June–January inclusive), group size (excluding pups), number of female group members of breeding age); whether the female was lactating; and the time of sample collection (AM or PM).

Subordinate restraint due to the likelihood of infanticide by the dominant

As dominant females are only infanticidal when pregnant (Clutton-Brock et al., 2001; Young and Clutton-Brock, 2006), there is marked temporal variation in the likelihood of infanticide by the dominant. If subordinate females exercise restraint due in part to the likelihood of infanticide, they might therefore be predicted to show associated temporal variation in their estrogen levels, to avoid conceiving at times when the dominant is likely to be pregnant, and hence infanticidal, when their own litter is eventually born (~70 days later; Doolan and Macdonald, 1997). As dominant females are pregnant throughout much of the conceptive season, producing an average of 2.8 litters per year (Clutton-Brock et al., 2001), perhaps the only time that a subordinate female could conceive with virtual certainty that the dominant will not be heavily pregnant when her own litter is born, is soon after the dominant (within 2 weeks, as the dominant often undergoes a postpartum conception, Moss et al., 2001). We therefore tested the prediction that, if subordinate females exercise restraint in response to threat of infanticide by the dominant, they should show elevated estrogen levels during the fortnight following the dominant female’s conception, relative to other times (times when the dominant female is in late pregnancy, and times when the dominant female is not pregnant).

We used a GLMM to investigate whether subordinate females do modulate their estrogen levels in accordance with the reproductive state of the dominant female in the manner predicted. The dominant female’s reproductive state was fitted as a four-level factor: (i) fortnight following conception (which was always during the conceptive season); (ii) later in her pregnancy (which was always during the conceptive season); (iii) non-pregnant (during the conceptive season); and (iv) non-pregnant (during the non-conceptive season). To investigate whether any detected changes in estrogen levels across these contexts might be due instead to correlated variation in the physiological stress experienced by subordinate females, we used a second GLMM to test whether subordinate female fecal GC metabolite concentrations also varied across these same four contexts. To ensure that the two GLMMs used data arising from exactly the same set of fecal samples, the analyses made use of a set of 64 samples, each evaluated for both estrogen and GC metabolite concentrations. The samples were collected from 30 subordinate females of breeding age who were within their groups (neither evicted nor within 2 weeks of return from eviction; n=7 groups) and not pregnant at the time of sampling. Natural logarithm transformations were used to normalize both the total estrogen and GC data for analysis. The two GLMMs controlled for variation in female age (in days, log-transformed), body condition (residuals of body weight on age), whether the female had unrelated males within her group (immigrants since she was born), whether the female was lactating, group size (excluding pups), number of female group members of breeding age and the time of sample collection (AM or PM), to ensure that these variables neither confounded the comparisons nor yielded variation that may shroud the effects of interest.

Results

The analyses reported below investigate three possible explanations for the estrogen levels of subordinate females within their groups being markedly lower than those of dominant females.

Stress-related suppression of subordinate females while within their groups

There was no evidence to suggest that the low estrogen levels of subordinate females could be attributed to chronic stress suffered while within their groups, as their fecal GC metabolite concentrations (hereafter referred to as ‘GC levels’) during this time were comparable to those of dominant females (Table 1;).

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Factors affecting the fecal glucocorticoid metabolite concentrations of female meerkats</th>
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<tbody>
<tr>
<td></td>
<td>Full model</td>
</tr>
<tr>
<td></td>
<td>$\chi^2$</td>
</tr>
<tr>
<td>Lactating (yes, no)</td>
<td>9.87</td>
</tr>
<tr>
<td>Sample collection time (AM, PM)</td>
<td>7.88</td>
</tr>
<tr>
<td>Ln age (days)</td>
<td>4.77</td>
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<tr>
<td>Peak conceptive season (yes, no)</td>
<td>4.40</td>
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<tr>
<td>Body condition</td>
<td>2.12</td>
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<tr>
<td>Group size (excluding pups)</td>
<td>1.18</td>
</tr>
<tr>
<td>Females &gt;9 months old</td>
<td>0.55</td>
</tr>
<tr>
<td>Breeding experience (nulli, primi, multi)</td>
<td>1.51</td>
</tr>
<tr>
<td>Dominance status (dominant, subordinate)</td>
<td>0.43</td>
</tr>
<tr>
<td>Unrelated males within the group (yes, no)</td>
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</tr>
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</table>

<table>
<thead>
<tr>
<th></th>
<th>Minimal model</th>
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<tbody>
<tr>
<td>Constant</td>
<td>4.13 0.16</td>
</tr>
<tr>
<td>Lactating (yes &gt; no)</td>
<td>-0.40 0.13</td>
</tr>
<tr>
<td>Sample collection time (PM &gt; AM)</td>
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<tr>
<td>Ln age (days)</td>
<td>-0.33 0.15</td>
</tr>
<tr>
<td>Peak conceptive season (yes &gt; no)</td>
<td>-0.30 0.14</td>
</tr>
</tbody>
</table>

Results are from a GLMM based on a sample of 181 fecal samples collected from 14 dominants and 41 subordinates from 10 groups (all were non-pregnant females of breeding age, within their groups). Fecal glucocorticoid data were log transformed for analysis.

* Residuals of body weight on age.
This comparison controlled for significant elevations of GC levels during the peak conceptive season (Table 1; Fig. 1b) and in younger females (Table 1; Fig. 1c) and significant effects of both lactation status and sample collection time (Table 1). There was no evidence to suggest that the GC levels of a particular subset of subordinate females were elevated above those of dominants as might be expected if dominants targeted only a subset of subordinates who might otherwise attempt to breed (Young et al., 2006), as dominance status did not interact significantly with any of the other terms tested.

Subordinate restraint due to factors that may act regardless of the dominant’s presence

Females showed significantly lower fecal total-estrogen metabolite concentrations (hereafter referred to as ‘estrogen levels’) when in poorer body condition (Table 2; Fig. 2a), but not in response to a lack of unrelated males within their groups, young age (all females were of breeding age; over 9 months old) or a lack of prior breeding experience (Table 2). This analysis controlled for significant elevations of estrogen levels during the peak conceptive season and during lactation (Table 2). Substantial differences in the estrogen levels or dominant and subordinate females remained, however, when all of the above effects were controlled (Table 2; Fig. 2b), suggesting that any restraint exercised in response to these factors alone cannot account entirely for the low estrogen levels of subordinate females.

Subordinate restraint due to the likelihood of infanticide by the dominant

The estrogen levels of subordinate females varied significantly in association with the reproductive state of the dominant female (Table 3; Fig. 3a), showing the pattern that one would predict if they were exercising restraint in response to the likelihood of infanticide by the dominant (who is only infanticidal when pregnant; Clutton-Brock et al., 2001). Subordinate females exhibited markedly higher estrogen levels in the fortnight following conception by the dominant female.
The estrogen and GC analyses controlled for significant effects of body condition and lactation status, respectively, along with a number of other potentially confounding variables (Table 3).

Discussion

Our findings suggest that the low mean estrogen levels of subordinate female meerkats cannot be readily attributed to chronic stress suffered while within their groups, as their GC levels during this time were comparable with those of dominants. The low estrogen levels of subordinates would appear to be due instead to subordinates exercising physiological restraint; down-regulating their own reproductive endocrine axes so as to maximize their fitness given their circumstances.

While our analyses suggest that females may exercise a degree of physiological restraint when in poor body condition (with those who are lighter for their age showing lower estrogen levels), substantial differences in the estrogen levels of subordinate and dominant females remained after we controlled for this effect, along with each of the other factors that could favor restraint regardless of the presence of the dominant. Perhaps the most likely explanation for this residual difference in estrogen levels is that subordinates also exercise restraint due in part to the presence and/or likely actions of the dominant female (who becomes infanticidal when pregnant, Clutton-Brock et al., 2001). In accordance with this hypothesis, the estrogen levels of subordinate females appear to be modulated in association with temporal variation in the likelihood of infanticide by the dominant (a pattern that cannot be attributed to correlated variation in the GC levels of subordinates). Together these findings suggest that, while stress imposed by the dominant does appear to play a key role in the suppression of subordinate reproduction (during periodic temporary evictions; (Young et al., 2006), the low estrogen levels of subordinate females within their groups most likely reflect a degree of physiological restraint.
self-restraint due to factors both independent of, and arising from, the presence and/or likely actions of the dominant.

Recent work has indicated that stress-related suppression could prove difficult to detect with simple comparisons of the average GC levels of dominants and all subordinates, as dominants may target only a subset of their subordinates who might otherwise attempt to breed (Young et al., 2006). It seems unlikely that a key role for stress among subordinate females might otherwise attempt to breed (Young et al., 2006). It seems unlikely that a key role for stress among subordinate females 

An in-depth analysis of stress-related suppression is necessary to understand the underlying mechanisms. The findings of our GC level comparisons contrast with those of an earlier study, which reported that dominant female meerkats were more likely to have detectable levels of cortisol in their blood than subordinates (Carlson et al., 2004). At least two potential explanations exist for this disparity, both of which suggest that the findings reported here, using non-invasive techniques, provide the more accurate reflection of the patterns of baseline GC concentrations among meerkat females. First, the earlier study used blood samples taken 4–6 min after capture, leaving it possible that capture stress and/or anesthesia had affected the animals’ plasma cortisol concentrations prior to sampling (the difference that was detected could therefore constitute a difference in stress-responsiveness rather than in baseline GC concentrations per se). Second, as the comparisons in the earlier study had to be conducted on the basis of whether or not cortisol was detected in each sample, they only weakly reflect the patterns of actual GC concentrations in the blood samples taken.

While our analyses suggest that subordinate females exercise physiological restraint due in part to factors that may act regardless of the presence of the dominant, only one such factor proved important: females had lower estrogen levels when in poor condition (when they are also less likely to conceive; Clutton-Brock et al., 2001). As subordinate females lose an average of 4.2% of their body weight when they are temporarily driven from their groups by the dominant female (Young et al., 2006), one could argue that even this effect may be due in part to the actions of the dominant. The association between body condition and estrogen levels cannot be attributed solely to eviction-induced weight loss though, as evictees recover their weight loss within a month of their return (Young & Clutton-Brock, unpublished data), yet the association remains significant when all samples collected within 3 months of an evictee’s return are excluded from the data set. Indeed, as the association exists for all females (dominants and subordinates alike; Table 2), it would appear to constitute a generalized response to poor body condition.

We found no evidence that females exercised physiological restraint in response to any of the other factors that could reduce their expected payoff from maintaining their fertility regardless of the presence of the dominant (specifically young age, limited breeding experience and a lack of unrelated males within their groups). This latter finding contrasts with that of studies based on data from the early years of our project, when females did show both reduced estrogen levels and lower conception rates when lacking unrelated males within their groups (O’Riain et al., 2000; Clutton-Brock et al., 2001). This difference probably reflects the markedly higher rates at which our groups are know visited by prospecting males from other groups, affording the females in the current analyses access to unrelated breeding partners even when lacking them within their groups (females commonly mate with these prospecting males; Young et al., 2005, 2007). Accordingly, recent analyses suggest that subordinate females are no longer less likely to breed when lacking unrelated males within their groups either (Clutton-Brock et al., in review).
Perhaps the most likely explanation for the two-fold difference in mean estrogen levels that exists between dominant and subordinate females even after the factors discussed above have been controlled (Fig. 2b) is that subordinates may also exercise restraint due to the presence and/or likely actions of the dominant. Subordinates are now believed to exercise a degree of physiological restraint in the presence of their same-sex dominant in a number of social vertebrates (e.g. common marmosets, Abbott et al., 1997; Saltzman, 2003; naked mole-rats, Faulkes and Abbott, 1997; Cryptomys damarensis, Clarke et al., 2001), but the precise reasons for this are not well understood (Young, in press). Subordinates might exercise restraint in the dominant’s presence simply because their own young would suffer fitness costs from being reared alongside the dominant’s (e.g. due to competition for care), or instead because the dominant has the capacity to disrupt and/or punish subordinate attempts to breed (e.g. with mate guarding, Komdeur et al., 1999; infanticide, Digby, 2000; or expulsion from the group, Dierkes et al., 1999). While dominant interference of this kind has now been documented in a broad range of taxa, evidence actually linking the expression of subordinate restraint with the likelihood of such interference remains elusive. Our finding that the estrogen levels of subordinate females vary in association with the likelihood that the dominant will be pregnant (and hence infanticidal, Clutton-Brock et al., 2001) when any litter they conceive is eventually born is of particular interest.

The estrogen levels of subordinate females were substantially higher in the fortnight following conception by the dominant female than at other times (either later in the dominant’s pregnancy or when the dominant was not pregnant). This variation cannot be readily explained by subordinates experiencing differing levels of physiological stress across these contexts (as their GC levels were comparable across these contexts) or by correlated variation in factors known to cause variation in meerkat estrogen levels (as all such factors were controlled in the analysis). The most plausible explanation therefore appears to be that subordinate females modulate their own estrogen levels in response to variation in the reproductive state of the dominant female. Such an association might be expected if subordinates were exercising restraint due to costs that their own young would suffer from competing with those of the dominant. However, if this was the case, subordinates would be expected to favor conceiving, and so probably show peak estrogen levels, when the dominant had yet to conceive (to ensure that their own pups would be older than any produced by the dominant and thus dominate competition for care; S.J. Hodge unpublished data), yet the opposite appears to be true. The observed pattern, of peak estrogen levels in the fortnight following conception by the dominant female, is consistent instead with subordinates exercising restraint due to the threat of infanticide by the dominant female, as subordinate litters conceived in the fortnight following the dominant’s are almost guaranteed to be born when the dominant is no longer pregnant, and hence not infanticidal (Clutton-Brock et al., 2001). While this particular finding suggests that the threat of infanticide may contribute to selection for restraint among subordinates, the threat of interference by other means could also play a role (e.g. the elevated risk of abortion due to temporary evictions by the dominant, Young et al., 2006).

Our findings suggest that, while subordinate females do appear to suffer stress-related reproductive failure during periodic temporary evictions by the dominant female (Young et al., 2006), their low estrogen levels while residing within their groups may instead reflect a degree of subordinate restraint. This has broad implications because, while many studies seek to establish whether physiological suppression arises from chronic stress imposed by dominants or from subordinate restraint, both processes may act in concert in a given species, with dominants employing stress-related suppression in a targeted manner to guard against lapses in restraint at critical times (Young et al., 2006; Young, in press). Our findings also provide support for the hypothesis that subordinates exercise restraint due in part to the threat of dominant interference, which constitutes a plausible general explanation for subordinates exercising restraint in the presence of their same-sex dominants (Abbott et al., 1997; Faulkes and Abbott, 1997; Johnstone and Cant, 1999; Hamilton, 2004; Young, in press). Attempts to identify the causes of physiological suppression in vertebrate societies should be cautious therefore when rejecting a role for dominant interference in favor of subordinate restraint, as the threat of dominant interference may commonly be the reason why subordinates exercise restraint.

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