Elevated glucocorticoid concentrations during gestation predict reduced reproductive success in subordinate female banded mongooses


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Dominant females in social species have been hypothesized to reduce the reproductive success of their subordinates by inducing elevated circulating glucocorticoid (GC) concentrations. However, this 'stress-related suppression' hypothesis has received little support in cooperatively breeding species, despite evident reproductive skews among females. We tested this hypothesis in the banded mongoose (Mungos mungo), a cooperative mammal in which multiple females conceive and carry to term in each communal breeding attempt. As predicted, lower ranked females had lower reproductive success, even among females that carried to term. While there were no rank-related differences in faecal glucocorticoid (fGC) concentrations prior to gestation or in the first trimester, lower ranked females had significantly higher fGC concentrations than higher ranked females in the second and third trimesters. Finally, females with higher fGC concentrations during the third trimester lost a greater proportion of their gestated young prior to their emergence from the burrow. Together, our results are consistent with a role for rank-related maternal stress in generating reproductive skew among females in this cooperative breeder. While studies of reproductive skew frequently consider the possibility that rank-related stress reduces the conception rates of subordinates, our findings highlight the possibility of detrimental effects on reproductive outcomes even after pregnancies have become established.

1. Introduction

In animal societies, subordinate females often have lower reproductive success than dominant females. The stress-related suppression hypothesis proposes that dominant females suppress subordinate reproduction through behaviours that lead to chronic elevations in circulating glucocorticoids (GCs) and consequent reproductive downregulation [1–4]. Notably though, compelling support for this hypothesis remains scarce in cooperatively breeding societies, where reproductive skews among females are frequently apparent ([1,2]; but see [3,5]). Stress-related suppression might only be necessary, however, in the subset of cooperative breeders in which subordinate females do still attempt to breed, as complete reproductive restraint by subordinates might otherwise obviate the need for dominants to stress their subordinates [3,6,7]. Furthermore, stress-related suppression could actually be difficult to detect using the approach most-commonly employed to...
test it (comparisons of the average GC levels of dominants and subordinates), if dominants target only a subset of likely breeders and do so only during periods when subordinate reproduction would otherwise be costly to dominants [3,5,6]. These suggestions have led to calls for further tests in cooperatively breeding species in which subordinates do attempt to breed, focusing on those subordinates attempting to breed at the same time as their dominants [3,6].

While socially induced GC elevations have frequently been considered a potential cause of reduced conception rates among subordinates, they also have the potential to compromise the outcomes of established pregnancies. For example, elevated GCs during pregnancy may impact in utero or early post-natal development and affect offspring health, condition and survival [6,7]. While studies of cooperatively breeding mammals have shown that being subjected to aggression by the dominant female is associated with increased abortion rates among subordinates [3,8], whether rank-related maternal stress compromises reproductive outcomes among subordinates that do manage to carry to term has yet to be investigated. If subordinate reproductive success was reduced as a result of elevated GC concentrations during gestation, then one might make three predictions: pregnant females of lower social rank will have (i) reduced reproductive success and (ii) elevated GC concentrations during gestation, and (iii) females experiencing higher gestational GCs will have reduced reproductive success.

Here, we test these three predictions with a detailed investigation of faecal glucocorticoid (fGC) concentrations and reproductive success in female banded mongooses (Mungos mungo). Banded mongooses live in stable cooperatively breeding groups comprising a ‘core’ of breeding adults (one to five females and three to seven males) that reproduce three to four times per year, alongside a subset of younger individuals that breed occasionally [9]. Aggression received by pregnant subordinates can result in eviction and abortion [8], but pregnant subordinates do often breed successfully alongside pregnant dominants [9]. The rank-related patterns of reproductive success among females that carry to term have yet to be investigated, along with the role that GCs may play in generating them.

2. Material and methods

We studied a population of banded mongooses living in Queen Elizabeth National Park, Uganda (0°12′ S, 29°33′ E) between December 2010 and April 2014. All animals were marked and habituated to close observation (less than 5 m). Groups were observed every 1–4 days to record all breeding events. We ran habituated to close observation (less than 5 m). Groups were observed every 1–4 days to record all breeding events. We ran

3. Results

Lower ranking females that carried to term experienced lower reproductive success than higher ranking females, both when measured as the number of assigned offspring ($\chi^2 = 4.18$, $p = 0.041$; figure 1a) and the proportion of fetuses surviving to emergence ($\chi^2 = 4.29$, $p = 0.038$; figure 1c). There was no effect of rank on the number of fetuses carried by a female ($\chi^2 = 0.027$, $p = 0.87$). We found a significant interaction between female rank and pregnancy stage on fGC concentrations: lower ranking females did not differ from higher ranking females prior to conception or during the first trimester but had elevated fGCs during the second and third trimesters ($\chi^2 = 4.18$, $p = 0.041$; figure 2). Females experiencing higher fGC concentrations during the third trimester had fewer assigned offspring than those with lower GCs ($\chi^2 = 5.26$, $p = 0.022$; figure 1b) and a lower proportion of their fetuses survived to emergence ($\chi^2 = 4.07$, $p = 0.044$; figure 1d). Full model outputs are included in the electronic supplementary material S1.
4. Discussion

Our findings are consistent with the hypothesis that subordinate female banded mongooses exhibit reduced reproductive success as a result of rank-related maternal stress during gestation. Lower ranked females had lower reproductive success than higher ranked females (despite conceiving litters of the same size), both when measured as the proportion of fetuses surviving to emergence and the number of emergent offspring. Although higher and lower ranked females had...
similar fGC concentrations prior to gestation and during the first trimester, lower ranked females showed significantly elevated fGC concentrations during the second and third trimesters. These results highlight the potential that stress-related suppression of subordinate reproduction arises through gestational effects that compromise offspring survival either during the latter stages of pregnancy or soon after birth (prior to emergence from the burrow). Accordingly, females that experienced higher fGC concentrations during the third trimester had fewer emergent pups and a lower proportion of fetuses surviving to emergence.

Rank-related differences in reproductive success among female mammals commonly occur due to differences in conception rates, either because subordinate females exercise reproductive restraint or because their ability to conceive is compromised by active interference by dominant females [18,19]. By contrast, we have demonstrated a rank-related difference in reproductive success within females that carry to term. As there was no observable rank-related variation in litter size in utero, this rank-related difference in reproductive success could well have arisen from pre-natal developmental impacts on offspring survival either during late pregnancy or during the early post-natal period. A role for rank-related maternal stress during late gestation in generating these effects on offspring survival would be consistent with experimental evidence that late-gestational GC elevations can inhibit offspring development [4,20]. In the absence of experimental evidence of a role for maternal GC elevations, however, it is also possible that alternative mechanisms, such as early post-natal infanticide [21], play a role in generating the observed rank-related variation in offspring survival from detection as a fetus to emergence from the burrow.

The stress-related suppression hypothesis posits that elevated GC concentrations observed in lower ranking females are a result of aggression from dominant females. However, conspicuous aggression among female banded mongooses is rare outside of eviction events [9]. As such, the elevated GC concentrations observed here may not be a product of overt aggression. Our findings cannot be attributed instead to simple age effects, in which younger females struggle to meet the resource-demands of gestation (and hence exhibit differential GC elevations), as our analyses control for variation in absolute age and attribute variation in both reproductive success and gestational GC concentrations to variation in rank per se. However, the gestational GC elevations of lower ranked females could arise at least in part from energetic differences during gestation. For example, subordinates may be competitively excluded from resources by dominant females. Alternatively, as intra-sexual conflict among females may frequently be resolved without overt physical conflict, these GC elevations could also reflect responses to more subtle rank-related outcomes, such as social isolation [22]. Either way, our findings highlight the possibility that stress-related suppression of subordinate reproduction may occur in the absence of conspicuous aggression.

**Ethics.** All research was carried out under permit from Uganda Wildlife Authority (UWA) and Uganda National Council for Science and Technology (UNCST). All methods used received ethical approval from UWA, UNCST, and the Ethical Review Committees of the University of Exeter and Chester Zoo.

**Data accessibility.** All data analysed in this study are available in the electronic supplementary material S2.

**Authors’ contributions.** J.L.S. conceived the study, designed the study, organized and carried out fieldwork, organized hormone analyses, carried out parentage assignment and all statistical analyses and drafted the manuscript; H.J.N. carried out genetic analyses and commented on the manuscript; H.H.M., E.I.K.V. and F.J.T. all organized and carried out fieldwork and commented on the manuscript; S.L.W. managed hormone analysis and advised on collection of faecal samples; M.A.C. managed fieldwork and supervised the design of the study, analysis and drafting of manuscript; A.J.Y. supervised design of the study, analysis and drafting of manuscript. All authors approve the final version and agree to be accountable for all aspects of the work.

**Competing interests.** We declare we have no competing interests.

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**References**


