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The cost of dominance: suppressing subordinate reproduction affects the reproductive success of dominant female banded mongooses

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Social species show considerable variation in the extent to which dominant females suppress subordinate reproduction. Much of this variation may be influenced by the cost of active suppression to dominants, who may be selected to balance the need to maximize the resources available for their own offspring against the costs of interfering with subordinate reproduction. To date, the cost of reproductive suppression has received little attention, despite its potential to influence the outcome of conflict over the distribution of reproduction in social species. Here, we investigate possible costs of reproductive suppression in banded mongooses, where dominant females evict subordinates from their groups, thereby inducing subordinate abortion. We show that evicting subordinate females is associated with substantial costs to dominant females: pups born to females who evicted subordinates while pregnant were lighter than those born after undisturbed gestations; pups whose dependent period was disrupted by an eviction attained a lower weight at independence; and the proportion of a litter that survived to independence was reduced if there was an eviction during the dependent period. To our knowledge, this is the first empirical study indicating a possible cost to dominants in attempting to suppress subordinate breeding, and we argue that much of the variation in reproductive skew both within and between social species may be influenced by adaptive variation in the effort invested in suppression by dominants.

Keywords: reproductive skew; cooperative breeding; eusociality; conflict; cooperation

1. INTRODUCTION

Conflict over access to the resources required to breed is common in social species [1–3], reaching a peak in cooperative breeders, where reproduction is often limited to a single pair within each group, and where non-breeders provide care for the breeders' offspring [4–6]. This conflict appears to have selected for the direct suppression of subordinate reproduction by dominants [7–11], both to limit competition over the resources required for offspring care [12] and to maximize contributions by helpers, who tend to reduce their investment in care when they breed themselves [13]. There is, however, considerable interspecific variation in the extent of suppression ('reproductive skew'), from complete monopolization of reproduction (social hymenoptera [14]; naked mole rats [15]) to apparent egalitarianism (banded mongooses [16]; lions [17]). Moreover, skew can vary considerably within species, even those usually thought of as relatively despotic (e.g. meerkats [5,18]).

Variation in reproductive skew has been a persistent focus of attention (reviewed in [2]) because it may help to explain the paradox of reproductive altruism and it influences the evolutionary payoffs of most social behaviour [19]. Initially, thinking was heavily influenced by theoretical models that assumed, explicitly or implicitly, stable outcomes generated after what amounted to negotiation between dominants and subordinates [11,20–23]. However, recent empirical evidence suggests that variation in reproductive skew may instead be largely determined by taxon-specific idiosyncrasies of evolutionary history, ecology and social structure [14,24,25]. These influence the relative payoffs to dominants in attempting to monopolize breeding, and to subordinates in attempting to challenge dominants.

A largely overlooked issue, which may profoundly influence the payoffs of conflict over reproduction, is that the cost to dominants in attempting to suppress subordinates is unlikely to be trivial [21]. Selection may therefore act on dominants to invest in suppression only when the costs are low relative to the potential benefits [25,26]. Much variation in the distribution of reproduction within cooperative societies may therefore be a consequence of adaptive variation in the effort invested in suppression by dominants, although evidence for this is currently very limited. An effective way to investigate whether suppression imposes costs on dominants is to

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examine species where suppression only occurs periodically, and where the mechanisms of suppression are distinct from behaviours involved in 'routine' dominance interactions. This enables clear identification of when suppression is, and is not, occurring, allowing a comparison of dominant reproductive success between the two contexts. The social mongooses provide an excellent opportunity to do this, as dominants suppress subordinates by temporarily or permanently evicting them from the group (reviewed in [11,21]), but not in every breeding attempt. Eviction degrades subordinates' condition and raises stress levels, preventing them from entering oestrus or inducing them to abort [10,27]. However, despite its effectiveness at preventing subordinate reproduction, eviction probably carries considerable costs to dominants: sustained attacks are likely to be energetically expensive; may interrupt foraging and reduce food intake; could carry a risk of injury to dominants; and may disrupt provisioning of any dependent offspring from previous breeding attempts.

Here, we investigate the cost of evictions to dominant female banded mongooses (*Mungos mungo*). In this species, groups contain between one and 12 potential breeding females, and reproductive skew fluctuates widely, with between one and 10 females attempting to breed in synchrony in each breeding attempt [11]. Competition is often intense and temporary eviction of subordinates is common [11,16,28], typically occurring during oestrus or when females are in the latter stages of gestation. Eviction therefore often occurs when dominant females are already pregnant with their next litter, which may affect foetal development. Therefore, we expect pups born to dominants who evicted subordinates during gestation to be smaller than those born after undisturbed gestations. Evictions are also extremely violent and disruptive to normal behaviour, with attacks and chases occurring throughout foraging sessions, scattering groups and interrupting foraging. Such disruption may have a profound effect on the development of dependent pups: post-weaning, banded mongoose pups are cared for in exclusive relationships with a single helper (their 'escort'). When separated from their escorts, pups receive very little food [29], with pup provisioning rate, growth rate and survival positively correlated with the strength of the pup–escort association [30]. Therefore, we expect that evictions occurring while there are dependent pups in a group will reduce the strength of pup–escort associations, reduce pup growth rate and increase pup mortality.

2. METHODS

(a) *Study site and data collection*

Between April 2000 and February 2002, and between April 2003 and October 2005, we monitored 99 breeding attempts that produced at least one emerging pup from 11 groups in Queen Elizabeth National Park, Uganda (0°12′ S; 27°54′ E; see [16] for habitat and climate details). Individually marked animals were habituated to close (less than 5 m) observation on foot and accurate ages (±2 days) were known for most animals (92%). Individuals aged 0–3 months were classified as *pups* and more than three months as *helpers* (animals as young as three months provision pups; M. Bell 2004, personal observation).

(b) *Group structure, breeding and conflict*

Banded mongooses live in large family groups (in this study, average number of adults = 29, range 5–40) and are one of the few cooperative species where subordinates regularly breed (this study, median breeding females = 4, range 1–12). Groups breed two to four times each year [16,31], with pregnancy identified at *ca* 40 days by abdominal swelling and weight increase [16,28]. Females come into oestrus in synchrony and all pregnant females usually give birth on the same night [28,32], producing communal litters (this study; median litter size = 5, range 1–23). Births were identified by substantial over-night weight loss; changes in female shape; the appearance of suckle marks around distended nipples; and the onset of babysitting behaviour (variable number of adults remaining at a den while the rest of the group forages). Females usually enter oestrus within 10 days of giving birth (this study; median 9 days, range 2–27), becoming pregnant while pups from the previous litter are still dependent.

In around a quarter of breeding attempts (27 out of the 99 monitored during this period), a variable number of (usually pregnant) females were attacked by older, larger females and forced to leave the group (median number evicted = 7, range 1–12; we defined evictions as cases where at least one adult female left her group for at least one day as a consequence of aggression from other females). Evictees spent about a week out of their groups (median 5 days, range 1–39), following their groups at a distance and attempting to return several times each day, triggering prolonged chases.

Identifying a single 'dominant' female is problematic, so for each breeding attempt we classified females as dominant if they contributed to the communal litter, were observed actively evicting other females and were not themselves evicted. The remaining females were classified as 'subordinate' (after [11]). Using this classification, groups contained between one and five dominant females (mean ± s.d. = 2.90 ± 0.91) and 0 to 12 subordinate females (1.46 ± 1.43), with dominants always being the oldest females in the group.

(c) *Pup care and the escort system*

After birth, pups remain in dens for 3–4 weeks. When they emerge, they spend 3–5 days approaching different helpers, after which most pups form an exclusive association with a single adult (termed an escort), with whom pups spend 70 per cent or more of their time, and from whom they receive most of their food (median = 100% [30,31,33]; for details of escort characteristics and the pup–escort relationship, see [34,35]). During a foraging session, pups follow escorts closely (usually within 10 cm), begging constantly. Associations remain stable for 9–13 weeks [31]. Pups generally become nutritionally independent at *ca* 90 days, when the associations break down. Pups with stronger associations are fed more, grow faster and are more likely to survive to independence [30]. For the purposes of this investigation, we define the period between emergence from the den and 90 days of age as the 'dependent period'.

To quantify associations between pups and helpers, once each litter started foraging, we conducted 2 h of scan observations on three mornings each week until 90 days. Scans commenced when the group began foraging (*ca* 07.00 am), and at 5 min intervals, for each pup, we recorded distance to (±10 cm) and identity of the nearest helper. Pups that were within 2 m of the same individual for more than 50 per cent of time observed were classed as having an escort for that day, and the remainder were classed as having no escort for that day (after [30]). For each breeding attempt, we calculated the proportion of observation days on which each pup had an escort (the 'association index'), which was a continuous variable, ranging from 0 to 1. Although some pups spend the entire dependent period with the same helper, and others temporarily switch helpers, we use the *total* number of days that a pup had an escort, regardless of whether the identity of the helper changed (see [30,35] for further details).

(d) *Weight data*

All animals were caught by hand and weighed when they first emerged from the den (average weight at first weighing = 192.6 g ± 2.51 s.e.; average age at first weighing = 31.5 days ± 0.27 s.e.). They were subsequently trained to climb on an electronic laboratory scale before foraging in the morning (*ca* 07.30; accuracy ± 1.5 g; weight collected on three consecutive mornings each week). For each individual, age-controlled weight was calculated as the residual from a linear regression across individuals of mass (gram) over age in days (the relationship between mass and age is linear during the first three months of life [36]).

(e) *Assigning of maternity*

Maternity cannot be determined observationally, so we used microsatellite DNA analysis to assign maternity and investigate the effect of eviction during gestation on the pups of dominant females. DNA was extracted from tissue samples using lysis with proteinase K followed by a phenol : chloroform purification, and genotyped at 14 polymorphic microsatellite loci (see electronic supplementary material for details). Maternity was assigned at 95% confidence and included as candidate mothers all females who were known to be pregnant in that breeding attempt.

(f) *Statistical analysis*

We carried out simple parametric tests in MINITAB (all tests two-tailed), and constructed linear models using GENSTAT 8.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Where analysis involved repeated sampling within individuals, groups or litters, we used linear-mixed models (LMMs) or generalized linear-mixed models (GLMMs). Random terms were retained in models unless the variance component was found to be unmeasurable (less than 10^{-5}). See electronic supplementary material for full details of all explanatory variables investigated in each model.

(g) *Specific questions*

(i) *Does evicting subordinates during pregnancy affect pup weight at emergence?*

From the total dataset, we identified nine females with assigned maternity to pups produced after either (i) normal gestations ('undisturbed') or (ii) gestations where they had been observed actively evicting subordinates and were not themselves attacked ('disturbed'). We then compared the weight at first weighing for pups produced after the disturbed gestations with that of pups produced after the undisturbed gestation immediately preceding the disturbed gestations, giving a sample comprising 57 pups born into seven disturbed and seven undisturbed litters, in two groups (average interval between the two births = 65 days, range 58–92 days). We constructed an LMM, with pup weight at first weighing as the response variable, and mother identity and litter as random factors. Whether or not the gestation was disturbed was fitted as the main term of interest. To control for changes in maternal condition between the two breeding attempts, we fitted mother's weight at conception as a covariate, calculated as average morning weight during the period 70–60 days prior to birth (see also [36]).

(ii) *Does an eviction during the dependent period affect the strength of pup–escort associations?*

We analysed 296 pups: 124 females and 172 males from 56 litters in eight groups. Fourteen per cent of the litters for which data were available (eight out of 56) were disrupted by eviction during the dependent period, affecting 64 pups (22%). In all cases, the females conducting the eviction had contributed to the communal litter, with no contributions by other females. For each pup, the number of days during which a pup was classified as having an escort was fitted as the response variable, in a GLMM with a binomial error structure and a logit link function, and the total number of days observed was fitted as the binomial total. We included Group and Litter as random terms. Whether or not the litter was disturbed was fitted as the main term of interest, with age-controlled weight at first weighing, litter size, eviction during gestation, helper–pup ratio, rainfall during the dependent period, pup sex and group size as covariates.

(iii) *Does an eviction during the dependent period affect pup weight at independence?*

We analysed 110 pups: 37 females and 73 males, from 30 litters in six groups, with average weight at independence = 427.05 g (range 173–651.8 g). Twenty per cent of the litters for which data were available (six out of 30) were disturbed by eviction during the dependent period, affecting 22 pups (20%). In all cases, the females conducting the eviction had contributed to the communal litter, with no contributions by other females. For each pup, we calculated weight at independence as the average morning weight (in grams) between 90 and 95 days old. We fitted this as the response variable in an LMM, with Group and Litter as random factors. Whether or not the litter was disturbed was fitted as the main term of interest, with age-controlled weight at first weighing, association index, rainfall during the dependent period, eviction during gestation, litter size, pup sex, pack size and pup–helper ratio as covariates.

(iv) *Is the proportion of pups in a litter who survive to independence affected by an eviction during the dependent period?*

We analysed 98 litters (17 disrupted by eviction, 81 undisturbed) in eight groups. In all cases, the females conducting the eviction had contributed to the communal litter, with no contributions by other females. We constructed a GLMM with number of pups surviving to 90 days as the response variable, and total litter size (number of pups counted at first emergence) as the binomial total. We fitted Group as a random term. Whether or not the litter was disturbed was fitted as the main term of interest, with rainfall during gestation, the average age-controlled weight of the litter, eviction during gestation, number of breeding females, rainfall during the dependent period, helper–pup ratio, litter size and pack size as covariates.

3. RESULTS

(a) *Pup weight at emergence*

The average weight of pups born to a mother was lower if she had been observed actively evicting subordinates during gestation than when gestations had been undisturbed (LMM: $\chi^2 = 5.53$, $p = 0.019$; figure 1*a*; electronic supplementary material, table S1), after controlling for effects of the age at which the pups were first weighed ($\chi^2 = 5.08$, $p < 0.001$) and rainfall during gestation ($\chi^2 = 7.64$, $p = 0.006$). We also confirm previous analyses [37] that maternal weight at conception affects pup weight at emergence ($\chi^2 = 8.26$, $p = 0.004$).

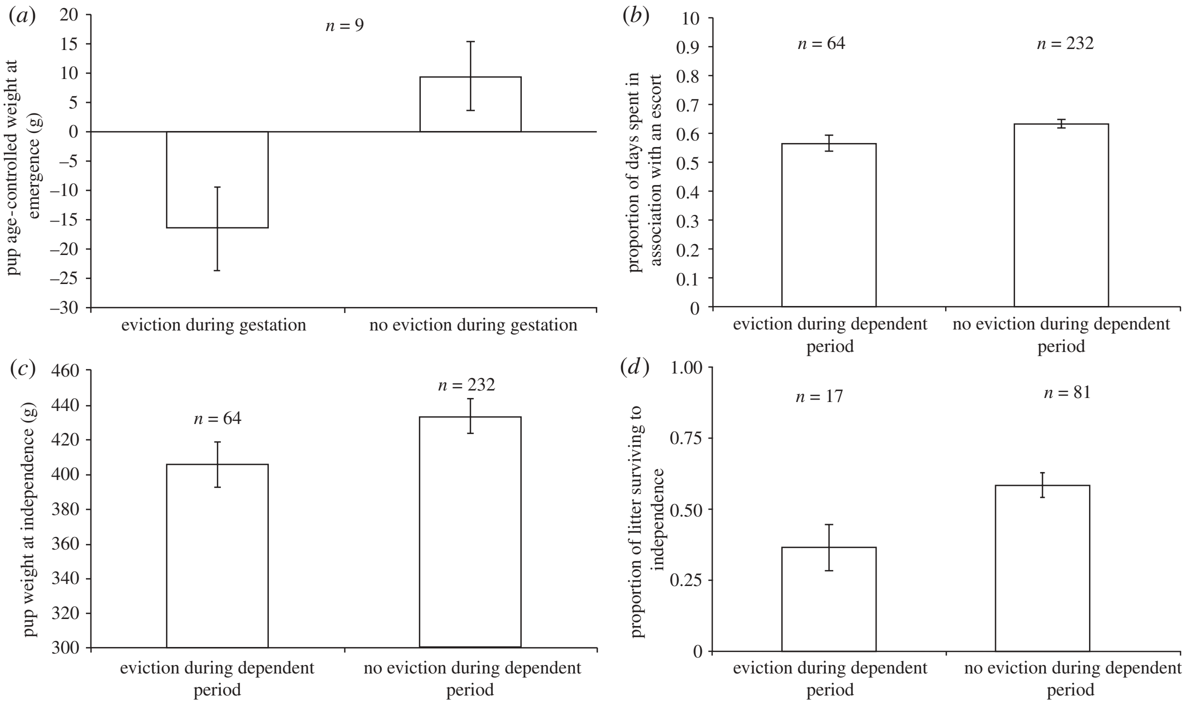

Figure 1. (*a*) The effect of eviction during gestation on pup age-controlled weight at emergence (LMM: $\chi^2 = 5.53$, $p = 0.019$; data are average age-controlled weights (±s.e.) of pups born to dominant females that experienced both interrupted and uninterrupted gestations); (*b*) the effect of eviction during the dependent period on the proportion of days pups spent in association with an escort (GLMM: $\chi^2 = 6.62$, $p = 0.01$; data are average proportion of days spent in association with an escort for pups in undisturbed litters and litters interrupted by an eviction, ±s.e.); (*c*) the effect of eviction during the dependent period on pup weight at independence (LMM: $\chi^2 = 6.87$, $p = 0.009$; means ± s.e.); and (*d*) effect of eviction event during the dependent period on the proportion of an emerging litter that survives to independence at 90 days (GLMM: $\chi^2 = 14.65$, $p < 0.001$; means ± s.e.).

(b) *Pup–escort association strength*

Pups exposed to eviction events during their dependent period spent fewer days in close association with an escort than those with an undisturbed dependent period (GLMM: $\chi^2 = 6.62$, $p = 0.01$; figure 1*b*; electronic supplementary material, table 2), after controlling for an interaction between age-controlled weight at emergence and litter size ($\chi^2 = 8.55$, $p = 0.003$). There was also a marginal negative effect of eviction during gestation ($\chi^2 = 3.06$, $p = 0.081$).

(c) *Pup weight at independence*

After controlling for a positive effect of weight at emergence, pups exposed to eviction events during their dependent period were lighter at 90 days than those with an undisturbed dependent period (LMM: $\chi^2 = 6.87$, $p = 0.009$; figure 1*c*; electronic supplementary material, table S3). We also confirmed previous analyses (e.g. [30]), finding that pups who spent a greater proportion of their dependent period in close association with a helper were significantly heavier than those who spent less time with a helper ($\chi^2 = 10.3$, $p = 0.001$), and found a positive effect of rainfall during the dependent period ($\chi^2 = 10.21$, 0.001). There was also a marginal negative effect of eviction during gestation ($\chi^2 = 3.37, p = 0.079$).

(d) *Proportion of a litter surviving to independence (90 days)*

A smaller proportion of pups survived in litters disrupted by eviction events during the dependent period than in litters with an undisturbed dependent period (GLMM: $\chi^2 = 14.65$, $p < 0.001$; figure 1*d*; electronic supplementary material, table S4) after controlling for effects of rainfall during gestation ($\chi^2 = 20.75$, $p < 0.001$) and the average age-controlled weight at emergence of all pups in the litter ($\chi^2 = 16.26$, $p < 0.001$). There was also a marginal negative effect of eviction during gestation ($\chi^2 = 3.97$, $p = 0.05$).

4. DISCUSSION

These data reveal that evicting subordinate females is associated with considerable negative effects for the offspring subsequently produced by dominant females: pups born to females who had evicted subordinates during gestation were lighter than those born after undisturbed gestations; pups whose dependent period was disrupted by an eviction were lighter at independence; and the proportion of a litter surviving to independence was reduced if there was an eviction during the dependent period. To our knowledge, this is the first empirical evidence indicating that attempting to restrict subordinate reproduction may be costly to dominants, and as such has important implications for our understanding of the outcome of conflict over the distribution of reproduction in social species.

Reduced emergence weight in pups born after their mothers had evicted subordinates is probably owing to a combination of factors, including: energy expenditure during the prolonged chases and fights; raised maternal stress levels; and fewer lactating females during the period between birth and emergence [11]. The latter may be particularly important because suckling occurs communally, and females do not appear to discriminate against other females' pups. As these and previous (e.g. [36]) analyses reveal, numerous social and environmental factors (such as rainfall and maternal weight at conception) are important in determining emergence weight. That the effect of eviction remains after controlling for these suggests that evicting subordinates imposes a substantial drain on maternal resources. Nevertheless, the sample size for this analysis is small and data are restricted to two groups, so the results must be treated as suggestive.

Reduced weight at independence in pups exposed to evictions during the dependent period is likely to be owing to the disruption of the pup–escort associations revealed in our analysis. Pups receive more than 90 per cent of their food from their escorts [33], and are generally provisioned at very low rates when separated from their escorts [29]. Therefore, pups that spend less time with their escorts are likely to receive much less food, and may be forced to start foraging for themselves earlier, when they are likely to be less efficient foragers [38]. Reduced food intake probably also explains the increased mortality in eviction-disrupted litters, although this may be owing to increased predation risk, since predators tend to target pups separated from their escorts (M. Bell 2004, personal observation).

That eviction during gestation does not appear to have significant effects on growth and survival after emergence is surprising, but probably owing to the effect on weight at emergence, which accounts for very significant variation within the models. More broadly, the association between eviction events, reduced emergence weight and declines in pup growth and survival may be driven by an increased probability of eviction when resources available to breeding females become restricted, rather than by a direct effect of evictions *per se*. However, our models include rainfall (a proxy for food availability), and either group size or helper–pup ratio (a measure of the help available to dependent pups), so it seems that the negative effect of eviction occurs *in addition* to any negative effect of resource restriction.

The negative effects of eviction on pup weight at emergence and independence are likely to have profound long-term effects on pup fitness. Size at emergence determines competitive ability in early life [37]; rapid growth rates during development reduce the age and size at which females first breed [30], and size at adulthood affects reproductive success [30,37,39] and probability of later eviction [40]. Hence these data imply that attempting to restrict subordinate reproduction has profound consequences for dominant fitness. That dominants endure these costs suggests that their fitness would be even more adversely affected if subordinates bred successfully—yet dominants appear unaffected when few subordinates breed [11], probably because the escort system limits competition between pups [33] and resources are abundant. However, as the number of breeding females increases, and communal litter size increases, the reproductive success of dominants does decline markedly—and eviction occurs [11]. By contrast, in meerkats, the presence of a single extra breeder can impose considerable costs on the dominant [26], and aggression, eviction or infanticide occurs in most breeding attempts [10,27]. Yet even here, dominants only suppress when the timing of subordinate breeding maximizes the degree of conflict over available resources [41].

Our results indicate that the cost of preventing competitors from breeding can be substantial, suggesting that dominants may be under selection to optimize their investment in targeted aggression. Substantial costs of interference with subordinate reproduction are likely to be widespread [3,17,41] and may impose important constraints on the ability of single individuals to monopolize group reproduction. This means that, while social structure and patterns of relatedness appear to set the evolutionary limits within which subordinates can tolerate restraints on reproduction [14,42], the actual distribution of reproduction within groups may be determined by conflict [19,21,43–45], with the relative costs of such conflict potentially decisive in determining the outcome.

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