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Author-supplied statements

Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
A previous study found no adverse effects of trapping and anaesthesia on pregnant females [31], and all methods were carried out in accordance with the Association for the Study of Animal Behaviour (ASAB) guidelines. All field work was conducted under permissions from Uganda Wildlife Authority (UWA) and Uganda National Council for Science and Technology (UNCST), and animal research methods approved by the ethical review panel of the University of Exeter.

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
Data supporting this manuscript are available on Figshare, at https://doi.org/10.6084/m9.figshare.5572408.v1

Conflict of interest

I/We declare we have no competing interests

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This paper has multiple authors and our individual contributions were as below

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MC and EI conceived the study and designed it with guidance from GKZ. EI, EV, HM and FT conducted and interpreted analyses. EI, EV and MC prepared the manuscript and GKZ, HM and FT contributed with critical revising; all authors approved the final version and agree to be held accountable for the content therein.

Spontaneous abortion as a response to reproductive conflict in the banded mongoose

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Abstract

When breeding females compete for limited resources, the intensity of this reproductive conflict can determine whether the fitness benefits of current reproductive effort exceed the potential costs to survival and future fertility. In group-living species, reproductive competition can occur through post-natal competition among the offspring of co-breeding females. Spontaneous abortion could be a response to such competition, allowing females to curtail reproductive expenditure on offspring that are unlikely to survive and to conserve resources for future breeding opportunities. We tested this hypothesis using long-term data on banded mongooses, *Mungos mungo*, in which multiple females within a group give birth synchronously to a communal litter that is cared for by other group members. As predicted, abortions were more likely during dry periods when food is scarce, and in breeding attempts with more intense reproductive competition. Within breeding events, younger, lighter females carrying smaller fetuses were more likely to abort, particularly those that were also of lower rank. Our results suggest that abortion may be a means by which disadvantaged females conserve resources for future breeding attempts in more benign conditions, and highlight that female reproductive competition may be resolved long before the production of offspring.

Keywords: banded mongoose, abortion, female reproductive competition, cooperative species, reproductive suppression

Introduction

Female reproductive conflict, that is, competition over the distribution of reproduction among females in a social unit, is typically more subtle than male-male competition and hence easily overlooked [1]. Yet females use a variety of strategies to compete over access to and control of resources essential to the survival and reproductive success of their offspring. In reindeer (*Rangifer tarandus*), for example, dominant females monopolize access to superior foraging patches, gain weight during the winter, and consequently breed earlier and more often, producing calves that grow faster than those of subordinate females [2]. Cooperatively breeding animals exhibit more overt forms of competition, whereby dominant females and other non-breeding subordinate females aggressively suppress subordinate female reproduction through direct aggression and infanticide [3].

Spontaneous abortion in response to social cues can be a strategy for a female to save time and resources, in order to raise future offspring with better survival probabilities [4]. For example, in rodents, females commonly abort or reabsorb fetuses in the presence of a new unknown male ('The Bruce effect' [5,6]). Spontaneous abortions have also been found to increase in wild female geladas (*Theropithecus gelada*) if the dominant male in the group is replaced [7]. We investigated whether patterns of abortion reflect the intensity of reproductive conflict in wild banded mongooses (*Mungos mungo*) in which offspring of several females compete for food and access to adult helpers or 'escorts' in communal litters [8]. We made two predictions. First, we predicted that abortion should be more frequent in breeding attempts with more intense reproductive competition, as measured by female group size and resource abundance. Second, within breeding attempts, we predicted that lower-rank females, females in poorer condition and those with smaller fetuses should be more likely to spontaneously abort, particularly when competition is high [8,9].

Methods

Study population

We collected data from a wild population of banded mongooses living on and around the Mweya Peninsula, Queen Elizabeth National Park, Uganda (0°12'S, 29°54'E) between September 1999 and February 2015. For a detailed description of the climate, habitat and the population see [10]. All individuals in the population are individually identified and groups were visited daily to determine pregnancy, parturition and abortion dates. Pregnancy was confirmed by ultrasound scans and palpation of the abdomen during routine capture, and parturition and abortion detected from subsequent rapid changes in body shape and weight (for details of capture and anaesthesia see [11]). Abortions were defined as confirmed pregnancies that lasted < 60 days (mean gestation period [12]) and produced no viable pups. There were also 9 direct observations of spontaneous abortion of unviable neonates. In the banded mongoose, groups of individuals are periodically evicted from their natal group and the violent eviction events are known to increase the risk of abortion [13]. Therefore, to focus on spontaneous pregnancy loss, abortions from breeding attempts where an eviction event occurred were excluded from these analyses.

Predictors of abortion

Rainfall in the study site correlates with invertebrate abundance (e.g. [14]) so cumulative rainfall for 60 days before the birth of the communal litter was used as a proxy for resource abundance during gestation. In the banded mongoose, pups born in communal litters compete for helpers postnatally, and the breeding success of dominant females declines with increasing female group size [15]. Probability of violent evictions where older females expel younger females also increases with group size [15, 16], and the per capita reproductive success of the remaining females increases after eviction events [17], so the number of adult (>1 years old) females was used as a proxy of the intensity of reproductive competition. Ranked age (range 1-11, 1 = oldest female in the group) which describes vulnerability to eviction [9] was used as proxy of dominance status, by dividing it by the number of adult females in the group to get a relative rank score (range 0.09-1) that is comparable across different group sizes. Adult weight varies with rainfall and availability of invertebrate prey (e.g. [18]) and it predicts survival [18] as well as competitive ability [19], so female weight on the closest weighing event prior to the estimated conception date was used as a proxy for female condition. Fetus size was measured from ultrasound scans (see [19] and ESM) for the subset of data where this was available.

Statistical analyses

Available data varied across females and breeding attempts, so in order to maximise sample size the analysis was conducted in three stages (see ESM for full details, and [20] for the full datasets used in the analyses). First, we looked at whether any abortions occurred in a breeding event (Y/N, N = 461 communal litters from 18 groups; breeding events where an eviction occurred were left out), with rainfall during gestation (mm) and female group size as predictors; female group size was also fitted as a quadratic term, to allow for possible negative effects of both small and large group size on probability of abortion. Second, we looked at individual level predictors of a particular female aborting (Y/N) in 207 confirmed pregnancies from 93 females in 8 social groups, within the 57 litters in which abortions occurred and for which we had complete data for the predictor variables: female weight at conception (g), relative age rank, primiparity (Y/N), number of females, and rainfall during gestation (mm). We included two-way interactions between weight and rainfall, female group size and rank, to test for condition-specific effects of resource levels and competitive environment. Third, we ran a separate model of whether a particular female aborted (Y/N), with average fetus size (mm^2), relative age rank, number of females and two-way interactions between weight and rank, weight and female group size, and weight and fetus size as predictors, in the subset of data (76 pregnancies from 17 females, 8 litters, 6 groups) where fetus size measurements were available; fetus gestational age was included as a covariate to control for capture at different times during pregnancy. Generalised linear mixed models (GLMMs) with a binomial error structure and logit link function were fitted using lme4 package [21] in R version 3.1.0 [22]. Group was included as a random factor in all analyses, and female and litter identity in the individual level analyses (see ESM for details). The significance of each fixed effect was assessed by comparing the likelihood ratio of the maximal model to that of the model without the fixed effect [21]. Non-significant interactions were removed to allow the significance of the main effects to be tested [23], but models were not simplified further, to avoid problems associated with stepwise model reduction (e.g. [23, 24]).

Results

Abortions occurred in 133 (29%) out of 461 group breeding attempts, with 2.06 ± 1.26 (mean ± S.D.) females aborting in each. Out of 830 pregnancies that were confirmed by palpation and ultrasound, 361 (43%) were not carried to term. This is a conservative estimate of the overall abortion rate: most abortions occurred in the second trimester (average 43 days) and those occurring before pregnancy could be confirmed (<30 days) would go undetected.

As predicted, among litters, abortion was more likely when rainfall was low (β ± SE = -0.272 ± 0.110, χ^2_1 = 6.36, P = 0.012; Fig. 1a) and when more females were co-breeding (β ± SE = 0.372 ± 0.180, χ^2_1 = 4.54, P = 0.033; Fig. 1b); the quadratic effect of female group size was not significant (β ± SE = -0.023 ± 0.013, χ^2_1 = 3.41, P = 0.065). Within litters, abortion probability was higher for females of lower rank, particularly in females that also had lower weight at conception (interaction weight × rank: β ± SE = -1.097 ± 0.552, χ^2_1=4.157, P=0.042; Fig. 2a; all other terms P > 0.19, see ESM Table S2). Females with larger fetuses were less likely to abort, and abortion probability declined with increasing fetus size more steeply in lighter than in heavier females (β ± SE = 0.025 ± 0.011, χ^2_1 = 9.79, N = 76, P = 0.002; Fig. 2b). No other terms predicted abortion probability at the individual level (ESM Table S3).

Discussion

Spontaneous abortion was common in banded mongooses, with 43% of detected pregnancies not carried to term. Equally high reproductive failure rates have been found in other mammals (e.g. [25]). Across litters, abortions were more common during dry periods, when invertebrate pray is scarce, suggesting that resource limitation is an important determinant of pregnancy outcome. However, controlling for the effect of rainfall, the probability of abortion also increased with increasing female group size, suggesting that reproductive competition is also an important determinant of abortion risk. Reproductive competition is intense among female banded mongooses, and is manifested in conspicuous and violent behaviour such as infanticide and eviction of reproductive rivals. Our results show that conflict over reproduction may be resolved in subtle ways that are more difficult to detect, through termination of pregnancy before offspring are produced.

On an individual level, similar to red squirrels (*Sciurus vulgaris* [26]) and caribou (*Rangifer tarandus* [27]), female condition (measured as weight at conception) in conjunction with the females' social rank predicted abortion probability. As predicted, relatively young females were more likely to abort, and this effect of age rank on abortion probability was amplified for females that were in poor condition. We know from previous work that younger and lighter females are particularly responsive to reproductive competition, producing larger fetuses when female group size is large [19]. In this study we have shown that larger fetuses are less likely to be aborted, and this relationship is particularly steep for lighter females. Taken together, these findings support the idea that those females that cannot (or do not) respond to reproductive competition by increasing their fetus size instead abort their litter, conserving resources for future reproductive events that are more likely to succeed. It is also the case that lighter and younger females are more likely to forego reproduction entirely, particularly when resources are scarce (28). Our results highlight that reproductive conflict among females may often be resolved in subtle and complex ways, long before offspring are produced and without any associated aggression or agonistic behaviour.

At the study site, rainfall correlates with invertebrate prey abundance, and dry periods are linked with increased post-natal competition for food and access to helpers [8,14,18]. In such circumstances, low ranking and light females may gain from aborting their pregnancy to reallocate resources to a future breeding attempt in more benign and less competitive conditions [25], especially as their offspring tend to be smaller at birth and are particularly susceptible to infanticide by older, socially dominant females [12,15]. Breeding may also entail higher costs to lighter or less experienced females, and disproportionately compromise their survival or future reproduction [29, 30]. The long-term fitness consequences of abortion remain unknown at present, but overall our results suggest that spontaneous abortion patterns may evolve as a response to potentially costly female reproductive conflict.

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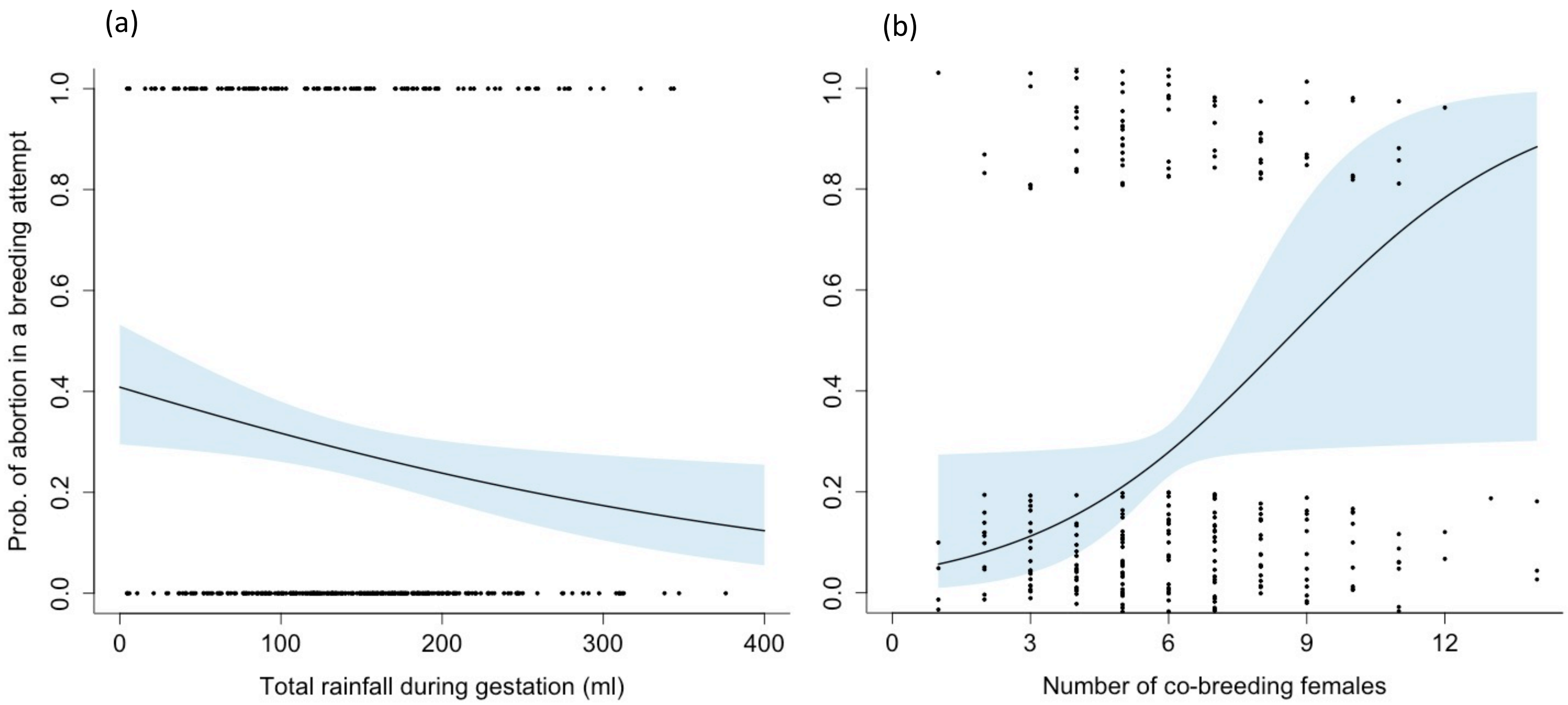
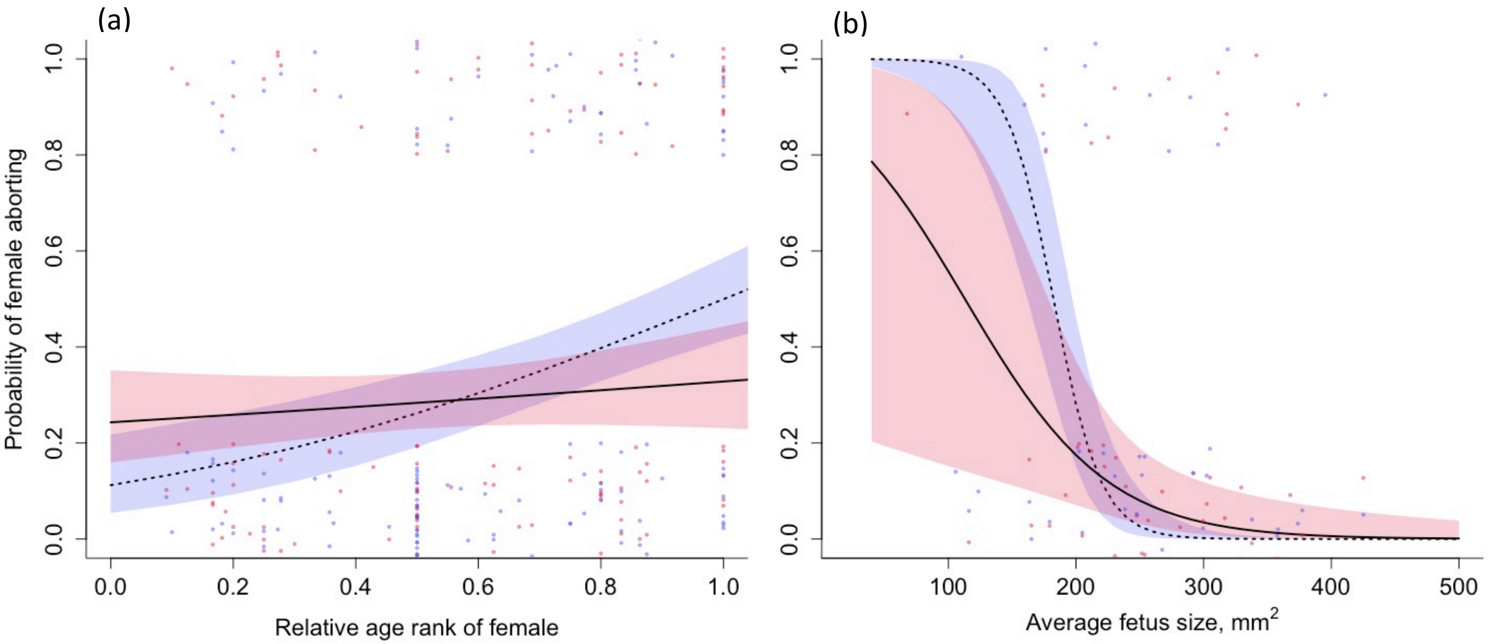
FIGURES

Figure 1. Litter-level predictors of abortion in wild banded mongooses. Abortions were more likely to occur in a given breeding attempt (a) when rainfall was low, and (b) in breeding attempts under more intense reproductive competition (when more females were co-breeding). The line and shaded area represent model predictions ± SE from a binomial GLMM, accounting for the random effect of group identity, and the points are raw data (jittered for clarity in b).

Figure 2. Figure 2. Individual level predictors of abortion probability in wild banded mongooses. For a given female, in breeding attempts where abortions occurred, individual probability of abortion (a) increased with decreasing relative rank (1 = lowest rank), particularly in light females (blue) as compared to heavier females (red), and (b) decreased more steeply with increasing fetus size in light females (blue) than in heavy females (red). The lines and shaded areas represent model predictions ± SE from binomial GLMMs, plotted for light (25% quartile = 1200g: dotted line, blue area) and heavy females (75% quartile = 1550g: solid line, red area) after accounting for the random effects of female, litter and group identity. Dots are raw datapoints, jittered for clarity. Note that in the analyses female weight was used as a continuous predictor, and weight categories are drawn for illustration only.


(a)
Prob. of abortion in a breeding attempt
0.0
0.2
0.4
0.6
0.8
1.0
0
100
200
300
400
Total rainfall during gestation (ml)
(b)
0.0
0.2
0.4
0.6
0.8
1.0
0
3
6
9
12
Number of co-breeding females


(a)
(b)
Probability of female aborting
0.0
0.2
0.4
0.6
0.8
1.0
Relative age rank of female
100
200
300
400
500
Average fetus size, mm^2