

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

E. Inzani¹, H. H. Marshall^{1,2}, F.J. Thompson¹, G. Kalema-Zikusoka³, M.A. Cant¹ & E.I.K. Vitikainen^{1,4*}

Address:

1. Centre for Ecology and Conservation, Penryn Campus, University of Exeter, UK
2. Centre for Research in Ecology, Evolution and Behaviour, University of Roehampton, UK
3. Conservation Through Public Health, Entebbe, Uganda
4. Organismal and Evolutionary Biology research programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Finland

*Corresponding author: emma.vitikainen@helsinki.fi

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

26 rank. Our results suggest that abortion may be a means by which disadvantaged females conserve
27 resources for future breeding attempts in more benign conditions, and highlight that female
28 reproductive competition may be resolved long before the production of offspring.

29

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

For Review Only

32 Introduction

33

34 Female reproductive conflict, that is, competition over the distribution of reproduction among females
35 in a social unit, is typically more subtle than male-male competition and hence easily overlooked [1].

36 Yet females use a variety of strategies to compete over access to and control of resources essential to
37 the survival and reproductive success of their offspring. In reindeer (*Rangifer tarandus*), for example,
38 dominant females monopolize access to superior foraging patches, gain weight during the winter, and
39 consequently breed earlier and more often, producing calves that grow faster than those of
40 subordinate females [2]. Cooperatively breeding animals exhibit more overt forms of competition,
41 whereby dominant females and other non-breeding subordinate females aggressively suppress
42 subordinate female reproduction through direct aggression and infanticide [3].

43

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

56

57

58 **Methods**

59

60 *Study population*

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

74

75 *Predictors of abortion*

76 Rainfall in the study site correlates with invertebrate abundance (e.g. [14]) so cumulative rainfall for 60
77 days before the birth of the communal litter was used as a proxy for resource abundance during
78 gestation. In the banded mongoose, pups born in communal litters compete for helpers postnatally,
79 and the breeding success of dominant females declines with increasing female group size [15].
80 Probability of violent evictions where older females expel younger females also increases with group
81 size [15, 16], and the per capita reproductive success of the remaining females increases after eviction

82 events [17], so the number of adult (>1 years old) females was used as a proxy of the intensity of
83 reproductive competition. Ranked age (range 1-11, 1 = oldest female in the group) which describes
84 vulnerability to eviction [9] was used as proxy of dominance status, by dividing it by the number of
85 adult females in the group to get a relative rank score (range 0.09-1) that is comparable across
86 different group sizes. Adult weight varies with rainfall and availability of invertebrate prey (e.g. [18])
87 and it predicts survival [18] as well as competitive ability [19], so female weight on the closest weighing
88 event prior to the estimated conception date was used as a proxy for female condition. Fetus size was
89 measured from ultrasound scans (see [19] and ESM) for the subset of data where this was available.

90

91 *Statistical analyses*

92 Available data varied across females and breeding attempts, so in order to maximise sample size the
93 analysis was conducted in three stages (see ESM for full details, and [20] for the full datasets used in
94 the analyses). First, we looked at whether any abortions occurred in a breeding event (Y/N, N = 461
95 communal litters from 18 groups; breeding events where an eviction occurred were left out), with
96 rainfall during gestation (mm) and female group size as predictors; female group size was also fitted as
97 a quadratic term, to allow for possible negative effects of both small and large group size on probability
98 of abortion. Second, we looked at individual level predictors of a particular female aborting (Y/N) in
99 207 confirmed pregnancies from 93 females in 8 social groups, within the 57 litters in which abortions
100 occurred and for which we had complete data for the predictor variables: female weight at conception
101 (g), relative age rank, primiparity (Y/N), number of females, and rainfall during gestation (mm). We
102 included two-way interactions between weight and rainfall, female group size and rank, to test for
103 condition-specific effects of resource levels and competitive environment. Third, we ran a separate
104 model of whether a particular female aborted (Y/N), with average fetus size (mm²), relative age rank,
105 number of females and two-way interactions between weight and rank, weight and female group size,
106 and weight and fetus size as predictors, in the subset of data (76 pregnancies from 17 females, 8 litters,

107 6 groups) where fetus size measurements were available; fetus gestational age was included as a
108 covariate to control for capture at different times during pregnancy. Generalised linear mixed models
109 (GLMMs) with a binomial error structure and logit link function were fitted using lme4 package [21] in
110 R version 3.1.0 [22]. Group was included as a random factor in all analyses, and female and litter
111 identity in the individual level analyses (see ESM for details). The significance of each fixed effect was
112 assessed by comparing the likelihood ratio of the maximal model to that of the model without the fixed
113 effect [21]. Non-significant interactions were removed to allow the significance of the main effects to
114 be tested [23], but models were not simplified further, to avoid problems associated with stepwise
115 model reduction (e.g. [23, 24]).

116

117 **Results**

118

119 Abortions occurred in 133 (29%) out of 461 group breeding attempts, with 2.06 ± 1.26 (mean \pm S.D.)
120 females aborting in each. Out of 830 pregnancies that were confirmed by palpation and ultrasound,
121 361 (43%) were not carried to term. This is a conservative estimate of the overall abortion rate: most
122 abortions occurred in the second trimester (average 43 days) and those occurring before pregnancy
123 could be confirmed (<30 days) would go undetected.

124

125 As predicted, among litters, abortion was more likely when rainfall was low ($\beta \pm SE = -0.272 \pm 0.110$, χ^2_1
126 $= 6.36$, $P = 0.012$; Fig. 1a) and when more females were co-breeding ($\beta \pm SE = 0.372 \pm 0.180$, $\chi^2_1 = 4.54$,
127 $P = 0.033$; Fig. 1b); the quadratic effect of female group size was not significant ($\beta \pm SE = -0.023 \pm 0.013$,
128 $\chi^2_1 = 3.41$, $P = 0.065$). Within litters, abortion probability was higher for females of lower rank,
129 particularly in females that also had lower weight at conception (interaction weight \times rank: $\beta \pm SE = -$
130 1.097 ± 0.552 , $\chi^2_1 = 4.157$, $P = 0.042$; Fig. 2a; all other terms $P > 0.19$, see ESM Table S2). Females with
131 larger fetuses were less likely to abort, and abortion probability declined with increasing fetus size
132 more steeply in lighter than in heavier females ($\beta \pm SE = 0.025 \pm 0.011$, $\chi^2_1 = 9.79$, $N = 76$, $P = 0.002$; Fig.
133 2b). No other terms predicted abortion probability at the individual level (ESM Table S3).

134

135 Discussion

136

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

147

148 On an individual level, similar to red squirrels (*Sciurus vulgaris* [26]) and caribou (*Rangifer tarandus*
149 [27]), female condition (measured as weight at conception) in conjunction with the females' social rank
150 predicted abortion probability. As predicted, relatively young females were more likely to abort, and
151 this effect of age rank on abortion probability was amplified for females that were in poor condition.
152 We know from previous work that younger and lighter females are particularly responsive to
153 reproductive competition, producing larger fetuses when female group size is large [19]. In this study
154 we have shown that larger fetuses are less likely to be aborted, and this relationship is particularly
155 steep for lighter females. Taken together, these findings support the idea that those females that
156 cannot (or do not) respond to reproductive competition by increasing their fetus size instead abort
157 their litter, conserving resources for future reproductive events that are more likely to succeed. It is
158 also the case that lighter and younger females are more likely to forego reproduction entirely,
159 particularly when resources are scarce (28). Our results highlight that reproductive conflict among

160 females may often be resolved in subtle and complex ways, long before offspring are produced and
161 without any associated aggression or agonistic behaviour.

162

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

173

174 **Acknowledgements**

175 We are grateful to N. Guma, E. Asalu, M. Driciru and the wardens and staff of Queen Elizabeth National
176 Park for continuous logistical support. We thank Francis Mwanguhya, Solomon Kyabulima, Kenneth
177 Mwesige, Robert Businge and Solomon Ahabyona for assistance in the field, and previous Banded
178 Mongoose Research Project researchers, particularly Jason Gilchrist, Matt Bell and Sarah Hodge and
179 Neil Jordan, for their contribution to the long-term data. We thank four anonymous reviewers whose
180 detailed comments greatly improved this manuscript. The study was funded by NERC grants
181 (NE/E015441/1; NE/G019657/1; NE/J010278/1) and an ERC grant (grant number 309249) to MAC.

182

183 **References**

184

- 185 1. Stockley, P. & Bro-Jørgensen, J. 2011 Female competition and its evolutionary consequences in
186 mammals. *Biological Reviews* **86**, 341–366. (doi:10.1111/j.1469-185X.2010.00149.x)
- 187 2. Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M. E., Røed, K. H., Nieminen, M. &
188 Weladji, R. B. 2004 Social rank in female reindeer (*Rangifer tarandus*): effects of body mass,
189 antler size and age. *J Zool* **263**, 365–372. (doi:10.1017/S0952836904005382)
- 190 3. Creel, S. R. & Creel, N. M. 1991 Energetics, reproductive suppression and obligate communal
191 breeding in carnivores. *Behav Ecol Sociobiol* **28**, 263–270.
- 192 4. Stearns, S. C. 1992 *The Evolution of Life Histories*. Oxford, UK: Oxford University Press.
- 193 5. Bruce, H. M. 1959 An exteroceptive block to pregnancy in the mouse. *Nature* **184**, 105.
194 (doi:10.1038/184105a0)
- 195 6. Mahady, S. J. & Wolff, J. O. 2002 A field test of the Bruce effect in the monogamous prairie vole
196 (*Microtus ochrogaster*). *Behav Ecol Sociobiol* **52**, 31–37. (doi:10.1007/s00265-002-0484-0)
- 197 7. Roberts, E. K., Lu, A., Bergman, T. J. & Beehner, J. C. 2012 A Bruce effect in wild geladas. *Science*
198 **335**, 1222–1225. (doi:10.1126/science.1213600)
- 199 8. Hodge, S. J., Bell, M. B. V., Mwanguhya, F., Kyabulima, S., Waldick, R. C. & Russell, A. F. 2009
200 Maternal weight, offspring competitive ability, and the evolution of communal breeding. *Behav*
201 *Ecol* **20**, 729–735. (doi:10.1093/beheco/arp053)
- 202 9. Cant, M. A., Nichols, H. J., Johnstone, R. A. & Hodge, S. J. 2014 Policing of reproduction by hidden
203 threats in a cooperative mammal. *PNAS* **111**, 326–330. (doi:10.1073/pnas.1312626111)
- 204 10. Cant, M. A., Vitikainen, E. & Nichols, H. J. 2013 Demography and Social Evolution of Banded
205 Mongooses-Chapter Six. *Adv Study Behav* **45**, 407–445. (doi:10.1016/B978-0-12-407186-
206 5.00006-9)
- 207 11. Jordan, N. R., Mwanguhya, F., Kyabulima, S., Ruedi, P. & Cant, M. A. 2010 Scent marking within
208 and between groups of wild banded mongooses. *J Zool* **280**, 72–83. (doi:10.1111/j.1469-
209 7998.2009.00646.x)
- 210 12. Cant, M. A. 2000 Social control of reproduction in banded mongooses. *Animal Behaviour* **59**,
211 147–158. (doi:10.1006/anbe.1999.1279)
- 212 13. Gilchrist, J. S. 2006 Female eviction, abortion, and infanticide in banded mongooses (*Mungos*
213 *mungo*): implications for social control of reproduction and synchronized parturition. *Behav.*
214 *Ecol.* **17**, 664–669. (doi:10.1093/beheco/ark012)
- 215 14. Marshall, H. H., Vitikainen, E. I. K., Mwanguhya, F., Businge, R., Kyabulima, S., Hares, M. C.,
216 Inzani, E., Kalema-Zikusoka, G., Mwesige, K., Nichols, H. J., Sanderson, J. L., Thompson, F. J., &
217 Cant, M. A. 2017 Lifetime fitness consequences of early-life ecological hardship in a wild mammal
218 population. *Ecol Evol* **57**, 1–13. (doi:10.1002/ece3.2747)
- 219 15. Cant, M.A., Hodge, S.J., Bell, M.B.V., Gilchrist, J.S. & Nichols, H.J. 2010 Reproductive control via

- 220 eviction (but not the threat of eviction) in banded mongooses. *Proc R Soc B* **277**, 2219–26. (doi:
221 10.1098/rspb.2009.2097)
- 222 16. Thompson, F. J., Marshall, H. H., Sanderson, J. L., Vitikainen, E. I. K., Nichols, H. J., Gilchrist, J. S.,
223 Young, A.J., Hodge, S.J. & Cant, M. A. 2016 Reproductive competition triggers mass eviction in
224 cooperative banded mongooses. *Proc R Soc B* **283**, 20152607. (doi: 10.1098/rspb.2015.2607)
- 225 17. Thompson, F.J., Marshall, H.H., Vitikainen, E. I. K. & Cant, M. A Causes and consequences of
226 intergroup conflict in cooperative banded mongooses. *Animal Behaviour*. Elsevier Ltd; 2017 Apr
227 1;126:31–40.
- 228 18. Marshall, H. H., Sanderson, J. L., Mwanghuya, F., Businge, R, Kyabulima, S., Hares, M. C., Inzani,
229 E., Kalema-Zikusoka, G., Mwesige, K., Thompson, F. J., Vitikainen, E. I. K. & Cant, M. A. 2016
230 Variable ecological conditions promote male helping by changing banded mongoose group
231 composition. *Behav Ecol* **27**:978–987 (doi: 10.1093/beheco/arw006)
- 232 19. Inzani, E. L., Marshall, H. H., Sanderson, J. L., Nichols, H. J., Thompson, F. J., Kalema-Zikusoka, G.,
233 Hodge, S. J., Cant, M. A. & Vitikainen, E. I. K. 2016 Female reproductive competition explains
234 variation in prenatal investment in wild banded mongooses. *Sci Rep* **6**, 20013–6.
235 (doi:10.1038/srep20013)
- 236 20. Inzani, E. L., Marshall, H. H., Thompson, F. J., Kalema-Zikusoka, G., Cant, M. A. & Vitikainen, E. I.
237 K. 2019 Data from: Spontaneous abortion as a response to reproductive conflict in the banded
238 mongoose. FigShare digital depository (<https://doi.org/10.6084/m9.figshare.5572408.v1>)
- 239 21. Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015 Fitting Linear Mixed-Effects Models Using
240 lme4. *J Stat Soft* **67**, 1–48. (doi:10.18637/jss.v067.i01)
- 241 22. R Core Team 2016 *R: A Language and Environment for Statistical Computing*. R Foundation for
242 Statistical Computing, Vienna, Austria.
- 243 23. Engqvist, L. 2005 The mistreatment of covariate interaction terms in linear model analyses of
244 behavioural and evolutionary ecology studies. *Animal Behaviour* **70**, 967–971.
245 (doi:10.1016/j.anbehav.2005.01.016)
- 246 24. Forstmeier, W., & Schielzeth, H. 2011 Cryptic multiple hypotheses testing in linear models:
247 Overestimated effect sizes and the winner's curse. *Behav. Ecol. Sociobiol.* **65**, 47–55.
248 (doi: 10.1007/s00265-010-1038-5)
- 249 25. Wasser, S. K. & Barash, D. P. 1983 Reproductive suppression among female mammals:
250 implications for biomedicine and sexual selection theory. *Q Rev Biol* **58**, 513–538.
- 251 26. Wauters, L. & Dhondt, A. A. 1989 Body Weight, Longevity and Reproductive Success in Red
252 Squirrels (*Sciurus vulgaris*). *J Anim Ecol* **58**, 637. (doi:10.2307/4853)
- 253 27. Cameron, R. D., Smith, W. T., Fancy, S. G., Gerhart, K. L. & White, R. G. 2011 Calving success of
254 female caribou in relation to body weight. *Can Zool* **71**, 480–486. (doi:10.1139/z93-069)
- 255 28. Nichols, H.J., Bell M.B.V., Hodge S.J. & Cant M.A 2012 Resource limitation moderates the
256 adaptive suppression of subordinate breeding in a cooperatively breeding mongoose. *Behav Ecol*
257 **23**:635–42. (doi: 10.1093/beheco/ars008)
- 258 29. Hanssen, S. A., Hasselquist, D., Folstad, I. & Erikstad, K. E. 2005 Cost of reproduction in a long-

- 259 lived bird: incubation effort reduces immune function and future reproduction. *Proc R Soc B* **272**,
260 1039–1046. (doi:10.1098/rspb.2005.3057)
- 261 30. Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I. & Monaghan, P. 2003 Age-specific
262 reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and
263 processes in a natural population. *J Anim Ecol* **72**, 765–776. (doi:10.1046/j.1365-
264 2656.2003.00750.x)
- 265 31. Gilchrist, J. S., Oтали, E. & Mwanguhya, F. 2004 Why breed communally? Factors affecting
266 fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*). *Behav*
267 *Ecol Sociobiol* **57**, 119–131. (doi:10.1007/s00265-004-0837-y)

For Review Only

268 FIGURES

269

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

275

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



