

1 **Female reproductive competition explains variation in prenatal**  
2 **investment in wild banded mongooses**

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26 **Abstract**

27 Female intrasexual competition is intense in cooperatively breeding species where offspring  
28 compete locally for resources and helpers. In mammals, females have been proposed to  
29 adjust prenatal investment according to the intensity of competition in the postnatal  
30 environment (a form of 'predictive adaptive response'; PAR). We carried out a test of this  
31 hypothesis using ultrasound scanning of wild female banded mongooses in Uganda. In this  
32 species multiple females give birth together to a communal litter, and all females breed  
33 regularly from one year old. Total prenatal investment (size times the number of fetuses)  
34 increased with the number of potential female breeders in the group. This relationship was  
35 driven by fetus size rather than number. The response to competition was particularly  
36 strong in low weight females and when ecological conditions were poor. Increased prenatal  
37 investment did not trade off against maternal survival. In fact we found the opposite  
38 relationship: females with greater levels of prenatal investment had elevated postnatal  
39 maternal survival. Our results support the hypothesis that mammalian prenatal  
40 development is responsive to the intensity of postnatal competition. Understanding  
41 whether these responses are adaptive requires information on the long-term consequences  
42 of prenatal investment for offspring fitness.

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45 **Key words:** Female reproductive conflict; prenatal investment; cooperative breeding;

46 predictive adaptive responses; intrasexual competition

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52 **Introduction**

53 Intrasexual competition is usually most severe among males, because males generally have  
54 higher variance in reproductive success than females<sup>1</sup>. This is manifested through  
55 conspicuous traits such as aggression and weaponry<sup>2</sup>. In cooperatively breeding species,  
56 female competition for reproduction is also intense, leading to overt and sometimes  
57 aggressive competition<sup>3</sup>. Because the cost of producing young is higher for females  
58 compared to males, theory suggests females will often resolve conflict without recourse to  
59 overt violence, for example, through the use of signals or threats<sup>4</sup>.

60

61 Recently, it has been suggested that females may compete over reproduction via maternal  
62 effects on offspring growth. In hyenas (*Crocuta crocuta*) and red squirrels (*Tamiasciurus*  
63 *hudsonicus*), for example, there is evidence that mothers prime their offspring to face  
64 competitive social environments through hormonal signaling (androgens or  
65 glucocorticoids[GCs]<sup>5,6</sup>). Experimental manipulations of population density in other taxa  
66 have also shown that offspring size is increased in response to adverse conditions (increased  
67 competition) rather than producing more offspring<sup>7-11</sup>. These effects can be interpreted as a  
68 form of 'predictive adaptive response' (PAR), whereby mothers (or, potentially, offspring  
69 themselves) are hypothesized to adjust the developmental trajectory to ensure a match  
70 between offspring phenotype and the environment experienced postnatally or in later life<sup>12-</sup>  
71 <sup>15</sup>. However, no study of wild mammals has directly tested whether mothers adjust prenatal  
72 investment according to the postnatal environment, and in particular the intensity of  
73 reproductive competition.

74

75 We carried out this test in a wild cooperatively breeding mammal, the banded mongoose  
76 (*Mungos mungo*)<sup>16</sup>. Banded mongooses are small diurnal carnivores which live in stable  
77 groups of ~20 adults plus pups. Multiple females (mean = 3.5 females, range 1 to 13) give

78 birth together in each breeding attempt, usually on the same day. Groups breed on average  
79 four times per year, experiencing considerable variation in environmental conditions (i.e.  
80 rainfall) which is strongly linked to invertebrate prey abundance<sup>17,18</sup>. Females compete  
81 postnatally using infanticide, but can escape infanticide through birth synchrony<sup>19</sup>. Offspring  
82 compete for access to lactating females and helpers (called “escorts”) who provision and  
83 protect pups after they emerge from the den. There is also evidence of prenatal maternal  
84 impacts on offspring competitiveness: mothers that are heavier at conception produce  
85 larger pups which have competitive advantage when competing for alloparental care;  
86 increasing pup survival<sup>20</sup>.

87

88 We carried out ultrasound scans on 59 breeding females from 8 groups of banded  
89 mongooses to test (1) whether mothers adjust prenatal investment in response to  
90 reproductive competition, and (2) the consequences of variation in prenatal investment for  
91 mothers and offspring.

92

### 93 **Methods**

#### 94 *Study site*

95 We studied a population of banded mongooses living on and around Mweya Peninsula,  
96 Queen Elizabeth National Park (QENP), Uganda (0°12'S, 27°54'E) between May 2000 and  
97 November 2013. For a detailed description of the climate, habitat and the population see  
98 Cant *et al.* 2013<sup>18</sup>. Rainfall data was provided by Uganda Institute of Ecology Meteorological  
99 Station and, later, using a rain gauge.

100

#### 101 *Study population*

102 All individuals in the population are known and individually marked with either colour-coded  
103 collars (7 g) or unique shave patterns (for details of trapping protocol and anesthesia are

104 given elsewhere; Ketamine<sup>21</sup>; Isoflurane<sup>22</sup>). The identity of breeding females was  
105 determined from changes in body shape, ultrasound scans and palpation<sup>23,24</sup>. Each group  
106 was visited daily to determine accurate parturition dates. Since parturition can be  
107 determined precisely but conception cannot, we calculated the age of fetuses  
108 retrospectively assuming an average 60 day gestation (the mean period between peak mate  
109 guarding and birth<sup>23</sup>). Group size and the number of females were counted as the total  
110 number of individuals or females over 1 year old in each group for each communal litter.  
111 Individuals are habituated to step onto electronic scales to determine an accurate weight  
112 which allows regular weighing events without capture. Female weight at the time of  
113 conception was calculated using the closest weighing event prior ( $\pm 10$  days from  
114 conception) to the estimated conception date; if possible weights for all females within the  
115 same group came from the same weighing event.

116

#### 117 *Measuring fetus size and number*

118 Number of fetuses was counted under anesthesia by palpating the abdomen, and a cross-  
119 sectional ultrasound scan of each fetus was obtained using an ultrasound scanner (SIUI CTS-  
120 900V, UK) and ultrasound gel (Anagel, UK). Trapping females within the last few weeks of  
121 pregnancy was avoided and most trapping was conducted 3-4 weeks after oestrus. Previous  
122 study has shown no adverse effects of trapping and palpating pregnant females<sup>24</sup>. The age  
123 of the fetus at the time of the ultrasound scan was calculated retrospectively from the litter  
124 birth date and the scan date, assuming a gestation length of 60 days (average female  
125 gestation length<sup>23</sup>).

126

127 We used the cross-sectional area ( $\text{mm}^2$ ) of each fetus as measured from the ultrasound  
128 images as an estimate of fetus size. Fetuses were measured on average at  $30 \pm 7$  (mean  $\pm$  sd)  
129 days post conception when they are still roughly spherical in shape to minimize noise arising

130 from different angles of the scan cross-section. The outline of a fetus was identified by the  
131 black pixilation of the fluid-filled amniotic sac and the white pixilation of the womb tissue  
132 and the amniotic sac membrane around the fetus. The mean of two perpendicular  
133 measurements of the diameter were taken using the computer software Image J (1.47c<sup>25</sup>)  
134 and used to calculate the elliptical area of the fetus (see Figure 1).

135

### 136 *Statistics*

137 We analyzed fetus sizes and the number of fetuses using general linear mixed models  
138 (LMMs) and generalized linear mixed models (GLMMs) in R version 3.1.0 using lme4 package  
139 R1.1-6<sup>26,27</sup>. GLMMs had either a poisson error structure with log-link function or binomial  
140 error structure with logit link function. Female, litter and group identities were included as  
141 random factors in analyses to account for the repeated sampling. Fixed terms included were  
142 female weight at conception, female age (months), number of adult females present in the  
143 group, group size and the total rainfall during gestation (ml). Because groups were trapped  
144 at different stages of pregnancy, fetus age (days) was included as a covariate when analyzing  
145 fetus size. Correlations between variables fitted in the same models as fixed effects were  
146 lower than the levels indicated by Freckleton<sup>28</sup> to cause model fitting issues such as variance  
147 inflation in effect estimates (max  $r = 0.48$ ). We obtained a minimal model via sequential  
148 removal of least significant factors, starting with 2-way interactions. Each factor was then  
149 added back into the minimum model in order to confirm removal was not contingent on the  
150 order of removal<sup>29</sup>.

151

152 To investigate if mothers adjust their prenatal investment in response to reproductive  
153 competition we estimated total prenatal investment by multiplying the average fetus size by  
154 the number of fetuses carried for each pregnancy. Variation in prenatal investment could be  
155 due to individual female adjustment in response to competition (a within-individual effect)

156 or be the result of consistent differences between individuals. We tested the relative  
157 importance of within- versus between-individual effects using the method described by van  
158 de Pol & Wright<sup>30</sup>, which separates out the effect sizes in the fitted model attributable to  
159 variation within versus between individuals. To test the consequences of variation in  
160 prenatal investment for mothers and offspring we focused on pup survival to 3 months (y/n)  
161 using logistic regression, and pup weight (controlled age at capture <90 days) as well as  
162 female reproductive effort and survival. Maternity assignments for pups were based on 43  
163 microsatellite loci as described in Sanderson *et al.*<sup>31</sup>. As individual fetus scans cannot be  
164 matched to pups an average fetus size was used in these analyses. Relative fetus size was  
165 calculated as the average fetus size in each female's litter relative to average fetus size for all  
166 females within a breeding attempt. We tested whether prenatal investment predicted  
167 female participation in the next group litter (y/n) using a GLMM with binomial errors. We  
168 tested whether there was a trade-off between current investment in reproduction and  
169 female survival using Cox regression with backward selection of terms (Wald Chi-square).  
170 This analysis included total group size, number of females, and the average fetus size and  
171 number of fetuses as predictors, and to avoid repeat sampling used only the last  
172 reproductive event on record for each female. This analysis was conducted in SPSS  
173 21.0.0.0<sup>32</sup>.

174

#### 175 *Ethical Statement*

176 Research was carried out under a permit from Uganda Wildlife Authority (UWA) and Uganda  
177 National Council for Science and Technology (UNCST), and all methods approved by UWA,  
178 UNCST and the Ethical Review panel of the University of Exeter. All methods were carried  
179 out in accordance with the Guidelines for the Treatment of Animals in Behavioural Research  
180 and Teaching published by the Association for the Study of Animal Behaviour<sup>33</sup>.

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182

183 **Results**

184 *(1) Do mothers adjust prenatal investment in response to reproductive competition?*

185 The total prenatal investment (fetus size x number of fetuses carried) of females increased  
186 with the number of other adult females in the group during pregnancy, and with a female's  
187 weight at conception (LMM, number of females,  $\chi^2_1=5.65$ ,  $N=142$ ,  $P=0.017$ , female weight:  
188 (LMM,  $\chi^2_1=12.60$ ,  $N=142$ ,  $P<0.001$ ). This relationship was driven by fetus size rather than  
189 number: mean fetus size increased with the number of females in the group; increased more  
190 steeply in lighter females, and in breeding attempts featuring lower rainfall (LMM, 2 way  
191 interaction of female number with: weight,  $\chi^2_1=4.23$ ,  $N=360$  scans,  $P=0.040$ ; rainfall,  $\chi^2_1$   
192  $=4.91$ ,  $N=360$ ,  $P=0.027$ ; Figure 2). Neither total group size nor female age influenced fetus  
193 size (see Supplementary Information (SI) Table S1). Within-female variation was a better  
194 predictor of fetal size in response to reproductive competition than between-female  
195 variation (LMM, within-female variation,  $\chi^2_1=4.51$ ,  $N=360$ ,  $P=0.034$ , between-female  
196 variation,  $\chi^2_1=3.38$ ,  $N=360$ ,  $P=0.066$ ; SI Table S2). The number of fetuses was only  
197 influenced by female age, peaking at 4 years of age before declining (GLMM poisson,  $\chi^2_1$   
198  $=10.36$ ,  $N=361$ ,  $P=0.001$ ). There was no significant relationship between fetus size and the  
199 number of fetuses (LMM,  $\chi^2_1=1.03$ ,  $N=581$ ,  $P=0.31$ ). Thus individual females produced  
200 larger fetuses, but no fewer of them, when faced with competition from other female  
201 breeders.

202

203 *(2) What are the consequences of variation in prenatal investment for mothers and*  
204 *offspring?*

205 Female reproductive success (number of assigned pups at emergence) increased with the  
206 number of fetuses during gestation, (GLMM poisson,  $\chi^2_1=5.44$ ,  $N=153$  females,  $P=0.02$ ; SI  
207 Table S3). However, larger fetuses did not translate into a greater number of assigned pups



208 (GLMM poisson,  $\chi^2_1=0.76$ , N =151 pups,  $P =0.38$ ). Fetus size also did not influence pup  
209 weight at 3 months (LMM,  $\chi^2_1=0.37$ , N =115 pups,  $P =0.54$ ; SI Table S4), nor survival to 3  
210 months (GLMM, binomial,  $\chi^2_1=0.12$ , N =131 pups,  $P =0.72$ ). Relative fetus size (measured  
211 relative to other scanned females in a particular breeding attempt) also did not predict a  
212 female's share of total group reproductive success (GLMM binomial,  $\chi^2_1=1.14$ , N =153,  $P$   
213 =0.29) nor pup survival to 3 months (GLMM binomial,  $\chi^2_1=1.09$ , N =131,  $P =0.30$ ). Thus, we  
214 found no evidence that the production of larger fetuses translated into improved success in  
215 postnatal reproductive competition, at least in the short term.

216

217 Finally, we found no evidence of a cost of prenatal investment to mothers in terms of future  
218 survival or reproduction. In fact, higher total prenatal investment was associated with higher  
219 post-scan survival of mothers (Cox regression, Wald  $\chi^2_1=6.57$ , N =360,  $P =0.010$ ; Figure 3).  
220 Again this relationship was driven by fetus size rather than number (SI Table S5). Females  
221 that invested more prenatally were not less likely to reproduce in the next breeding attempt  
222 (GLMM binomial,  $\chi^2_1=0.35$ , N =164,  $P =0.061$ ; SI Table S6). Thus we found no evidence of a  
223 survival cost to mothers of elevated prenatal investment, nor did mothers compensate for  
224 high prenatal investment by reducing reproductive effort in the next breeding attempt.

225

## 226 **Discussion**

227 Female banded mongooses produced larger, but no fewer, offspring when there were more  
228 adult females in the group. Since all adult females breed in most breeding attempts, this is  
229 consistent with the hypothesis that females strategically up-regulate prenatal investment in  
230 the face of elevated postnatal reproductive competition. Such responses may be  
231 particularly likely to evolve in breeding systems where females co-breed regularly. Females  
232 showed steeper increases in prenatal investment when ecological conditions were harsh,  
233 and when they were in relatively poor body condition, two factors which are expected to

234 exacerbate the intensity of postnatal competition among offspring<sup>34</sup>. We found no evidence  
235 that increased prenatal investment incurred future costs to females in terms of reproduction  
236 or survival. On the contrary, females that invested more prenatally showed improved future  
237 survival (Figure 3). A positive relationship between current reproductive investment and  
238 future survival is expected where females vary considerably in quality or access to resources,  
239 since high quality females may be able to divert more resources to offspring production  
240 without compromising their somatic function (the 'big house big car' effect<sup>35,36</sup>).

241

242 Increasing fetus size in response to increased social competition is a subtle way in which  
243 females could compete over reproduction within social groups without risking the costs of  
244 fighting or killing offspring<sup>3,4</sup>. However, we found no detectable benefit (in terms of short-  
245 term reproductive success) associated with increased investment in fetus size. Neither  
246 absolute fetus size nor fetus size relative to other co-breeders predicted the number of  
247 offspring that survived to emerge from the den. The lack of any detectable advantage to  
248 elevated prenatal investment is surprising, and may reflect a high level of noise associated  
249 with high pup mortality due to intra- or intergroup infanticide and predation<sup>18,19</sup>. It may also  
250 be that the benefits of increased prenatal investment are realised later in the life of the  
251 offspring. Studies of human famine and laboratory rodents, for example, suggest that early  
252 life environments can influence health and fitness across the lifespan, not just in the short  
253 term<sup>13</sup>.

254

255 Our findings offer an interesting contrast to studies of social birds and fish, in which  
256 dominant females produce smaller eggs or a larger number of eggs when there are many  
257 helpers in the group<sup>37-40</sup>. In banded mongooses, all group members contribute to rearing  
258 young, but prenatal investment did not vary with the potential number of helpers  
259 (measured by total group size). Our findings suggest that the intensity of reproductive

260 competition, rather than the availability of helpers, is the main determinant of variation in  
261 prenatal investment in this species. Larger pups have better access to adult group members  
262 who provide parental care and, upon emergence, aggressively defend access to the best  
263 helpers or 'escorts'<sup>41</sup>. Where postnatal competition among offspring has characteristics of  
264 contest competition, the best response to competition will be to invest more resources per  
265 offspring prenatally, rather than to produce more of them<sup>42,43</sup>. Producing a larger number of  
266 offspring could also bring benefits, but at the unavoidable cost of intensified competition  
267 among littermates.

268

269 Our study complements previous studies which suggest that mothers use hormones to  
270 influence the development of their offspring *in utero* to improve their success in the  
271 postnatal environment, a form of PAR<sup>13,44</sup>. The PAR hypothesis has been criticized because  
272 long term forecasts of environmental conditions are inherently unreliable<sup>14,15</sup>. In cooperative  
273 breeders, however, the quality of the postnatal environment is largely determined by the  
274 number of breeders competing for reproduction and the number of helpers available to  
275 offspring. These features of social groups remain stable over the course of offspring  
276 development, from gestation to nutritional independence, so are highly predictable.  
277 Cooperative birds and mammals, including humans, are thus likely candidates to evolve  
278 PARs. We found evidence that female banded mongooses respond to reproductive  
279 competition by adjusting prenatal investment, consistent with the PAR hypothesis, but we  
280 did not find evidence that this response is adaptive. To test the PAR hypothesis fully will  
281 require study of the consequences of variation in prenatal investment across the lifetime of  
282 offspring in animals exposed to natural predators and pathogens.

283

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291

292 **Author contributions:**

293 MC, EV, SH and EI designed research; EV and SH collected data; MC and GK supervised field  
294 project; EI, FT HM and EV analysed data; HN and JS carried out genetic analysis; MC, EI and  
295 EV drafted the paper; all authors contributed to the final version.

296

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399 **Figure legends:**

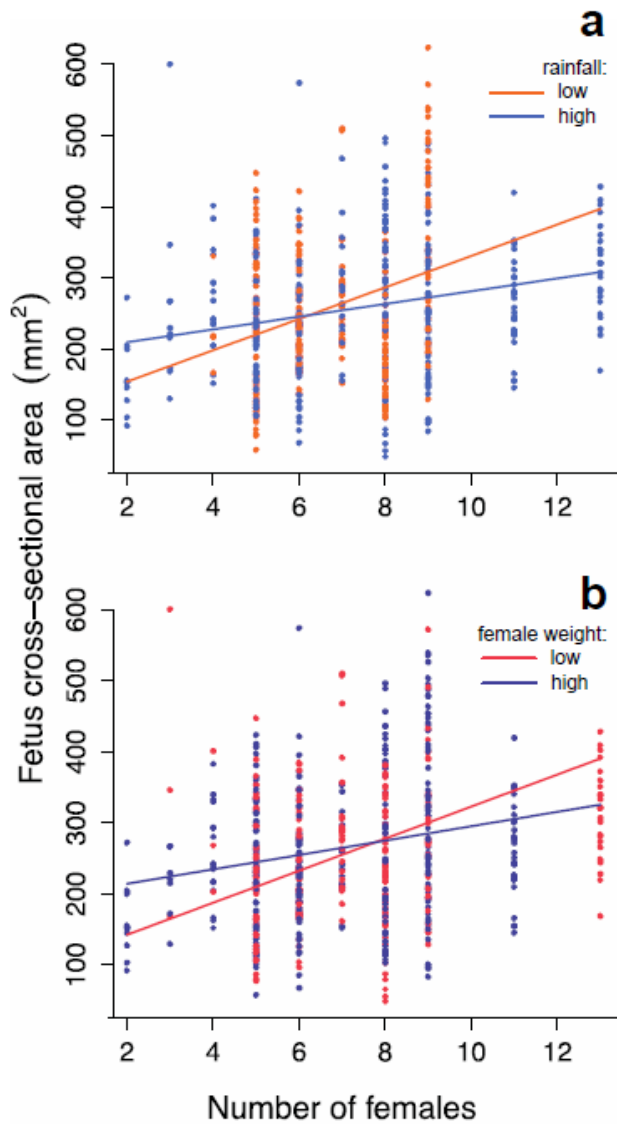


400

401 **Figure 1.** Cross-sectional ultrasound scan of individual fetus with 2 perpendicular

402 measurements A and B used to calculate the cross-sectional area  $(A/2 \times B/2 \times \pi)$ .

403

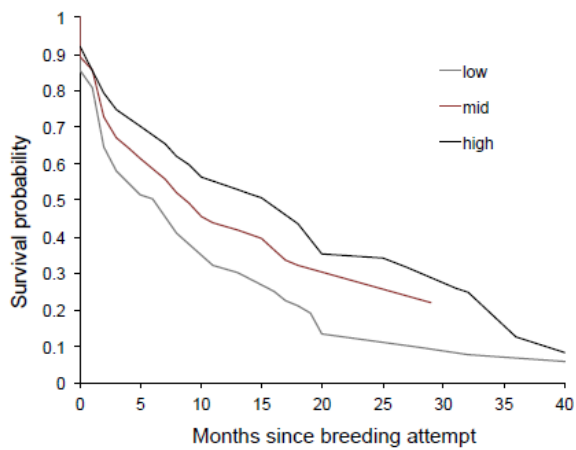


404

405 **Figure 2.** Variation in prenatal investment as a function of the number of adult females in  
 406 the group at conception. (a) Fetus cross-sectional area increases more sharply when rainfall  
 407 is low (orange line) compared to high (light blue line); (b) Lighter females (red line) show the  
 408 steepest increase in fetus size with female number compared to heavier females (dark blue  
 409 line). Female weight (mean±sd =1447±201g) and rainfall (mean±sd=128.3±40.9ml) are  
 410 continuous variables that have been categorized for illustrative purposes using the 25% and  
 411 75% quartiles.

412

413



414

415 **Figure 3.** Maternal survival as a function of prenatal investment. Mothers that invested

416 more prenatally survived longer. Fetus size (mean±sd =247.90±100.88mm<sup>2</sup>) has been

417 categorized for illustrative purposes using the 25% (179.54mm<sup>2</sup>), mean and 75%

418 (319.09mm<sup>2</sup>) quartiles.

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