1 **Female reproductive competition explains variation in prenatal**

2 **investment in wild banded mongooses**

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6 Emma L. Inzani, Harry H. Marshall, Jennifer L. Sanderson, Hazel J. Nichols, Faye J. Thompson,

7 Gladys Kalema-Zikusoka, Sarah J. Hodge, Michael A. Cant* & Emma I.K. Vitikainen

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10 Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall TR10

11 8FE

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14 *Corresponding author: m.a.cant@exeter.ac.uk

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Abstract

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

Introduction

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

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

We carried out this test in a wild cooperatively breeding mammal, the banded mongoose (*Mungos mungo*)[16]. Banded mongooses are small diurnal carnivores which live in stable 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[17,18]. Females compete

81   postnatally using infanticide, but can escape infanticide through birth synchrony[19]. 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[20].

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[18]. 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[21]; Isoflurane[22]). The identity of breeding females was

105   determined from changes in body shape, ultrasound scans and palpation[23,24]. 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[23]). 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 (±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 palpitating 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 palpitating pregnant females[24]. 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[23]).

126

127   We used the cross-sectional area (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 ± 7 (mean ± sd)

129   days post conception when they are still roughly spherical in shape to minimize noise arising

5

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[25])

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[26,27]. 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[28] 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[29].

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[30], 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.*[31]. 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[32].

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[33].

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182

Results

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

The total prenatal investment (fetus size x number of fetuses carried) of females increased

with the number of other adult females in the group during pregnancy, and with a female's

weight at conception (LMM, number of females, χ^2_1 =5.65, N =142, *P* =0.017, female weight:

(LMM, , χ^2_1 =12.60, N =142, *P* < 0.001). This relationship was driven by fetus size rather than

number: mean fetus size increased with the number of females in the group; increased more

steeply in lighter females, and in breeding attempts featuring lower rainfall (LMM, 2 way

interaction of female number with: weight, χ^2_1 =4.23, N =360 scans, *P* = 0.040; rainfall, χ^2_1

=4.91, N =360, *P* =0.027; Figure 2). Neither total group size nor female age influenced fetus

size (see Supplementary Information (SI) Table S1). Within-female variation was a better

predictor of fetal size in response to reproductive competition than between-female

variation (LMM, within-female variation, χ^2_1 =4.51, N =360, *P* =0.034, between-female

variation, χ^2_1 =3.38, N =360, *P* =0.066; SI Table S2). The number of fetuses was only

influenced by female age, peaking at 4 years of age before declining (GLMM poisson, χ^2_1

=10.36, N =361, *P* =0.001). There was no significant relationship between fetus size and the

number of fetuses (LMM, χ^2_1 =1.03, N =581, *P* =0.31). Thus individual females produced

larger fetuses, but no fewer of them, when faced with competition from other female

breeders.

(2) What are the consequences of variation in prenatal investment for mothers and

offspring?

Female reproductive success (number of assigned pups at emergence) increased with the

number of fetuses during gestation, (GLMM poisson, χ^2_1 =5.44, N =153 females, *P* =0.02; SI

Table S3). However, larger fetuses did not translate into a greater number of assigned pups

8

208   (GLMM poisson, χ^2_1 =0.76, N =151 pups, P =0.38). Fetus size also did not influence pup

209   weight at 3 months (LMM, χ^2_1 =0.37, N =115 pups, P =0.54; SI Table S4), nor survival to 3

210   months (GLMM, binomial, χ^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, χ^2_1 =1.14, N =153, P

213   =0.29) nor pup survival to 3 months (GLMM binomial, χ^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 χ^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, χ^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

9

234   exacerbate the intensity of postnatal competition among offspring[34]. 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[35,36]).

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[3,4]. 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[18,19]. 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[13].

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[37-40]. 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'[41]. 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[42,43]. 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[13,44]. The PAR hypothesis has been criticized because

272   long term forecasts of environmental conditions are inherently unreliable[14,15]. 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.

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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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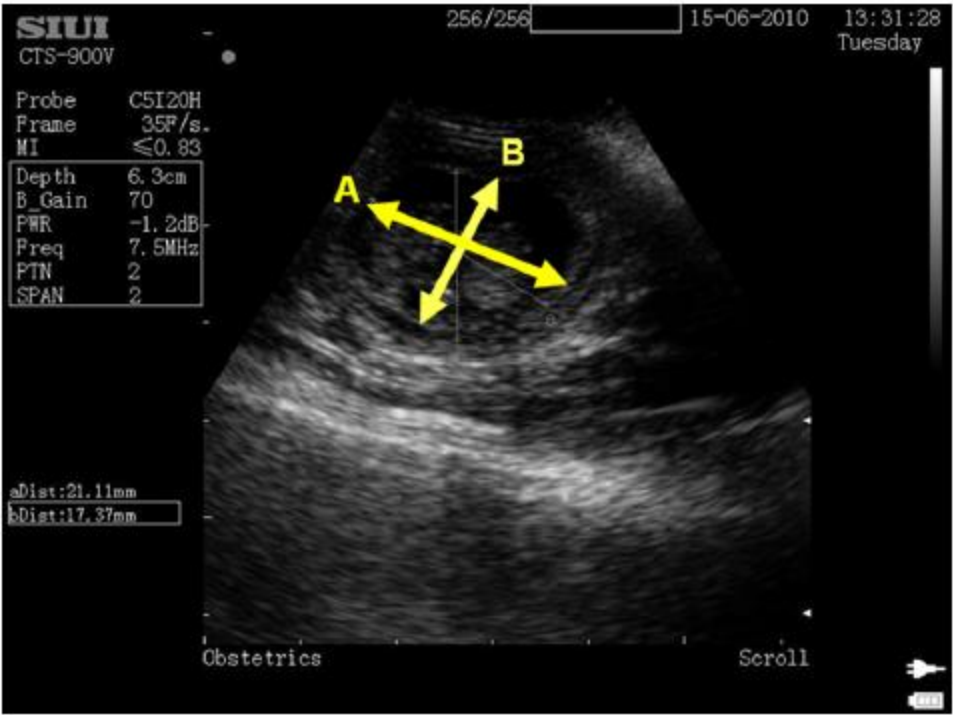397
398

Figure legends:

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

measurements A and B used to calculate the cross-sectional area (A/2 x B/2 x π).
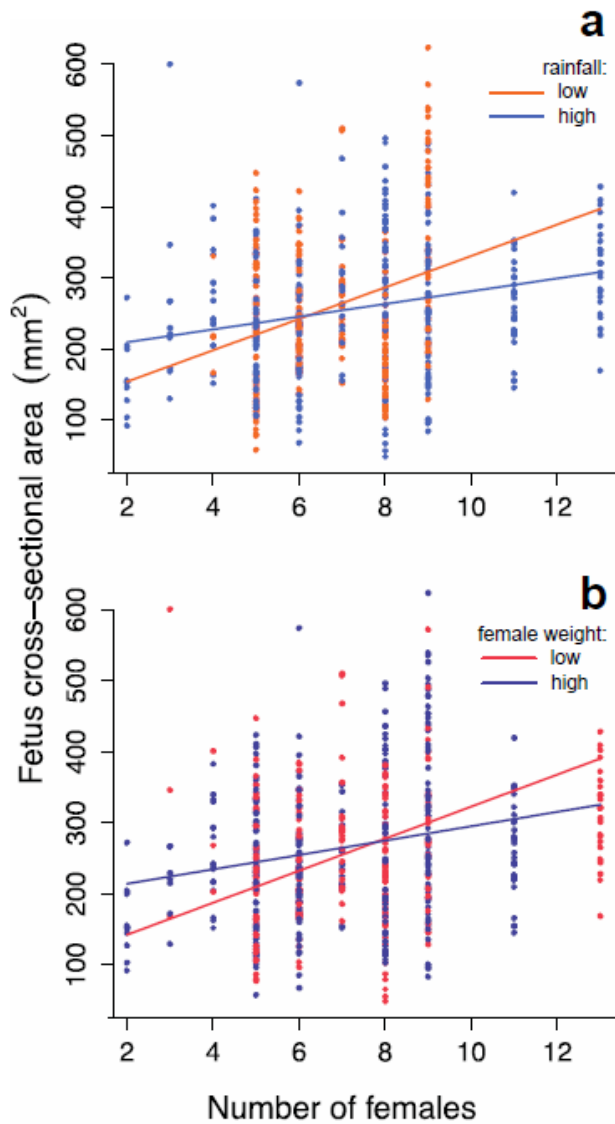
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Figure 2. Variation in prenatal investment as a function of the number of adult females in

the group at conception. (a) Fetus cross-sectional area increases more sharply when rainfall

is low (orange line) compared to high (light blue line); (b) Lighter females (red line) show the

steepest increase in fetus size with female number compared to heavier females (dark blue

line). Female weight (mean±sd =1447±201g) and rainfall (mean±sd=128.3±40.9ml) are

continuous variables that have been categorized for illustrative purposes using the 25% and
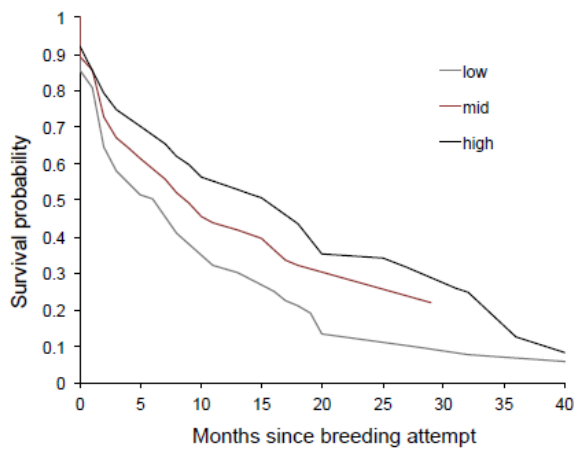
75% quartiles.

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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^2) has been

417 categorized for illustrative purposes using the 25% (179.54mm^2), mean and 75%

418 (319.09mm^2) quartiles.

419

420