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Lifetime fitness consequences of early-life ecological hardship in a wild mammal population

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1 **Lifetime fitness consequences of early-life ecological**
2 **hardship in a wild mammal population**

3

4 Harry H. Marshall^{1,*}, Emma I. K. Vitikainen¹, Francis Mwanguhya², Robert Businge², Solomon
5 Kyabulima², Michelle C. Hares¹, Emma Inzani¹, Gladys Kalema-Zikusoka³, Kenneth Mwesige², Hazel J.
6 Nichols⁴, Jennifer L. Sanderson¹, Faye J. Thompson¹ and Michael A. Cant¹

7

8 ¹ Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall, TR10 9FE, UK

9 ² Banded Mongoose Research Project, Queen Elizabeth National Park, Kasese District, Uganda

10 ³ Conservation Through Public Health, Entebbe, Uganda

11 ⁴ School of Natural Science and Psychology, Liverpool John Moores University, Liverpool, L3 3AF, UK

12

13 *Corresponding author: Harry H. Marshall, Centre for Ecology and Conservation, University of
14 Exeter, Penryn Campus, Cornwall, TR10 9FE, UK. Tel.: +44 (0)1326 256274. Fax: +44 (0)1326 371859.

15 E-mail: h.marshall@exeter.ac.uk

16

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18

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20

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23 **Abstract**

24

25 1. Early-life ecological conditions have major effects on survival and reproduction. Numerous
26 studies in wild systems show fitness benefits of good quality early-life ecological conditions
27 ('silver spoon' effects).

28 2. Recently, however, some studies have reported that poor quality early-life ecological
29 conditions are associated with later-life fitness advantages and that the effect of early-life
30 conditions can be sex-specific. Furthermore, few studies have investigated the effect of the
31 variability of early-life ecological conditions on later-life fitness.

32 3. Here we test how the mean and variability of early-life ecological conditions affect the
33 longevity and reproduction of males and females using 14 years of data on wild banded
34 mongooses (*Mungos mungo*).

35 4. Males that experienced highly variable ecological conditions during development lived
36 longer and had greater lifetime fitness, while those that experienced poor early-life
37 conditions lived longer but at a cost of reduced fertility. In females there were no such
38 effects.

39 5. Our study suggests that exposure to more variable environments in early life can result in
40 lifetime fitness benefits whereas differences in the mean early-life conditions experienced
41 mediates a life history trade-off between survival and reproduction. It also demonstrates
42 how early-life ecological conditions can produce different selection pressures on males and
43 females.

44 **Introduction**

45 What does not kill me makes me stronger. Friedrich Nietzsche (1889), *Twilight of the Idols*

46

47 The principle that a good start in life can have many advantages later on is well-recognised in
48 ecology and evolution (Lindström 1999; Monaghan 2008). Indeed, numerous ecological studies have
49 shown that favourable early-life ecological conditions have positive ‘silver-spoon’ effects on
50 individuals’ later-life survival (Reid *et al.* 2003; Van de Pol *et al.* 2006; Cartwright *et al.* 2014; Wong &
51 Kölliker 2014) and reproduction (Nussey *et al.* 2007; Millon *et al.* 2011; Hayward, Rickard & Lummaa
52 2013; Douhard *et al.* 2014; Balbontin & Moller 2015).

53

54 Recently however, there has been growing evidence that the effect of early-life ecological
55 conditions on later-life fitness is not so straightforward. First, some studies have found indications
56 that poor – rather than good – early-life ecological conditions can have favourable effects on fertility
57 or survival in later life (Wilkin & Sheldon 2009; Garratt *et al.* 2015; Rubenstein *et al.* 2016). For
58 example, male superb starlings (*Lamprotonis superbus*) which hatched in a low prebreeding rainfall
59 year (an indicator of poor ecological conditions in this system) had lower rates of DNA methylation
60 which in turn was associated with a greater probability of breeding in later life (Rubenstein *et al.*
61 2016). There is also evidence that, despite an overall positive effect of favourable early-life ecological
62 conditions on fitness, cohorts of male great tits (*Parus major*) born in poor years live longer and have
63 greater reproductive success (Wilkin & Sheldon 2009). It has been proposed, but not tested, that this
64 relationship could arise because of increased maternal investment during harsh periods (Rubenstein
65 *et al.* 2016), or stronger selection during periods of hardship (Wilkin & Sheldon 2009; Garratt *et al.*
66 2015). These findings may also relate to a widely recognised phenomenon in laboratory animals and
67 humans that dietary restriction, without malnutrition, has beneficial effects such as increased
68 longevity (e.g. McCay, Crowell & Maynard 1935; Fontana *et al.* 2004; Masoro 2006; Colman *et al.*
69 2009; Zhang *et al.* 2013). Second, there is evidence that individuals can adjust life history trajectories

70 to achieve similar lifetime fitness, despite differing early life conditions (Gluckman, Hanson &
71 Spencer 2005; Taborsky 2006; Monaghan 2008; Nettle & Bateson 2015). For example, Seychelles
72 warblers (*Acrocephalus sechellensis*) born into unfavourable ecological conditions have shorter
73 lifespans, but also start to breed earlier with no difference in the length of the reproductive lifespan
74 compared to individuals born during periods of abundance (Hammers *et al.* 2013; Cartwright *et al.*
75 2014). Third, early-life effects in later life are often manifested in one sex but not the other (Kruuk *et al.*
76 1999; Wilkin & Sheldon 2009; Millon *et al.* 2011; Ancona & Drummond 2013; Wong & Kölliker
77 2014; Garratt *et al.* 2015; Rubenstein *et al.* 2016). In red deer (*Cervus elaphus*), females that
78 experience lower temperatures in early life have reduced reproductive success, but males show no
79 such relationship (Kruuk *et al.* 1999). In the European earwig (*Forficula auricularia*), low food
80 availability during development reduces lifetime reproductive success in females but not males
81 (Wong & Kölliker 2014).

82

83 Ecological conditions in a given space and time can be characterised by their average value,
84 and also by how much they vary around this average. Despite this, previous studies have (implicitly
85 or explicitly) tended to focus on the effect of the average early-life ecological conditions on later-life,
86 and not considered the effect of their variability. Yet, environmental variability can have profound
87 implications on ecological and evolutionary processes (e.g. Botero *et al.* 2014). For example,
88 theoretical work has shown that direction and strength of the correlation between maternal and
89 offspring phenotype, i.e. the maternal effect, should be affected by the magnitude and predictability
90 of the environment's fluctuations (Hoyle & Ezard 2012; Kuijper & Hoyle 2015). There are also
91 instructive examples from studies of human medicine and psychology suggesting that the variability
92 of conditions experienced during early-life may have important later-life implications. First, exposure
93 to a narrower variety of pathogens during childhood can impair the development of the immune
94 system, resulting in inappropriate immune responses in adulthood and the dramatic increase in
95 allergic diseases observed in Western societies over the last few decades (the "hygiene hypothesis":

96 Strachan 1989, 2000; Wills-Karp, Santeliz & Karp 2001; Yazdanbakhsh, Kremsner & van Ree 2002).
97 Second, exposure to a wide variety of psychological stressors during childhood may have important
98 effects on aspects of cognitive development, with evidence that a stressful childhood, while
99 impinging on health and wellbeing, may also produce adults who perform better in cognitive tasks
100 which involve an element of stress (Frankenhuis & de Weerth 2013; Frankenhuis, Panchanathan &
101 Nettle 2015).

102

103 In this study we test the sex-specific effects of the mean and variability of early-life
104 ecological conditions on later-life survival and reproductive success in wild banded mongooses
105 (*Mungos mungo*, Fig. 1). We use a 14 year data set describing ecological conditions (measured by
106 annual rainfall) and mongoose body condition, survival and reproduction to address two questions.
107 First, how do early-life ecological conditions influence early-life social environment, body condition
108 and survival? This question is stimulated by previous studies which have argued that the effects of
109 early-life ecological conditions on later life may result from changes in the amount of care received
110 during development (Rubenstein *et al.* 2016) or the quality of offspring that survive to adulthood
111 (Wilkin & Sheldon 2009; Garratt *et al.* 2015). Second, how do early-life ecological conditions affect
112 lifetime survival and reproductive success? We test whether the effects of both the mean and
113 variability of early-life ecological conditions on later-life survival and reproduction represent a classic
114 silver-spoon effect (Reid *et al.* 2003; Van de Pol *et al.* 2006; Nussey *et al.* 2007) or support more
115 recent indications that poor early-life conditions can be advantageous (Wilkin & Sheldon 2009;
116 Garratt *et al.* 2015; Rubenstein *et al.* 2016). We also test whether the later-life effects we find (i) are
117 due to a life-history trade-off between survival and reproduction (Hammers *et al.* 2013; Cartwright
118 *et al.* 2014) and (ii) differ between males and females (Kruuk *et al.* 1999; Wilkin & Sheldon 2009;
119 Millon *et al.* 2011).

120

121

122 **Materials and Methods**

123 **Study System**

124 We conducted our study between September 1999 and March 2014 on a long-term study population
125 of banded mongooses on the Mweya Peninsula in Queen Elizabeth National Park, Uganda (0°12'S,
126 27°54'E). Cant et al. (2013; 2016), and references therein, provide detailed descriptions of our study
127 site and banded mongoose biology. Here, we provide information about both specific to this study.

128

129 Banded mongooses (Fig. 1) are diurnal carnivores (<2kg) that live in stable, mixed-sex groups
130 of around 10 to 30 individuals and whose diet mainly consists of small invertebrates (Rood 1975).
131 Individuals sexually mature around the age of 1 year old (Cant *et al.* 2016) and all individuals within a
132 group reproduce to some extent, though contributions to reproduction are skewed towards older
133 individuals (Nichols *et al.* 2010, 2012). Their average lifespan is around 3.5 years (males = 42 months,
134 females = 38 months, max = 149 months, Cant *et al.* 2016) and survival rates are constant across all
135 ages (Cant *et al.* 2016; Marshall *et al.* 2016). At our equatorial study site reproduction occurs all year
136 round and is not synchronised between groups. Reproduction is, however, highly synchronised
137 within groups: around four times per year, all pregnant females in a group give birth in an
138 underground den to a large communal litter, usually on the same morning (Cant 2000; Hodge, Bell &
139 Cant 2011). Pups remain in the den for approximately their first 30 days, after which they move with
140 the rest of the group and are cared for by adult 'escorts' for around a further 60 days (Gilchrist 2004;
141 Gilchrist & Russell 2007). We are able to individually recognise the mongooses in our study
142 population using unique hair-shave patterns or coloured collars. Radio collars weighing 26 to 30 g
143 (Sirtrack Ltd, Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd, Dorset, UK) are
144 fitted to one to two individuals in each group to allow them to be located. Most individual are
145 trained to step onto an electronic balance in return for a small milk reward. Two groups have access
146 to human refuse (Otali & Gilchrist 2004) and so were excluded from this study (and also a previous

147 complementary study investigating the effects of ecological conditions during adulthood, Marshall *et*
148 *al.* 2016).

149

150 **Data Collection**

151 *Ecological conditions*

152 We collected climate data daily from a weather station situated centrally at our study site. We
153 selected rainfall as our measure of ecological conditions since it is relatively variable at Mweya
154 (mean monthly rainfall \pm s.d. = 61 ± 41 mm, $n = 152$ months) whilst temperature is reasonably
155 constant (mean of monthly mean maximum daily temperature \pm s.d. = 29.5 ± 1.5 °C, $n = 162$ months)
156 (Marshall *et al.* 2016). We defined an individual's 'early life' to be its first year of development based
157 on growth and age at sexual maturity. Banded mongooses' major growth phase occurs in their first
158 year (zone i in Fig. 2) and one year is also the approximate age at which females become regular
159 breeders and males first obtain paternity (Cant *et al.* 2016). In addition, the pattern of rainfall at our
160 study site operates over a 12 month period: two wet seasons, one shorter (March-May) and one
161 longer (August-December), divided by two dry seasons (Jan-Feb and June-July; Fig. 3a, Marshall *et al.*
162 2016). Consequently we used the mean and standard deviation of the monthly rainfall in
163 mongooses' first year of life as our measure of the mean and variability of early-life ecological
164 conditions (Fig. 3b). At our study site the mean and standard deviation of monthly rainfall within a
165 year are not correlated (Pearson's $r = 0.11$, $p = 0.73$, $n = 13$ years). This standard deviation is,
166 however, positively correlated with the maximum monthly rainfall in the year ($r = 0.91$, $p < 0.001$, n
167 $= 13$) and negatively correlated with the minimum rainfall in the year ($r = -0.71$, $p = 0.007$, $n = 13$).
168 Thus, a high standard deviation in monthly rainfall over a 12-month period indicates a period with
169 greater extremes of low and high monthly rainfall. As you would expect, mean monthly rainfall in a
170 year is moderately positively correlated with both the minimum ($r = 0.46$, $p = 0.12$, $n = 13$) and
171 maximum ($r = 0.32$, $p = 0.28$, $n = 13$) monthly rainfall.

172

173 We further explored the ecological relevance of rainfall at our study site by measuring its
174 effect on invertebrates (banded mongooses' predominant food source; Rood 1975) using monthly
175 pitfall trap transects set between August 2013 and February 2015. At the end of each month we set
176 pitfall traps on 40-m transects at four randomly chosen locations. Each transect consisted of five
177 pitfall traps set at 10-m intervals along the transect line. Pitfall traps consisted of smooth-side plastic
178 drinking cups (9 cm tall with circular tops 7 cm in diameter) buried so that their rims were flush with
179 the level of the ground. These were filled with water to c.3 cm deep and a drop of detergent to
180 break the water's surface tension and ensure captured invertebrates fell into the water rather than
181 being caught on its surface. The traps were collected after 24 hours and their contents were sieved
182 out and frozen in ziplock bags in a -20°C freezer. At a later date the contents of the pitfall traps in
183 each transect were then sorted and the invertebrates were identified to order level. Following Rood
184 (1975), we identified mongoose prey as those invertebrates belonging to the orders Blattodea,
185 Coleoptera, Diplopoda, Formicidae and Orthoptera. We measured the abundance and diversity of
186 invertebrate prey collected in each transect. Abundance was measured as the total number of
187 individuals in all five orders. Diversity was calculated using the Shannon-Weiner index of diversity to
188 measure the distribution of these individuals across the five orders. The Shannon-Weiner index (H)
189 for a particular transect was calculated as:

190

$$191 \quad H = -\sum_{i=1}^s p_i \ln p_i$$

192

193 Here, s is the total number of orders and p_i is the proportional abundance of the i th order in that
194 transect. Our sampling yielded measures of mongoose invertebrate prey abundance and diversity
195 from 36 transects from 9 months (some monthly samples were lost).

196

197 *Banded mongooses*

198 We visited our study groups for at least 20 minutes every 1-3 days, during which we noted the
199 presence or absence of individuals. We could distinguish between absences due to dispersal from
200 the group and due to death since in banded mongooses dispersal involves the simultaneous eviction
201 of multiple individuals from the group, often with a conspicuous period of aggression within the
202 group beforehand (Cant *et al.* 2010; Thompson *et al.* 2016). In contrast, death involves the
203 permanent disappearance of single individuals. We were able to weigh most individuals once a week
204 in the morning before foraging started by training them to step on electronic scales in return for a
205 small milk reward. We identified female pregnancy by visual swelling of the abdomen and confirmed
206 this by palpation and ultrasound scans during trapping (Cant 2000; Inzani *et al.* 2016). Births occur
207 overnight in an underground den, and were identified by the absence of pregnant females the
208 following morning and a subsequent change in their body shape and mass loss (Cant 2000). To assign
209 parentage DNA was extracted from 2 mm skin samples taken from individuals when they were first
210 trapped (either as newly emerged pups or newly arrived immigrants). This DNA was then genotyped
211 using a panel of 43 polymorphic microsatellite markers (see further details of DNA analysis and
212 parentage assignment in Sanderson *et al.* 2015). See Hodge (2007) and Jordan *et al.* (2010) for
213 further details of the trapping procedure.

214

215 To answer part of our first question about whether early-life ecological conditions affect
216 early-life social environment, we measured the amount of social care an individual received as a pup
217 and the social rank of their parents. The amount of escorting (social care) a mongoose pup receives
218 has been shown to affect its condition and survival during development and later-life reproduction
219 (Gilchrist, Otali & Mwanguhya 2004; Hodge 2005). Similarly, parental social rank has been shown to
220 influence individuals' access to resources and growth in early-life, and reproduction in later-life in
221 other systems (Altmann & Alberts 2005; Charpentier *et al.* 2008; Huchard *et al.* 2013). We measured
222 the amount of escorting received by a pup as the proportion of group visits they were observed

223 being escorted by an adult during the escorting period. Pups were defined as being escorted if they
224 were within 30 cm of the same adult for more than 50% of the group visit time (Gilchrist 2004;
225 Sanderson *et al.* 2014). Social dominance increases with age in banded mongooses (e.g. Nichols *et al.*
226 2010; Cant *et al.* 2014) and so parental rank was measured as the parent's age-rank within the group
227 on the day of an individual's birth.

228

229 **Statistical analyses**

230 *Effects of ecological conditions on invertebrate prey abundance and diversity*

231 Prior to our main analyses, we explored the ecological relevance of our rainfall measures. To do this
232 we fitted models predicting invertebrate prey abundance and species diversity in each monthly
233 pitfall trap transect. In these models we included the following fixed effects: the total rainfall in the
234 past 30 days to test for shorter-term rainfall effects, the mean and standard deviation of the
235 monthly rainfall in the past 12 months to test for longer-term rainfall effects and the quadratic terms
236 of this mean and standard deviation to test for any non-linear effects. We included collection month
237 as a random intercept. The abundance data were overdispersed but not zero-inflated so we also
238 included an observation-level random effect in the abundance model and fitted it using a Poisson
239 log-normal error structure and log link function (Harrison 2014). The diversity model was fitted using
240 a normal error structure and its residuals checked to ensure they were normally distributed with a
241 homogeneous variance.

242

243 *Effects of early-life ecological conditions on banded mongooses*

244 Mirroring our research questions, we conducted our analyses of the effect of early-life ecological
245 conditions in two stages: (1) effects during early-life, and (2) lifetime fitness effects, fitting our
246 models to males and females separately. Banded mongooses are fully grown and reach sexual
247 maturity between the ages of 1 and 2 years (zone ii in Fig. 2; Cant *et al.* 2016). Therefore in stage 2
248 of our analyses, we only included individuals who had survived to 2 years old to ensure we only

249 included fully developed individuals (zone iii in Fig. 2). Table 1 lists the models we fitted in each stage
250 and details how the response variable in each model was measured, the sample sizes used, the
251 random effects included and the models' error structure and link functions. In all models we fitted
252 the mean and standard deviation of the monthly rainfall in an individual's first year of life as fixed
253 effects. To test for the possibility of a life-history trade-off between survival and reproduction our
254 models of lifespan also included whether an individual had successfully reproduced in their lifetime
255 (0/1) and the interaction between this and the first-year rainfall variables. Our model of adult mass
256 also included an individual's age as a control variable, whilst our model predicting the amount of
257 social care received as a pup also included the ratio of adults (potential escorts) to pups in the group
258 as a control variable. Banded mongoose reproduction is synchronised within groups, but not
259 between groups, and in our equatorial study population reproduction occurs all year round.
260 Consequently, population-wide cohort effects, which can lead to spurious findings in the analysis of
261 life history traits (Murray 2006; Grosbois *et al.* 2008), are not expected in this system. Within-group
262 reproductive synchrony does form cohorts of individuals born in the same communal litter who all
263 experience the same early-life ecological conditions, and we controlled for this in stage 1 of our
264 analysis by including breeding attempt as a random effect in our models (Table 1). It was not
265 necessary to control for within-group cohort effects in stage 2 of our analyses because the high
266 mortality rate in our population (e.g. 57% mortality between 1 and 3 months old, Hodge *et al.* 2009;
267 see full survival curve in Cant *et al.* 2016) meant that individuals included in these analyses were
268 almost entirely from unique breeding attempts.

269

270 We conducted our analyses using generalized linear mixed effect models (GLMMs). The
271 residuals of models fitted using normal error structures (mass at 1 year old and adult mass) were
272 checked to ensure they were normally distributed with constant variance. Models fitted to count
273 data used a Poisson error structure unless they were overdispersed. Where this occurred, following
274 Harrison (2014), models were fitted using a Poisson log-normal error structure and an observation-

275 level random effect (lifespan models) unless the data were zero-inflated in which case a negative
276 binomial error structure was used (lifetime reproductive success models). We used the same model
277 selection procedure to our complementary study of the effect of ecological conditions during
278 adulthood on banded mongooses (Marshall *et al.* 2016). We used likelihood ratio tests, comparing
279 the full model to a model without a particular variable, to test the significance of this variable's
280 effect (Forstmeier & Schielzeth 2011). Where interactions did not have a significant effect we
281 dropped these from our final model to allow us to test the significance of the main effects in these
282 non-significant interactions (Engqvist 2005). We did not reduce our model further due to the issues
283 with stepwise model reduction techniques (Whittingham *et al.* 2006; Mundry & Nunn 2009;
284 Forstmeier & Schielzeth 2011). Correlations between variables fitted in models as fixed effects –
285 including the correlation between the mean and standard deviation of the monthly rainfall in a
286 mongoose's first year – were lower than the levels previously shown to cause model fitting issues
287 such as variance inflation in effect estimates (max $r = 0.36$, Freckleton 2011). We performed all
288 analyses in R (R Core Team 2014), fitting GLMMs using the lme4 package (Bates *et al.* 2014).

289 Table 1: Details of the models fitted in each stage of our analyses. Samples sizes are shown for males (M) and females (F) as models were fitted separately
 290 to data from each sex. All models included the mean and standard deviation of the monthly rainfall in an individual's first year of life as fixed effects.

		<u>Sample size</u>				<u>Model fitting</u>				
Models predicting how early-life ecological conditions affect:	Measured as	individuals		packs		breeding attempts		random effects	error structure	link function
		M	F	M	F	M	F			
<u>Stage 1: effects during early life</u>										
Maternal rank	The age-rank of an individual's mother in the pack at the time of their birth	104	84	10	9	63	48	breeding attempt, pack	Poisson	log
Paternal rank	The age-rank of an individual's father in the pack at the time of their birth	86	63	10	9	53	43	breeding attempt, pack	Poisson	log
Social care received ¹	The proportion of group visits an individual was observed being escorted as a pup	49	41	5	5	27	21	breeding attempt, pack	binomial	logit
Mass at 1 year	Individual's mass (grams) at 1 year old (\pm 30 days)	47	15	6	2	27	12	breeding attempt, pack	normal	identity
Survival to 1 year	Binary denoting if an individual survived to 1 year old.	357	300	14	13	132	117	breeding attempt, pack	binomial	logit
<u>Stage 2: lifetime fitness effects</u>										
Body condition* ²	Mass (grams)	80	41	8	8			individual, pack	normal	identity
Successful reproduction in lifetime	Binary denoting if an individual was assigned as parent to a pup during their lifetime	61	43	9	8			pack	binomial	logit
Relative fertility of successful reproducers	Proportion of all genotyped pups born whilst an individual was resident in a pack that they were assigned as parent to	19	22	5	5			pack	binomial	logit
Lifetime reproductive success	Total number of pups an individual was assigned in its lifetime	58	37	9	8			pack	negative binomial	log
Lifespan ³	Age (years) at which an individual died	60	43	9	8			pack, observation-level	Poisson log-normal	log

*Models fitted to 174 and 90 records of male and female masses, respectively. Also included as fixed effects: ¹ number of adults (potential escorts) in the group, ² an individual's age, ³ whether an individual had successfully reproduced in their lifetime (0/1) and the interaction between this and the first-year rainfall variables

291 **Results**

292 **Effects of ecological conditions on invertebrate prey abundance and diversity**

293 Invertebrate prey abundance was predicted by the pattern of rainfall in the preceding 12 months:
294 prey abundance increased with the mean monthly rainfall in the previous 12 months ($\beta \pm \text{s.e.} = 0.16$
295 ± 0.06 , $\chi^2 = 5.70$, $p = 0.017$; Fig. 4a) and decreased with the standard deviation of monthly rainfall in
296 the previous 12 months ($\beta \pm \text{s.e.} = -0.11 \pm 0.04$, $\chi^2 = 4.50$, $p = 0.034$; Fig. 4b). Invertebrate prey
297 abundance was not affected by the amount of rainfall in the past 30 days ($\chi^2 = 2.14$, $p = 0.14$; model
298 intercept $\pm \text{s.e.} = -2.53 \pm 2.96$). There was no evidence for a quadratic relationship between
299 invertebrate abundance and either rainfall measure (mean rainfall: $\chi^2 = 0.79$, $p = 0.38$; s.d. rainfall: χ^2
300 $= 2.96$, $p = 0.09$). Invertebrate prey diversity was not predicted by any rainfall measure (linear terms,
301 mean rainfall: $\chi^2 = 3.19$, $p = 0.07$, s.d. rainfall: $\chi^2 = 1.99$, $p = 0.16$; quadratic terms, mean rainfall: $\chi^2 =$
302 0.24 , $p = 0.63$, s.d. rainfall: $\chi^2 = 1.35$, $p = 0.24$; rainfall in last 30 days: $\chi^2 = 0.71$, $p = 0.40$; model
303 intercept $\pm \text{s.e.} = 1.82 \pm 0.96$). It appears, therefore, that invertebrate prey abundance at our site is
304 influenced by longer-, rather than shorter-term patterns in rainfall. This is consistent with other
305 studies showing that ground-dwelling invertebrates can have long life cycles (e.g. 2 years in
306 millipedes, Lewis 1971) and that their abundance can be more greatly influenced by longer-term
307 rainfall patterns (Kwok *et al.* 2016).

308

309 **Effects of early-life ecological conditions on banded mongooses**

310 Early-life ecological conditions, as measured by the mean and variability of rainfall in a mongoose's
311 first year, did not predict the amount of social care received in their first year or their survival to 1
312 year old (Table 2). Early-life conditions did not have a significant effect on body mass at one year old,
313 however there was a trend for males born in more variable years to be heavier at one year old ($p =$
314 0.06 , Table 2).

315

316 Early life conditions did have consistent effects on reproduction and survival in adult males
317 (Table 3). Males born into years with more variable rainfall generally had better lifetime
318 reproductive success and survival in later-life (Fig. 5, right-hand panels), whilst the effect of the
319 amount of first-year rainfall indicated a potential life-history trade-off (Fig. 5, left-hand panels).
320 Males that experienced more variable first-year rainfall were heavier in adulthood (Fig. 5b) and more
321 likely to sire a pup during their lifetime (Fig. 5d). The variability of first-year rainfall did not affect
322 successful males' relative fertility (the proportion of all pups born into their group that they sired,
323 Fig. 5f) but males born in more variable rainfall years did live longer (Fig. 5h). Ultimately, this
324 translated into males born in more variable rainfall years having greater lifetime reproductive
325 success (Fig. 5j). Males born into years with less rainfall were heavier in adulthood (Fig. 5a).
326 However, in contrast to the effect of the variability of first-year rainfall, the amount of first-year
327 rainfall did not affect the chance of a male siring at least one pup in their life (Fig. 5c). However, if a
328 male was a successful sire in their lifetime, those born into years with more rainfall had greater
329 relative fertility (Fig. 5e) but lived shorter lives (Fig. 5g). This translated in the amount of first-year
330 rainfall having no effect on males' overall lifetime reproductive success (Fig. 5i).

331

332 The mean and variability of first-year rainfall had almost no effects on female mass,
333 reproduction and survival (Table 3). The one exception was that successfully breeding females born
334 in years with more variable rainfall had a lower relative fertility, i.e. were mother to a lower
335 proportion of all pups born into their group during their lifetime (Table 3).

336 Table 2: Models predicting the effect of early-life ecological conditions on early-life social environment, body condition and survival. Parameter estimates (\pm
 337 standard errors) for models fitted to males and females are shown, along with likelihood-ratio chi-square statistics and p-values.

Model predicting	Explanatory variable	Males				Females			
		β	s.e.	χ^2	p	β	s.e.	χ^2	p
Maternal rank	Intercept	0.34	0.67			0.64	0.74		
	Mean monthly rainfall in first year	0.004	0.01	0.17	0.68	0.01	0.01	0.31	0.58
	S.D. monthly rainfall in first year	0.01	0.01	2.00	0.16	-0.004	0.01	0.49	0.49
Paternal rank	Intercept	0.40	0.75			0.17	0.87		
	Mean monthly rainfall in first year	0.01	0.01	1.33	0.25	0.01	0.01	0.47	0.49
	S.D. monthly rainfall in first year	-0.01	0.01	0.66	0.42	0.002	0.01	0.10	0.75
Social care received	Intercept	-0.22	2.91			3.37	2.04		
	Mean monthly rainfall in first year	0.02	0.04	0.33	0.56	-0.04	0.03	2.15	0.14
	S.D. monthly rainfall in first year	-0.02	0.04	0.24	0.63	-0.02	0.03	0.42	0.51
	Ratio of adults to pups in the group	-0.02	0.14	0.02	0.90	-0.18	0.11	2.12	0.15
Mass at 1 year old	Intercept	1329.35	248.83			1082.51	222.98		
	Mean monthly rainfall in first year	-4.48	2.90	2.33	0.13	0.40	3.64	0.04	0.84
	S.D. monthly rainfall in first year	3.72	1.95	3.68	0.06	0.20	1.38	0.02	0.88
Survival to 1 year	Intercept	-0.12	1.53			1.78	1.55		
	Mean monthly rainfall in first year	-2.52E-04	0.02	1.36E-04	0.99	-0.03	0.02	2.04	0.15
	S.D. monthly rainfall in first year	-0.001	0.01	0.01	0.94	-4.70E-04	0.01	0.001	0.97

338

339 Table 3: Models predicting the effect of early-life ecological conditions on lifetime reproduction and survival. Parameter estimates (\pm standard errors) for
 340 models fitted to males and females are shown, along with likelihood-ratio chi-square statistics and p-values. Significant effects of early-life ecological
 341 conditions are highlighted in bold.

Model predicting	Explanatory variable	Males				Females			
		β	s.e.	χ^2	p	β	s.e.	χ^2	p
Body condition	Intercept	1451.14	113.43			1211.50	303.06		
	Age	17.26	4.26	16.08	<0.001	12.61	7.91	2.51	0.11
	Mean monthly rainfall in first year	-3.68	1.81	4.26	0.04	0.19	4.76	2.00E-05	0.99
	S.D. monthly rainfall in first year	2.89	1.05	7.49	0.006	0.81	1.32	0.43	0.51
Successful reproduction in lifetime	Intercept	-7.10	4.63			2.96	4.72		
	Mean monthly rainfall in first year	0.06	0.05	1.76	0.19	-0.04	0.07	0.40	0.53
	S.D. monthly rainfall in first year	0.07	0.03	5.41	0.02	0.01	0.04	0.06	0.81
In successful reproducers, proportion of potential pups assigned in lifetime	Intercept	-6.77	1.59			5.02	3.30		
	Mean monthly rainfall in first year	0.08	0.03	9.47	0.002	-0.08	0.05	3.44	0.06
	S.D. monthly rainfall in first year	1.40E-03	0.01	0.01	0.91	-0.04	0.02	5.24	0.02
Lifetime reproductive success	Intercept	-3.61	3.58			0.46	4.28		
	Mean monthly rainfall in first year	0.01	0.06	0.02	0.89	-0.01	0.06	2.49	0.11
	S.D. monthly rainfall in first year	0.08	0.04	5.14	0.02	-0.002	0.03	3.11	0.08
Lifespan	Intercept	6.47	0.64			7.50	0.60		
	Mean monthly rainfall in first year	-3.12E-04	0.01			-0.01	0.01	0.37	0.54
	S.D. monthly rainfall in first year	0.015	0.005	7.27	0.01	-0.01	0.01	2.23	0.14
	Successfully reproduced in lifetime (1/0)	2.53	0.95			0.54	0.13	18.03	<0.001
	Successfully reproduced in lifetime x								
	Mean monthly rainfall in first year	-0.03	0.02	4.27	0.04	-0.02	0.02	1.02	0.31
S.D. monthly rainfall in first year	0.02	0.01	3.19	0.07	-0.01	0.01	0.24	0.62	

342 Discussion

343

344 Early-life ecological conditions had lifetime consequences for male banded mongooses. More
345 variable early-life conditions had positive effects on males' lifespan and lifetime reproductive
346 success, suggesting a relaxation of life-history trade-off constraints. In contrast, changes in mean
347 early-life conditions influenced males' relative fertility and lifespan in opposite directions resulting in
348 no overall effect on lifetime reproductive success, suggesting a life-history trade-off. In Figure 6 we
349 use a simple graphical model (adapted from Saeki, Tuda & Crowley 2014) to illustrate these different
350 effects of variability and mean early-life conditions. Unlike in males, females' early-life ecological
351 conditions had almost no effect on patterns of survival and reproduction.

352

353 Males who experienced more variable rainfall in early-life lived longer and had greater
354 lifetime reproductive success. We have shown previously that more variable rainfall is associated
355 with higher adult mortality in mongooses (Marshall *et al.* 2016) and our results here also indicate an
356 association with lower food abundance suggesting that years with more variable rainfall are generally
357 unfavourable. These findings, therefore, contrast with previous studies of wild animals showing that
358 favourable early-life ecological conditions have positive effects on survival and reproduction in later
359 life (e.g. *Haematopus ostralegus* Van de Pol *et al.* 2006; *Cervus elaphus* Nussey *et al.* 2007; *Forficula*
360 *auricularia* Wong & Kölliker 2014). Evidence for later-life fitness advantages of unfavourable early-
361 life ecological conditions has been shown in two wild bird systems, but this was based on a single
362 measure of fitness (probability of breeding in *Lamprolornis superbus* Rubenstein *et al.* 2016) or was
363 found within an overall positive effect of early-life ecological conditions on fertility and survival
364 (*Parus major* Wilkin & Sheldon 2009). Increased adult survival was also shown in female roe deer
365 (*Capreolus capreolus*) that survived periods of high juvenile mortality (Garratt *et al.* 2015). Our study
366 uses multiple measures of fitness to directly link later-life fitness advantages to unfavourable early-
367 life ecological conditions (rather than measures of early-life mortality) in a wild mammal system.

368 Moreover, our results show that these later-life advantages are not explained by the impact of early
369 life conditions on offspring survival (i.e. selection), parental investment, or the social environment as
370 suggested previously (Wilkin & Sheldon 2009; Garratt *et al.* 2015; Rubenstein *et al.* 2016).

371

372 Why might more variable ecological conditions be associated with increased fitness payoffs,
373 without any apparent costs (Figure 6a)? Previous studies investigating the effect of the variability of
374 early-life ecological conditions on later-life performance in a wild animal system are lacking. One
375 possibility is that more varied early-life conditions might influence individuals' physiological or
376 cognitive development such that they are able to cope with a greater range of environmental
377 challenges in later-life. This hypothesis is supported by the fact that, at our study site, years with
378 greater variation in monthly rainfall values were also those with greater maximum and lower
379 minimum monthly rainfalls. Furthermore, comparing the range of monthly rainfall values males
380 experienced during early-life to the range of monthly values they would experience during a typical
381 male lifespan (42 months, Cant *et al.* 2016), those born in highly variable periods (the top third of
382 early-life s.d. rainfall values) experienced $93\% \pm 7\%$ (mean \pm s.d., $n = 50$ males) of the typical lifetime
383 range whilst those born in low variability periods (the bottom third of early-life s.d. values)
384 experienced $63\% \pm 8\%$ ($n = 55$ males). Our results do not support the possibility that a more variable
385 early-life rainfall conferred advantages through a more diverse diet. However, there are parallels
386 between our hypothesis that early-life variability may have beneficial impacts on physiological or
387 cognitive development and findings from the medical literature. First, experiencing a wide variety of
388 pathogens during childhood is recognised to be important in the development of the human
389 immune system, with a lack of early-life immunological challenges leading to inappropriate immune
390 responses in adulthood and allergic diseases (the "hygiene hypothesis": Strachan 1989, 2000; Wills-
391 Karp *et al.* 2001; Yazdanbakhsh *et al.* 2002). Second, experiencing a variety of childhood
392 psychological stressors is thought to have positive effects on some cognitive abilities in adults under
393 stress (Frankenhuis & de Weerth 2013; Frankenhuis *et al.* 2015). Finally, it may be that reduced

394 early-life food availability is beneficial. In laboratory models and humans dietary restriction has
395 repeatedly been shown to increase lifespan (e.g. McCay *et al.* 1935; Fontana *et al.* 2004; Masoro
396 2006; Colman *et al.* 2009; Zhang *et al.* 2013). In support of this recent ecological studies have shown
397 that restrictions on early-life diet can have benefits such as reduced oxidative damage in zebra
398 finches, *Taeniopygia guttata*, and wild yellow-legged gulls, *Larus michahellis* (Noguera *et al.* 2011;
399 Noguera, Monaghan & Metcalfe 2015). The link between our hypothesis and these biomedical
400 findings is speculative at present, but there is clearly much scope for research to elucidate the
401 mechanisms underlying the early-life effects reported here.

402

403 Mean early-life ecological conditions, rather than having an effect on overall fitness payoffs,
404 appeared to mediate a life-history trade-off (Figure 6b). Depending on mean conditions during
405 development, males apparently adopted a ‘live-fast, die-young’ or ‘live-slow, die-old’ strategy and
406 achieved similar lifetime fitness as a consequence. These findings are consistent with life-history
407 theory that individuals trade-off allocating resources between somatic maintenance and
408 reproduction (Kirkwood & Rose 1991; Reznick & Yang 1993; Zera & Harshman 2001), and support
409 the general hypothesis that conditions during development have an important influence on this life-
410 history resource allocation across an individuals’ lifetime (Gluckman *et al.* 2005; Taborsky 2006;
411 Monaghan 2008; Nettle & Bateson 2015). Nonetheless, empirical studies demonstrating the effect of
412 early-life conditions on life-history trade-offs are uncommon (Hammers *et al.* 2013; Cartwright *et al.*
413 2014), with many more studies showing directly positive (or negative) ‘silver-spoon’ effects of early-
414 life conditions on lifetime fitness (Van de Pol *et al.* 2006; Nussey *et al.* 2007; Hayward *et al.* 2013;
415 Wong & Kölliker 2014; Rubenstein *et al.* 2016). Our results provide evidence for both life-history
416 trade-off and ‘silver-spoon’ type effects of early- life ecological conditions. Poor average early-life
417 conditions shifted life histories towards the slower end of the survival versus reproduction trade-off,
418 whilst more variable early-life conditions had beneficial effects on both survival and reproduction.

419 This highlights the importance of considering the variability, as well as the average, of early-life
420 conditions in understanding their consequences for individuals' lifetime fitness.

421

422 Why did early-life ecological conditions only have consistent effects on males', and not
423 females', later-life fitness? Previous studies have suggested that sex-differences in the effect of
424 early-life ecological conditions may be due to sex-differences in: (1) body size (Kruuk *et al.* 1999;
425 Millon *et al.* 2011; Ancona & Drummond 2013), (2) the amount of care received during development
426 (Kruuk *et al.* 1999; Rubenstein *et al.* 2016), (3) the effect of early-life conditions on the development
427 of reproductive organs (Wong & Kölliker 2014) and (4) selection pressures for plasticity to later-life
428 conditions (Wilkin & Sheldon 2009; Ancona & Drummond 2013; Garratt *et al.* 2015). We are able to
429 rule out explanations (1) and (2) here since banded mongooses show little sexual dimorphism and
430 early-life ecological conditions did not predict the amount of care pups received. We have no direct
431 evidence to rule out explanation (3) but we consider it unlikely since female reproductive organs are
432 more costly to develop and so this would predict later-life fitness effects in females rather than
433 males (as Wong & Kölliker 2014 found), which is the opposite to what we found. There is, however,
434 evidence to support explanation (4) that banded mongoose females are under greater selection to
435 exhibit higher levels of plasticity to ecological conditions experienced in adulthood. Adult females'
436 mass and survival are more sensitive than males' to ecological conditions experienced during
437 adulthood (Marshall *et al.* 2016). Females in better condition are more fecund and have more
438 competitive offspring (Hodge *et al.* 2009; Inzani *et al.* 2016) and they reduce their costly helping
439 behaviour more than males when food availability is lower (Bell 2010). These effects are all likely to
440 increase selection on females to adapt to the ecological conditions they experience during
441 adulthood, masking any effects of the conditions they experienced in early-life. In addition, females
442 also start breeding at an earlier age than males (Cant *et al.* 2016) and are pregnant for an average of
443 30% of their adult lives (Marshall HH *et al.*, unpublished data). Whilst this last point may impair
444 females' ability to respond to changes in ecological conditions whilst they are pregnant (Marshall *et*

445 *al.* 2016) it may increase the pressure to adapt to these changes outside of pregnancy. These results
446 contribute to the growing picture that the effect of early-life ecological conditions on later-life
447 fitness are often sex-specific (Millon *et al.* 2011; Rubenstein *et al.* 2016), and highlight sex-
448 differences in plasticity to later-life ecological conditions as a mechanism producing this sex-specific
449 effect (Wilkin & Sheldon 2009; Ancona & Drummond 2013).

450

451 Finally, despite the multiple effects of early-life ecological conditions in later-life, we found
452 no immediate effects of early life conditions on social care received or offspring survival. There was a
453 trend for males to be heavier at 1 year old after a more variable early-life, however this effect was a
454 non-significant trend ($p = 0.06$) and so needs further investigation. This agrees with other studies
455 showing that early-life conditions can influence individuals in later-life without having impacts on
456 early-life health or survival (Rosa *et al.* 2014; Andrews *et al.* 2015). For example, in the European
457 starling, *Sturnis vulgaris*, competitive disadvantage during development does not affect chick growth
458 or mass a year later, but disadvantaged birds experience greater telomere attrition as chicks (Nettle
459 *et al.* 2015b) and, as adults, impaired flight performance and altered foraging and cognitive
460 behaviour (Andrews *et al.* 2015; Bateson *et al.* 2015; Nettle *et al.* 2015a; O’Hagan *et al.* 2015). Such
461 “cryptic” or “carry-over” effects of early-life conditions may be mediated by physiological
462 mechanisms that only manifest themselves in later life (Andrews *et al.* 2015; Nettle *et al.* 2015b). A
463 greater understanding of how environmental conditions during development affect individuals’
464 physiology may be key in understanding why these conditions influence individuals’ health,
465 behaviour and fitness in later-life, with implications for evolutionary and biomedical science
466 (Gluckman *et al.* 2005; Nettle & Bateson 2015).

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478

479 **Data Accessibility**

480 The data used in this paper will be made available on Figshare upon acceptance for publication.

481

482 **Author Contributions**

483 HHM and MAC conceived the study; All authors contributed to the design of the demographic data
484 collection protocols; FM, RB, SK and KN collected the behavioural and demographic data collection;
485 HJN conducted the genetic analyses; JLS performed the parentage assignments; HHM performed the
486 statistical analyses and wrote the first draft of the manuscript; All authors contributed to subsequent
487 manuscript revisions.

488

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704 **Figure legends**

705

706 Figure 1: Banded mongooses (*Mungos mungo*) moving as a group and inspecting what lies ahead.

707 Photo credit: Feargus Cooney.

708

709 Figure 2: Banded mongoose mass change with age. Panel a shows all data and panel b zooms in on

710 data from individuals between the ages of 0 and 3 years. In both panels the vertical dotted lines

711 divide the data into masses from individuals aged 0 to 1 year (zone i), 1 to 2 years (zone ii) and over

712 2 years (zone iii).

713

714 Figure 3: The rainfall pattern (a) within and (b) between years at our study site: the Mweya

715 Peninsula, Uganda. Panel a shows the mean (\pm standard error) rainfall recorded in each month (n =

716 152 months, month 1 = January). Panel b shows the mean (filled circles and solid line) and standard

717 deviation (open circles and dashed line) of the monthly rainfall within each year. Rainfall data for

718 2002 is incomplete and so not shown.

719

720 Figure 4: The effect of (a) the mean and (b) the standard deviation of monthly rainfall in the past 12

721 months on invertebrate prey abundance. Note the log scale on the y axis.

722

723 Figure 5: Male mongooses' reproduction and survival and the mean (left-hand panels) and variability

724 (right-hand panels) of rainfall in their first year. Panels show the effect on adult males': mass (a,b),

725 probability of siring at least one pup (c,d); in those that did sire a pup, the proportion of all pups

726 born into their group that they sired (e,f); their lifespan (g,h); the total number of pups they sired in

727 their lifetime (i,j). Lines show significant relationships predicted by models (see Table 3). Non-

728 significant relationships are not plotted. In panel g the data and predicted relationships are split by

729 into males who successfully reproduced in their lifetime (purple) and those who did not (black).

730

731 Figure 6: Graphical illustration of the hypothesised effect of changes in the (a) variability and (b)

732 mean of early-life rainfall on life-history trade-off and allocation patterns (after Saeki *et al.* 2014).

733 The thin grey lines represent fitness isoclines along which all positions return an equal payoff. The

734 thick dashed line represents the reference trade-off slope for an individual (here straight lines for

735 simplicity) and the yellow dot represents the reference optimal allocation of resources to survival

736 and reproduction (where the trade-off slope is tangential to the isocline). In panel a) the thick red

737 lines and dots show how an (i) increase or (ii) decrease in the variability of early-life rainfall relaxes

738 or increases the life-history trade-off constraints leading to higher or lower fitness payoffs. In panel

739 b) the thick blue lines and dots represent how an (iii) increase or (iv) decrease in mean early-life

740 rainfall leads to changes in an individual's trade-off slope and optimal allocation of resources but no

741 change in their overall fitness payoff.

742

743 Figure 1

744

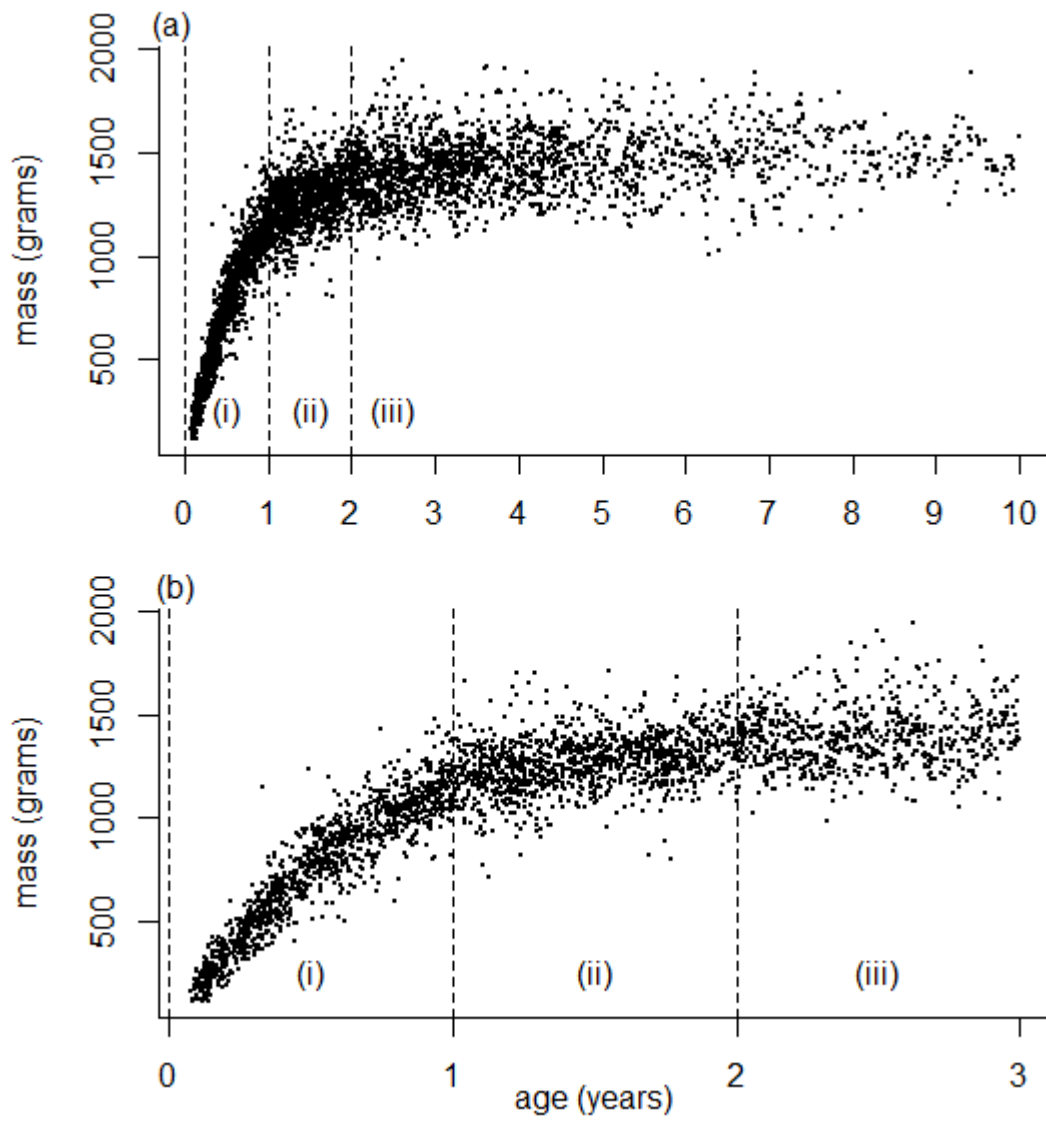


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747 Figure 2

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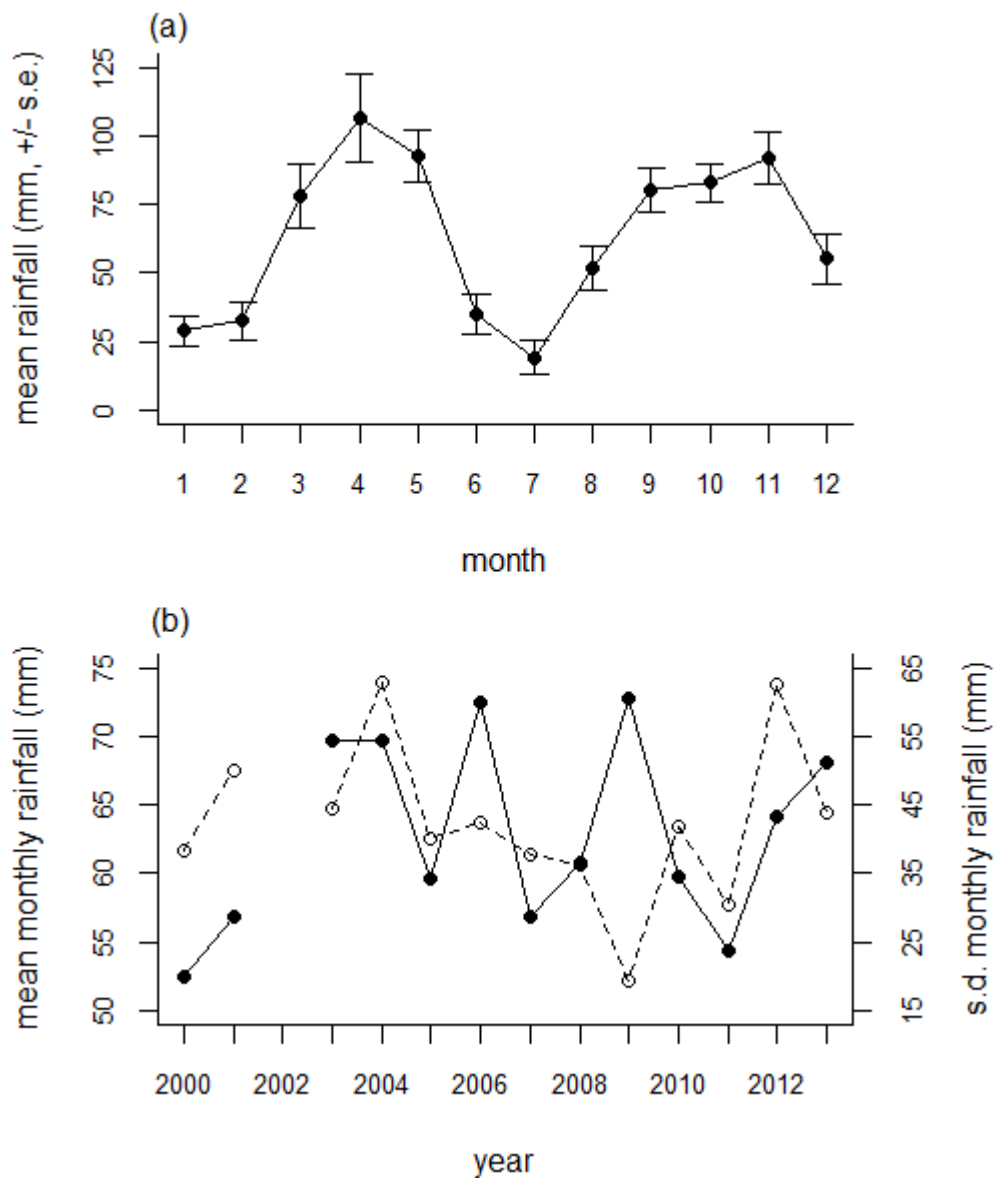


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751 Figure 3

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Figure 4

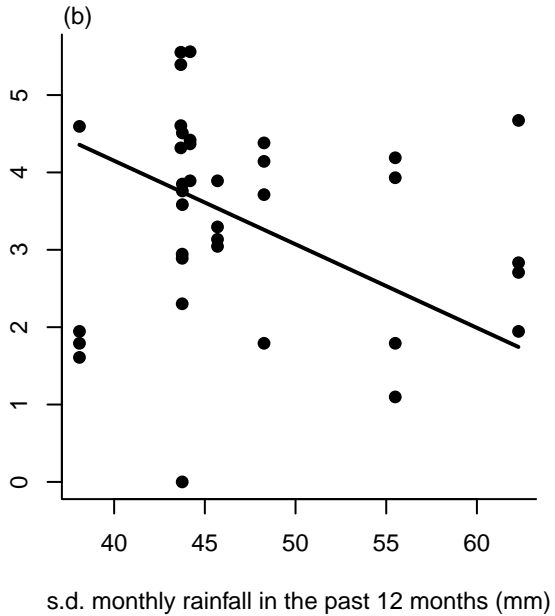
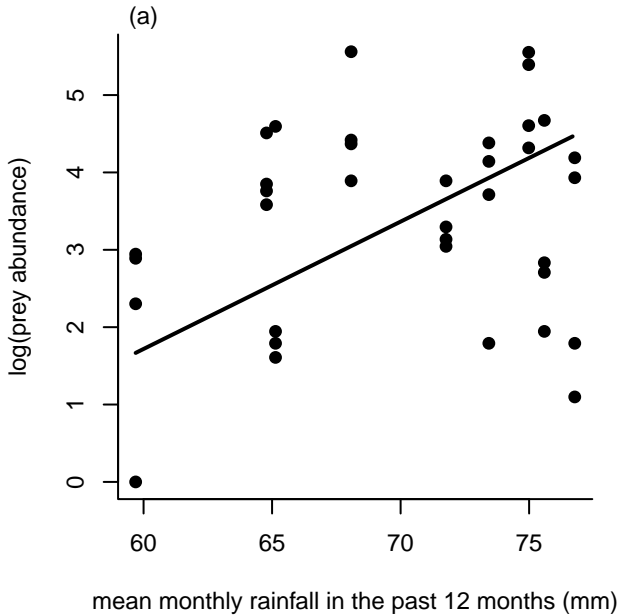


Figure 5

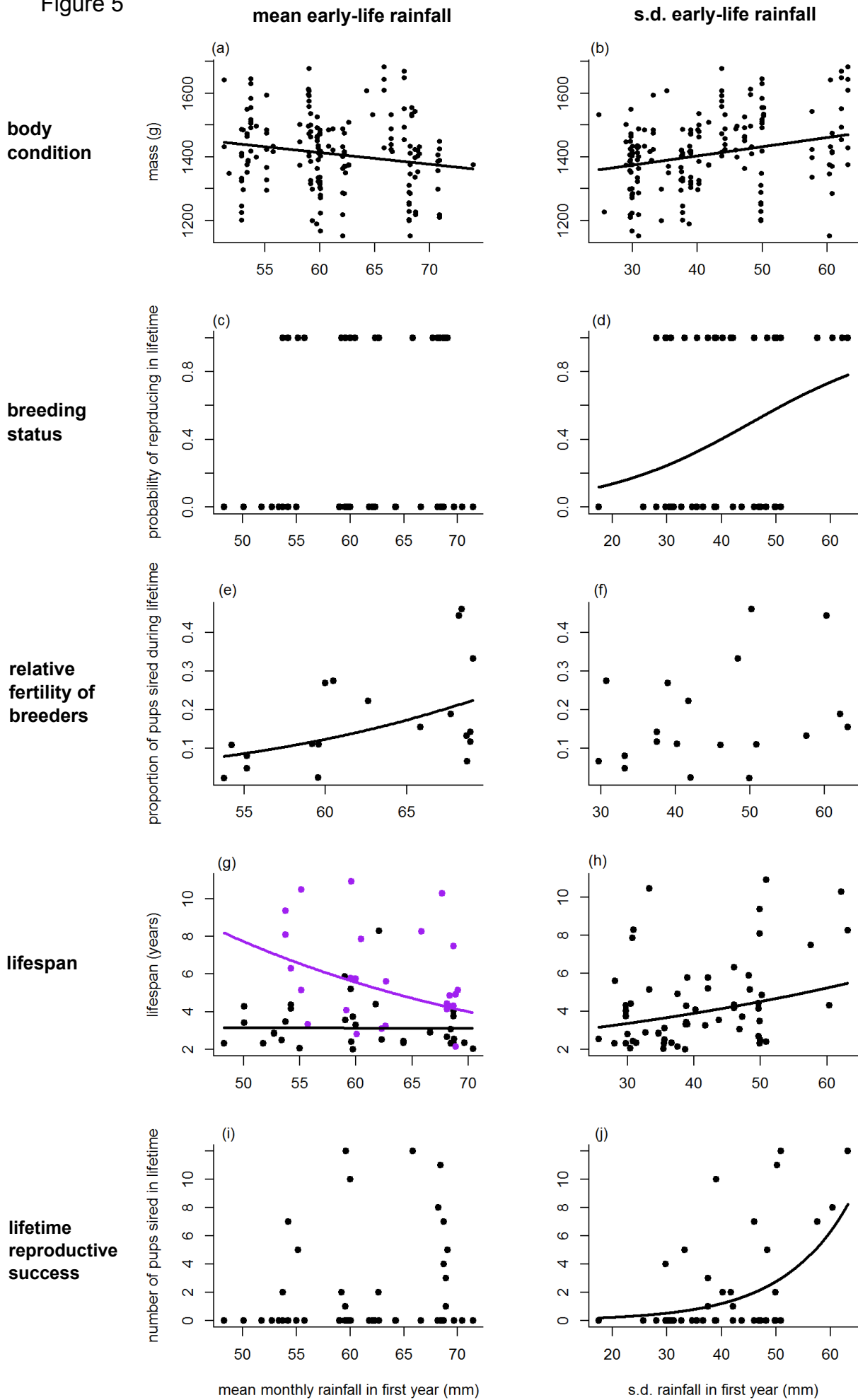


Figure 6

