1 **Lifetime fitness consequences of early-life ecological**

2 **hardship in a wild mammal population**

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Abstract

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

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

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

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

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

Introduction

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

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

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

76   *al.* 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

Materials and Methods

Study System

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

Banded mongooses (Fig. 1) are diurnal carnivores (<2kg) that live in stable, mixed-sex groups of around 10 to 30 individuals and whose diet mainly consists of small invertebrates (Rood 1975). Individuals sexually mature around the age of 1 year old (Cant *et al.* 2016) and all individuals within a group reproduce to some extent, though contributions to reproduction are skewed towards older individuals (Nichols *et al.* 2010, 2012). Their average lifespan is around 3.5 years (males = 42 months, females = 38 months, max = 149 months, Cant *et al.* 2016) and survival rates are constant across all ages (Cant *et al.* 2016; Marshall *et al.* 2016). At our equatorial study site reproduction occurs all year round and is not synchronised between groups. Reproduction is, however, highly synchronised within groups: around four times per year, all pregnant females in a group give birth in an underground den to a large communal litter, usually on the same morning (Cant 2000; Hodge, Bell & Cant 2011). Pups remain in the den for approximately their first 30 days, after which they move with the rest of the group and are cared for by adult 'escorts' for around a further 60 days (Gilchrist 2004; Gilchrist & Russell 2007). We are able to individually recognise the mongooses in our study population using unique hair-shave patterns or coloured collars. Radio collars weighing 26 to 30 g (Sirtrack Ltd, Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd, Dorset, UK) are fitted to one to two individuals in each group to allow them to be located. Most individual are trained to step onto an electronic balance in return for a small milk reward. Two groups have access 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 ± s.d. = 61 ± 41 mm, n = 152 months) whilst temperature is reasonably

155 constant (mean of monthly mean maximum daily temperature ± 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 mongoooses' 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 there 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   $H = -\sum_{i=1}^{s} p_i \ln p_i$

192

193 Here, *s* is the total number of orders and p_i is the proportional abundance if 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% mortalty 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).

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 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.

Models predicting how early-life ecological conditions affect:	Measured as	Sample size individuals M	F	packs M	F	breeding attempts M	F	Model fitting random effects	error structure	link function
Stage 1: effects during early life										
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 (± 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
Stage 2: lifetime fitness effects										
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

Results

Effects of ecological conditions on invertebrate prey abundance and diversity

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

Effects of early-life ecological conditions on banded mongooses

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

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 (±

337 standard errors) for models fitted to males and females are shown, along with likelihood-ratio chi-square statistics and p-values.

		Males				Females			
Model predicting	Explanatory variable	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 (± 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

Discussion

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

Males who experienced more variable rainfall in early-life lived longer and had greater lifetime reproductive success. We have shown previously that more variable rainfall is associated with higher adult mortality in mongooses (Marshall *et al.* 2016) and our results here also indicate an association with lower food abundance suggesting that years with more variable rainfall ae generally unfavourable. These findings, therefore, contrast with previous studies of wild animals showing that favourable early-life ecological conditions have positive effects on survival and reproduction in later life (e.g. *Haematopus ostralegus* Van de Pol *et al.* 2006; *Cervus elaphus* Nussey *et al.* 2007; *Forficula auricularia* Wong & Kölliker 2014). Evidence for later-life fitness advantages of unfavourable early-life ecological conditions has been shown in two wild bird systems, but this was based on a single measure of fitness (probability of breeding in *Lamprotornis superbus* Rubenstein *et al.* 2016) or was found within an overall positive effect of early-life ecological conditions on fertility and survival (*Parus major* Wilkin & Sheldon 2009). Increased adult survival was also shown in female roe deer (*Capreolus capreolus*) that survived periods of high juvenile mortality (Garratt *et al.* 2015). Our study uses multiple measures of fitness to directly link later-life fitness advantages to unfavourable early-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% ± 7% (mean ± 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% ± 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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Data Accessibility

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

Author Contributions

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

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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 (± 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.
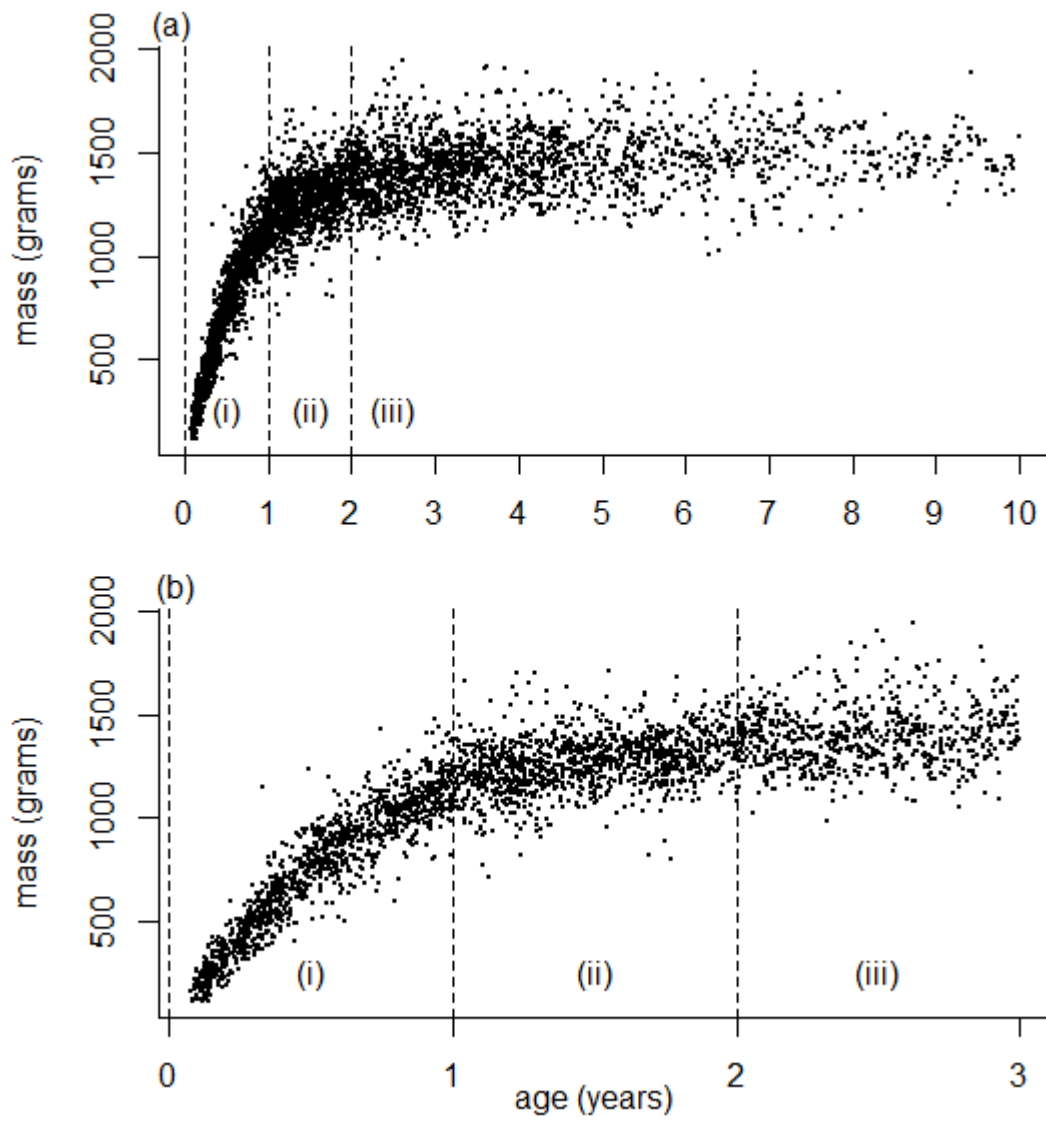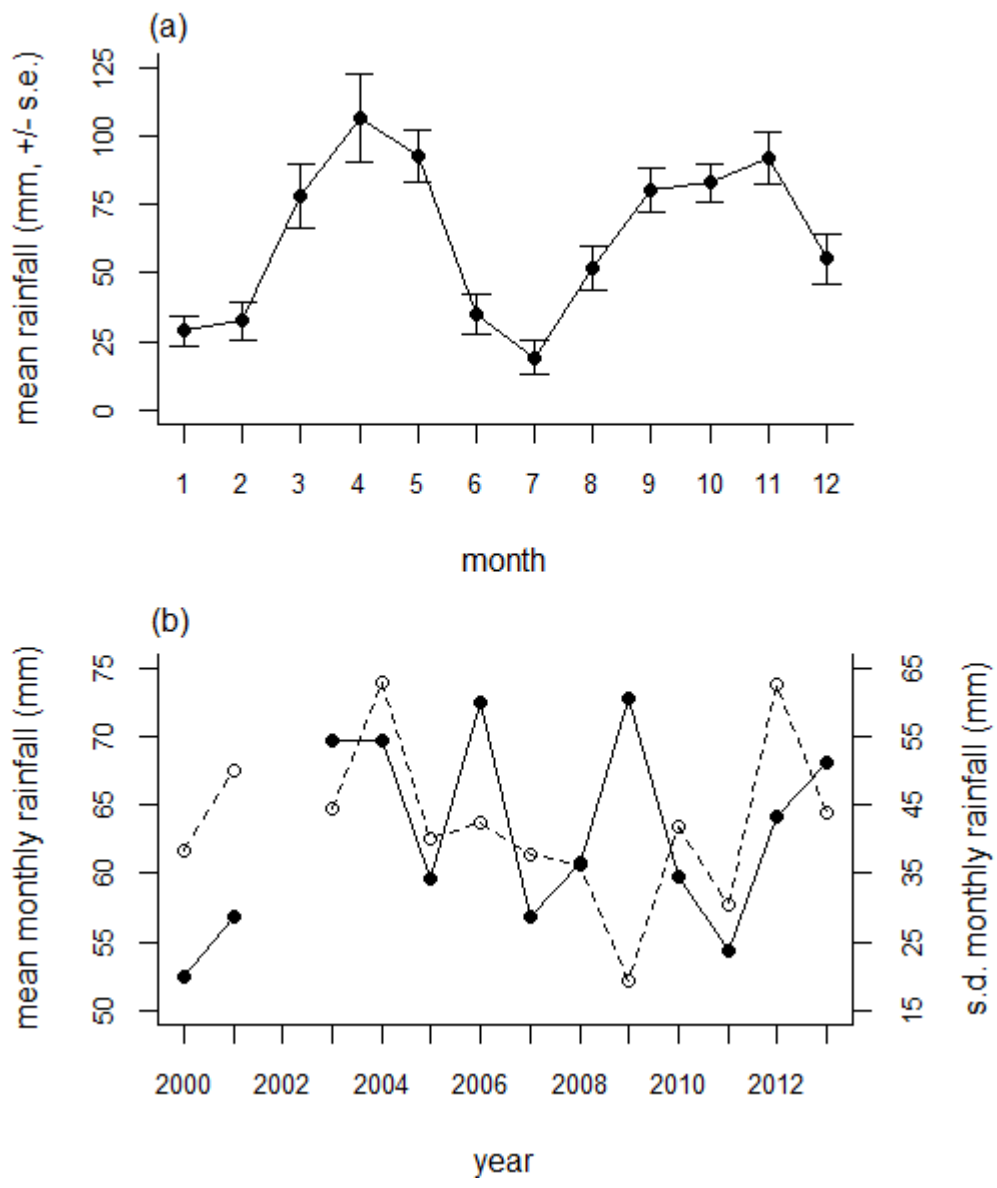
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743   Figure 1

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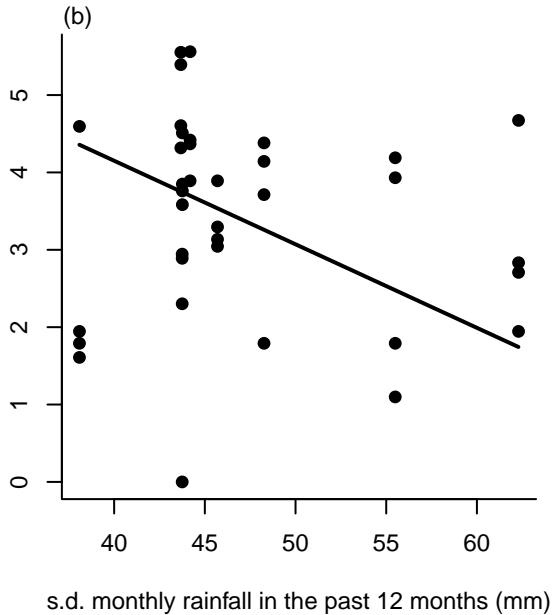746

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751   Figure 3

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Figure 4
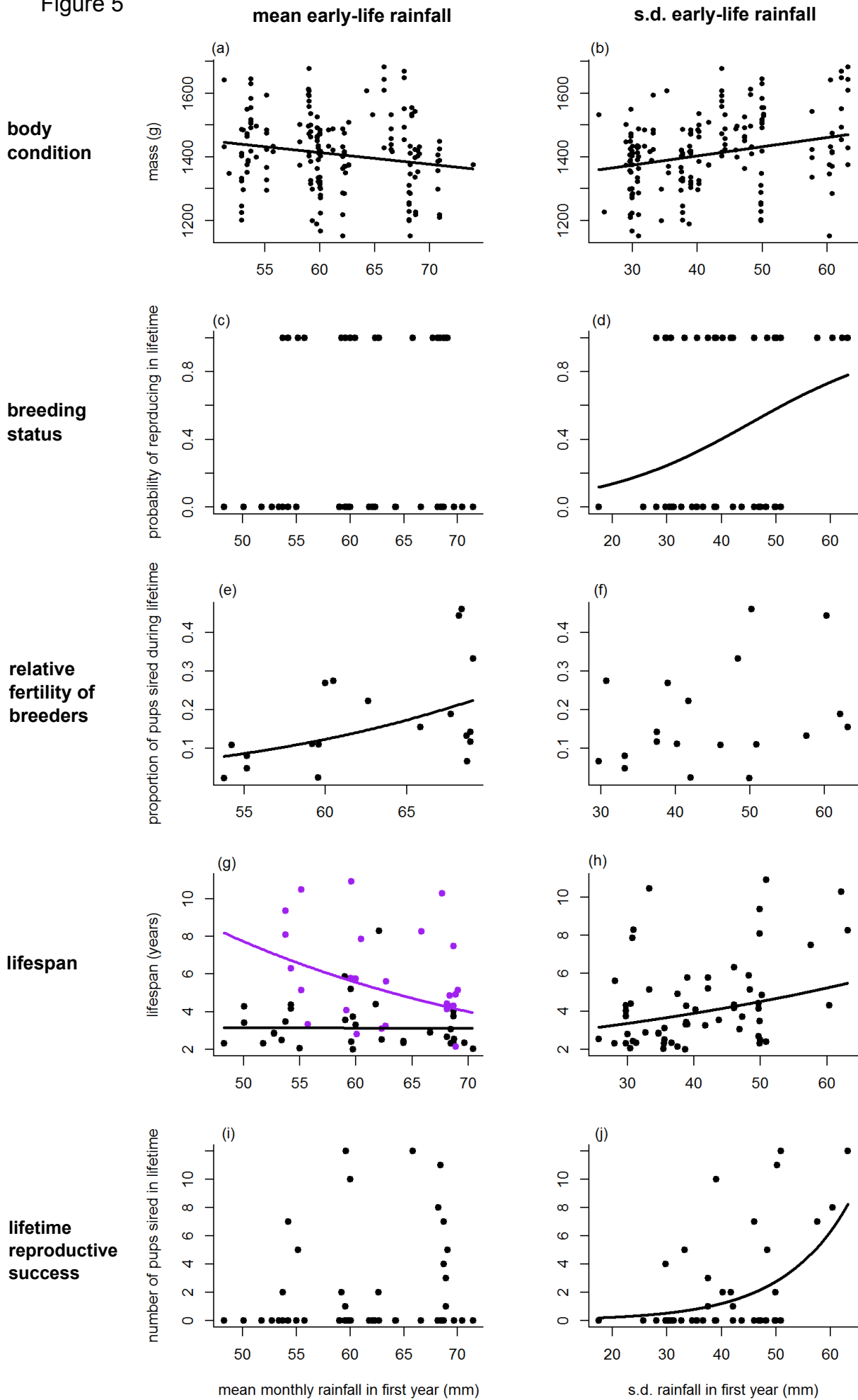
Figure 5

Figure 6