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

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

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

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

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

Data Collection

Ecological conditions

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

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

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

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

Banded mongooses

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

To answer part of our first question about whether early-life ecological conditions affect early-life social environment, we measured the amount of social care an individual received as a pup and the social rank of their parents. The amount of escorting (social care) a mongoose pup receives has been shown to affect its condition and survival during development and later-life reproduction (Gilchrist, Otali & Mwanguhya 2004; Hodge 2005). Similarly, parental social rank has been shown to influence individuals’ access to resources and growth in early-life, and reproduction in later-life in other systems (Altmann & Alberts 2005; Charpentier *et al.* 2008; Huchard *et al.* 2013). We measured the amount of escorting received by a pup as the proportion of group visits they were observed being escorted by an adult during the escorting period. Pups were defined as being escorted if they were within 30 cm of the same adult for more than 50% of the group visit time (Gilchrist 2004; Sanderson *et al.* 2014). Social dominance increases with age in banded mongooses (e.g. Nichols *et al.* 2010; Cant *et al.* 2014) and so parental rank was measured as the parent's age-rank within the group on the day of an individual's birth.

Statistical analyses

Effects of ecological conditions on invertebrate prey abundance and diversity

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

Effects of early-life ecological conditions on banded mongooses

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

We conducted our analyses using generalized linear mixed effect models (GLMMs). The residuals of models fitted using normal error structures (mass at 1 year old and adult mass) were checked to ensure they were normally distributed with constant variance. Models fitted to count data used a Poisson error structure unless they were overdispersed. Where this occurred, following Harrison (2014), models were fitted using a Poisson log-normal error structure and an observation-level random effect (lifespan models) unless the data were zero-inflated in which case a negative binomial error structure was used (lifetime reproductive success models). We used the same model selection procedure to our complementary study of the effect of ecological conditions during adulthood on banded mongooses (Marshall *et al.* 2016). We used likelihood ratio tests, comparing the full model to a model without a particular variable, to test the significance of this variable's effect (Forstmeier & Schielzeth 2011). Where interactions did not have a significant effect we dropped these from our final model to allow us to test the significance of the main effects in these non-significant interactions (Engqvist 2005). We did not reduce our model further due to the issues with stepwise model reduction techniques (Whittingham *et al.* 2006; Mundry & Nunn 2009; Forstmeier & Schielzeth 2011). Correlations between variables fitted in models as fixed effects – including the correlation between the mean and standard deviation of the monthly rainfall in a mongoose's first year – were lower than the levels previously shown to cause model fitting issues such as variance inflation in effect estimates (max $r = 0.36$, Freckleton 2011). We performed all 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.

		Sample size						Model fitting		
Models predicting how early-life ecological conditions affect:	Measured as	individuals M	individuals F	packs M	packs F	breeding attempts M	breeding attempts F	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, $\chi^2 = 5.70$, $p = 0.017$; Fig. 4a) and decreased with the standard deviation of monthly rainfall in the previous 12 months (β ± s.e. = -0.11 ± 0.04, $\chi^2 = 4.50$, $p = 0.034$; Fig. 4b). Invertebrate prey abundance was not affected by the amount of rainfall in the past 30 days ($\chi^2 = 2.14$, $p = 0.14$; 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: $\chi^2 = 0.79$, $p = 0.38$; s.d. rainfall: $\chi^2 =2.96$, $p = 0.09$). Invertebrate prey diversity was not predicted by any rainfall measure (linear terms, mean rainfall: $\chi^2 = 3.19$, $p = 0.07$, s.d, rainfall: $\chi^2 = 1.99$, $p = 0.16$; quadratic terms, mean rainfall: $\chi^2 = 0.24$, $p = 0.63$, s.d. rainfall: $\chi^2 = 1.35$, $p = 0.24$; rainfall in last 30 days: $\chi^2 = 0.71$, $p = 0.40$; model 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).

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

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

Table 2: Models predicting the effect of early-life ecological conditions on early-life social environment, body condition and survival. Parameter estimates (± 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

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

		Males				Females			
Model predicting	Explanatory variable	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.

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

Why might more variable ecological conditions be associated with increased fitness payoffs, without any apparent costs (Figure 6a)? Previous studies investigating the effect of the variability of early-life ecological conditions on later-life performance in a wild animal system are lacking. One possibility is that more varied early-life conditions might influence individuals' physiological or cognitive development such that they are able to cope with a greater range of environmental challenges in later-life. This hypothesis is supported by the fact that, at our study site, years with greater variation in monthly rainfall values were also those with greater maximum and lower minimum monthly rainfalls. Furthermore, comparing the range of monthly rainfall values males experienced during early-life to the range of monthly values they would experience during a typical male lifespan (42 months, Cant *et al.* 2016), those born in highly variable periods (the top third of early-life s.d. rainfall values) experienced 93% ± 7% (mean ± s.d., n = 50 males) of the typical lifetime range whilst those born in low variability periods (the bottom third of early-life s.d. values) experienced 63% ± 8% (n = 55 males). Our results do not support the possibility that a more variable early-life rainfall conferred advantages through a more diverse diet. However, there are parallels between our hypothesis that early-life variability may have beneficial impacts on physiological or cognitive development and findings from the medical literature. First, experiencing a wide variety of pathogens during childhood is recognised to be important in the development of the human immune system, with a lack of early-life immunological challenges leading to inappropriate immune responses in adulthood and allergic diseases (the "hygiene hypothesis": Strachan 1989, 2000; Wills-Karp *et al.* 2001; Yazdanbakhsh *et al.* 2002). Second, experiencing a variety of childhood psychological stressors is thought to have positive effects on some cognitive abilities in adults under stress (Frankenhuis & de Weerth 2013; Frankenhuis *et al.* 2015). Finally, it may be that reduced early-life food availability is beneficial. In laboratory models and humans dietary restriction has repeatedly been shown to increase lifespan (e.g. McCay *et al.* 1935; Fontana *et al.* 2004; Masoro 2006; Colman *et al.* 2009; Zhang *et al.* 2013). In support of this recent ecological studies have shown that restrictions on early-life diet can have benefits such as reduced oxidative damage in zebra finches, *Taeniopygia guttata*, and wild yellow-legged gulls, *Larus michahellis* (Noguera *et al.* 2011; Noguera, Monaghan & Metcalfe 2015). The link between our hypothesis and these biomedical findings is speculative at present, but there is clearly much scope for research to elucidate the mechanisms underlying the early-life effects reported here.

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

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

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

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

References

Altmann, J. & Alberts, S.C. (2005) Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral Ecology and Sociobiology*, **57**, 490–501.

Ancona, S. & Drummond, H. (2013) Life history plasticity of a tropical seabird in response to El Nino anomalies during early life. *PLoS ONE*, **8**, e72665.

Andrews, C., Viviani, J., Egan, E., Bedford, T., Brilot, B., Nettle, D. & Bateson, M. (2015) Early life adversity increases foraging and information gathering in European starlings, Sturnus vulgaris. *Animal Behaviour*, **109**, 123–132.

Balbontin, J. & Moller, A. (2015) Environmental conditions during early life accelerate the rate of senescence in a short-lived passerine bird. *Ecology*, **96**, 948–959.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. Available from: http://cran.rproject.org/package=lme4

Bateson, M., Emmerson, M., Ergün, G., Monaghan, P. & Nettle, D. (2015) Opposite effects of early-life competition and developmental telomere attrition on cognitive biases in juvenile European starlings. *Plos One*, **10**, e0132602.

Bell, M.B. V. (2010) Sex and age influence responses to changes in the cost of cooperative care in a social carnivore. *Behavioral Ecology*, **21**, 1118–1123.

Botero, C.A., Weissing, F.J., Wright, J. & Rubenstein, D.R. (2014) Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences*, **112**, 184–189.

Cant, M.A. (2000) Social control of reproduction in banded mongooses. *Animal behaviour*, **59**, 147–158.

Cant, M.A., Hodge, S.J., Bell, M.B. V, Gilchrist, J.S. & Nichols, H.J. (2010) Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2219–2226.

Cant, M.A., Nichols, H.J., Johnstone, R.A. & Hodge, S.J. (2014) Policing of reproduction by hidden threats in a cooperative mammal. *Proceedings of the National Academy of Sciences*, **111**, 326–330.

Cant, M.A., Nichols, H.J., Thompson, F.J. & Vitikainen, E. (2016) Banded mongooses: demography, life history, and social behavior. *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution and Behavior* (eds W.D. Koenig), & J.L. Dickinson), pp. 318–337. Cambridge University Press, Cambridge, UK.

Cant, M.A., Vitikainen, E. & Nichols, H.J. (2013) Demography and social evolution of banded mongooses. *Advances in the Study of Behavior*, **45**, 407–445.

Cartwright, S.J., Nicoll, M.A.C., Jones, C.G., Tatayah, V. & Norris, K. (2014) Anthropogenic natal environmental effects on life histories in a wild bird population. *Current Biology*, **24**, 536–540.

Charpentier, M.J.E., Tung, J., Altmann, J. & Alberts, S.C. (2008) Age at maturity in wild baboons: genetic, environmental and demographic influences. *Molecular Ecology*, **17**, 2026–2040.

Colman, R.J., Anderson, R.M., Johnson, S.C., Kastman, E.K., Kosmatka, K.J., Beasley, T.M., Allison, D.B., Cruzen, C., Simmons, H.A., Kemnitz, J.W. & Weindruch, R. (2009) Caloric restriction delays disease onset and mortality in rhesus monkeys. *Science*, **325**, 201–204.

Douhard, M., Plard, F., Gaillard, J.-M., Capron, G., Delorme, D., Klein, F., Duncan, P., Loe, L.E. & Bonenfant, C. (2014) Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20140276.

Engqvist, L. (2005) The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour*, **70**, 967–971.

Fontana, L., Meyer, T.E., Klein, S. & Holloszy, J.O. (2004) Long-term calorie restriction is highly effective in reducing the risk for atherosclerosis in humans. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 6659–6663.

Forstmeier, W. & Schielzeth, H. (2011) Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner’s curse. *Behavioral Ecology and Sociobiology*, **65**, 47–55.

Frankenhuis, W.E., Panchanathan, K. & Nettle, D. (2015) Cognition in harsh and unpredictable environments. *Current Opinion in Psychology*, **7**, 76–80.

Frankenhuis, W.E. & de Weerth, C. (2013) Does Early-Life Exposure to Stress Shape or Impair Cognition? *Current Directions in Psychological Science*, **22**, 407–412.

Freckleton, R.P. (2011) Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioral Ecology and Sociobiology*, **65**, 91–101.

Garratt, M., Lemaître, J.F., Douhard, M., Bonenfant, C., Capron, G., Warnant, C., Klein, F., Brooks, R.C. & Gaillard, J.M. (2015) High juvenile mortality is associated with sex-specific adult survival and lifespan in wild roe deer. *Current Biology*, **25**, 759–763.

Gilchrist, J.S. (2004) Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behavioral Ecology*, **15**, 952–960.

Gilchrist, J.S., Otali, E. & Mwanguhya, F. (2004) Why breed communally? Factors affecting fecundity in a communal breeding mammal: The banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology*, **57**, 119–131.

Gilchrist, J.S. & Russell, A.F. (2007) Who cares? Individual contributions to pup care by breeders vs non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*). *Behavioral Ecology and Sociobiology*, **61**, 1053–1060.

Gluckman, P.D., Hanson, M.A. & Spencer, H.G. (2005) Predictive adaptive responses and human evolution. *Trends in Ecology & Evolution*, **20**, 527–533.

Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A.P. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.

Hammers, M., Richardson, D.S., Burke, T. & Komdeur, J. (2013) The impact of reproductive investment and early-life environmental conditions on senescence: Support for the disposable soma hypothesis. *Journal of Evolutionary Biology*, **26**, 1999–2007.

Harrison, X.A. (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, **2**, e616.

Hayward, A.D., Rickard, I.J. & Lummaa, V. (2013) Influence of early-life nutrition on mortality and reproductive success during a subsequent famine in a preindustrial population. *Proceedings of the National Academy of Sciences*, **110**, 13886–13891.

Hodge, S.J. (2005) Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2479–2484.

Hodge, S.J. (2007) Counting the costs: the evolution of male-biased care in the cooperatively breeding banded mongoose. *Animal Behaviour*, **74**, 911–919.

Hodge, S.J., Bell, M.B. V & Cant, M.A. (2011) Reproductive competition and the evolution of extreme birth synchrony in a cooperative mammal. *Biology Letters*, **7**, 54–56.

Hodge, S.J., Bell, M.B.V., Mwanguhya, F., Kyabulima, S., Waldick, R.C. & Russell, A.F. (2009) Maternal weight, offspring competitive ability, and the evolution of communal breeding. *Behavioral Ecology*, **20**, 729–735.

Hoyle, R.B. & Ezard, T.H.G. (2012) The benefits of maternal effects in novel and in stable environments. *Journal of The Royal Society Interface*, 2403–2413.

Huchard, E., Charpentier, M.J., Marshall, H.H., King, A. J., Knapp, L.A. & Cowlishaw, G. (2013) Paternal effects on access to resources in a promiscuous primate society. *Behavioral Ecology*, **24**, 229–236.

Inzani, E.L., Marshall, H.H., Sanderson, J.L., Nichols, H.J., Thompson, F.J., Kalema-Zikusoka, G., Hodge, S.J., Cant, M.A. & Vitikainen, E.I.K. (2016) Female reproductive competition explains variation in prenatal investment in wild banded mongooses. *Scientific Reports*, **6**, 20013.

Jordan, N., Mwanguhya, F., Kyabulima, S., Ruedi, P. & Cant, M.A. (2010) Scent marking within and between groups of wild banded mongooses. *Journal of Zoology*, **280**, 72–83.

Kirkwood, T.B.L. & Rose, M.R. (1991) Evolution of senescence: late survival sacrificed for reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **332**, 15–24.

Kruuk, L.E., Clutton-Brock, T.H., Rose, K.E. & Guinness, F.E. (1999) Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1655–1661.

Kuijper, B. & Hoyle, R.B. (2015) When to rely on maternal effects and when on phenotypic plasticity ? *Evolution*, **69**, 950–968.

Kwok, A.B.C., Wardle, G.M., Greenville, A.C. & Dickman, C.R. (2016) Long-term patterns of invertebrate abundance and relationships to environmental factors in arid Australia. *Austral Ecology*, **41**, 480–491.

Lewis, J. (1971) The life history and ecology of the millipede Tymbodesmus falcatus (Polydesmida : Gomphoclesmidae) in northern Nigeria with notes on Sphenodesmus sheribongensis. *Proceedings of the Zoological Society of London*, **164**, 551–563.

Lindström, J. (1999) Early Developnment and fitness in birds and mammals. *Trends in Ecology and Evolucion*, **14**, 343–348.

Marshall, H.H., Sanderson, J.L., Mwanghuya, F., Businge, R., Kyabulima, S., Hares, M.C., Inzani, E., Kalema-Zikusoka, G., Mwesige, K., Thompson, F.J., Vitikainen, E.I.K. & Cant, M.A. (2016) Variable ecological conditions promote male helping by changing banded mongoose group composition. *Behavioral Ecology* , **27**, 978–987.

Masoro, E.J. (2006) Dietary restriction-induced life extension: A broadly based biological phenomenon. *Biogerontology*, **7**, 153–155.

McCay, C.M., Crowell, M.F. & Maynard, L.A. (1935) The effect of retarded growth upon the length of life span and upon the ultimate body size. *The Journal of Nutrition*, **5**, 63–79.

Millon, A., Petty, S.J., Little, B. & Lambin, X. (2011) Natal conditions alter age-specific reproduction but not survival or senescence in a long-lived bird of prey. *Journal of Animal Ecology*, **80**, 968–975.

Monaghan, P. (2008) Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 1635–1645.

Mundry, R. & Nunn, C.L. (2009) Stepwise model fitting and statistical inference: turning noise into signal pollution. *American Naturalist*, **173**, 119–123.

Murray, D.L. (2006) On improving telemetry-based survival estimation. *Journal of Wildlife Management*, **70**, 1530–1543.

Nettle, D., Andrews, C.P., Monaghan, P., Brilot, B.O., Bedford, T., Gillespie, R. & Bateson, M. (2015a) Developmental and familial predictors of adult cognitive traits in the European starling. *Animal Behaviour*, **107**, 239–248.

Nettle, D. & Bateson, M. (2015) Adaptive developmental plasticity: what is it, how can we recognize it and when can it evolve? *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151005.

Nettle, D., Monaghan, P., Gillespie, R., Brilot, B., Bedford, T. & Bateson, M. (2015b) An experimental demonstration that early-life competitive disadvantage accelerates telomere loss. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20141610.

Nichols, H.J., Amos, W., Cant, M.A., Bell, M.B.V. & Hodge, S.J. (2010) Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose. *Animal Behaviour*, **80**, 649–657.

Nichols, H.J., Bell, M.B. V., Hodge, S.J. & Cant, M.A. (2012) Resource limitation moderates the adaptive suppression of subordinate breeding in a cooperatively breeding mongoose. *Behavioral Ecology*, **23**, 635–642.

Noguera, J., Lores, M., Alonso-Alvarez, C. & Velando, A. (2011) Thrifty development: early-life diet restriction reduces oxidative damage during later growth. *Functional Ecology*, 1144–1153.

Noguera, J., Monaghan, P. & Metcalfe, N. (2015) Interactive effects of early and later nutritional conditions on the adult antioxidant defence system in zebra finches. *Journal of Experimental Biology*, **218**, 2211–2217.

Nussey, D.H., Kruuk, L.E.B., Morris, A. & Clutton-Brock, T.H. (2007) Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biology*, **17**, 1000–1001.

O'Hagan, D., Andrews, C.P., Bedford, T., Bateson, M. & Nettle, D. (2015) Early life disadvantage strengthens flight performance trade-offs in European starlings, *Sturnus vulgaris*. *Animal Behaviour*, **102**, 141–148.

Otali, E. & Gilchrist, J.S. (2004) The effects of refuse feeding on body condition, reproduction, and survival of banded mongooses. *Journal of Mammalogy*, **85**, 491–497.

Van de Pol, M., Bruinzeel, L.W., Heg, D., Van der Jeugd, H.P. & Verhulst, S. (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **75**, 616–626.

R Core Team. (2014) R: A language and environment for statistical computing. Version 3.1.1. Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org/.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*. *Journal of Animal Ecology*, **72**, 36–46.

Reznick, D. & Yang, A.P. (1993) The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. *Ecology*, **74**, 2011–2019.

Rood, J. (1975) Population dynamics and food habits of the banded mongoose. *East African Journal of Ecology*, **13**, 89–111.

Rosa, R., Baptista, M., Lopes, V.M., Pegado, M.R., Paula, J.R., Trübenbach, M.C., Leal, R.C. & Repolho, T. (2014) Early-life exposure to climate change impairs tropical shark survival. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20141738.

Rubenstein, D.R., Skolnik, H., Berrio, A., Champagne, F.A., Phelps, S. & Solomon, J. (2016) Sex-specific fitness effects of unpredictable early life conditions are associated with DNA methylation in the avian glucocorticoid receptor. *Molecular Ecology*, **8**, 1714-1728.

Saeki, Y., Tuda, M. & Crowley, P.H. (2014) Allocation tradeoffs and life histories: A conceptual and graphical framework. *Oikos*, **123**, 786–793.

Sanderson, J.L., Wang, J., Vitikainen, E.I.K., Cant, M.A. & Nichols, H.J. (2015) Banded mongooses avoid inbreeding when mating with members of the same natal group. *Molecular Ecology*, **24**, 3738–3751.

Sanderson, J.L., Young, A.J., Hodge, S.J., Kyabulima, S., Walker, S.L. & Cant, M. a. (2014) Hormonal mediation of a carry-over effect in a wild cooperative mammal (ed C McArthur). *Functional Ecology*, **28**, 1377-1386.

Strachan, D.P. (1989) Hay fever, hygiene, and household size. *British Medical Journal*, **299**, 1259–1260.

Strachan, D.P. (2000) Family size, infection and atopy: the first decade of the “hygiene hypothesis”. *Thorax*, **55 Suppl 1**, S2–S10.

Taborsky, B. (2006) The influence of juvenile and adult environments on life-history trajectories. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 741–750.

Thompson, F.J., Marshall, H.H., Sanderson, J.L., Vitikainen, I.K., Nichols, H.J., Gilchrist, J.S., Young, A.J., Hodge, S.J. & Cant, M.A. (2016) Reproductive competition triggers mass eviction in cooperative banded mongooses. *Proceedings of the Royal Society B: Biological sciences*, **283**, 20152607.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, **75**, 1182–1189.

Wilkin, T.A. & Sheldon, B.C. (2009) Sex differences in the persistence of natal environmental effects on life histories. *Current Biology*, **19**, 1998–2002.

Wills-Karp, M., Santeliz, J. & Karp, C.L. (2001) The germless theory of allergic disease: revisiting the hygiene hypothesis. *Nature Reviews Immunology*, **1**, 69–75.

Wong, J.W.Y. & Kölliker, M. (2014) Effects of food restriction across stages of juvenile and early adult development on body weight, survival and adult life history. *Journal of Evolutionary Biology*, **27**, 2420–2430.

Yazdanbakhsh, M., Kremsner, P.G. & van Ree, R. (2002) Allergy, parasites, and the hygiene hypothesis. *Science*, **296**, 490–494.

Zera, A.J. & Harshman, L.G. (2001) The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, **32**, 95–126.

Zhang, C., Li, S., Yang, L., Huang, P., Li, W., Wang, S., Zhao, G., Zhang, M., Pang, X., Yan, Z., Liu, Y. & Zhao, L. (2013) Structural modulation of gut microbiota in life-long calorie-restricted mice. *Nature Communications*, **4**, 2163.

Figure legends

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

Figure 2: Banded mongoose mass change with age. Panel a shows all data and panel b zooms in on data from individuals between the ages of 0 and 3 years. In both panels the vertical dotted lines divide the data into masses from individuals aged 0 to 1 year (zone i), 1 to 2 years (zone ii) and over 2 years (zone iii).

Figure 3: The rainfall pattern (a) within and (b) between years at our study site: the Mweya Peninsula, Uganda. Panel a shows the mean (± standard error) rainfall recorded in each month (n = 152 months, month 1 = January). Panel b shows the mean (filled circles and solid line) and standard deviation (open circles and dashed line) of the monthly rainfall within each year. Rainfall data for 2002 is incomplete and so not shown.

Figure 4: The effect of (a) the mean and (b) the standard deviation of monthly rainfall in the past 12 months on invertebrate prey abundance. Note the log scale on the y axis.

Figure 5: Male mongooses' reproduction and survival and the mean (left-hand panels) and variability (right-hand panels) of rainfall in their first year. Panels show the effect on adult males': mass (a,b), probability of siring at least one pup (c,d); in those that did sire a pup, the proportion of all pups born into their group that they sired (e,f); their lifespan (g,h); the total number of pups they sired in their lifetime (i,j). Lines show significant relationships predicted by models (see Table 3). Non-significant relationships are not plotted. In panel g the data and predicted relationships are split by into males who successfully reproduced in their lifetime (purple) and those who did not (black).

Figure 6: Graphical illustration of the hypothesised effect of changes in the (a) variability and (b) mean of early-life rainfall on life-history trade-off and allocation patterns (after Saeki *et al.* 2014). The thin grey lines represent fitness isoclines along which all positions return an equal payoff. The thick dashed line represents the reference trade-off slope for an individual (here straight lines for simplicity) and the yellow dot represents the reference optimal allocation of resources to survival and reproduction (where the trade-off slope is tangential to the isocline). In panel a) the thick red lines and dots show how an (i) increase or (ii) decrease in the variability of early-life rainfall relaxes or increases the life-history trade-off constraints leading to higher or lower fitness payoffs. In panel b) the thick blue lines and dots represent how an (iii) increase or (iv) decrease in mean early-life rainfall leads to changes in an individual's trade-off slope and optimal allocation of resources but no change in their overall fitness payoff.

Figure 1

Figure 2

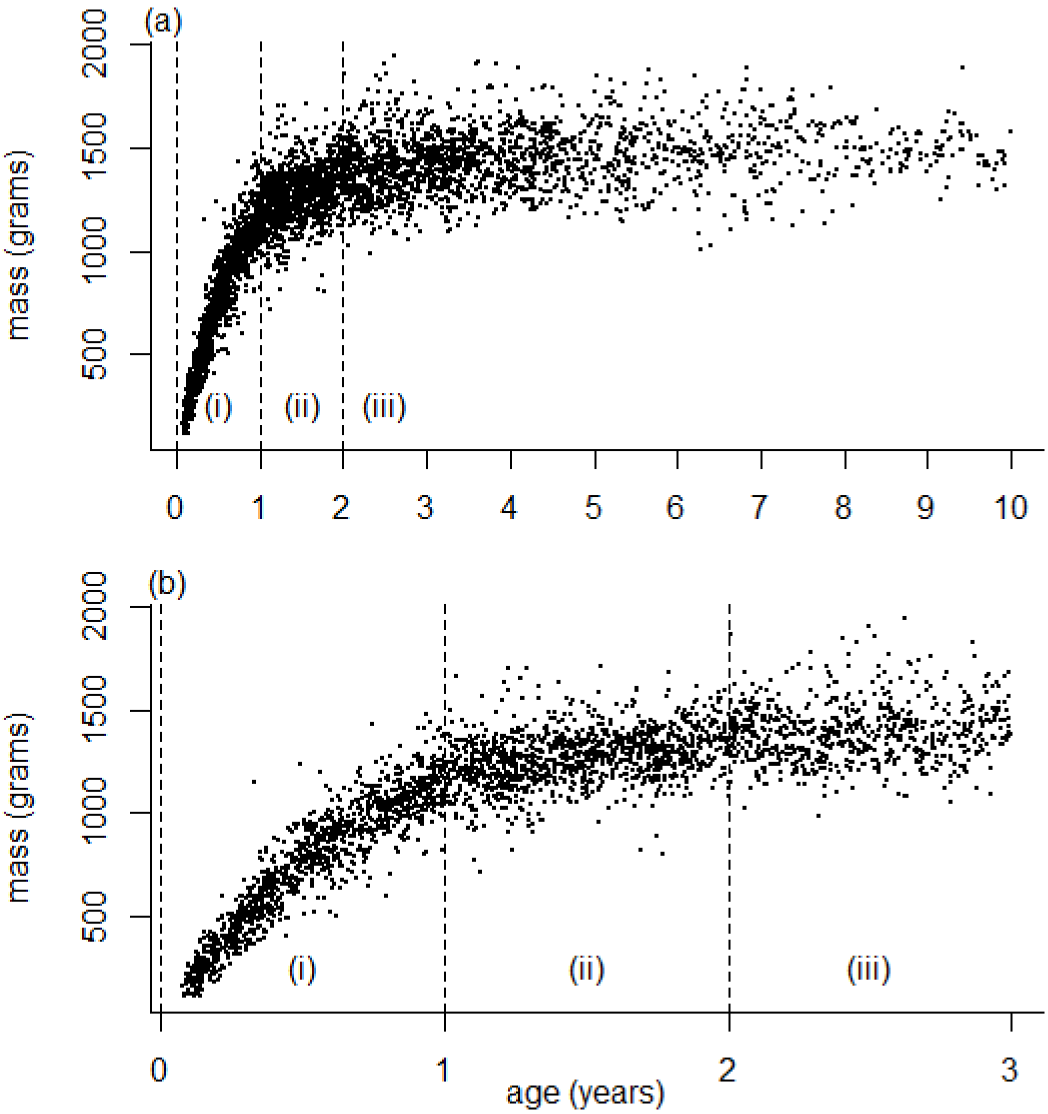

(a)
mass (grams)
500
1000
1500
2000
(i)
(ii)
(iii)
0
1
2
3
4
5
6
7
8
9
10
(b)
mass (grams)
500
1000
1500
2000
(i)
(ii)
(iii)
0
1
2
3
age (years)

Figure 3

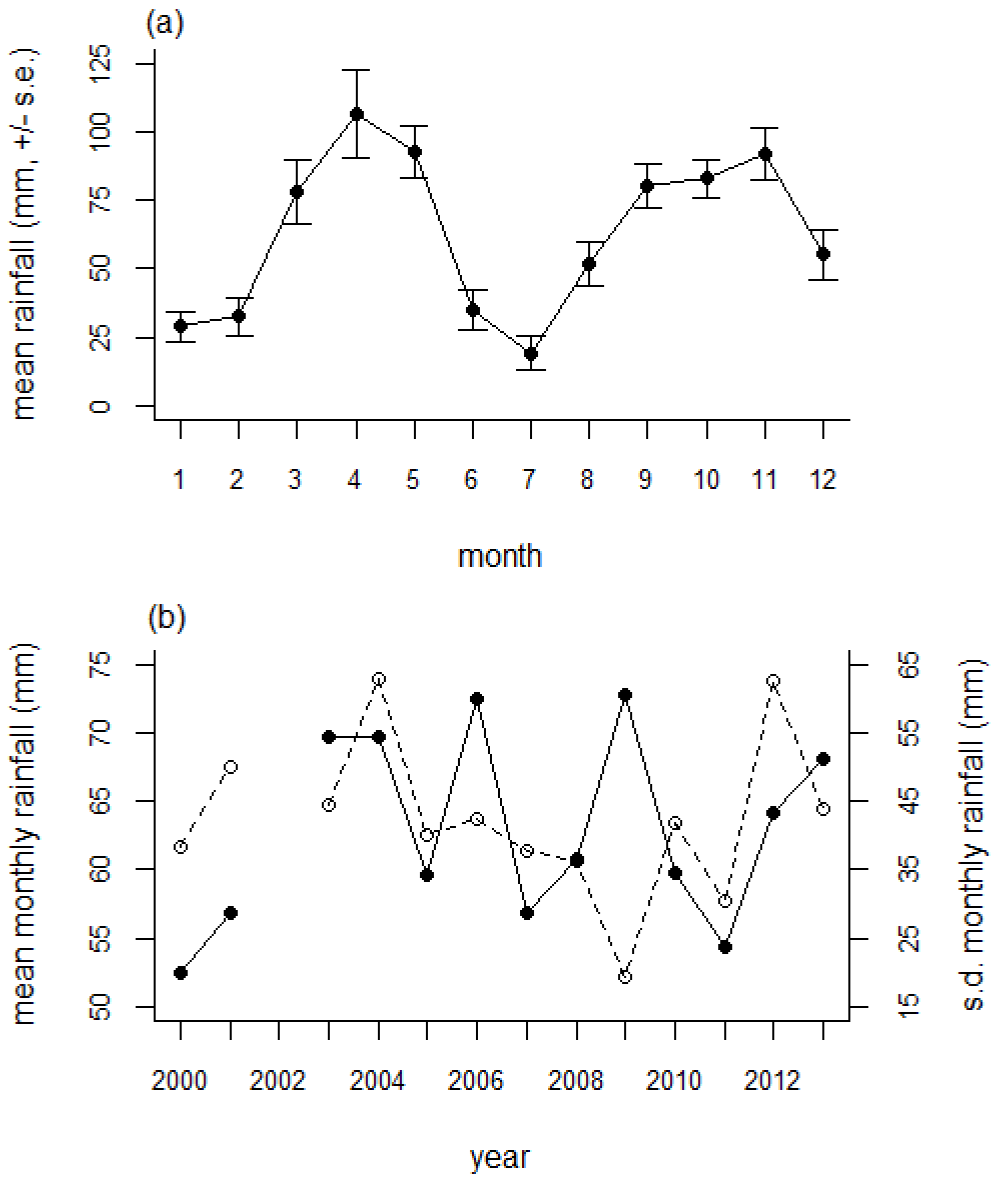

(a)
mean rainfall (mm, +/- s.e.)
0
25
50
75
100
125
1
2
3
4
5
6
7
8
9
10
11
12
month
(b)
mean monthly rainfall (mm)
50
55
60
65
70
75
s.d. monthly rainfall (mm)
15
25
35
45
55
65
2000
2002
2004
2006
2008
2010
2012
year

Figure 4

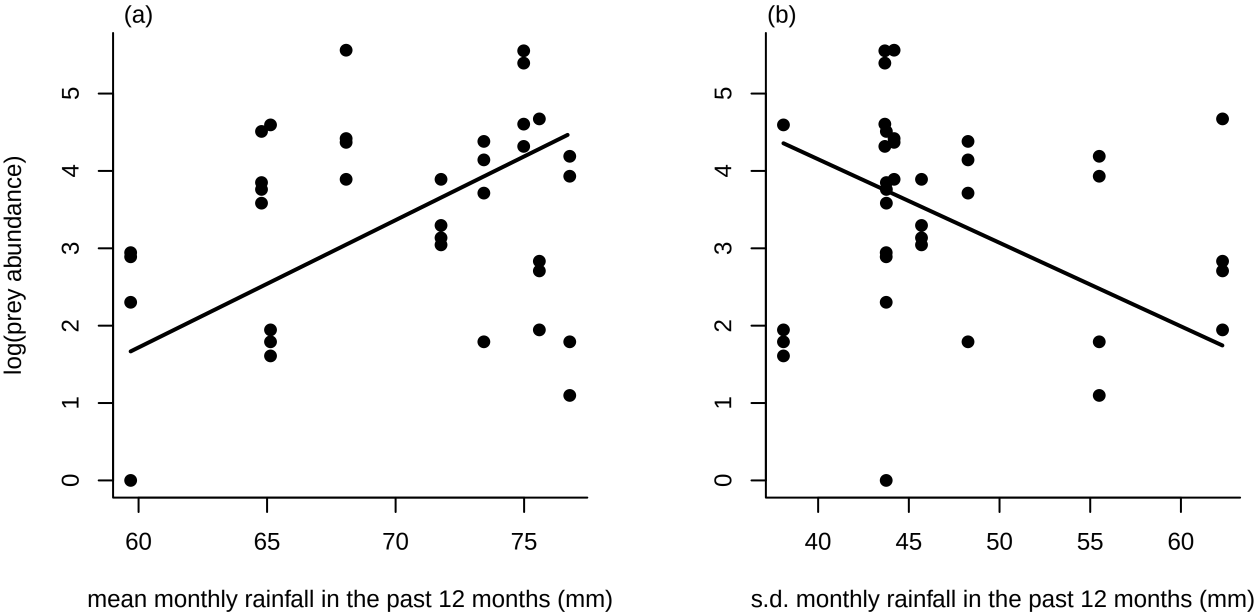
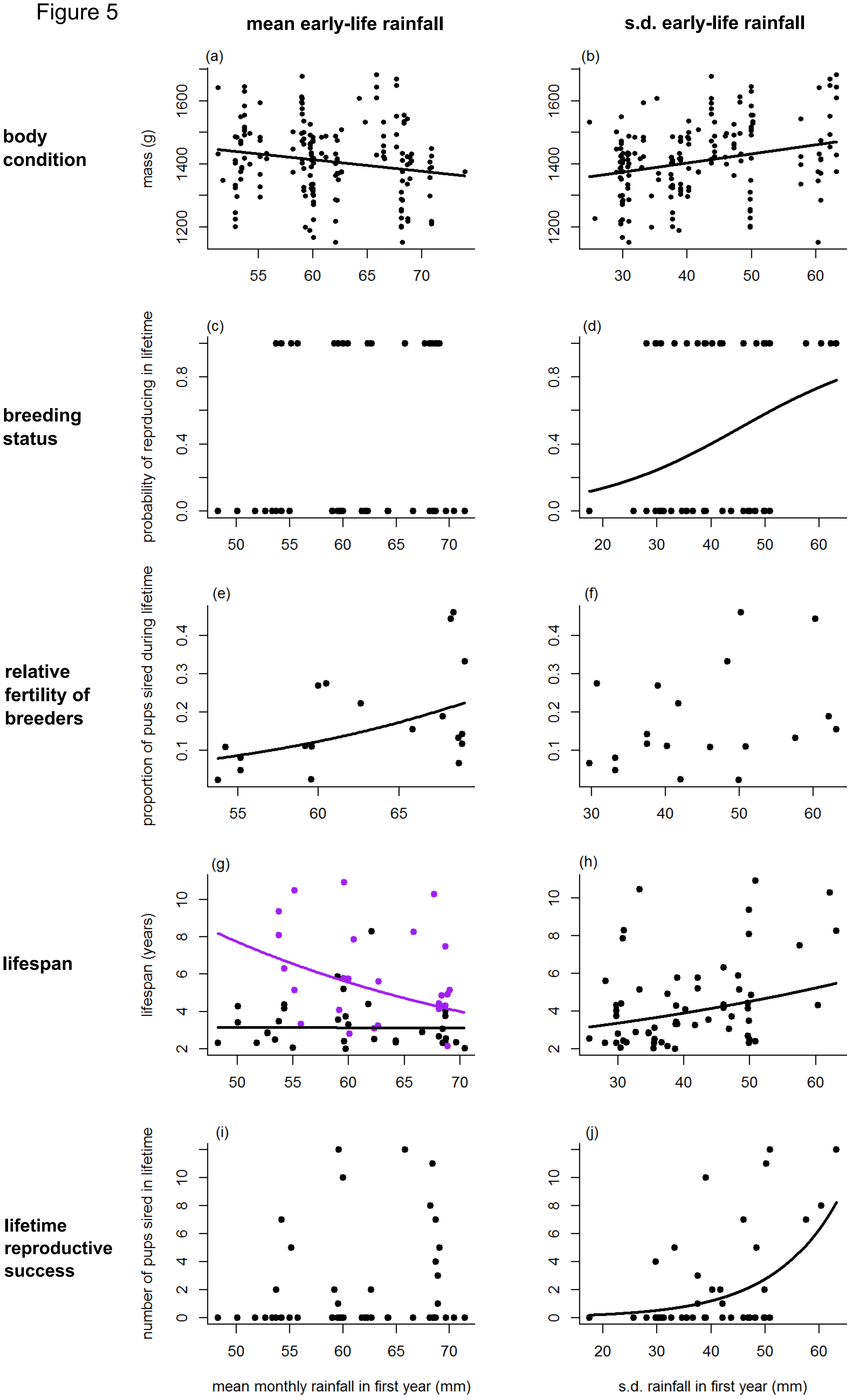
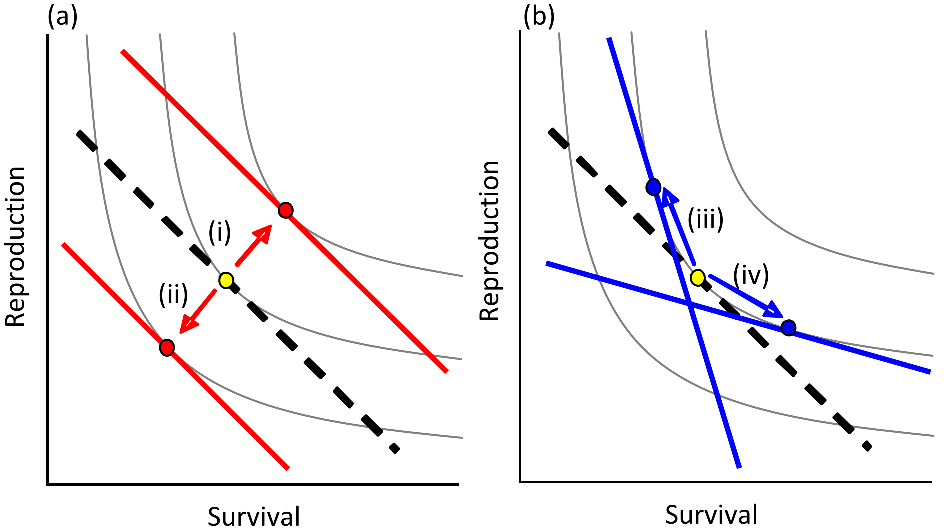

(a)
(b)
log(prey abundance)
0
1
2
3
4
5
60
65
70
75
40
45
50
55
60
mean monthly rainfall in the past 12 months (mm)
s.d. monthly rainfall in the past 12 months (mm)

Figure 5



mean early-life rainfall
s.d. early-life rainfall
body condition
breeding status
relative fertility of breeders
lifespan
lifetime reproductive success
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
mass (g)
1200
1400
1600
55
60
65
70
30
40
50
60
probability of reprducing in lifetime
0.0
0.4
0.8
50
55
60
65
70
20
30
40
50
60
proportion of pups sired during lifetime
0.1
0.2
0.3
0.4
55
60
65
30
40
50
60
lifespan (years)
2
4
6
8
10
50
55
60
65
70
30
40
50
60
number of pups sired in lifetime
0
2
4
6
8
10
50
55
60
65
70
20
30
40
50
60
mean monthly rainfall in first year (mm)
s.d. rainfall in first year (mm)

Figure 6


(a)
Reproduction
Survival
(i)
(ii)
(b)
Reproduction
Survival
(iii)
(iv)