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Evolution of differential maternal age effects on male and female offspring development and longevity

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Running headline: Sex-specific maternal age effects

Summary

1 Maternal age effects on life-history traits, including longevity, are widespread and can be seen as a manifestation of ageing. However, little is known about how maternal lifespan may influence the maternal age effect. At a given chronological age, a long-lived parent may be at a younger biological age than a short-lived parent, and thus have a less severe parental age effect. However, earlier work using experimentally evolved short- and long-lived lines did not support this hypothesis.

2 We scored developmental time and longevity of 14995 individual seed beetles, *Callosobruchus maculatus* derived from replicate short-lived and long-lived lines created via artificial selection on male lifespan.

3 Offspring from older mothers had shorter lifespan, which is consistent with most of the literature.

4 We found support for the hypothesis that detrimental maternal age effects evolve to be weaker under selection for long lifespan. However, this finding was only apparent in males, suggesting that maternal age affects male and female offspring differently.

5 These results suggest that sex-dependent parental age effects should be incorporated in the studies of longevity and ageing evolution and that selection on one sex can cause evolution of parental age effects in the other sex.

Key-words: Ageing, *Callosobruchus maculatus*, Eclosion success, Sex-specific response

INTRODUCTION

Ageing, defined as the decline in physiological and reproductive performance and the increase in probability of death with age, is a nearly universal phenomenon (Hamilton 1966; Rose 1991; Charlesworth 1994; Hughes & Reynolds 2005). Variation in the ageing rates, combined with different levels of extrinsic mortality, results in within and among species variation in lifespan. Lifespan is heritable (Johnson & Wood 1982; Klebanov *et al.* 2000; Kemkes-Grottenthaler 2004; Fox *et al.* 2004a), often sexually dimorphic (Trivers 1985; Bonduriansky *et al.* 2008; Maklakov & Lummaa 2013), and evolves rapidly in the laboratory (Rose 1984; Zwaan, Bijlsma & Hoekstra 1995; Partridge, Prowse & Pignatelli 1999; Remolina *et al.* 2012; Berg & Maklakov 2012).

Although lifespan is heritable, it can vary considerably among an individual's offspring. One key factor contributing to such variation is parental age (Lansing 1947; Gavrilov & Gavrilova 1997; Priest, Mackowiak & Promislow 2002). The influence of parental age on offspring longevity has been a particularly hot topic in recent human studies, but has also been investigated in animal systems. The prevailing view is that offspring lifespan decreases with increased parental age (known as the "Lansing effect "; Lansing 1947; Rockstein 1957; Tracey 1958; O´Brian 1961; Kiritani & Kimura 1967; Gavrilov & Gavrilova 1997; Priest *et al.* 2002; García-Palomares *et al.* 2009; but see Fox, Bush & Wallin 2003). Moreover, the parental age effect is frequently specific to both parent and offspring sex. Maternal age is often the strongest factor affecting offspring lifespan (Butz & Hayden 1962; Priest *et al.* 2002), although, intriguingly, in humans the father's age appears to play a bigger role (Gavrilov & Gavrilova 1997; Kemkes-Grottenthaler 2004).

A few studies have also investigated whether parental age affects sons and daughters differently. Interestingly, in humans, paternal age strongly influences the lifespan of daughters while neither maternal nor paternal age had a significant effect on the lifespan of sons (Gavrilov & Gavrilova 1997; Kemkes-Grottenthaler 2004). Unlike in humans, in model laboratory organisms it has been possible to experimentally partition parental age effects and sex-specific offspring effects. However, there have been relatively few studies and the results are mixed. One such study of fruit flies found that paternal age effects more strongly influenced the lifespan of sons, while maternal age effects more strongly influenced the lifespan of daughters (Priest *et al.* 2002), the latter finding has also been reported in an early experiment by Butz & Hayden (1962). Also in mice, maternal age seems mostly to influence daughters (Carnes, Riesch & Schlupp 2012). In seed beetles, previous seminal work has shown that while maternal age affects males more than females, the overall effect was positive, contrary to a more common pattern observed in other systems (Fox *et al.* 2003).

Despite accumulating empirical evidence for parental age effects, very little is known about how parental lifespan should influence the parental age effect on offspring lifespan. This is important, since at a given chronological age, a long-lived parent may be at a younger biological age than a short-lived parent, and thus have a less severe parental age effect. Since parental age effects are often caused by similar mechanisms that are involved in ageing (such as mutation load or trade-offs between early and late function) (Priest *et al.* 2002; Kemkes-Grottenthaler 2004; Kong *et al.* 2012), it is likely that these effects will differ among long- and short-lived parents. Since the parental age effect has been shown to differ among genotypes (Priest *et al.* 2002), it has the potential to be influenced by the evolution of parental lifespan.

We set out to test this hypothesis in long-lived and short-lived lines of the seed beetle *Callosobruchus maculatus* Fabricius (Berg & Maklakov 2012). The seed beetle *C. maculatus* is a model organism for studies of experimental life-history evolution (Messina 2004; Fricke & Arnqvist 2007; Maklakov, Bonduriansky & Brooks 2009), since it has a short generation time, thrives in a laboratory environment, and is facultatively aphagous (i.e. does not require food or water once it emerges as an adult) (Fox 1993b; Fox *et al.* 2003). In this study, we used the lines that had been selected for long and short adult male lifespan, which resulted in the evolution of significant differences in longevity in both sexes because of intersexual genetic correlation for this trait (Berg & Maklakov 2012). We used these lines to test for sex- and selection-specific maternal age effects on offspring lifespan.

MATERIALS AND METHODS

Study system

C. maculatus is a very common pest of stored legumes. Females paste their eggs onto the host bean's surface. Larvae hatch a few days later and burrow directly into the bean, using it as a food resource until hatching out as reproductively mature adults between 23-27 days after the egg is laid. *C. maculatus* are capital breeders, obtaining all of the resources required for survival and reproduction during the larval stage (Fox 1993b; Fox *et al.* 2003). Females live shorter than males, and the adult lifespan is normally between 6 and 20 days, depending upon factors such as temperature and host plants (Fox *et al.* 2004b, Fox *et al.* 2011, Berg & Maklakov 2012).

The long- and short-life selection lines used in our experiment were derived from a heterogeneous South Indian population ("SI USA") obtained from C. W. Fox at the University of Kentucky, USA. Originally collected in 1979 from infested mung beans (*Vigna radiata*) in Tirunelveli, India (Mitchell 1991), this stock population has been maintained in our lab for over 80 generations. The beetles have been cultured exclusively on mung beans and kept in climate chambers at 30°C, 50% relative humidity and a 14:10 hr light-dark cycle.

Artificial selection on male lifespan

Prior to this experiment, we selected directly on male lifespan for a total of nine generations to create four replicate "long-life" selection lines where males lived on average 40% longer than in four “short-life” selection lines. For details of the selection procedure, see Berg & Maklakov (2012).

Maternal age effects

We allowed each of the lines to mate at random for two generations before assessing maternal age effects in order to reduce any residual parental effects. Beans, each bearing a single hatched egg, were then isolated in individual “virgin chambers” (containers with separate wells for each bean) prior to hatching. For each of the four long-life and four short-life selection lines, a one-day old virgin female was paired with a one-day old virgin male from the unselected baseline population (n = 20 pairs per line), in order to eliminate any systematic male effects. Pairs were placed in a 60 mm Petri dish with approximately 75 beans (“Day 1” dishes). We chose this number of beans, since females can lay up to 65 eggs per day (Berg, unpublished data), and we wanted to provide enough beans so that no more than one egg would be laid on each bean. After 24 hours, the males were removed and discarded, females were moved to a new dish with 75 fresh beans (“Day 2” dishes), and the initial dishes were stored in the climate chamber. After 24 hours, the female was moved to a new dish with 75 fresh beans (“Day 3”), and the Day 2 dishes were stored. This process was repeated one additional time (“Day 4+”). The females were allowed to remain in the fourth dish until death. Dishes were monitored daily, and the date of death of each female was recorded.

All hatched eggs from all days (Day 1 through Day 4+) were placed in individually marked virgin chambers and monitored daily until eclosion. The age at eclosion, sex, and age at death were recorded for all offspring. This gives an accurate estimate of lifespan from all maternal ages, but because females were left in Day 4+, their eggs could be laid over several days, and therefore the development time (but not lifespan) from Day 4+ will be overestimated. We therefore performed all analyses that included development time both with and without Day 4+.

We collected data on the offspring of 20 females of each of the 8 lines. On average, we scored 94 offspring per female, resulting in a total of 14995 offspring scored. 6147 beetles emerged from eggs laid during Day 1, 2808 from Day 2, 2764 from Day 3 and 3236 from Day 4+.

Statistical analysis

We tested the effect of maternal age and selection background on adult emergence success in a generalized mixed effect model implemented in a Bayesian MCMC framework using the package *MCMCglmm* (Hadfield 2010) in *R* 2.15.3 (R Development Core Team 2011). For all models, one day was subtracted from maternal age, to have the model intercept at day one. Emergence success was treated as a binary response variable (yes/no), selection background (long/short life) as a fixed factor and maternal age and age^2 as covariates estimating the direction (the age term) and curvature (the age^2 term) of the maternal age effect. Line was treated as a random effect, and because several offspring of each mother were scored, we also included maternal ID as a random effect to avoid pseudoreplication. Model selection using DIC (the Bayesian equivalent to AIC) was performed to find the minimal model.

All offspring that emerged from the beans were scored for development time and lifespan, which were investigated in separate mixed effect models with offspring sex and selection background as fixed factors, maternal age and age^2 as covariates, and line and maternal ID were fitted as random effects. Response variables were log transformed to meet the assumptions of normality. Since the maternal age effect influenced both development time and ageing, we also ran a similar model for lifespan that, in addition to the factors above, also included mean-centered development time as a covariate. Since development time from Day 4+ could be overestimated (see above), we analysed maternal age effects on development time, as well as the role of development time for lifespan both with and without the inclusion of Day 4+.

RESULTS

Egg-to-adult survival was very high. On average 97.6% of all eggs produced adults, and the eclosion success increased significantly with increased maternal age (posterior mode: 0.366, 95% HPD interval: 0.127; 0.715, pMCMC: 0.015). The increase was linear, since the effect of maternal age^2 was not significant (posterior mode: -0.115, 95% HPD interval: -0.212; -0.004, pMCMC: 0.061). Selection background had no effect on egg-to-adult survival (posterior mode: 0.198, 95% HPD interval: -0.387; 0.563, pMCMC: 0.583).

Development time was affected by selection background, offspring sex and maternal age (Table 1, Fig. 1). We found that increased maternal age resulted in an increase in the development time of her offspring (with a positive quadratic component), but this effect was line specific. In lines selected for short male lifespan, offspring produced by young mothers took longer to develop than offspring from long-lived lines. However, this effect disappeared with increased maternal age (maternal age × selection treatment interaction), resulting in similar development time to the lines selected for long lifespan when laid by old mothers. Sons developed faster than daughters in both selection backgrounds, but the difference in development time between the selected lines was larger in daughters. A strong sign of a maternal age effect on development time in both selection backgrounds was also present when data from Day 4+ was included (Table 1).

We found that mothers from the lines selected for long lifespan produced offspring that had a longer life than offspring of mothers from short lifespan lines, and that offspring lifespan in both selection backgrounds decreased with increased maternal age (Table 2, Fig. 2a). Daughters lived substantially longer than sons, and the maternal age effect was specific to both offspring sex and the selection background of the line. The maternal age effect was stronger for sons from short-life lines than for sons from long-life lines, but this effect was most pronounced in offspring born during the first two days of a mothers adult lifespan, as indicated by the interaction between selection treatment, sex and maternal age. We also found that the quadratic curvature differed between lines and offspring sex, most noticeable for males of the short lived lines, who not only had the largest drop in offspring lifespan between maternal age 1 and 2, but then a small increase in offspring lifespan for age 3 and 4+. No obvious difference in maternal age effect between the selected lines was present for daughters.

When development time was used as a covariate, we found that long development time was associated with short lifespan, with a similar effect in both sexes and selection treatments (Table 2, Fig. 2b). Much of the difference in lifespan between the lines was explained by development time, but not the sex difference in lifespan. Offspring born to young (day 1) mothers had longer lifespan than expected when controlling for development time, suggesting that other factors than development time are responsible for the maternal age effect on offspring lifespan. Again, an interaction between selection treatment, sex and maternal age indicated that the negative effect on maternal age in the short-lived lines was most pronounced in sons produced during the first two days. An interaction between offspring sex and maternal age^2 indicates a different shape of the maternal age effect between sons and daughters, and this effect was present in all selected lines. When data from the Day 4+ treatment was included, it did not affect the pattern found (see Table S1 in Supporting Information).

DISCUSSION

We found that offspring of older mothers had reduced lifespan, which is consistent with the large body of literature on the negative impact of older parents across the animal kingdom (Lansing 1947; Rockstein 1957; Tracey 1958; O´Brian 1961; Butz & Hayden 1962; Kiritani & Kimura 1967; Gavrilov & Gavrilova 1997; Klass 1977; Priest *et al.* 2002; Kemkes-

Grottenthaler 2004; Tucić *et al.* 2004, but see Fox, Bush & Wallin 2003). Our main finding, however, is that the maternal age effect on offspring lifespan had evolved in long-lived lines, and that this evolutionary response was sex-specific: increased maternal age is less damaging for offspring lifespan when mothers are from a long-lived genetic background, and this effect is stronger for sons than for daughters. This effect was however only present during the first two days of maternal age. We found that development time increased with maternal age, likely because of a reduction in maternal provisioning, but that the sex-specific maternal age effect on offspring lifespan was present even after controlling for the strong negative effect of long development time on lifespan.

Maternal age effects that reduce offspring lifespan are common (but see Fox *et al.* 2003, discussed below) and are believed to be caused by a number of mechanisms including maternal provisioning, the accumulation of late acting deleterious mutations, and trade-offs between early- and late-life function (Priest *et al.* 2002). Since these two latter mechanisms are also key explanations for the evolution of lifespan and ageing, and that genetic variation for maternal age effects are present in nature (Priest *et al.* 2002), there is a potential for maternal age effects to be influenced by the evolution of ageing. We therefore investigated whether lines artificially selected for long or short male lifespan would also differ in maternal age effects. We found not only that individuals whose mothers were from lines selected for long life lived longer, but also that the maternal age effect that caused a reduction in offspring lifespan was weaker in the long-life lines, especially for sons. Since long-lived females likely had a lower biological age at a given chronological age compared to the short-lived females, this result suggests that long maternal lifespan reduces the negative effect of maternal age on offspring lifespan. Notably, the effect was most pronounced during the first days of female adult life, with a large drop in offspring lifespan laid by 2-day-old mothers from the short-lived lines. Female *C. maculatus* are known to lay most eggs during the first days of adult life (Fox 1993a; Tatar & Carey 1995), indeed 60% of total eggs produced in this experiment were laid during the first two days. This suggests that the maternal age effect may have a large fitness impact.

Interestingly, the only previous study that investigated the evolution of maternal age effects in short-lived and long-lived experimental lines reported negative results. When comparing lines of the bean weevil *Acanthoscelides obtectus* selected for early or late reproduction, no difference in the maternal age effect on offspring lifespan between the selected lines was found (Tucić *et al.* 2004). The difference between the studies may lie in the biology of these species suggesting that evolution of long-life may not always manifest itself in the reduction of detrimental parental age effects. Clearly, more experimental work is needed before we can make broad cross-taxonomic generalizations regarding the evolution of parental age effects in response to selection for age-specific life-histories.

The evolution of maternal age effect in our study was specific to offspring sex: the reduction of the maternal age effect in long-lived lines mainly affected sons, not daughters. While sex difference in maternal age effects on offspring lifespan is common, there is substantial variation across species, and even populations within species, regarding which sex is affected stronger (Butz & Hayden 1962; Priest *et al.* 2002; Fox et al, 2003; Carnes *et al.* 2012). Generally, our finding of stronger response in males is in line with stronger maternal effects in general (Fox, Czesak & Wallin (2004b) and maternal age effects in particular (Fox et al. 2003) on male lifespan in *C. maculatus*. Sexual selection often causes males to invest heavily into energetically costly traits (Sheldon *et al.* 1998, Brooks 2000, Tomkins et al. 2004, Bussiere *et al.* 2008, Kwan *et al.* 2008, Sharp & Agrawal 2013) and recent work found that male *C. maculatus* are indeed more sensitive to environmental changes (Berger *et al.* 2014). Male *C. maculatus* spend a lot of energy in mate search even in the absence of females; therefore, low-condition sons produced by older mothers could be paying relatively higher price than low-condition daughters.

Since a well-known maternal age effect in *C. maculatus* is a reduction in maternal investment in egg size, resulting in longer development time for offspring hatching from smaller eggs (Fox 1993b, 1994), we also investigated the maternal age effect on development time. In agreement with previous work, we found that offspring from older mothers took longer to develop. In addition, we found a strong effect of our selection treatment, where offspring from long-life lines had shorter development times, a difference that was especially pronounced for young mothers, while the maternal-age effect on development time was weak in the short lived lines. Although we did not measure egg size, the pattern is consistent with previous findings in *C. maculatus* of a negative correlation between egg size and development time, and reduced egg size and increased offspring development time with maternal age (Fox 1993b, 1994). Since the females from long-life lines were larger than females from short-life lines (Berg *et al.* submitted), and there is a positive correlation between female body size and egg size in *C. maculatus* (Fox 1993b), our results suggest that the large females of the long-life lines lay large eggs, especially when young, resulting in offspring with short development time and long lifespan. Although neither egg size nor offspring size was measured here, previous research suggests there is no maternal age effect on offspring size in *C. maculatus* (Fox 1993b), despite the fact that old mothers lay small eggs, possibly because they take longer to develop and still hatch at a common size.

Although the maternal age effect on development time, probably caused by a reduction in egg size with age, is a likely mechanism explaining a major part of the parental age effect, this effect alone does not explain the patterns we found. By investigating the maternal age effect on lifespan after controlling for the strongly negative effect of increased development time, the maternal age effect was still present, resulting in longer lifespan than expected for offspring born to newly eclosed females. Not surprisingly, the lifespans of beetles from the two selection lines were more similar after controlling for development time, since the lines selected for long life had shorter development time. It is possible that ageing of eggs caused this effect, or other factors related to maternal provisioning that do not affect development time. It is also interesting to note that also Fox *et al.* (2011) have found sex-specific responses in lifespan, but in their case as a response to novel conditions, further suggesting that the lifespan of the two sexes respond differently in *C. maculatus*.

While our study is consistent with most of the literature on parental age effects that show that older parents produce shorter-lived offspring, our results differ from the only other similar study on *C. maculatus*, in which Fox *et al.* (2003) found a positive effect of maternal age on offspring lifespan, but only for very old mothers (day 6+) which are outside the range of our study. The authors hypothesized that their unexpected results may have been caused by the reduced eclosion success of offspring from older mothers in their experiment, resulting in condition-dependent survival. In other words, the subset of offspring from old mothers that did eclose were in high condition and, therefore, lived longer. In our study, we did not find a decrease in eclosion success with maternal age (rather a small increase) and, consequently, condition-dependent mortality did not influence our estimate of the maternal age effect. The fact that our results showed negative effects of maternal age suggest that differences in egg-to-adult survival, as argued by Fox *et al.* (2003), can influence the estimates of the maternal age effect on lifespan.

Selection on late age of reproduction (Rose 1984; Luckinbill *et al.* 1984; Partridge *et al.* 1999) or direct selection on long-lived individuals (Zwaan *et al.* 1995; Hunt *et al*. 2006, Berg & Maklakov 2012) result in the evolution of long life, but at the same time the offspring of old parents have reduced lifespan (Lansing 1947; Priest *et al.* 2002). Therefore, the processes driving maternal age effects have often been seen as distinct from those underlying ageing. Here we show that the detrimental effect of old maternal age on the lifespan of offspring evolves rapidly and is diminished in mothers from long-lived lines. Moreover, sons were affected more than daughters, suggesting that maternal age effects can play an important role in shaping sexual dimorphism in lifespan and ageing. More broadly, our findings confirm that parental age effects can be viewed as a manifestation of ageing (Priest *et al*. 2002) and call for a further integration of the two fields.

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Data Accessibility

Data deposited in the Dryad repository: http://doi.org/10.5061/dryad.2320n

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1. The influence of maternal age (Day 1-4+), selection treatment and offspring sex on the log of offspring lifespan, after controlling for offspring development time.

Table 1. The influence of maternal age, selection treatment and offspring sex on the log of development time of the offspring. Results are presented separately for analyses including maternal age 1-3 and maternal age 1-4+.

	Development time (maternal age 1 - 3)			Development time (maternal age 1 - 4+)		
Parameter	Posterior mode	95% HPD interval	pMCMC	Posterior mode	95% HPD interval	pMCMC
Intercept	3.127	3.103; 3.151	<0.001	3.129	3.106; 3.151	<0.001
Selection treatment (short → long)	-0.025	-0.059; 0.009	0.124	-0.026	-0.057; 0.008	0.117
Sex (female → male)	-0.019	-0.022; -0.017	<0.001	-0.019	-0.022; -0.017	<0.001
Maternal age	-0.007	-0.014; -0.001	0.041	-0.023	-0.027; -0.019	<0.001
Maternal age^2	0.004	0.001; 0.007	0.034	0.013	0.011; 0.014	<0.001
Selection treatment × Sex	0.004	0.001; 0.008	0.025	0.004	0.001; 0.008	0.024
Selection treatment × Maternal age	0.019	0.009; 0.027	<0.001	0.018	0.011; 0.022	<0.001

Selection treatment × Maternal age^2	-0.005	-0.009; 0.000	0.063	-0.003	-0.005; -0.001	<0.001

Table 2. The influence of maternal age, selection treatment and offspring sex on the log of offspring adult lifespan and lifespan residuals after controlling for development time. Lifespan is calculated on data from all maternal ages (1-4+), while lifespan residuals is calculated using data from the first three maternal ages.

	Lifespan			Lifespan residuals		
Parameter	Posterior mode	95% HPD interval	pMCMC	Posterior mode	95% HPD interval	pMCMC
Intercept	3.294	3.244; 3.347	<0.001	3.307	3.254; 3.360	<0.001
Development time	-	-	-	-0.380	-0.434; -0.316	<0.001
Selection treatment (short → long)	0.050	-0.027; 0.118	0.217	0.032	-0.043; 0.110	0.346
Sex (female → male)	-	-0.380; -	<0.00	-	-0.391; -	<0.00

	0.367	0.355	1	0.378	0.366	1
Maternal age	-0.036	-0.054; -0.018	<0.001	-0.087	-0.109; -0.059	<0.001
Maternal age^2	0.007	0.002; 0.014	0.020	0.035	0.021; 0.046	<0.001
Selection treatment × Sex	0.043	0.024; 0.057	<0.001	0.048	0.030; 0.064	<0.001
Selection treatment × Maternal age	-0.021	-0.046; 0.003	0.086	0.043	0.014; 0.072	0.004
Selection treatment × Maternal age^2	0.005	-0.002; 0.014	0.136	-0.028	-0.042; -0.013	<0.001
Sex × Maternal age	-0.084	-0.102; -0.053	<0.001	-0.070	-0.102; -0.042	<0.001
Sex × Maternal age^2	0.029	0.020; 0.037	<0.001	0.025	0.009; 0.038	0.002
Selection treatment × Sex × Maternal age	0.088	0.062; 0.130	<0.001	0.040	0.026; 0.056	<0.001
Selection treatment × Sex × Maternal age^2	-0.031	-0.044; -0.021	<0.001	-	-	-

Figure 1. Development time (±SE) in log days for female (circles) and male (triangles) offspring of mothers with an adult age of 1, 2, 3 or 4+ days from long lived (closed symbols) or short lived (open symbols) lines.

Figure 2. (a) Adult lifespan and (b) residuals of adult lifespan after controlling for the effect of development time in log days (±SE) for female (circles) and male (triangles) offspring of mothers with an adult age of 1, 2, 3 or 4+ days from long lived (closed symbols) or short lived (open symbols) lines. Lifespan residuals were converted to original units by adding the grand mean.

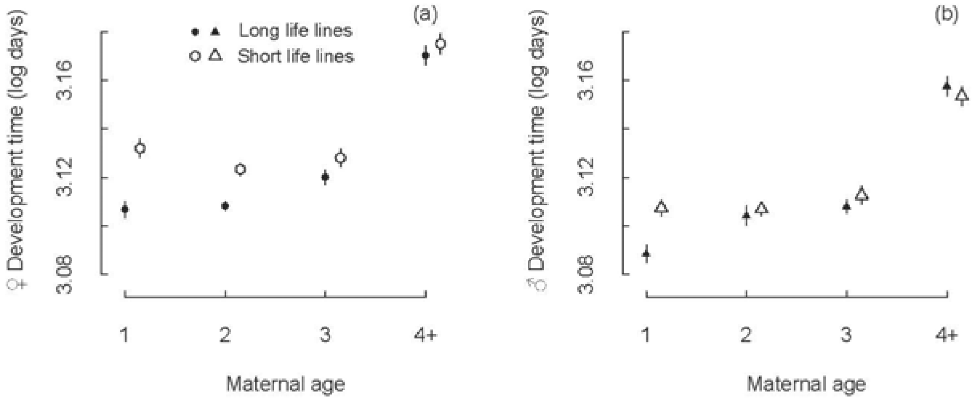

Figure 1

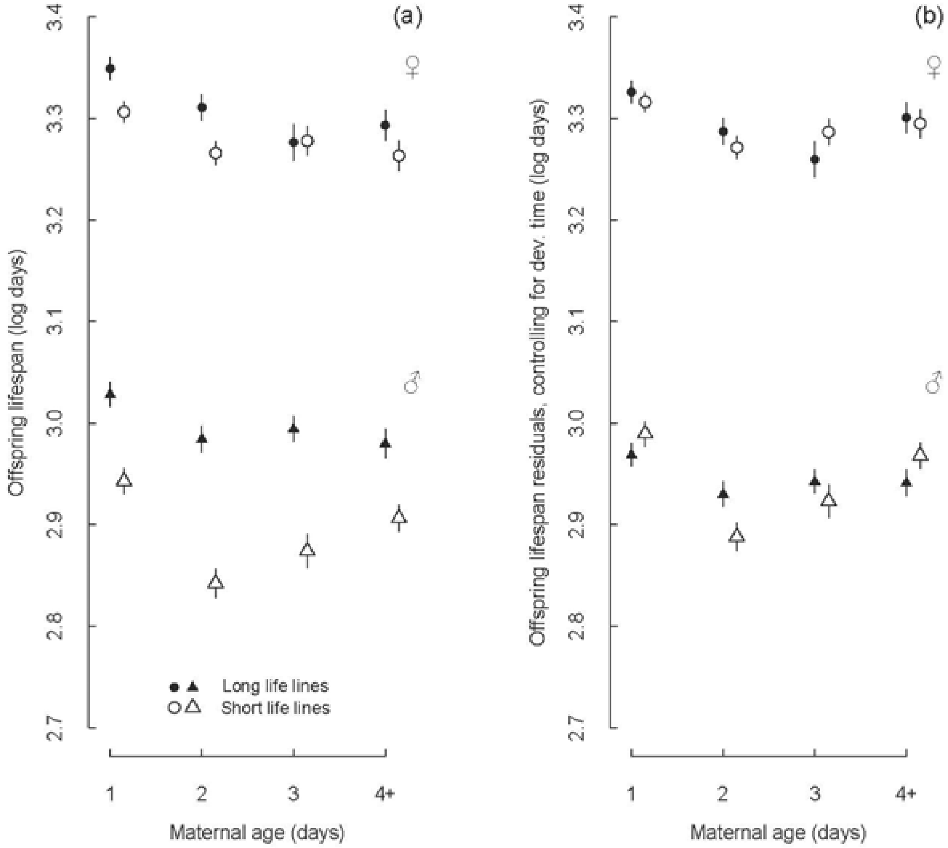
(a)
(b)
Offspring lifespan (log days)
Offspring lifespan residuals, controlling for dev. time (log days)
3.4
3.3
3.2
3.1
3.0
2.9
2.8
2.7
♀
♂
● ▲ Long life lines
○ △ Short life lines
1
2
3
4+
Maternal age (days)

Figure 2