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Sexual selection did not contribute to the evolution of male lifespan under curtailed age at reproduction in a seed beetle

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Abstract. 1. Sexual selection is a powerful evolutionary force that is hypothesised to play an important role in the evolution of lifespan. Here we test for the potential contribution of sexual selection to the rapid evolution of male lifespan in replicated laboratory populations of the seed beetle, *Callosobruchus maculatus*.

2. For 35 generations, newly hatched virgin male beetles from eight different populations were allowed to mate for 24 h and then discarded. Sexual selection was removed in half of these populations by enforcing random monogamy.

3. Classic theory predicts that because of sexual competition, males from sexually selected lines would have higher age-specific mortality rates and shorter lifespan than males from monogamous lines.

4. Alternatively, condition-dependent sexual selection may also favour genes that have positive pleiotropic effects on lifespan and ageing.

5. Males from all eight populations evolved shorter lifespans compared with the source population. However, there was no difference in lifespan between males from populations with or without sexual selection. Thus, sexual selection did not contribute to the evolution of male lifespan despite the fact that such evolution did occur in our study populations.

Key words. Ageing, beetles, life-history, senescence, sexual selection.

Introduction

The evolution of life histories involves a trade-off between investment in reproduction and somatic maintenance (Stearns, 1992). As selection on late-life performance is weak as a result of extrinsic mortality (Medawar, 1952; Williams, 1957; Charlesworth, 1994), the organisms may evolve life history schedules, where survival and reproductive performance in late life are traded for survival and reproductive performance in early life (Partridge & Barton, 1993). This model was originally championed by Williams (1957) and is known as antagonistic pleiotropy. Another process that is likely to reduce longevity is the accumulation of deleterious mutations whose actions are largely confined to late life (Medawar, 1952; Charlesworth, 1994), resulting in increased intrinsic mortality rate with age. Both processes are likely to contribute to the evolution of lifespan and ageing (Partridge & Barton, 1993; Snoke & Promislow, 2003; Hughes & Reynolds, 2005).

Optimal ageing and lifespan are predicted to evolve from the balance between opposing selection pressures for investment in current versus future reproduction (Partridge & Barton, 1993). Sexual selection can in theory affect the evolution of lifespan by modifying sex-specific life history optima (Svensson & Sheldon, 1998; Promislow, 2003; Bonduriansky *et al.*, 2008). Because of sex differences in variance in reproductive success, males are more likely to sacrifice lifespan for current reproduction than females. Therefore, males may adopt a 'live fast, die young' strategy if the benefits of high investment in early reproduction outweigh the costs of reduced investment in somatic maintenance or increased probability of injury (reviewed in Bonduriansky *et al.*, 2008), resulting in

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higher mortality rates and lower lifespan of males compared with females. This hypothesis predicts that sexual selection will lead to increased investment in reproduction early in life in males at the expense of late-life survival. For example, male crickets selected for shorter lifespan reached their peak levels of sexual advertisement earlier than those selected for long lifespan (Hunt *et al.*, 2006). Alternatively, it has been argued that sexual selection on male physiological performance may favour alleles with positive pleiotropic effects on lifespan (Bonduriansky *et al.*, 2008). Under this hypothesis, sexual selection via male–male competition and mate choice may lead to the evolution of more robust males with decelerated ageing and improved survival. Empirical tests of these hypotheses should advance our understanding of the role of sexual selection in the evolution of lifespan.

How can we investigate the role of sexual selection in the evolution of sex-specific lifespan experimentally? One potential route is to remove any benefits of late-life reproduction in a given sex and compare the resulted change in lifespan for populations with and without sexual selection. Under this scenario, antagonistically pleiotropic alleles that increase early-life fitness at the cost of late-life fitness would accumulate. Such accumulation is predicted because there will be no opposing selection on late-life performance. Importantly, this would be true for any antagonistically pleiotropic trait, including those that are not under sexual selection. Additionally, maladaptive late-life mutations would also accumulate at a higher rate. The two factors—antagonistically pleiotropic natural selection and mutation accumulation—are predicted to reduce lifespan regardless of the contribution of sexual selection to lifespan evolution. However, the experimental removal of sexual selection will make it possible to elucidate any additional role for antagonistically pleiotropic sexually selected traits.

While sexual selection and sexual conflict are likely to contribute to the evolution of senescence, there are only a few experimental evolution studies of this subject and they all address rather different questions, and therefore differ in experimental design (Promislow *et al.*, 1998; Maklakov *et al.*, 2005; Hunt *et al.*, 2006; Maklakov *et al.*, 2007a; Zajitschek *et al.*, 2007; Maklakov *et al.*, 2009). Two studies that directly tested for the potential of sexual selection to contribute to the evolution of lifespan via antagonistic pleiotropy reached different conclusions. Hunt *et al.* (2006) reported an extremely rapid response of black field crickets (*Teleogryllus commodus*) to artificial selection on lifespan. After only five generations of selection on adult longevity, males selected for shorter lifespan started to call sooner and spend more time calling than males selected for longer lifespan. This result directly supports the role of sexual selection in the evolution of lifespan via antagonistic pleiotropy. In a different study, Maklakov *et al.* (2007a) showed that virgin females of *Callosobruchus maculatus* seed beetles from sexually selected populations lived shorter than their counterparts from populations with enforced monogamy after 35 generations of selection. However, there was no effect of sexual selection on virgin male lifespan and mortality rates. This was particularly surprising provided that males, but not females, were selected under curtailed adult lifespan and could live and reproduce only for ~12% of their normal adult life. We hypothesised that the selective effect of sexual competition (sexual selection versus random monogamy) could become apparent if we allow males to compete for matings with females, such that pleiotropic traits that may have evolved in a sexually selected population can be expressed (Maklakov *et al.*, 2007a). In this study, we directly tested this hypothesis by comparing the survival of reproducing males from different selection regimes and found that, despite the evolution of shortened male lifespan during the experiment, there was no difference in lifespan between males from populations with or without sexual selection.

Materials and methods

Animals

Callosobruchus maculatus is a world-wide pest that infests stored legumes. Females cement their eggs on the outer surface of the host bean and the larvae bore inside to finish their development. After about 21 days at 30 °C, the adult individuals emerge. Adults are polygamous, mate readily and are characterised by a scramble competition for mates. Mated females generally resist male mating attempts, but do re-mate several times in their lives (Arnqvist *et al.*, 2005). These beetles are facultative capital breeders and can be maintained without additional food and water. *C. maculatus* has been widely used as a model species for studies of lifespan and mortality rates (Tatar & Carey, 1994; Fox *et al.*, 2003a, b, 2004a, b) because adult beetles are short-lived and can be easily raised in large numbers. Importantly, the laboratory environment represents a close approximation of seed storages in which *C. maculatus*, and other species of seed beetles, evolved for many generations (Fox *et al.*, 2003a; Messina & Karren, 2003; Maklakov *et al.*, 2007b). Beetles were reared on black-eyed beans (*Vigna unguiculata*) under controlled environmental conditions at 30 °C ± 0.5° and 45% RH ± 10% with a LD 12:12 h cycle.

Population maintenance

The base population used in this study was created by mass-mating three beetle populations, which were originally collected in three adjacent locations in Nigeria (Fricke & Arnqvist, 2007) to increase the genetic variation prior to the start of the selection experiment. After five generations, we established 16 replicated selection lines and manipulated their mating system and their host beans (for details see Fricke & Arnqvist, 2007). Only the eight populations that evolved on their ancestral host, the black-eyed bean, were used in this study. Briefly, we either enforced monogamy (M) upon four of the lines or allowed the other four to be polygamous (P). Males and females were collected as virgins and then allowed to interact for 24 h, after which the males were discarded and the females of each line were collected and transferred into a 1-litre glass jar containing *c.* 120 g of black-eyed beans. The animals for the next generation were obtained from the beans haphazardly selected from each population jar. Females were left there to oviposit until their natural death. In the monogamous treatment, a female was given one male at random to mate with, whereas in the

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polygamous treatment, each individual encountered two mates in sequential order. Females were held singly with one male and after 3 h of interaction the males within one line were rotated around and stayed with their new mate for the remaining hours of the 24-h cycle. Importantly, females in these lines do re-mate within 24 h with polygamous lines, mating on average 1.43 ± 0.09 and monogamous lines 1.31 ± 0.08 times (Fricke & Arnqvist, 2007).

The M lines were started with 50 pairs each, whereas the P lines were made up of 57 pairs each, so that the effective population size was held equal with $N_e \sim 80$ (see Fricke & Arnqvist, 2007) in both treatments. In the P regime, males would be selected for increased mating success with mated females despite female resistance (i.e. selection for more persistent males). Furthermore, in the P regime, males would be selected for higher success in sperm competition that could favour behavioural (e.g. long copulations), morphological (e.g. genitalia that allows for longer copulations) and/or physiological (e.g. faster metabolism allowing for faster movement or more motile sperm) adaptations that would benefit males but could be harmful to females (Das *et al.*, 1980; Ronn *et al.*, 2006, 2007; Hotzy & Arnqvist, 2009).

The base population was propagated in parallel with the selection lines, to function as a control. For each generation ~150 beetles were collected at random and transferred on 120–140 g of host beans. We expect sexual selection to be more intense in our base population than in our polygamy treatment, as the sexes were allowed to interact for longer and each individual encountered a greater number of potential mates. We thus note that our polygamy treatment is characterised by a reduction in sexual selection compared with conditions that are natural to laboratory populations of these beetles.

Experimental procedure

After 35 generations of selection and three generations of relaxed selection, we collected virgin males from each of the eight replicate lines and from the base population and tested lifespan and mortality rates in mixed-sex groups. Three groups of ~20 males each (mean $\pm$ SE $-$ 20 ± 0.2, range -18–22, $n = 540$ beetles) for each of the nine populations were placed together with identical numbers of virgin females from the base population in ø 9-cm Petri-dishes with 30 g of black-eyed beans, where the sexes could interact freely. Male cohorts were weighed at the beginning of the experiment and we recorded the number of dead individuals daily.

Statistical analysis

The longevity data were analysed using a mixed linear model where Selection was included as a fixed factor with three levels (M, P and B), and Population nested as a random factor within Selection. Body Mass of the cohort was used as a covariate.

We used a standard approach to describe age-specific mortality by comparing the fit of survival data to four different models: Gompertz, Gompertz-Makeham, Logistic and Logistic-Makeham (Promislow *et al.*, 1999) using the maximum likelihood approach implemented in the WinModest software (Pletcher, 1999). In most cases in this study, the mortality patterns of male cohorts were best described by the simple Gompertz model, $\mu_x = \alpha e^{\beta x}$, where μ_x is the mortality hazard at age x, α (Gompertz intercept) is the baseline mortality rate, and β (Gompertz slope) is the rate of senescence (rate of increase in mortality with age) (Promislow *et al.*, 1999). We extracted the estimates of baseline mortality rate (which was subsequently log-transformed) and the rate of senescence for all cohorts and analysed them using the same statistical approach as for longevity data. As baseline mortality rate and rate-of-senescence are correlated, we modelled the effect of selection on the rate of senescence both directly (Rate of Senescence I) and using baseline mortality as a covariate (Rate of Senescence II) and present the results of both models, as well as the actual data. The analysis was conducted in SAS Analyst 9.1 (SAS Institute Inc., Cary, NC, U.S.A.), apart from the baseline mortality model, which was run in JMP 7 (SAS Institute Inc., Cary, NC, U.S.A.) as an unbounded variance components model.

Results

There was a significant effect of selection on mean male lifespan (Table 1). Males from P and M populations lived on average 2.43 days (28.3%) shorter than males from the base population (B) (Table 2, Fig. 1). At the same time, there was no difference in lifespan between male cohorts from P and M

Table 1. The effects of the selection regime on longevity, baseline mortality (Gompertz intercept, In α) and rate of senescence (Gompertz slope, β). All mixed models control for average body mass of beetles in each cohort and the second model for rate of senescence additionally controls for baseline mortality (Rate of Senescence II, see text). The "–" sign indicates that estimates of the effect were lower than zero. Significant effects are highlighted in bold. Please refer to Table 2 and Figs 1 and 2 for the direction of the effects.

Source/Statistic	DF	DFDen	*F*-ratio/ Z-value	*P*-value
Longevity				
Selection	**2**	**7.07**	**7.05**	**0.021**
Population [Selection]			1.48	0.069
Body mass	1	20.4	0.09	0.771
Baseline mortality				
Selection	2	7.02	1.37	0.314
Population [Selection]			—	—
Body mass	1	16.14	3.47	0.081
Rate of senescence I				
Selection	2	7.52	1.70	0.246
Population [Selection]			0.65	0.259
Body mass	1	22.2	1.94	0.177
Rate of Senescence II				
Selection	**2**	**6.99**	**5.22**	**0.041**
Population [Selection]			1.54	0.062
Body mass	1	18.2	0.06	0.802
Baseline mortality	**1**	**17.1**	**357.37**	**<0.0001**

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Table 2. Mean values ± SE of longevity, baseline mortality (Gompertz intercept, In α) and rate of senescence (Gompertz slope, β) based on three male cohorts for each of nine populations.

Mating System	Population	Longevity	In α	β
Base	**1**	8.61 ± 0.32	−6.662 ± 0.946	0.675 ± 0.156
Polygamy	**2**	6.03 ± 0.20	−6.501 ± 1.097	0.974 ± 0.208
Polygamy	**3**	5.58 ± 0.10	−5.147 ± 0.232	0.796 ± 0.062
Polygamy	**4**	7.28 ± 0.09	−5.643 ± 1.163	0.646 ± 0.108
Polygamy	**5**	5.93 ± 0.12	−6.908 ± 0.525	1.089 ± 0.084
Monogamy	**6**	6.40 ± 0.24	−4.794 ± 0.399	0.594 ± 0.072
Monogamy	**7**	6.30 ± 0.03	−6.565 ± 0.980	0.950 ± 0.317
Monogamy	**8**	6.03 ± 0.33	−5.567 ± 0.258	0.798 ± 0.027
Monogamy	**9**	5.83 ± 0.17	−5.260 ± 0.367	0.779 ± 0.161

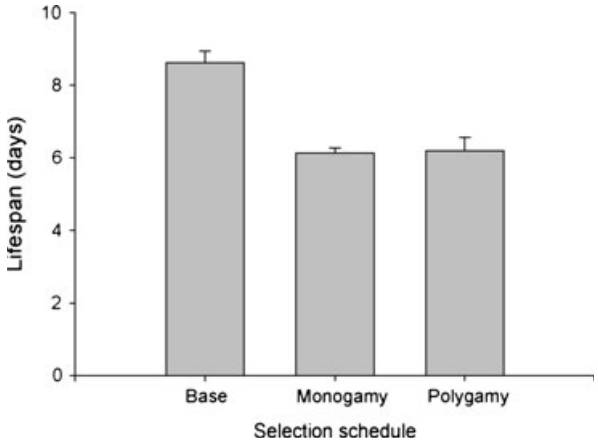

Fig. 1. The effect of selection schedule (Base—control population, Polygamy or Monogamy experimental treatments) on lifespan of mated males (mean ± SE). The values are averaged across replicate vials within populations and then across populations in two experimental treatments.

populations (Tukey–Kramer within-model post hoc comparisons: B vs M, $t_{1,8.23} = 3.67$, $P = 0.006$; B vs P, $t_{1,8.99} = 3.50$, $P = 0.007$, P vs M, $t_{1,6.04} = 0.13$, $P = 0.902$; Table 2, Fig. 1).

Table 2 provides the values for the baseline mortality rates and rates-of-senescence obtained from the Gompertz model using the WinModest software (Pletcher, 1999). There was no effect of selection on either parameter (Table 1). A close examination of Fig. 2 suggests that the difference in mortality rates between M and P populations on one hand, and the base population on the other, may be masked by a negative correlation between the two Gompertz parameters, because the regression lines for the P and M populations cross. Indeed, analysing the rate-of-senescence while keeping the baseline mortality rate constant shows a significant effect of selection (Table 1).

There was no effect of male origin (M, P or B) on lifespan or mortality rates of cohabiting females from the B population (all $P > 0.15$).

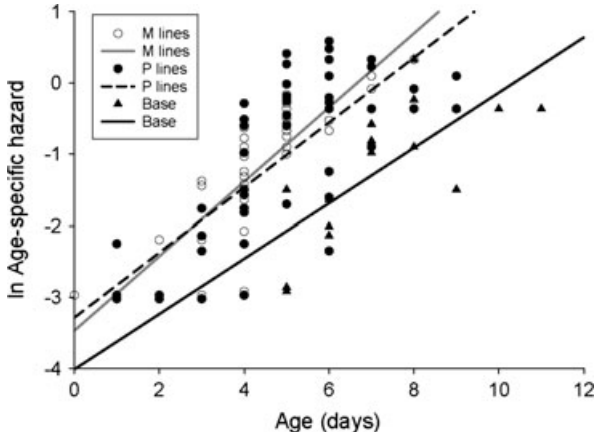

Fig. 2. The effect of selection schedule (Base—control population, Polygamy or Monogamy experimental treatments) on age-specific mortality hazard of mated males. Filled and open dots and filled triangles represent the actual data points, whereas the intercepts of regression lines represent initial mortality rate (Gompertz intercept) and the slopes represent the change in mortality rate with age (Gompertz slope).

Discussion

We show that male beetles from populations that evolved under curtailed reproductive lifespan for 35 generations lived 28.3% shorter than males from the source population. At the same time, the mating system of these beetle populations (i.e. monogamy versus polygamy)—the primary experimental manipulation of our study—did not have a discernible effect on the evolution of male lifespan or mortality rates.

There is strong theoretical foundation for the hypothesis that sexual selection should play an important role in the evolution of lifespan and ageing (Promislow, 2003; Graves, 2007; Bonduriansky *et al.*, 2008). However, very few experimental evolution studies have been conducted to test this hypothesis (Promislow *et al.*, 1998; Hunt *et al.*, 2006; Maklakov *et al.*, 2007a; Maklakov *et al.*, 2009). In our first study of the evolution of lifespan and ageing in these populations, we found that sexual selection affected lifespan in virgin females, but not in virgin males (Maklakov *et al.*, 2007a). We then suggested that males from sexually selected populations might have evolved pleiotropic traits that improve their reproductive performance at the expense of survival, but our ability to reveal these effects was limited as we only tested the survival of virgin cohorts (Maklakov *et al.*, 2007a). Nevertheless, we now report that sexual selection did not affect the evolution of male lifespan when measured in mated cohorts and under conditions that represent the recent evolutionary history of this species (Fox *et al.*, 2003a; Messina & Karren, 2003).

Collectively, these results provide further evidence that at least some of the alleles that affect longevity are sex-specific. There is substantial evidence for sex-specific effects of loci that affect longevity in *D. melanogaster* (Nuzhdin *et al.*, 1997; Vieira *et al.*, 2000; Leips & Mackay, 2002; Spencer *et al.*, 2003). Quantitative genetic studies also suggest that sex-specific loci are affecting longevity in the seed beetles

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C. maculatus and *Stator limbatus* (Fox *et al.*, 2004b; Fox *et al.*, 2006). Our studies of the evolution of male and female longevity in populations of *C. maculatus* with and without sexual selection suggest that female longevity was affected by mating system, whereas male longevity was not.

Why did sexual selection not affect lifespan of either virgin (Maklakov *et al.*, 2007a) or mated *C. maculatus* male beetles (this study)? It might be that there was little standing genetic variation for male reproductive traits that affect lifespan in the source population on which selection could operate. However, as this population was created by mixing three different populations of seed beetles it should harbour a relatively large amount of genetic variation. This is further confirmed by significant effects of selection on other traits (Fricke, 2006; Fricke & Arnqvist, 2007; Maklakov *et al.*, 2007a). Thus, it would be that only traits affecting male lifespan were lacking sufficient amounts of genetic variation. Alternatively, it is possible that the span of 35 generations was not sufficient for sexual selection to affect the evolution of male lifespan. Such possibilities would always remain a potential explanation for a lack of response. However, provided that (1) the mating system regime affected female lifespan (Maklakov *et al.*, 2007a); and (2) male lifespan was shortened in all experimental populations but was unaffected by the mating system, we suggest that our current results provide evidence against the importance of sexual selection for the evolution of male lifespan in this species on a short-time scale. We note, however, that the sexual selection treatment in our study was relatively weak and higher levels of sexual selection could produce a different outcome (but see Maklakov *et al.*, 2009).

Our results are unlikely to be affected by inbreeding for two main reasons. First, we carefully adjusted the effective population size in our experimental populations (see Methods), such that we do not expect significant differences between monogamous and polygamous populations. Second, the predicted approximate effective population size in all our lines was at least ~80, and this should be enough to avoid inbreeding effects over the time scale of 35 generations.

The population genetic theory of ageing suggests that evolution under curtailed lifespan as imposed upon males in our experiment, can result in short-lived male beetles via two distinct but not mutually exclusive processes—mutation accumulation (Medawar, 1952) and/or antagonistic pleiotropy (Williams, 1957). As males could not reproduce beyond the period of 24 h, deleterious mutations with effects that are largely confined to late age should accumulate. Alternatively, alleles that favour increased reproductive performance by males during the 24-h period at the expense of survival would be favoured. Given that we found an overall reduction in male lifespan, but no effect of the mating system treatment, we tentatively suggest that the observed pattern could result from mutation accumulation. We note that we cannot exclude the possibility of antagonistically pleiotropic effects of alleles that increase early survival at the expense of late survival. However, this possibility is, perhaps, less likely as the survival of male beetles during the first 24 h of their lives is very high (A.A.M. & C.F., pers. obs.).

In summary, we found that removal of sexual selection for 35 generations had no effect on longevity of reproducing males in populations selected under curtailed male lifespan, despite the observation that these populations did evolve shorter male lifespans compared with the source population. These results suggest that sexual selection may not always have a strong effect on lifespan evolution, at least on a short-term evolutionary scale. We do not imply that sexual selection does not play an important role in the evolution of male lifespan via antagonistic pleiotropy, because data from this (Bilde *et al.*, 2009) and other systems (Bonduriansky *et al.*, 2008) support this hypothesis. Rather, it is possible that extant sexual selection is not always the predominant force in lifespan evolution compared with natural selection (Maklakov *et al.*, 2009). It is theoretically possible that sexual selection acts both to accelerate and decelerate ageing and the relative importance of each of these potential effects could be system-specific (Maklakov *et al.*, 2009) and depend on the relative strength of 'good-genes' sexual selection versus sexual conflict (see also Holland, 2002; Hollis *et al.*, 2009). We currently have very few cases that investigated the role of sexual selection in the evolution of lifespan and ageing using an experimental evolution approach, and those utilized only a handful of taxa. We need more studies of lifespan evolution with and without sexual selection in different organisms, as well as a new range of experimental designs (Bonduriansky *et al.*, 2008).

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