Functional Ecology

British Ecological Society

*Functional Ecology* 2014, **28**, 469–478 doi: 10.1111/1365-2435.12179

# Sex-dependent evolution of life-history traits following adaptation to climate warming

**Björn Rogell*[1,2], William Widegren[1], Lára R. Hallsson[1,3], David Berger[1], Mats Björklund[1] and Alexei A. Maklakov*[1]**

[1]*Department of Animal Ecology, Evolutionary Biology Center, Uppsala University, Uppsala, SE-752 36, Sweden;* [2]*Shool of Biological Sciences, Monash University, Clayton, 3800, Australia; and* [3]*Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales, 2052, Australia*

## Summary

**1.** Thermodynamic processes increase metabolic rate and decrease longevity at high temperatures in ectotherms. However, how sustained long-term increase in temperature affects the evolution of longevity is poorly understood.

**2.** Stress theory of ageing predicts that increased longevity is positively genetically correlated with resistance to different types of environmental stressors implying that evolutionary trajectories of ageing may be mediated by correlative selection for robust phenotypes under thermal stress.

**3.** Here, we test this hypothesis by using replicate populations of the seed beetle *Callosobruchus maculatus*, evolving under two thermal environments: ancestral 30 °C and incremental increase towards novel 36 °C.

**4.** Beetles evolving under climate warming became larger, more fecund and lived longer than the beetles evolving under 30 °C across both environments. However, the increase in longevity was partly due to parental effects because after two generations of acclimatization it persisted only in males.

**5.** Our results support the hypothesis that evolution of stress resistance confers increased longevity through positive pleiotropy but demonstrate that such effects can be sex specific. These findings suggest that sex differences can evolve as correlated responses to selection under environmental change.

**Key-words:** adaptation, ageing, climate change, longevity, phenotypic plasticity, senescence, stress resistance

## Introduction

There is tremendous variation in longevity and ageing both within and across taxa (Promislow 1991; Roff 2001; Fox *et al*. 2006; Ricklefs 2010); however, the underlying reasons for this variation are not fully understood and have been a major topic of a recent debate. In 1957, G. C. Williams proposed antagonistic pleiotropy of fitness across age classes, that is, that genes conferring high fitness in younger age classes will induce costs later in life, as a possible cause for ageing. Such antagonistic alleles can go to fixation when there is a net fitness advantage, and ageing evolves as an adaptation generated by selection for high reproductive success early in life (Williams 1957). However, provided that genes have moderately age-specific effects, ageing may also evolve without antagonistic pleiotropy since alleles that are expressed during later life stages will be largely hidden from selection and therefore accumulate more mutations (Medawar 1952; Charlesworth 1994). Under both of these, not mutually exclusive, evolutionary scenarios, intrinsic life span is expected to correlate negatively with the level of extrinsic mortality of the population.

A major extension of the classic theory is the recent idea that evolution of ageing can be affected by the interactions between mortality rate, mortality source and the condition of individuals in the population (Abrams 1993; Williams & Day 2003; Williams *et al*. 2006). At the heart of this new theory lies an argument that if senescence in a given trait increases organism's susceptibility to an environmental hazard, increased mortality due to this hazard will increase selection against senescence in this trait (Williams & Day

*Correspondence authors. E-mail: alexei.maklakov@ebc.uu.se & bjorn.rogell@monash.edu

2003; Williams *et al.* 2006). Such condition-dependent mortality can result in a broad spectrum of evolutionary outcomes, often resulting in postponement of the onset of ageing (Williams & Day 2003). The effects on mean longevity can be equally variable and at least two empirical studies suggest that increased condition-dependent mortality can result in the evolution of longer intrinsic life span (Reznick *et al.* 2004; Chen & Maklakov 2012). The hypothesis that the evolution of ageing is driven by selection for genotypes robust to common sources of mortality is broadly in line with the large body of literature connecting stress resistance with increased longevity (reviewed in Parsons 1995; Kirkwood & Austad 2000; Sørensen, Nygaard Kristensen & Loeschcke 2003; Vermeulen & Loeschcke 2007). For example, extrinsic condition-dependent mortality by heat shock was used to demonstrate divergent evolution of longevity in lines that experience the same rate of extrinsic mortality, but differ in how this mortality is imposed (Chen & Maklakov 2012).

Increase in longevity and stress resistance often comes at the cost of reduced growth, fecundity or competitiveness (Sørensen, Nygaard Kristensen & Loeschcke 2003; Jenkins, McColl & Lithgow 2004). For example, in *Caenorhabditis elegans,* environmentally induced stress response improves survival by buffering effects of conditionally deleterious mutations. However, it also leads to reduced reproductive potential (Casanueva, Burga & Lehner 2012). Variation in ageing can thus be explained by trade-offs across different life-history traits (Stearns 1992; Baudisch 2008; Baudisch & Vaupel 2012; Danko *et al.* 2012), with positive pleiotropic effects between longevity and stress resistance (Kirkwood & Austad 2000; Shanley & Kirkwood 2000; Sørensen, Nygaard Kristensen & Loeschcke 2003; Vermeulen & Loeschcke 2007). However, life-history traits are also strongly affected by resource acquisition, and another possibility is that selection under stressful conditions benefits genotypes with high resource acquisition rates (Reznick, Nunney & Tessier 2000). Therefore, longevity, as well as other life-history traits, may be positively genetically correlated with resistance to different types of environmental hazards (Houle 1991; de Jong & van Noordwijk 1992; Rausher 1992; Lithgow *et al.* 1995; Parsons 1995; Kirkwood & Austad 2000; Robinson & Beckerman 2013).

Importantly, males and females often have different adaptive optima for life-history traits (Trivers 1972; Rice & Chippindale 2001), including life span (Promislow, Montgomerie & Martin 1992; Liker & Szekely 2005; Bonduriansky *et al.* 2008; Berg & Maklakov 2012). Thus, many of the alleles and allelic interactions that affect life span and other life-history characters are sex specific (Nuzhdin *et al.* 1997; Leips & Mackay 2002; Fox *et al.* 2006; Bilde *et al.* 2009; Magwire *et al.* 2010), and the evolution of these traits under stress is therefore likely to proceed along different trajectories in the two sexes. However, despite this prediction from life-history theory, few studies have investigated sex-specific evolutionary responses in life span and ageing under environmental change (but see Partridge *et al.* 1995 (novel temperature); Maklakov, Fricke & Arnqvist 2007; Maklakov & Fricke 2009 (novel mating system); Maklakov, Bonduriansky & Brooks 2009; [novel life-history schedule); Fox *et al.* 2011; (novel host plant)]. Even such a handful of studies produced different results: in the fruit fly *Drosophila melanogaster,* both sexes evolved higher longevity in their respective temperature environments (Partridge *et al.* 1995), while sex-specific evolution of longevity was reported in the three studies on the seed beetle *Callosobruchus maculatus* (Maklakov, Fricke & Arnqvist 2007; Maklakov, Bonduriansky & Brooks 2009; Maklakov & Fricke 2009; Fox *et al.* 2011). The difference between the studies may lie in the biological properties of the different study systems or may be driven by different agents of selection.

Here, we asked how sex-specific longevity, along with correlated life-history traits, evolves during adaptation to increasingly stressful temperatures in the seed beetle, *C. maculatus*. Due to the current increase in global temperature, there has been a strong focus on both ecological and evolutionary responses to novel thermal environment (Angilletta 2009; Hoffmann & Sgrò 2011; Walters, Blanckenhorn & Berger 2012). Temperature has profound effects on ectotherm life-history traits such as fecundity (Power *et al.* 2005), life span (Munch & Salinas 2009) and growth rate (Angilletta *et al.* 2003) that have been attributed to thermodynamic constraints on ectotherm metabolism (Gillooly *et al.* 2001; Brown *et al.* 2004). Accordingly, warmer climates as well as high temperatures in laboratory settings tend to increase adult mortality rates. Nevertheless, substantial interspecific variation in this temperature sensitivity suggests scope for adaptation (reviewed in Clarke 2003, 2006; Munch & Salinas 2009; Dell, Pawar & Savage 2011; Huey & Kingsolver 2011), and while the immediate effect of increased temperature on ectotherm life span is well described, the evolution of sex-specific evolutionary responses in life span in response to long-term and systematic increase in ambient temperature has received far less attention.

We used an experimental approach that simulated slow incremental increase in temperature from 30 °C to 36 °C degrees for 18 generations, followed by a period of constant temperature that stabilized at the upper value for another 13 generations. Such an approach is beneficial because it more closely approximates a potential change in a natural environment compared to an abrupt temperature change that is more commonly used in studies of laboratory adaptation (Huey & Rosenzweig 2009). This is relevant since the manner of an increase in temperature is likely to affect the evolutionary response. Seed beetles are capital breeders, and recent studies have shown that an increased temperature selects for increased body size (Hallsson & Björklund 2012a, b). If thermal tolerance is genetically linked to increased longevity and decelerated ageing via pleiotropic effects, then adaptation to a warming climate should result

in increased intrinsic life span. We thus predicted that lines that are adapted to warm conditions will exhibit higher fecundity (because of increased body size) and increased mean longevity. However, differences across sexes in resource acquisition and resource allocation towards somatic maintenance vs. reproduction can result in sex-specific evolution under novel thermal conditions. Since the trade-off between life span and reproduction is resolved differently between males and females in seed beetles (Bilde *et al*. 2009; Berg & Maklakov 2012), we were also interested in sex-specific responses to temperature adaptation.

## Materials and methods

### STUDY ORGANISM

The seed beetle (*C. maculatus*) is a pest of leguminous crops that colonized most of the tropical and subtropical regions of the world. *C. maculatus* do not require food or water at the adult stage in addition to resources accumulated at the larval stage to complete their reproductive cycle (Fox 1993), that is, they are facultatively aphagous. Females mate and start producing eggs on the day of eclosion. The eggs are glued onto the surface of the dry beans and hatched larvae bore into the beans to complete their life cycle. Adults emerge after 23–25 days at the intermediate temperature of 30 °C, to which the population used in this study had been adapted to for at least >90 generations (see below). *C. maculatus* have likely colonized human grain storages thousands of generations ago, which makes them an ideal laboratory organism as the laboratory environment closely approximates their 'natural' environment (Fox, Dublin & Pollitt 2003; Messina *et al*. 2009). Recent studies indicated that 36 °C is a suboptimal temperature for this species (Fox & Stillwell 2009).

### LABORATORY EVOLUTION LINES

The laboratory evolution lines were established from a large outbred population, which was created in 2002 by mass-mating three laboratory populations of Nigerian origin (known as Nigeria Mix; Fricke 2006). Several earlier studies found ample genetic variation for life-history and reproductive traits in this population (Fricke & Arnqvist 2007; Maklakov, Fricke & Arnqvist 2007). The population has been maintained by transferring 250–300 beetles each generation onto 120–140 g of host beans for >90 generations prior to this laboratory evolution experiment. Thus, the population does not suffer from inbreeding depression, and the large number of generations should have minimized linkage disequilibrium, which might have been prevalent in the laboratory founder population due to the admixture of genetically distinct lines. During the laboratory evolution experiment, the beetles were maintained at densities of 200 individuals per line in glass jars filled with 100 g of black-eyed beans (*Vinga unguiculata*). high-temperature lines ($n = 4$) and 'control' evolution lines ($n = 4$) were developed as part of a project to study adaptation to changing climatic conditions (Hallsson & Björklund 2012a,b,c). For the first 18 generations, four replicate lines were kept at a constant temperature of 30 °C (control), while the other four replicate lines were exposed to an incremental increase in temperature of 0·3 °C per generation (high-temperature). After the gradual increase in temperature had reached 36 °C for the high-temperature lines, the temperature was kept constant. During this second stage of the experiment, we increased the population size in all lines and maintained the beetles at ~500 individuals per jar with 200 g of beans. Further information on the initial lines can be found in Hallsson & Björklund (2012a, b). Previous studies with these new lines also indicated the presence of genetic variation for several traits, including fecundity and body size (Hallsson & Björklund 2012a, b).

## Experimental procedures

We conducted two different assays. In the first assay, we recorded longevity, body mass and development time, and it was preformed after 31 generations from the start of the experiment (henceforth 'longevity assay'). In the second assay, after 41 generations, we recorded lifetime offspring production (henceforth 'reproduction assay').

### LONGEVITY ASSAY

In order to separate genetic adaptation from phenotypic plasticity, we scored beetles which parents had been either directly moved to the test temperature as virgins, or been allowed to acclimatize at the test temperature for two generations prior to scoring of longevity. This was done by creating three replicates of each of the eight lines (four control lines and four high-temperature lines). While one of the replicates was kept in the native environment, the two others were moved into the novel environment, but at different times. The first translocated replicates were moved into the novel environment immediately and were hence allowed to acclimatize for two generations prior to longevity scoring ('acclimatized' assay). The remaining replica was moved the generation before the assay and may thus contain both environmental parental effects and immediate phenotypic responses ('non-acclimatized' assay). The 'acclimatized' and the 'non-acclimatized' assays were conducted simultaneously.

From the parental beetles placed at the test temperatures, we produced 48 male and 48 female virgin beetles from each line: test temperature: acclimatization treatment combination by isolating individual beans and monitoring them daily for emerging beetles. We used beetles from beans that had between three and five eggs only, to minimize variance in individual condition (in principle, there can be between one and ten beetles successfully hatching from one bean). The newly emerged focal beetles were then placed individually into 'virgin chambers' – 48-well plates from Falcon and scored for mortality on a daily basis. Development time was estimated as the number of days between placing the parental beetles together for mating and the date of eclosion of the focal beetles. Longevity was defined as the number of days between eclosion and death of the focal beetles. For each of the eight lines, two replicate estimates of weight at eclosion were taken per sex: test temperature: acclimation treatment combination, by taking the mean weight of two independent batches of 24 offspring not scored for longevity.

### REPRODUCTION ASSAY

For the reproduction assay, each replicate line was split among the two test temperatures and acclimatized to the test temperatures for two generations prior to the assay (performed after 41 generations; 23 generations under stable temperatures after the initial incremental increase of 18 generations). The non-acclimatized assay was omitted, since our main interest in this assay was in genetic response to novel temperature. We paired ten virgin males and females per line: test temperature combination. Each pair was placed in a Petri dish with 100 beans as egg-laying substrate, which is a sufficient amount to remove any density-dependent selection among offspring. Lifetime reproductive success was defined as the number of emerging adult offspring of both sexes from each pair.

### STATISTICAL ANALYSES

Our main objectives were to test if longevity, development time, lifetime reproductive success and body mass were affected by sex, selection regime and test temperature treatment.

When analysing the longevity data, we made two types of comparisons. First, we directly compared the longevity of beetles evolved under the control (30 °C) and high-temperature (36 °C) regime, at both test temperatures without acclimatization ('non-acclimatized' assay). In this comparison, both genetic effects and phenotypic plasticity could contribute to potential differences between selection regimes. Secondly, we compared the longevity of beetles evolved under the two temperature regimes, when beetles exposed to novel test temperatures had been allowed to acclimatize to them for two generations ('acclimatized' assay). This comparison includes mostly differences in genetic effects, because phenotypic effects are unlikely to carry over the two generations of acclimatization. The acclimatization was started two generations prior to scoring longevity, and all experimental beetles were thus of the same generation and were tested in parallel. We note that the two comparisons are full factorial designs asking different questions; first, the analysis of the 'non-acclimatized' assay compares the performance of high-temperature and control beetles when phenotypic plasticity and genetic effects are combined, and the analysis of the 'acclimatized' assay asks whether there has been a genetic change in lines that evolved under different temperatures.

We analysed how longevity and development time in *C. maculatus* were affected by selection (high-temperature vs. control regimes), test temperature (30 and 36 °C) and sex, as well as all possible interactions between these three factors using linear mixed-effect models. Replicate line, crossed by sex and test temperature, and nested within selection regime, was added as random effect to the model in order to avoid pseudo-replication. Lifetime reproductive success was analysed in the same way, except that sex was not included in the model as both parents contributed to offspring production. Because body mass had lower level of replication, it was only possible to include line nested within selection regime as random effect. All models were checked for homoscedasticity across experimental units using diagnostic plots, and life span was log-transformed in order to fulfil this assumption. All models were fit using a maximum likelihood algorithm implemented in the package *lme4* (Bates, Maechler & Bolker 2012) available for R (R Development Core Team 2009). The significance of the fitted model was assessed using analysis of variance (ANOVA) with type III sums of squares tested with an analysis of deviance on a chi-square distribution using the R package *car* (Fox 2002). Since the denominator degrees of freedom are not well defined for mixed models, we present analysis of deviance tables rather than the more traditional *F*-values.

In addition, to test the possibility that the observed differences in life span were induced by changes in body size between treatments, we fit a model with life span as response variable; sex, selection regime and test temperature as factorial explanatory variables; and body mass as a covariate. This analysis was performed on means of replicate line since life span and body mass were not measured on the same individuals. Since both body mass and life span were affected by the selection regime (see Results), both variables were scaled to a mean of zero and a standard deviation of unity within each treatment to avoid problems associated with collinearity among explanatory variables.

## Results

### NON-ACCLIMATIZED LONGEVITY ASSAY

We found that test temperature and sex had strong effects on life span in *C. maculatus*: higher temperature resulted in shorter life span across both selection regimes, and males lived shorter than females (Fig. 1, Table 1). The main effect of selection on life span (high-temperature vs. control) was significant, with lines adapted to high-temperature living longer than control lines at both test temperatures. This relationship was strongest in males as indicated by the significant interaction between selection regime and sex (Fig. 1, Table 1). The interaction between test temperature and selection regime was not significant (Table 1).

High test temperature caused direct increase in body mass through phenotypic plasticity and lines adapted to high temperature were larger than control beetles (Fig. 2, Table 1). In addition, there was a significant interaction between selection regime and sex, resulting from a strong sexual size dimorphism in the high-temperature lines that was practically absent in the control lines (Fig. 2, Table 1). All other interactions were non-significant, and body mass had no significant effects on life span within selection treatments ($P = 0{\cdot}30$). Females had significantly longer development times than males. However, there were no other significant effects on development time (Table 1).

### ACCLIMATIZED LONGEVITY ASSAY

We found significant effects of sex and test temperature on life span also in the acclimatized assay. The main effect of selection regime on life span was marginally significant, and in combination with the significant interaction

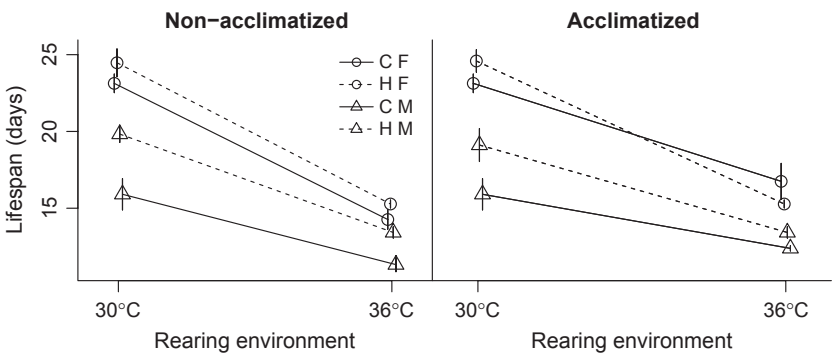


**Fig. 1.** The mean life span in days in the non-acclimatized and acclimatized assays across two test temperatures (30 and 36 °C). Control genotype is denoted as C, the High Temperature-adapted genotype is denoted as H, female F, and male M. Error bars represent ±1 SE.

**Table 1.** ANOVA table of the effect of treatment ('Treat.'; selected in 36 or 30 °C), trial temperature ('Temp.'; reared in 36 or 30 °C), sex, and their interactions on longevity, body mass and development time of acclimatized and non-acclimatized *Callosobruchus maculatus*. $\chi^2$ is the chi-square value, d.f. is the degrees of freedom and Pr(>$\chi^2$) the *P*-value

| | Longevity | | | Body mass | | | Development time | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | Pr(>$\chi^2$) | $\chi^2$ | d.f. | Pr(>$\chi^2$) | $\chi^2$ | d.f. | Pr(>$\chi^2$) |
| Acclimatized | | | | | | | | | |
| Temp. | 106·57 | 1 | <0·001 | 94·8 | 1 | <0·001 | 1·24 | 1 | 0·26 |
| Treat. | 3·84 | 1 | 0·05 | 57·5 | 1 | <0·001 | 1·85 | 1 | 0·17 |
| Sex | 139·64 | 1 | <0·001 | 7 | 1 | 0·008 | 24·36 | 1 | <0·001 |
| Temp.*Treat. | 3·4 | 1 | 0·07 | 0·33 | 1 | 0·57 | 4·22 | 1 | 0·04 |
| Temp.*Sex | 6·45 | 1 | 0·01 | 39 | 1 | <0·001 | 3·71 | 1 | 0·053 |
| Treat.*Sex | 10·02 | 1 | 0·001 | 0·25 | 1 | 0·62 | 24·72 | 1 | 0·03 |
| Temp.*Treat*Sex | 0·22 | 1 | 0·64 | 7·2 | 1 | 0·007 | 0·0025 | 1 | 0·96 |
| Non-acclimatized | | | | | | | | | |
| Temp. | 774·5 | 1 | <0·001 | 36·8 | 1 | <0·001 | 2·67 | 1 | 0·10 |
| Treat. | 8·3 | 1 | 0·003 | 80·4 | 1 | <0·001 | 0·007 | 1 | 0·93 |
| Sex | 273·6 | 1 | <0·001 | 13·5 | 1 | <0·001 | 26 | 1 | <0·001 |
| Temp.*Treat. | 0·92 | 1 | 0·33 | 1·38 | 1 | 0·24 | 0·05 | 1 | 0·82 |
| Temp.*Sex | 19·8 | 1 | <0·001 | 1·86 | 1 | 0·17 | 0·41 | 1 | 0·52 |
| Treat.*Sex | 20 | 1 | <0·001 | 22·3 | 1 | <0·001 | 0·29 | 1 | 0·59 |
| Temp.*Treat*Sex | 1·42 | 1 | 0·23 | 1·3 | 1 | 0·25 | 0·02 | 1 | 0·89 |

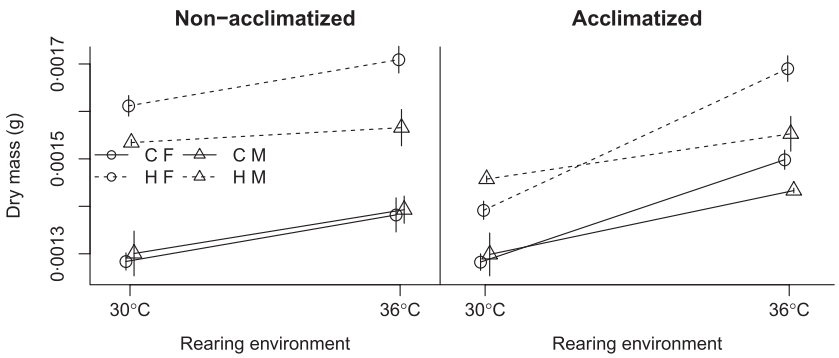


**Fig. 2.** The mean mass (g) in non-acclimated and acclimated *Callosobruchus maculatus* across two test temperatures (30 and 36 °C). Control line is denoted as C, the high-temperature-adapted line is denoted H, female F, and male M. Error bars represent ±1 SE.

between sex and selection regime, it indicates that the effect of selection observed in the non-acclimatized trial was still present, but only in males. The interaction between selection regime and test temperature was non-significant (Table 1).

Furthermore, in the acclimatized assay, we found that high test temperature increased the mass of the beetles and that lines evolving at the high-temperature selection regime were larger than control beetles (Fig. 2, Table 1). In this assay, we found a significant interaction between sex and test temperature, where females were smaller than males in 30 °C, but bigger in 36 °C (Fig. 2, Table 1). The three-way interaction was also significant because high-temperature', but not control beetles, exhibited crossing reaction norms for sex across the test temperatures. Other interactions were non-significant. Although body mass and life span were positively associated (Fig. 3), this association was not significant within selection regimes ($P = 0{\cdot}27$). As in the analysis of the data from the non-acclimatized assay, we found that development time was affected by sex, with females having a longer development time than males (Table 1). There were also marginally significant temperature *x* selection regime and sex *x* selection regime interactions for this trait.

### OFFSPRING PRODUCTION

High-temperature lines produced more offspring than control lines at both test temperatures ($\chi^2 = 9{\cdot}58$, d.f. = 1, $P = 0{\cdot}002$, Fig. 4). As expected, there were also large effects of test temperature on the number of offspring, with more offspring produced at 30 °C than at 36 °C ($\chi^2 = 51{\cdot}96$, d.f. = 1, $P < 0{\cdot}001$, Fig. 4). The interaction between selection and rearing environment was not significant ($\chi^2 = 0{\cdot}38$, d.f. = 1, $P = 0{\cdot}5$, Fig. 4). We also compared the proportional difference in offspring production between the selection regimes across temperatures by analysing data mean-scaled by the average offspring production for each temperature. However, even though there was a tendency for larger difference between selection regimes in 36 °C, implying that high-temperature lines might have a larger relative advantage

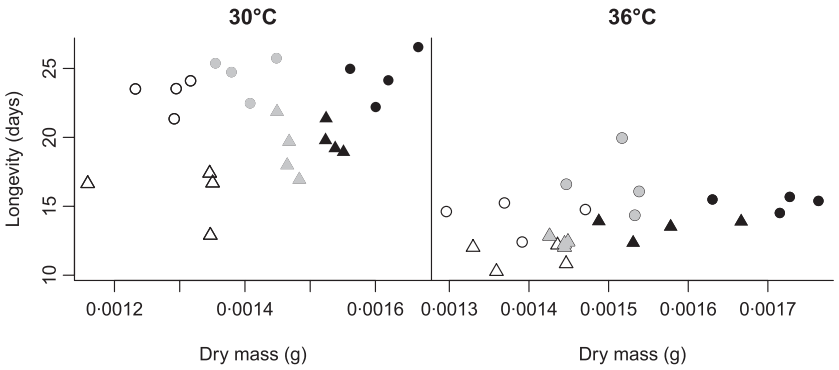


**Fig. 3.** Life span (days) plotted against mass (g) in the 30 °C and the 36 °C test temperatures. Each plot contains population means of the control and high-temperature-adapted lines of *Callosobruchus maculatus* where females are denoted by round symbols and males by wedges. Control lines are represented by unfilled symbols, high-temperature lines by filled symbols and the pre-acclimatized beetles by grey symbols (i.e. control lines acclimatized to 36 °C or high-temperature lines acclimatized to 30 °C).

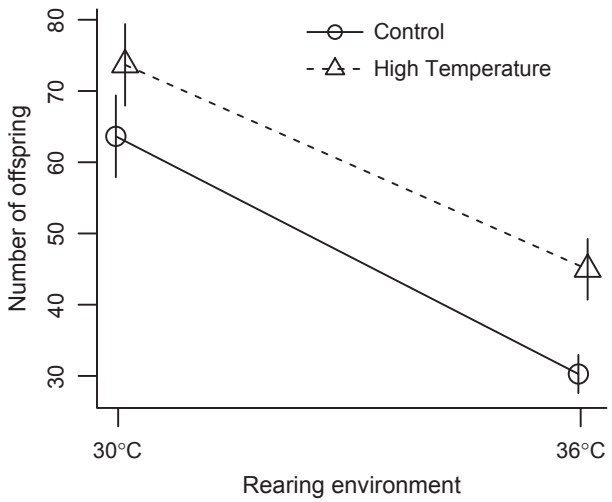


**Fig. 4.** The reproductive fitness (number of offspring) in control and high-temperature-adapted lines of *Callosobruchus maculatus* across two rearing environments (30 and 36 °C). The beetles were acclimatized to the test temperatures for two generations prior to the fitness assay. Error bars represent ±1 SE.

over control lines in the high test temperature compared to the control temperature (Fig. 4), the interaction between selection regime and test temperature remained non-significant also in this analysis ($\chi^2 = 3{\cdot}16$, d.f. = 1, $P = 0{\cdot}075$).

## Discussion

Longevity was decreased, and offspring production was lower at the high test temperature compared to the control (ancestral) temperature. However, in sharp contrast with previous work on *Drosophila* (Partridge *et al.* 1995), lines that evolved under high temperature had increased longevity and higher fecundity across both thermal environments compared to lines evolving under ancestral thermal conditions. Furthermore, increased longevity of high-temperature lines was observed in both sexes only when beetles were not acclimatized to the test temperatures, and while after two generations of acclimatization, the difference between selection regimes was apparent only in males. These results support the general hypothesis for evolution of increased intrinsic life span under stress, but also suggest that evolution under climate warming is likely to proceed along different trajectories in males and females.

Longevity has frequently been found to correlate positively with resistance to environmental stressors (Parsons 1995; Bijlsma & Loeschke 1997; Vermeulen & Loeschcke 2007) and since beetles evolving under high temperature lived longer in both test temperatures, our results support this notion. However, earlier work has shown that both sexes of fruit flies adapted to either 16·5 or 25 °C lived longer in their respective 'native' thermal environments (Partridge *et al.* 1995). What physiological, morphological or behavioural mechanism could explain the contrasting patterns observed across these two studies? Previous experiments with the same lines as used in this study showed that high-temperature lines were bigger than control beetles (Hallsson & Björklund 2012a, b), and our results suggest that this difference was maintained after 13 additional generations of evolution under 36 °C. A larger body size of a capital breeder is likely to reflect an increase in resources that may boost an organism's tolerance to desiccation. Previous laboratory experiments on other species have found that selection for starvation or desiccation resistance can lead to accumulation of resources and increased body mass (reviewed in Gibbs & Gefen 2009; Zera & Harshman 2009). Thus, the increased longevity could be directly linked to increased body size in high-temperature lines.

However, we found no support for a direct link between longevity and body size as there was no correlation between body size and longevity when controlling for the effect of selection treatment. Although this test has weak statistical power to pick up an effect due to very little variance in body size within selection regimes, previous studies on the relationship between body size and longevity in *C. maculatus* have also yielded incongruent results showing both significant genetic correlations between body size and life span (Moller, Smith & Sibly 1989; Messina & Fry 2003; D. Berg *et al.* unpublished data) as well as no relationship between the traits (Fox *et al.* 2004; Maklakov, Bonduriansky & Brooks 2009), suggesting that environmental conditions may be decisive in determining the

strength of this relationship. Moreover, while both sexes evolved larger body size in the stressful environment, only males showed a persistent increase in longevity after acclimatization. It thus seems likely that other traits, such as production of heat shock proteins known to buffer phenotypes against both extreme temperatures as well as other environmental stressors (Feder & Hofmann 1999; Hochachka & Somero 2002), reduced water loss (Hoffmann & Parsons 1993) and proportion of water content in the body (Gibbs, Chippindale & Rose 1997), are the causal factors contributing to differences in life span between the selected lines (Kearney *et al*. 2013). It is worth noting that, at least in *Drosophila*, short-term selection experiments on desiccation resistance do not change relative water content, while long-term selection experiments do (reviewed in Gibbs & Gefen 2009).

The increase in body size associated with high temperature is nevertheless notable as ectotherm size is usually observed to decrease in warm conditions (Atkinson & Sibly 1997; Angilletta 2009; Gardner *et al*. 2011). Furthermore, the increase was observed both as phenotypic plasticity and as an evolutionary response, strongly indicating that large size (or correlates thereof) is adaptive in hot temperature in *C. maculatus*. Though we are unaware of studies on other systems showing evolutionary increases in body size as a response to increased temperature, there are examples of increases through phenotypic plasticity (reviewed in Atkinson 1994; Kingsolver & Huey 2008).

In addition to stress resistance as a mechanism explaining larger size in hot temperatures, some theory suggests that increased fecundity selection may favour larger adult female body sizes at relatively warm temperatures (Frazier, Huey & Berrigan 2006; Berger, Walters & Gotthard 2008; Kingsolver & Huey 2008; Berger *et al*. 2012). This would further predict sex-specific selection for increased resource acquisition in the juvenile stage and/or sex-differences in adult life span through differential investment of resources into soma vs. reproduction.

Sex-specific response in longevity under environmental stress is in fact a general expectation based on life-history and sexual selection theories and the observation that males and females often show differences in trait optima and energy allocation to survival vs. reproduction (Trivers 1972; Lande 1980, 1981; Clutton-Brock & Parker 1992; Bonduriansky *et al*. 2008; Maklakov & Lummaa 2013). This is also the case in *C. maculatus* (Bilde *et al*. 2009; Berg & Maklakov 2012), and thus, differences between male and female reproductive strategies may have played a role in explaining why high-temperature females did not evolve increased longevity in the same way as males, but were still more fecund and, similar or even more so than males, bigger than control group beetles. In line with this hypothesis, seed beetle females have a considerable level of oogenesis in the absence of mating and even in the absence of oviposition substrate (Ouedraogo & Huignard 1981). Thus, the increased amount of resources acquired by the high-temperature group beetles may have been allocated to oogenesis in virgin females, while reproductive effort of virgin males may have remained unchanged across selection treatments, resulting in longer life only in high-temperature males.

Other traits could also have been important in generating the sex-specific response in life span. For example, reduced respiratory water loss can be associated with reduced activity levels (Williams, Rose & Bradley 1997) and can lead to increased longevity. Male beetles are much more active than females and this trait likely harbours sex-specific genetic variation in the ancestral population (Burgevin, Friberg & Maklakov 2013, D. Berg *et al*. unpublished data). A change in the relative strengths of sexual vs. natural selection on male activity levels between the high-temperature and control selection regimes may have reduced male activity in lines evolving at high temperatures and therefore affected the evolution of life span mostly in males.

Even so, it still remains unclear why the high-temperature line females lived longer than control females in the non-acclimatized trial, unless acclimatization changed the relative allocation of resource into reproduction vs. somatic maintenance, and did so in a sex-specific manner. Sex differences in plasticity, such as acclimatization responses, are commonly observed in ectotherms in general and seed beetles in particular (Stillwell *et al*. 2010). Furthermore, sex-specific plasticity is predicted to mediate sex-specific genetic responses as plasticity may weaken the strength of selection for genetic change (Whitlock 1996; Price, Qvarnström & Irwin 2003; Walters, Blanckenhorn & Berger 2012). We did find statistical support for sex-specific acclimatization in body mass, but no statistically consistent responses in longevity or development time (see Table S1–S4, Supporting information). Given our experimental design, it is also difficult to completely rule out the possibility that rapid genetic responses over the two generations of acclimatization could be responsible for the sex-specific differences in longevity between acclimatized and non-acclimatized beetles. Thus, the final verdict on the exact mechanism that led to the observed sex-specific life-history evolution must await further experimental investigation separating responses into their genetic and plastic components. We are unaware of any study that directly investigated the effects of sex-specific plasticity on adaptation to climatic conditions, but current studies in our laboratory are likely to shed light on this hypothesis.

## Conclusions

More than 99% of all taxa are ectothermic (Atkinson & Sibly 1997) and many of them are of large ecological and economic importance. How these organisms will respond to the current increase in global temperature is thus an important and challenging area of research (Huey & Kingsolver 1989; Clarke 2003, 2006; Deutsch *et al*. 2008; Angilletta 2009; Kellermann *et al*. 2012; Walters, Blanckenhorn & Berger 2012; Berger *et al*. 2013; Kingsolver *et al*. 2013).

Our results demonstrate that evolution of life-history traits during adaptation to climate warming can be rapid but proceed differently in the two sexes. While both sexes showed evolution of increased body size under high temperature, the evolution of longer life span was evident in males but not apparent in acclimatized females. As lines evolving under high temperature had higher reproductive performance, the lack of genetic response in female longevity could be driven by increased oogenesis. Although previous studies have shown that longevity may be genetically correlated with stress tolerance (Lithgow *et al*. 1995; Parsons 1995; Bubliy & Loeschcke 2005), the potential for sex specificity of these effects remains poorly acknowledged and has not been the focus of experimental tests (but see Partridge *et al*. 1995; Fox *et al*. 2011) despite expectations based on sexual selection theory and life-history optimization (Clutton-Brock & Parker 1992; Bonduriansky *et al*. 2008; Maklakov & Lummaa 2013). Because sexes often have profound differences in their life-histories, we suggest that our finding is likely to reflect a general pattern and may have important implications for how longevity evolves in populations adapting to a warming climate. More broadly, our results show that sexual dimorphism in life-history traits can evolve as correlative response to selection for stress resistance during adaptation to changing environments. Intriguingly, these data suggest that evolution under higher temperatures resulted in increased genetic values of three traits that are fundamental for population demography – body size, longevity and offspring production, across both novel and ancestral temperatures. It is likely that heat-adapted lines suffer trade-offs with other traits. However, despite measuring several key life-history traits in our data, we can find no clear support for costs associated with the fitness advantages.

## Acknowledgement

This study was supported by Swedish Research Council grants to AAM and DB and European Research Council Starting Grant-2010 to AAM.

## Data accessibility

Data from: Rogell, B., Widegren, W., Hallsson, L.R., Berger, D., Björklund, M. & Maklakov, A.A. (2013) Sex-dependent evolution of life-history traits following adaptation to climate warming. Data identifier: doi:10.5061/dryad.66r6s Journal manuscript number: FE-2013-00512.R1.

## References

Abrams, P.A. (1993) Does increased mortality favor the evolution of more rapid senescence? *Evolution*, **47**, 877–887.

Angilletta, M.J. (2009) *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford, UK.

Angilletta, M.J., Wilson, R.S., Navas, C.A.A. & James, R.S. (2003) Trade-offs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution*, **18**, 234–240.

Atkinson, D. (1994) Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.

Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology and Evolution*, **12**, 235–239.

Bates, D., Maechler, M. & Bolker, B. (2012). *lme4: Linear mixed-effects models using S4 classes*. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4

Baudisch, A. (2008) *Inevitable Senescence? Contributions to Evolutionary-Demographic Theory*. Springer, Berlin.

Baudisch, A. & Vaupel, J.W. (2012) Getting to the root of ageing. *Science*, **338**, 618–619.

Berg, E.C. & Maklakov, A.A. (2012) Sexes suffer from suboptimal lifespan because of genetic conflict in a seed beetle. *Philosophical Transactions of the Royal academy Sciences B*, **279**, 4296–4302.

Berger, D., Walters, R. & Gotthard, K. (2008) What limits insect fecundity? – Body size and temperature dependent egg maturation and oviposition in a butterfly. *Functional Ecology*, **22**, 523–529.

Berger, D., Olofsson, M., Gotthard, K., Wiklund, C. & Friberg, M. (2012) Ecological constraints on female fitness in a phytophagous insect. *The American Naturalist*, **180**, 464–480.

Berger, D., Postma, E., Blanckenhorn, W.U. & Walters, R.J. (2013) Quantitative genetic divergence and standing genetic (co)variance in thermal reaction norms along latitude. *Evolution*, **67**, 2385–2399.

Bijlsma, K. & Loeschke, V. (1997) *Stress Adaptation and Evolution*, 1st edn. Birkhäuser, Basel, Germany.

Bilde, T., Maklakov, A.A., Meisner, K., la Guardia, L. & Friberg, U. (2009) Sex differences in the genetic architecture of lifespan in a seed beetle: extreme inbreeding extends male lifespan. *BMC Evolutionary Biology*, **9**, 9–33.

Bonduriansky, R., Maklakov, A.A., Zajitschek, F. & Brooks, R. (2008) Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional Ecology*, **22**, 443–453.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Towards metabolic theory of ecology. *Ecology*, **85**, 1771–1789.

Bubliy, O.A. & Loeschcke, V. (2005) Correlated responses to selection for stress resistance and longevity in a laboratory population of *Drosophila melanogaster*. *Journal of Evolutionary Biology*, **18**, 789–803.

Burgevin, L., Friberg, U. & Maklakov, A.A. (2013) Intersexual correlation for same-sex sexual behaviour in an insect. *Animal Behaviour*, **85**, 759–762.

Casanueva, M.O., Burga, A. & Lehner, B. (2012) Fitness trade-offs and environmentally induced mutation buffering in isogenic *C. elegans*. *Science*, **335**, 82–85.

Charlesworth, B. (1994) *Evolution in Age-Structured Populations*. Cambridge University Press, Cambridge, UK.

Chen, H.Y. & Maklakov, A.A. (2012) Longer lifespan evolves under high rates of condition-dependent mortality. *Current Biology*, **22**, 2140–2143.

Clarke, A. (2003) Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology and Evolution*, **18**, 573–581.

Clarke, A. (2006) Temperature and the metabolic theory of ecology. *Functional Ecology*, **20**, 405–412.

Clutton-Brock, T.H. & Parker, G.A. (1992) Potential reproductive rates and the operation of sexual selection. *The Quarterly Reviews of Biology*, **67**, 437–456.

Danko, M.J., Kozlowski, J., Vaupel, J.W. & Baudisch, A. (2012) Mutation accumulation may be a minor force in shaping life history traits. *PLoS One*, **7**, e34146.

Dell, A.I., Pawar, S. & Savage, V.M. (2011) Systematic variation in the temperature dependence of physiological and ecological traits. *Proceedings of the National Academy of Sciences*, **108**, 10591–10596.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. *et al*. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, **105**, 6668–6672.

Feder, M.E. & Hofmann, G.E. (1999) Heat-shock proteins, molecular chaperones, and the stress response: evolutionary and ecological physiology. *Annual Review of Physiology*, **61**, 243–282.

Fox, C.W. (1993) Multiple mating, lifetime fecundity and female mortality of the Bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Functional Ecology*, **7**, 203.

Fox, J. (2002) *An R and S Plus Companion to Applied Regression*, 1st edn. Sage Publications, Inc. New York.

Fox, C.W., Dublin, L. & Pollitt, S.J. (2003) Gender differences in lifespan and mortality rates in two seed beetle species. *Functional Ecology*, **17**, 619–626.

Fox, C.W. & Stillwell, R.C. (2009) Environmental effects on sex differences in the genetic load for adult lifespan in a seed-feeding beetle. *Heredity*, **103**, 62–72.

Fox, C.W., Bush, M.L., Roff, D.A. & Wallin, W.G. (2004) Evolutionary genetics of lifespan and mortality rates in two populations of the seed beetle, *Callosobruchus maculatus*. *Heredity*, **92**, 170–181.

Fox, C.W., Scheibly, K.L., Wallin, W.G., Hitchcock, L.J., Stillwell, R.C. & Smith, B.P. (2006) The genetic architecture of lifespan and mortality rates: gender and species differences in inbreeding load of two seed-feeding beetles. *Genetics*, **174**, 763–773.

Fox, C.W., Wagner, J.D., Cline, S., Thomas, F.A. & Messina, F.J. (2011) Rapid evolution of lifespan in a novel environment: sex-specific responses and underlying genetic architecture. *Journal of Evolutionary Biology*, **38**, 182–196.

Frazier, M.R., Huey, R.B. & Berrigan, D. (2006) Thermodynamics constrains the evolution of insect population growth rates: "Warmer is better". *The American Naturalist*, **168**, 512–520.

Fricke, C. (2006) *Postmating Sexual Selection and Its Role in Population Divergence in Beetles*. Uppsala University, Uppsala, Sweden.

Fricke, C. & Arnqvist, G. (2007) Rapid adaptation to a novel host in a seed beetle (*Callosobruchus maculatus*): the role of sexual selection. *Evolution*, **61**, 440–454.

Gardner, J.L., Peters, A., Keearney, M.R., Joseph, L. & Heinsohn, R. (2011) Declining body size: a third universal response to warming? *Trends in Ecology and Evolution*, **26**, 285–291.

Gibbs, A.G., Chippindale, A.K. & Rose, M.R. (1997) Physiological mechanisms of evolved desiccation resistance in *Drosophila melanogaster*. *Journal of Experimental. Biology*, **200**, 1821–1832.

Gibbs, A.G. & Gefen, E.A. (2009) Physiological adaptations in laboratory environments. *Experimental Evolution* (eds T. Jr Garland & M.R. Rose), pp. 523–550. University of California Press, Berkley, CA.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.

Hallsson, L.R. & Björklund, M. (2012a) Selection in a fluctuating environment leads to decreased genetic variation and facilitates the evolution of phenotypic plasticity. *Journal of Evolutionary Biology*, **25**, 275–290.

Hallsson, L.R. & Björklund, M. (2012b) Selection in a fluctuating environment and the evolution of sexual dimorphism in the seed beetle *Callosobruchus maculatus*. *Journal of Evolutionary Biology*, **25**, 1564–1575.

Hallsson, L.R. & Björklund, M. (2012c) Sex-specific genetic variances in life-history and morphological traits of the seed beetle *Callosobruchus maculatus*. *Ecology and Evolution*, **2**, 128–138.

Hochachka, P.W. & Somero, G.N. (2002) *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*, 1st edn. Oxford University Press, New York.

Hoffmann, A.A. & Parsons, P.A. (1993) Direct and correlated responses to selection for desiccation resistance: a comparison of *Drosophila melanogaster* and *D. simulans*. *Journal of Evolutionary Biology*, **6**, 643–657.

Hoffmann, A.A. & Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Houle, D. (1991) Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution*, **45**, 630–648.

Huey, R.B. & Kingsolver, J.G. (1989) Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology and Evolution*, **4**, 131–135.

Huey, R. & Kingsolver, J.G. (2011) Variation in universal temperature dependence of biological rates. *Proceedings of the National Academy of Sciences*, **108**, 10377–10378.

Huey, R.B. & Rosenzweig, F. (2009) Laboratory evolution meets Catch-22: balancing simplicity and realism. *Experimental Evolution* (eds. T. Jr Garland & M.R. Rose), pp. 671–701. University of California Press, Berkley, CA.

Jenkins, N.L., McColl, G. & Lithgow, G.J. (2004) Fitness cost of extended lifespan in *Caenorhabditis elegans*. *Philosophical Transactions of the Royal academy Sciences B*, **271**, 2523–2526.

de Jong, G. & van Noordwijk, A.J. (1992) Acquisition and allocation of resources: genetic (CO) variances, selection, and life histories. *American Naturalist*, **139**, 749–770.

Kearney, M.R., Simpson, S.J., Raubenheimer, D. & Kooijman, S.A.L.M. (2013) Balancing heat, water and nutrients under environmental change: a thermodynamic niche framework. *Functional Ecology*, **27**, 950–966.

Kellermann, V., Overgaard, J., Hoffmann, A.A., Flojgaard, C., Svenning, J.C. & Loeschcke, V. (2012) Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences*, **109**, 16228–16233.

Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, **10**, 251–268.

Kingsolver, J.G., Diamond, S.E. & Buckley, L.B. (2013) Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional Ecology*, doi: 10.1111/1365-2435.12145.

Kirkwood, T.B.L. & Austad, S.N. (2000) Why do we age? *Nature*, **408**, 233–238.

Lande, R. (1980) Sexual dimorphism, sexual selection and adaptation in polygenic characters. *Evolution*, **34**, 292–305.

Lande, R. (1981) Model of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences*, **78**, 3721–3725.

Leips, J. & Mackay, T.F.C. (2002) The complex genetic architecture of *Drosophila* lifespan. *Experimental Ageing Research*, **28**, 361–390.

Liker, A. & Szekely, T. (2005) Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution*, **59**, 890–897.

Lithgow, G.J., White, T.M., Melov, S. & Johnson, T.E. (1995) Thermotolerance and extended life-span conferred by single-gene mutations and induced by thermal-stress. *Proceedings of the National Academy of Sciences*, **92**, 7540–7544.

Magwire, M.M., Yamamoto, A., Carbone, M.A., Roshina, N.V., Symonenko, A.V., Pasyukova, E.G. *et al.* (2010) Quantitative and molecular genetic analyses of mutations increasing *Drosophila* lifespan. *PLoS Genetics*, **6**, 1001037.

Maklakov, A.A., Bonduriansky, R. & Brooks, R.C. (2009) Sex differences, sexual selection, and ageing: an experimental evolution approach. *Evolution*, **63**, 2491–2503.

Maklakov, A.A. & Fricke, C. (2009) Sexual selection did not contribute to the evolution of male lifespan under curtailed age at reproduction in a seed beetle. *Ecological Entomology*, **34**, 638–643.

Maklakov, A.A., Fricke, F. & Arnqvist, G. (2007) Sexual selection affects lifespan and ageing in the seed beetle. *Aging Cell*, **6**, 739–744.

Maklakov, A.A. & Lummaa, V. (2013) Evolution of sex differences in lifespan and ageing: causes and constraints. *BioEssays*, **35**, 717–724.

Medawar, P.B. (1952) *An Unsolved Problem of Biology*. H.K. Lewis & Co., London.

Messina, F.J. & Fry, J.D. (2003) Environment-dependent reversal of a life history trade-off in the seed beetle *Callosobruchus maculatus*. *Journal of Evolutionary Biology*, **16**, 501–509.

Messina, F.J., Jones, J.C., Mendenhall, J.C. & Muller, A. (2009) Genetic modification of host acceptance by a seed beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Annals of the Entomological Society of America*, **102**, 181–188.

Moller, H., Smith, R.H. & Sibly, R.M. (1989) Evolutionary demography of a Bruchid beetle.1. Quantitative genetic-analysis of the female life-history. *Functional Ecology*, **3**, 673–681.

Munch, S.B. & Salinas, S. (2009) Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *Proceedings of the National Academy of Sciences*, **106**, 13860–13864.

Nuzhdin, S.V., Pasyukova, E.G., Dilda, C.L., Zeng, Z.B. & Mackay, T.F.C. (1997) Sex-specific quantitative trait loci affecting longevity in *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences*, **94**, 9734–9739.

Ouedraogo, A. & Huignard, J. (1981) Polymorphisms and ecological reactions in *Callosobruchus maculatus* F. (Coleoptera, Bruchidae) in Upper Volta. *The Ecology of Bruchids Attacking Legumes (Pulses)* (ed. V. Labeyrie), pp. 175–184. Springer, New York.

Parsons, P.A. (1995) Inherited stress resistance and longevity – a stress theory of ageing. *Heredity*, **75**, 216–221.

Partridge, L., Barrie, B., Barton, N.H., Fowler, K. & French, V. (1995) Rapid laboratory evolution of adult life-history traits in *Drosophila melanogaster* in response to temperature. *Evolution*, **49**, 538–544.

Power, M., Dempson, J.B., Reist, J.D., Schwarz, C.J. & Power, G. (2005) Latitudinal variation in fecundity among arctic charr populations in eastern north America. *Journal of Fish Biology*, **67**, 255–273.

Price, T.D., Qvarnström, A. & Irwin, D.E. (2003) The role of phenotypic plasticity in driving genetic evolution. *Philosophical Transactions of the Royal academy Sciences B*, **270**, 1433–1440.

Promislow, D.E.L. (1991) Senescence in natural populations of mammals – a comparative study. *Evolution*, **45**, 1869–1887.

Promislow, D.E.L., Montgomerie, R. & Martin, T.E. (1992) Mortality costs of sexual dimorphism in birds. *Proceedings of the Royal Society London*, **250**, 143–150.
R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
Rausher, M.D. (1992) The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution*, **46**, 616–626.
Reznick, D., Nunney, L. & Tessier, A. (2000) Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology and Evolution*, **15**, 421–425.
Reznick, D.N., Bryant, M.J., Roff, D., Ghalambor, C.K. & Ghalambor, D.E. (2004) Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature*, **431**, 1095–1099.
Rice, W.R. & Chippindale, A.K. (2001) Intersexual ontogenetic conflict. *Journal of Evolutionary Biology*, **14**, 685–693.
Ricklefs, R.E. (2010) Life-history connections to rates of ageing in terrestrial vertebrates. *Proceedings of the National Academy of Sciences*, **107**, 10314–10319.
Robinson, M.R. & Beckerman, A.P. (2013) Quantifying multivariate plasticity: genetic variation in resource acquisition drives plasticity in resource allocation to components of life history. *Ecology Letters*, **16**, 281–290.
Roff, D.A. (2001) *Life History Evolution*, 1st edn. Sinauer Associates, Chicago, IL.
Shanley, D.P. & Kirkwood, T.B.L. (2000) Calorie restriction and ageing: a life-history analysis. *Evolution*, **54**, 740–750.
Sørensen, J.G., Nygaard Kristensen, T. & Loeschcke, V. (2003) The evolutionary and ecological role of heat shock proteins. *Ecology Letters*, **6**, 1025–1037.
Stearns, S.C. (1992) *Evolution of Life Histories*. Oxford University Press, London, UK.
Stillwell, R.C., Blanckenhorn, W.U., Teder, T., Davidowitz, G. & Fox, C.W. (2010) Sex differences in phenotypic plasticity affects variation in sexual size dimorphism in insects: from physiology to evolution. *Annual Review of Entomology*., **55**, 227–245.
Trivers, R.L. (1972) Parental Investment and Sexual Selection. *Sexual Selection and the Descent of Man* (ed B. Campbell), pp. 136–179. Heineman, London.
Vermeulen, C. & Loeschcke, V. (2007) Longevity and the stress response in *Drosophila*. *Experimental Gerontology*, **42**, 153–159.
Walters, R.J., Blanckenhorn, W.U. & Berger, D. (2012) Forecasting extinction risk of ectotherms under climate warming: an evolutionary perspective. *Functional Ecology*, **26**, 1324–1338.
Whitlock, M.C. (1996) The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *American Naturalist*, **148**, 65–77.
Williams, G.C. (1957) Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, **11**, 398–411.
Williams, P.D. & Day, T. (2003) Antagonistic pleiotropy, mortality source interactions, and the evolutionary theory of senescence. *Evolution*, **57**, 1478–1488.
Williams, A.E., Rose, M.R. & Bradley, T.J. (1997) $CO_2$ release patterns in *Drosophila melanogaster*. The effect of selection for desiccation resistance. *Journal of Evolutionary Biology*, **200**, 615–624.
Williams, P.D., Day, T., Fletcher, Q. & Rowe, L. (2006) The shaping of senescence in the wild. *Trends in Ecology and Evolution*, **21**, 458–463.
Zera, A.J. & Harshman, L.G. (2009) Laboratory selection studies of life-history physiology in insects. *Experimental Evolution* (eds. T. Jr Garland & M.R. Rose), pp. 217–262. University of California Press, Berkley, CA.

*Received 3 February 2013; accepted 12 September 2013*
*Handling Editor: Charles Fox*

## Supporting Information

Additional Supporting information may be found in the online version of this article:

**Table S1.** ANOVA tables of the effect of Acclimatization, sex and their interaction of life span and development rate *Callosobruchus maculatus*
**Table S2.** Trait means for each Line:Selection regime ('Treatment'): Test temperature ('Temperature'):Sex combination for the acclimatized trial.
**Table S3.** Trait means for each Line:Selection regime ('Treatment'): Test temperature ('Temperature'):Sex combination for the nonacclimatized trial.
**Table S4.** Mean fecundity for each Line:Selection regime ('Treatment'): Test temperature ('Temperature') combination for the nonacclimatized trial.