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# Sex-specific selection under environmental stress in seed beetles

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## Abstract

Sexual selection can increase rates of adaptation by imposing strong selection in males, thereby allowing efficient purging of the mutation load on population fitness at a low demographic cost. Indeed, sexual selection tends to be male-biased throughout the animal kingdom, but little empirical work has explored the ecological sensitivity of this sex difference. In this study, we generated theoretical predictions of sex-specific strengths of selection, environmental sensitivities and genotype-by-environment interactions and tested them in seed beetles by manipulating either larval host plant or rearing temperature. Using fourteen isofemale lines, we measured sex-specific reductions in fitness components, genotype-by-environment interactions and the strength of selection (variance in fitness) in the juvenile and adult stage. As predicted, variance in fitness increased with stress, was consistently greater in males than females for adult reproductive success (implying strong sexual selection), but was similar in the sexes in terms of juvenile survival across all levels of stress. Although genetic variance in fitness increased in magnitude under severe stress, heritability decreased and particularly so in males. Moreover, genotype-by-environment interactions for fitness were common but specific to the type of stress, sex and life stage, suggesting that new environments may change the relative alignment and strength of selection in males and females. Our study thus exemplifies how environmental stress can influence the relative forces of natural and sexual selection, as well as concomitant changes in genetic variance in fitness, which are predicted to have consequences for rates of adaptation in sexual populations.

## Introduction

Males and females experience different selection pressures (Fisher, 1958; Lande, 1980; Andersson, 1994), which has been a major focus of evolutionary research on a large variety of topics such as the maintenance of sex (Agrawal, 2001), sexual conflict (Arnqvist & Rowe, 2005) and the evolution of sexual dimorphism (Clutton-Brock, 2007; Schärer *et al.*, 2012). Current research is highlighting the importance of ecological factors in determining the outcome of sexual selection and how sex differences can have major effects on the evolutionary response to environmental change (Bussiere *et al.*, 2008; Candolin & Heuschele, 2008; Svensson & Calsbeek, 2012; Grazer & Demont, 2014; Miller & Svensson, 2014; Robinson & Qvarnström, 2014; Rogell *et al.*, 2014). However, we still lack an understanding of whether there are systematic differences in how the two sexes respond to environmental stress, and what role the mating system plays in shaping such sex-specific environmental sensitivity and associated responses to environmental change.

It is often assumed that in most sexually reproducing species females invest large amounts of energy in producing offspring whereas males spend more resources on competing for access to females, presumably as an ultimate result of anisogamy (Bateman, 1948; Trivers, 1972; Schärer *et al.*, 2012; Parker, 2014). Although not all agree on the exact details of the implied causality (Dawkins & Carlisle, 1976; Sutherland, 1985; Kokko &

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Jennions, 2008), sexual selection is therefore generally expected to be stronger in males in polygamous species (Bateman, 1948; Andersson, 1994; Arnqvist & Rowe, 2005). Indeed, although a variety of different mating systems exist in nature, and the strength of sexual selection varies tremendously in accordance, the collated data as of to date support the general claim of stronger sexual selection in males (Janicke *et al.*, 2016).

A particular facet of such male bias is that sexual selection could increase adaptation in sexual populations (Manning, 1984; Agrawal, 2001; Siller, 2001; Lorch *et al.*, 2003). This assertion relies on that strong sexual selection targets and weeds out males of low genetic quality, and by doing so, removes mutations with generally deleterious effects from the population (Zahavi, 1975; Rowe & Houle, 1996; Tomkins & Radwan, 2004). This would reduce the mutation load on population fitness in sexually reproducing species at a low demographic cost (Agrawal, 2001; Siller, 2001), because females – who put the ultimate limit on population growth via their egg production – experience weaker selection and are relatively spared of the cost of adaptation (*sensu* Haldane, 1937). The relative strength of selection in males and females is therefore of considerable interest for predictions of demography and rates of adaptation in sexual populations (Whitlock & Agrawal, 2009).

As the strength of selection acting on any trait results from its covariance with fitness, the upper limit for the strength of selection is set by the mean-standardized variance in fitness $\boldsymbol{I} = \sigma_w^2/\bar{w}^2$, known as 'the opportunity for selection' (Crow, 1958). Moreover, $\boldsymbol{I}$'s additive genetic component, $\boldsymbol{I}_A$ (Houle, 1992), predicts the response to selection of fitness itself (Price, 1970). Sex-specific estimates of $\boldsymbol{I}$ and its subsequent partitioning into genetic and environmental components thus represent an empirically tractable means to explore the relative strength of, and response to, selection in males and females (Shuster & Wade, 2003; Krakauer & Webster, 2011). However, few empirical explorations of the environmental sensitivity of sex-specific strengths of selection are available due to a lack of systematic comparisons within species (but see Serbezov *et al.*, 2010; Byers & Dunn, 2012; Sharp & Agrawal, 2012; Janicke *et al.*, 2015). Moreover, male secondary sexual traits often show substantial genotype-by-environment interactions (GEI:s) (Bussiere *et al.*, 2008; Kolluru, 2014), implying spatio-temporal variation in selection and that the relative reproductive success of alternative genotypes varies across heterogeneous environments. Thus, efforts estimating the strength of sex-specific selection and the reproductive success of alternative male and female genotypes across different conditions are prerequisites for predicting the evolutionary fates of sexual populations facing environmental change (Candolin & Heuschele, 2008; Ingleby *et al.*, 2014; Miller & Svensson, 2014).

We here generate and test general predictions of environmental sensitivities and opportunities for selection in males and females based on simple fitness landscape theory (Fig. 1). In this framework, variances in the traits under selection are assumed to remain

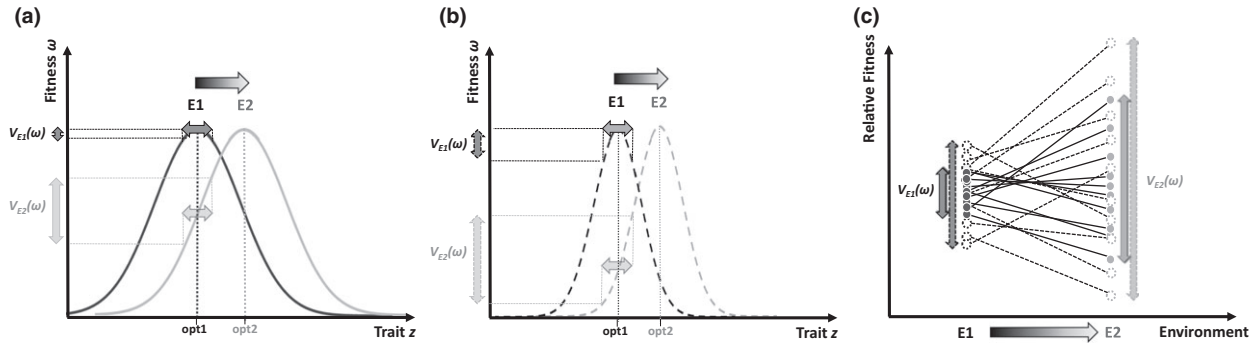


**Fig. 1** Predictions of the change in mean and variance in fitness under environmental stress. (a) In the ancestral environment (**E1**), stabilizing selection on trait $z$ is represented by the black curve, and variance in $z$ is represented by a horizontal double-headed arrow along the $x$-axis. The population is well adapted, and phenotype values are distributed around the trait mean which yields the maximum fitness (**opt1**). In this scenario, trait variance translates into a variance in fitness, $\boldsymbol{V_{E1}(\omega)}$, represented by a vertical double-headed arrow along the $y$-axis. If the environment changes rapidly (**E2**), the new trait optimum is shifted (light grey curve) to a new value of $z$ (**opt2**). However, phenotype values are still distributed around **opt1** and the population is now off-peak. Assuming the shape of the fitness function remains relatively unchanged, mean fitness decreases and variance in fitness increases in the new environment: $\boldsymbol{V_{E2}(\omega) > V_{E1}(\omega)}$. (b) Stronger stabilizing selection should yield a higher variance in fitness for the same phenotypic variance in $z$ (compare a and b). This is true when the population is on-peak and off-peak. (c) Analogously and as a result of a, environmental change induces genotype-by-environment interactions (GEI:s) and an inflation of genetic variance for fitness. Each genotype's relative fitness is represented by a point in the ancestral (**E1**) and novel (**E2**) environment. Again, stronger stabilizing selection (as in b; open symbols) is expected to result in stronger GEI:s than when selection is weak (as in a; closed symbols).

constant and unaffected by environmental stress. Although this assumption could be incorrect for any specific trait, it is in line with empirical data suggesting no general pattern of change in trait variance under stress (Hoffmann & Merilä, 1999; Agrawal & Whitlock, 2010). Instead, the theory predicts an inflation of variance in fitness when populations are moved into new environments as a result of these populations being pushed off their fitness peak (Martin & Lenormand, 2006; Fig. 1a). This inflation of fitness variance is predicted to be particularly pronounced when stabilizing selection is exceedingly strong (compare Fig. 1a, b), as might be the case for the strength of sexual selection on males relative to that on females. Analogously, we also expect increasingly pronounced GEI:s for traits under strong selection (Fig. 1c).

The dynamics of sexual selection in a natural population are likely to depend on all the phenotypes present in the population, that is, sexual selection is likely to be frequency dependent. Therefore, it may be difficult to make very detailed predictions for how reproductive fitness of different genotypes is affected under novel environmental settings that completely change the composition of phenotypes. Indeed, cases of sexual selection being disrupted by a change in the environment have been documented in both natural (Ahnesjo, 1995; Almada *et al.*, 1995) and laboratory populations (Janicke *et al.*, 2015). Here, studying the polyandrous seed beetle *Callosobruchus maculatus,* we therefore tested the outlined predictions of environmental sensitivity of fitness and GEI:s among individuals subjected to different environments when measured against a common standardized reference population, reared in the ancestral environment. Thus, although this approach sidesteps the natural situation in which focal individuals likely would compete and mate with individuals originating from the same environment as themselves, it provides a means to measure the environmental sensitivity of fitness and GEI:s in males and females independently. In other words, it directly assigns changes in mean and variance in fitness to variance in condition among tested focal individuals of a particular sex, reared in a particular environment.

We subjected males and females from 14 isofemale lines to two different environmental gradients by manipulating either developmental temperature or larval host plant species. We estimated sex-specific mean fitness across the gradients relative to the ancestral benign environment to assess sex-specific sensitivity to stress. We then estimated variances in relative fitness (i.e. $\boldsymbol{I}$) for each sex and in each environment and partitioned the variance into its genetic and environmental components across the juvenile and adult stage. This allowed us to test the following predictions: (i) male reproductive success should be more sensitive to environmental stress than female reproductive success, (ii) variances in fitness should increase under stress elevating both the opportunity for selection (Fig. 1a) and GEI:s (Fig. 1c), (iii) variance in male reproductive success should remain higher than variance in female reproductive success under stress (compare Fig. 1a, b), and (iv) male GEI:s for reproductive success (but not juvenile survival) should be more pronounced than female GEI:s as a result of increased fitness variance in novel environments (Fig. 1c).

## Materials and methods

### Study population

The beetle *C. maculatus* is a cosmopolitan capital breeder found in tropical and subtropical arid regions. Adults are facultatively aphagous (i.e. they do not require water or food to reproduce). Females lay eggs onto the surface of dry beans, and the larvae then develop inside the bean for about 3 weeks after which the sexually mature adults emerge (Fox *et al.*, 2011). Under laboratory conditions, egg to adult survival rates are usually well above 90% (e.g. Fricke & Arnqvist, 2004; Fox *et al.*, 2011). *Callosobruchus maculatus* serves as a model organism for the study of both pre- and post-copulatory sexual selection (e.g. Eady, 1991; Bilde *et al.*, 2008, 2009; Maklakov & Arnqvist, 2009). Males attempt mating frequently and females often resist mating attempts by kicking with the hind legs. Both sexes nevertheless usually mate multiply throughout their lifetime, leading to post-copulatory sexual selection on males. *Callosobruchus maculatus* is a widespread pest of seed storages; thus, the species is very well adapted to environmental conditions that are easily reproduced in the laboratory, making them a tractable model system (Fox *et al.*, 2003; Messina & Jones, 2009).

The study population was isolated from *Vigna unguiculata* (black-eyed beans) seed pods collected at a small-scale agricultural field close to Lome, Togo (06°10#N 01°13#E), during October and November 2010. The average annual temperature at this location is 26.6 °C (www.wordclimate.com). Virgin males and females emerging from the beans were paired randomly and each pair founded an isofemale line. In total, 41 lines were created. Lines were immediately expanded to a population size of approximately 300 adults that were then kept on *V. unguiculata* seeds under benign laboratory conditions (e.g. Arnqvist & Tuda, 2009) 29 °C, 50% RH and a 12-L: 12-D light cycle, for 25 generations prior to the experiments. The 14 lines used in this experiment were randomly selected from the 41 available lines (described in Berger *et al.*, 2014).

### Experimental design

We created two independent gradients of environmental stress by manipulating independently developmental temperature and larval host plant species. Starting from

the benign laboratory environment at which the lines were maintained (29 °C, black-eyed beans), we created two additional environments with stressful developmental temperatures: 34 °C and 37 °C (using black-eyed beans), and two additional environments with alternative hosts: *Vigna radiate* (mung bean) and *Vigna angularis* (adzuki bean) (at 29 °C). The level of stress was measured as percentage reduction in mean male and female fitness as compared to the original benign laboratory environment. Ten generations prior to the start of the experiment, we created an outbred standard reference population that focal individuals from each line would mate and compete with (See: 'Lifetime reproductive success' below) by pooling 10–20 individuals from each isofemale line and letting them mate at random.

The experiment was carried out over three consecutive generations, with all line/environment combinations represented in each generation. At the start of each generation, replicates of the isofemale lines were propagated in the five environments, whereas the reference population was propagated in the benign environment only. After 48 h of egg laying, adults were removed from the jars to keep larval density and competition at a moderate level. We confirmed that density did not have a negative impact on survival to adulthood and we do not comment on this further. In each generation, we measured the lines across the five environments for egg to adult survival and lifetime reproductive success (LRS) of the surviving adults. We then used these measures to calculate mean and variance (total and genetic) in fitness and the opportunity for selection (see 'Statistical analysis' in Material and methods).

### Juvenile survival

After the 48 h of egg laying, 48 beans per line and environment were selected at random and isolated. The eggs laid on the beans were counted a week later. The emerging adults were all counted and sexed. Assuming a 50/50 sex ratio of the eggs laid and no adjustment of this ratio depending on environmental conditions, for which there is no evidence in this species despite a comprehensive body of research (Edvardsson & Arnqvist, 2005), we calculated the egg to adult survival for each sex as the ratio of the number of males or females emerged divided by half of the total number of eggs laid.

### Adult lifetime reproductive success

We derived sex- and environment-specific estimates of adult LRS, by performing replicated assays on the emerging males and females from the 14 lines. Twenty to thirty days after eggs were laid in the various environments, virgin beetles started emerging and these focal individuals were immediately moved to the ancestral benign environment and allowed to compete against and mate with the individuals from the reference population (raised in the benign environment). Thus, the different environmental treatments only affected the focal individuals during the juvenile period. However, as *C. maculatus* acquires all its adult resources in the juvenile stage, the environmental stress imposed during this stage is predicted to have wide-ranging consequences across the full life cycle.

By competing focal individuals against references raised in the benign environment, we were able to estimate the change in LRS with environmental deterioration independently in each sex and with reference to the environment of origin. To estimate male LRS, a single virgin focal male, originating from one of the isofemale lines and developed in one of the five environments, was introduced together with one sterilized virgin male and two virgin females, all three from the reference population, into a Petri dish (90 mm ø) containing a surplus of *V. unguiculata* beans. Reference competitors were sterilized by irradiating them with a 100 Gy dose from a caesium-137 source. It has been shown that this sterilization method causes lasting sterility in males while leaving males active and their sperm competitive (Eady, 1991; Maklakov & Arnqvist, 2009). Males can mate multiply, and certainly with more than two females if given the opportunity, but remating with the same female also increases the chances of fertilization due to sperm competition. Presenting two female references should therefore capture the essential variation in male LRS.

Female LRS was estimated by placing the focal female with two reference males and a sterilized female reference competitor. This protocol ensured that females could remate and included potential competition between females for matings (as male ejaculates can have positive effects on female fecundity in this species (Fox, 1993a, b; Arnqvist *et al.*, 2005), as well as selection for female resistance to multiple mating attempts by males (as multiple mating and harassment can harm females: (Rönn *et al.*, 2007; Maklakov & Arnqvist, 2009). Focal and reference individuals were placed in the assays 0–24 h following adult emergence. The balanced sex ratios and equal set-ups used in the male and female assays ensured that sexual selection could act symmetrically in the sexes. The measure of LRS of the focal individuals corresponds to the number of adult offspring emerging from each assay. We scored in total 1034 females and 1047 males: on average 15 individuals per isofemale line × sex × environment combination.

### Statistical analysis

*Effects of environmental stress on sex-specific means*

Our analyses used maximum-likelihood estimates from linear mixed-effects models implemented in the lme4

package (Bates & Maechler, 2011) for R (R Core Team 2013). Juvenile survival was analysed in a generalized linear mixed-effects model with a binomial response (dead and alive) and logit link function, incorporating sex, environment and their interaction, as well as generation as fixed factors. Isofemale line crossed by sex and environment was included as a random effect. LRS was analysed as a normally distributed response variable in a model incorporating sex, environment, their interaction and generation as fixed factors and the same random effects as for the model on juvenile survival. Total fitness, calculated as the product of the line-level estimates for survival and reproductive success in each of the three generations, was analysed as a normally distributed response variable in a model incorporating the same fixed and random effects as the model for LRS. Separate models were run for the two types of environmental gradients.

*Effects of environmental stress on sex-specific opportunities for selection*

The opportunity for selection ($\boldsymbol{I}$) was calculated as defined by Crow (1958), where $\boldsymbol{I}_{\mathrm{JS}}$ is the opportunity for selection on juvenile survival, $\boldsymbol{I}_{\mathrm{LRS}}$ the opportunity for selection in adults, and $\boldsymbol{p}$ the fraction of individuals surviving to the adult stage:

$$\boldsymbol{I} = \boldsymbol{I}_{\mathrm{JS}} + \frac{1}{\boldsymbol{p}}\boldsymbol{I}_{\mathrm{LRS}} \tag{1}$$

$\boldsymbol{I}_{\mathrm{JS}}$ is calculated as the variance in juvenile survival ($V_{\mathrm{JS}}$) standardized by the squared mean juvenile survival $\left(\overline{\mathrm{JS}}^2\right)$. As for any binomially distributed variable, if mean survival probability is $p$, the variance in juvenile survival will be $p \times (1-p)$, so:

$$\boldsymbol{I}_{\mathrm{JS}} = \frac{V(\mathrm{JS})_{\mathrm{sex,env}}}{\overline{\mathrm{JS}}^2{}_{\mathrm{sex,env}}} = \frac{p \times (1-p)}{p^2} = \frac{1-p}{p} \tag{2}$$

$\boldsymbol{I}_{\mathrm{LRS}}$ is calculated as the variance ($V_{\mathrm{LRS}}$) in reproductive success of the individuals surviving to the adult stage standardized by the squared mean reproductive success of these individuals ($\overline{\mathrm{LRS}}^2$):

$$\boldsymbol{I}_{\mathrm{LRS}} = \frac{V(\mathrm{LRS})_{\mathrm{sex,env}}}{\overline{\mathrm{LRS}}^2{}_{\mathrm{sex,env}}} \tag{3}$$

We estimated sex- and environment-specific means and variances in LRS and juvenile survival in Bayesian mixed-effects models utilizing Markov chain Monte Carlo (MCMC) simulations implemented in the MCMCglmm package (Hadfield, 2010) for R. These models were equivalent to the described models using maximum-likelihood estimation, except for allowing more flexibility when estimating sex- and environment-specific opportunities for selection by incorporating a more specified structure for the random effects: Sex- and environment-specific variances for both the isofemale line and residual component were estimated while setting covariances to zero (using the 'idh' structure for the random effects variance–covariance matrix). A weak flat inverse-gamma prior was used for the random effects (V = 1 and $v$ = 0.002), to minimize the effect of prior information on posterior distributions (Hadfield, 2010). We ran 1 000 000 iterations of each model after discarding 500 000 iterations used to initiate the Markov chain. The thinning interval was set to 1000, thus resulting in 1000 stored posterior estimates of all variance components. To determine whether two estimates of $\boldsymbol{I}$ differed from each other, we calculated two-tailed $P$-values based on the posterior distributions. Mean-standardized genetic variance ($\boldsymbol{I}_{\mathrm{G}}$) was estimated as twice the variance explained by the isofemale line component (Hoffmann & Parsons, 1988).

*Sex-specific genotype-by-environment interactions*

To estimate sex-specific GEI:s, we again applied maximum-likelihood estimation. Separate models were run for the two environmental gradients. Juvenile survival was analysed as a binomial response using a logit link function, incorporating environment, sex and generation as fixed factors. LRS was mean-standardized per environment, generation and sex and analysed in models with no fixed effects. The random structure included isofemale line by environment and sex as well as the lower order terms for the line variance components, allowing estimation of interaction variances and testing for sex-specific GEI:s via hierarchical-likelihood ratio comparisons of full and reduced models using the car package (Fox & Weisberg, 2011). We subsequently also analysed the sexes separately to quantify the magnitude of GEI:s in each sex.

## Results

### Effects of environmental stress on mean survival and LRS

High temperature had a negative effect on juvenile survival, LRS and fitness in both sexes (Fig. 2a–c). In line with predictions, males suffered more than females in terms of total fitness (sex by environment interaction: $P$ = 0.015, Fig. 2c). This result was driven by male LRS being much more reduced by temperature than female LRS (sex by environment interaction: $P < 0.001$, Fig. 2b), whereas there was no consistent sex difference in the environmental sensitivity of juvenile survival (Fig. 2a). See Table S1 for a full summary of statistics.

Similar to the observations for temperature stress, male fitness tended to be more sensitive to host stress (Fig. 2f), although the sex by environment interaction for total fitness was not statistically significant (Table S2). The effect of host quality on the two fitness components was not consistent with that observed for

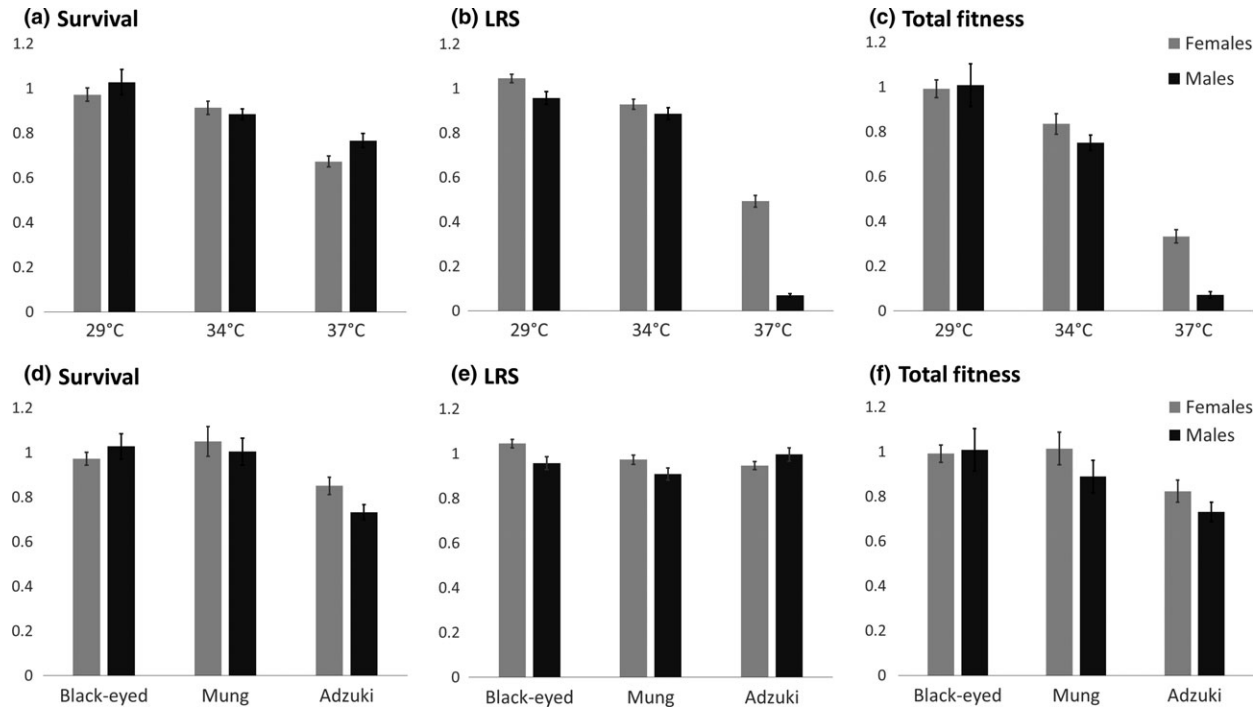


**Fig. 2** Sex-specific means of juvenile survival, adult LRS and total fitness along the two environmental gradients; temperature stress (a–c) and host stress (d–f). The error bars represent standard errors. Female values in grey and male values in black.

temperature stress. The sex by environment interaction was significant for adult LRS ($P = 0.016$), but driven by females tending to be more sensitive to development on adzuki beans and males to development on mung beans (Fig. 2e, Table S2), rather than an overall more pronounced stress sensitivity in males. Both sexes suffered reduced juvenile survival on adzuki beans and the effect was particularly pronounced in males (Fig. 2d); however, the sex by environment interaction was not statistically significant (Table S2).

## Effects of environmental stress on opportunities for selection

Temperature stress increased $\boldsymbol{I}$ for fitness in both sexes, driven by concomitant changes in the two underlying fitness components (Table 1, Fig. 3). Males consistently showed greater $\boldsymbol{I}_{\mathrm{LRS}}$ than females across temperatures (Table 1, Fig. 3b). No consistent sex-specific pattern was detectable for $\boldsymbol{I}_{\mathrm{JS}}$ (Fig. 3a). This resulted in an overall opportunity for selection that was generally male-biased under temperature stress (Fig. 3c, Table 1). $\boldsymbol{I}$ for fitness also seemed to increase under host stress, but foremost as a result of changes in $\boldsymbol{I}_{\mathrm{JS}}$ (Table 1, Fig. 3). The sex-specific pattern was very similar to that under temperature stress, with $\boldsymbol{I}_{\mathrm{LRS}}$ being consistently greater in males (Table 1, Fig. 3c).

Thus, as predicted from the Gaussian fitness landscape, $\boldsymbol{I}$ and its two underlying components generally increased with environmental stress in both males and females. Moreover, $\boldsymbol{I}_{\mathrm{LRS}}$ was significantly greater in males than females across all environments (Table 1, Fig. 3b), consistent with persistent male bias in the strength of sexual selection, whereas $\boldsymbol{I}_{\mathrm{JS}}$ never differed significantly between the sexes (Table 1, Fig. 3a). This resulted in $\boldsymbol{I}$ for fitness being consistently greater in males, although not significantly so at 34 °C (Table 1, Fig. 3c). Interestingly, and in line with predictions, temperature and host quality had similar effects on the opportunity for selection when accounting for the level of stress imposed by each environment (Fig. 3c). Although changes in (mean-standardized) $\boldsymbol{I}$ were partly driven by reductions in mean fitness, absolute variances also increased under stress (Table S3), demonstrating that the results were not solely attributable to mean scaling.

## Effects of environmental stress on $I_G$ and genotype-by-environment interactions

Our Bayesian estimates of $\boldsymbol{I}$*'s* genetic component ($\boldsymbol{I}_{\mathrm{G}}$) were low and hard to estimate, except for female LRS at 37 °C. Interpreting these estimates at face value, $\boldsymbol{I}_{\mathrm{G}}$ in both sexes increased with stress, in line with predictions, but were not greater in males. Moreover, male fitness and its components, juvenile survival and LRS, showed low broad-sense heritabilities, indicating a weak opportunity for a response to selection in this sex under stress (Fig. S1).

**Table 1** Bayesian estimates and significance tests of differences in the opportunity for selection in males ($I_M$) and females ($I_F$) across the different environments.

| | Juvenile survival | | | Lifetime reproductive success | | | Total fitness | | |
|---|---|---|---|---|---|---|---|---|---|
| Environment | $I_M$ | $I_F$ | *P*-value | $I_M$ | $I_F$ | *P*-value | $I_M$ | $I_F$ | *P*-value |
| 29 °C | 0.17 | 0.18 | 0.27 | 0.23 | 0.09 | 0.002 | 0.39 | 0.27 | 0.05 |
| 34 °C | 0.24 | 0.21 | 0.24 | 0.25 | 0.16 | < 0.001 | 0.50 | 0.42 | 0.062 |
| 37 °C | 0.46 | 0.70 | 0.09 | 3.80 | 0.98 | < 0.001 | 4.83 | 1.76 | < 0.001 |
| Black-eyed beans | 0.17 | 0.20 | 0.29 | 0.22 | 0.08 | < 0.001 | 0.39 | 0.30 | 0.042 |
| Mung beans | 0.27 | 0.29 | 0.46 | 0.24 | 0.12 | < 0.001 | 0.56 | 0.37 | 0.19 |
| Adzuki beans | 0.56 | 0.35 | 0.09 | 0.28 | 0.11 | < 0.001 | 0.84 | 0.50 | 0.004 |

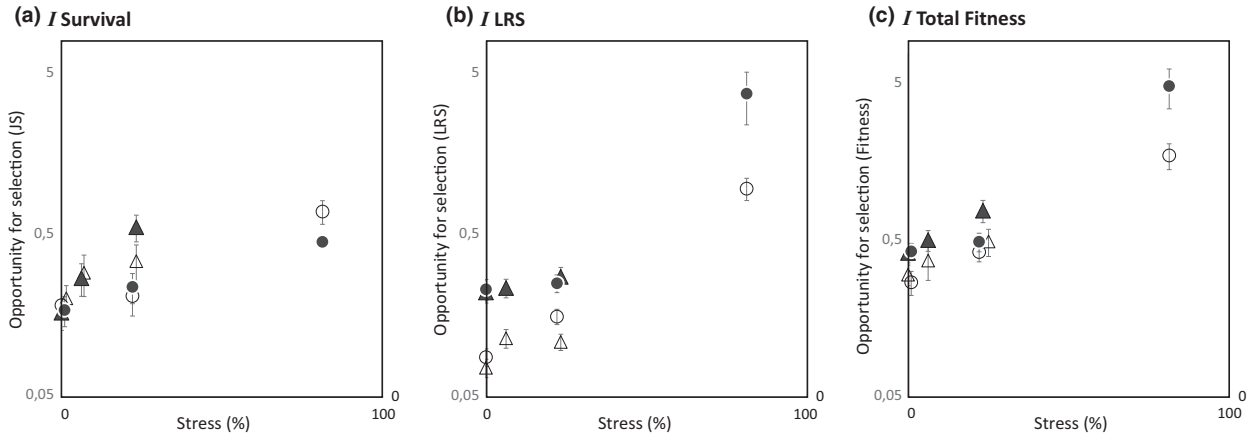


**Fig. 3** Sex-specific opportunities for selection in juvenile survival, adult lifetime reproductive success and total fitness as a function of the level of stress (expressed as a percentage of reduction in mean fitness as compared to ancestral conditions). The opportunity for selection is given by closed symbols in males and open symbols in females, under temperature stress (circles) and host stress (triangles), respectively. Error bars represent standard errors.

GEI:s accounted for a substantial fraction of the standing genetic variance in both juvenile survival and adult LRS across temperatures (Fig. 4), but there were also nontrivial amounts of variance accounted for by the overall effect of isofemale line, although effects were only statistically significant in females (Table 2). There were also marginally significant sex differences in GEI:s for the fitness components. Although ML estimates of genetic variances in LRS, in line with predictions from the Gaussian fitness landscape, increased in magnitude with temperature stress and were more pronounced in males, sex differences also seemed ascribed to differences in the relative ranking of genotypes across temperatures (Table 2 and Fig. 4).

GEI:s dominated genetic variance in juvenile survival across host plants and showed significant differences between the sexes. These sex differences seemed foremost to depend on differences in the ranking of different genotypes across hosts rather than sex differences in magnitude of the GEI:s (Table 2, Fig. 4). In contrast, there were no significant GEI:s for adult LRS, which showed low, but statistically significant, amounts of sex-specific genetic variance (Table 2, Fig. 4).

## Discussion

Sexual selection often acts more strongly in males in polygamous species (Wade & Shuster, 2004; Jones, 2009; Janicke *et al.*, 2016), which may offer population-level benefits to sexual reproduction (Manning, 1984; Agrawal, 2001; Siller, 2001; Lorch *et al.*, 2003). However, while central to predicting evolutionary responses and demographic processes under environmental change, less is known about how natural and sexual selection targets male and female phenotypes exposed to environmental stress. Here, we applied a simple Gaussian fitness landscape (Fig. 1) to generate and test predictions of changes in mean and variance in fitness, as well associated genotype-by-environment interactions (GEI:s), in males and females experiencing environmental stress. Our results imply that our application of the fitness landscape has relatively good explanatory power in terms of accurately predicting increased fitness variance among individuals raised in stressful environments (Fig. 3), and a consistent male bias in the strength of selection across environments (Figs 2 and 3). These results suggest that strong sexual

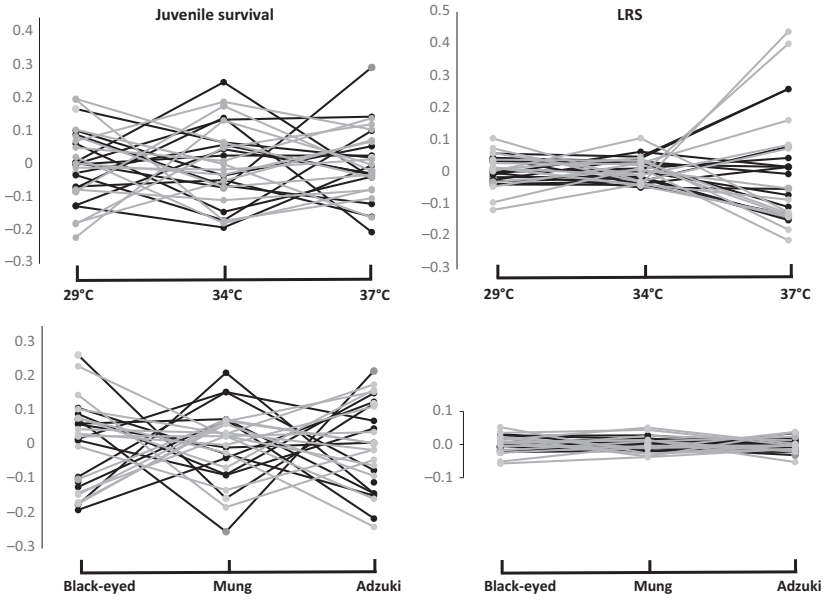


**Fig. 4** Male and female reaction norms for juvenile survival and adult lifetime reproductive success based on the 14 isofemale lines assayed under temperature and host stress. Black points and lines represent female genotypes and grey points and lines male genotypes. On the top row, the environment variable that changes is temperature and on the bottom row host plant species.

selection in males may indeed confer benefits to sexual populations exposed to changing environments by efficiently purging maladaptive alleles from the population at a low demographic cost (Manning, 1984; Agrawal, 2001; Siller, 2001). However, the details of these results were not entirely consistent across the two environmental gradients, and the genetic components underlying fitness variance were less predictable. Below we discuss these results in more detail with emphasis on the role of sex- and life stage-specific fitness effects in determining evolutionary responses to environmental stress.

Following predictions from sexual selection theory (Wade, 1979; Wade & Arnold, 1980), $\boldsymbol{I}_{\mathrm{LRS}}$ was consistently male-biased across environments, whereas $\boldsymbol{I}_{\mathrm{JS}}$ never differed significantly between the sexes (but see: Hunt *et al.*, 2004). In line with predictions from the Gaussian fitness landscape, the two environmental gradients had similar effects on $\boldsymbol{I}$ for total fitness over the comparable (low to intermediate) range of stress. However, one potentially important difference between the two environmental stressors is that the male-biased sensitivity to temperature stress was mainly due to sex differences in selection on adults (Figs 2a, b and 3a, b), whereas the small (and nonsignificant) male-biased sensitivity to host stress seemed to be ascribed to differences in juvenile survival (Figs 2d, e, and 3a, b). This illustrates that the type of environmental change studied can be of great importance as the mechanisms involved in a stress response will vary accordingly, and may be more or less sex-specific. For example, it is known that temperature has strong impact on male seed beetles through a reduction in sperm production (Fox *et al.*, 2006) and quality (Vasudeva, 2014). This may explain why temperature had a stronger effect on male reproductive success compared to host quality. Generally, such differences in the stage and sex specificity of environmental stress can prove crucial for responses to selection in sexual populations, because they may limit the potential for male-biased sexual selection to purge alleles decreasing juvenile viability in some environments. If so, the main cost of adaptation would be paid by both sexes in the juvenile stage, in turn weakening the relative importance of sexual selection on condition-dependent genetic variation in the adult stage.

While the opportunity for selection increased among stressed individuals, and generally more so in males, the response to selection ultimately relies on the genetic component of $\boldsymbol{I}$ (Fisher, 1930; Houle, 1992). Here, we applied the fitness landscape metaphor to predict that stress would reveal genetic variation for fitness (Fisher, 1930; Martin & Lenormand, 2006; Fig. 1). Indeed, genetic variance for $\boldsymbol{I}_{\mathrm{LRS}}$ was strongly inflated by temperature stress (Fig. 4b, Fig. S1), suggesting that there will be abundant genetic variation available for selection in hotter climates. However, we saw little increase in genetic variation under host stress. The level of stress imposed by the host gradient was much lower than that imposed by temperature, which may partly explain this discrepancy. Another explanation is that most of the cryptic genetic variation potentially revealed by host stress was suppressed – if individuals do not achieve their full genetic potential with scarce larval resources (Hoffmann & Merilä, 1999). Predictions of changes in genetic variance under stress are complicated by the fact that strong selection may both expose and erode genetic variation in fitness-related traits

**Table 2** Genetic effects for juvenile survival and lifetime reproductive success (LRS) estimated by isofemale line variance along the two environmental gradients. Full analyses estimating all hierarchical variance components were performed on the whole data set (Data = 'all') and then for each sex separately. *P*-values were calculated by likelihood ratio comparisons using a type III SS approach.

| Stress | Trait | Data | Component | Variance | $\chi^2$ | *P*-value |
|---|---|---|---|---|---|---|
| Temperature | Juvenile survival | Male | Line | 0.044 | 3.4 | 0.065 |
| | | | Line × E | 0.061 | 16 | < 0.001 |
| | | Female | Line | 0.059 | 6.4 | 0.011 |
| | | | Line × E | 0.038 | 10 | 0.0016 |
| | | All | Line | 0.047 | 6.1 | 0.013 |
| | | | Line × E | 0.020 | 1.7 | 0.20 |
| | | | Line × Sex | 0.0060 | 0.32 | 0.57 |
| | | | Line × E × Sex | 0.025 | 4.9 | 0.026 |
| | LRS | Male | Line | 0.019 | 0.77 | 0.38 |
| | | | Line × E | 0.026 | 1.7 | 0.19 |
| | | Female | Line | 0.017 | 4.3 | 0.039 |
| | | | Line × E | 0.013 | 5.5 | 0.019 |
| | | All | Line | 0.0014 | 0 | 1 |
| | | | Line × E | 0 | 0 | 1 |
| | | | Line × Sex | 0.015 | 1.8 | 0.18 |
| | | | Line × E × Sex | 0.019 | 3.3 | 0.071 |
| Host | Juvenile survival | Male | Line | 0.0035 | 0 | 1 |
| | | | Line × E | 0.089 | 33 | < 0.001 |
| | | Female | Line | $3.9 \times 10^{-08}$ | 0 | 1 |
| | | | Line × E | 0.12 | 43 | < 0.001 |
| | | All | Line | $9.2 \times 10^{-9}$ | 0 | 1 |
| | | | Line × E | 0.044 | 3.6 | 0.059 |
| | | | Line × Sex | $3.7 \times 10^{-7}$ | 0 | 1 |
| | | | Line × E × Sex | 0.052 | 15 | < 0.001 |
| | LRS | Male | Line | 0.0098 | 6.2 | 0.013 |
| | | | Line × E | 0.0012 | 0.11 | 0.74 |
| | | Female | Line | 0.0045 | 9.8 | 0.0018 |
| | | | Line × E | 0 | 0 | 1 |
| | | All | Line | 0.0029 | 0.96 | 0.33 |
| | | | Line × E | 0 | 0 | 1 |
| | | | Line × Sex | 0.0042 | 5.6 | 0.018 |
| | | | Line × E × Sex | $6.2 \times 10^{-12}$ | 0 | 1 |

(Merilä & Sheldon, 2000). Another example highlighting the complexity of understanding genetic variation in fitness comes from Wang *et al.* (2013) who measured environment-specific viability selection on 36 individual mutations inserted into two alternative genetic backgrounds of *Drosophila melanogaster* adapted to different environments in a 2 × 2 common garden design. Contrary to predictions based on fitness landscape theory, mutational variance was not higher for populations raised in the novel environment compared to their ancestral environment, but instead highly environment specific. Thus, even when genetic variation is abundant and estimated with precision, genetic selection in sexual populations may not be as accurately predicted by low-dimension fitness landscapes as previously demonstrated for unicellular organisms (e.g. Tenaillon, 2014).

In line with predictions, genetic variance in male LRS became particularly pronounced under temperature stress. However, only females showed statistically significant increases in genetic variance and GEI:s under temperature stress. Genetic variance for fitness is expected to be low compared to the environmental component, and this was especially true for male LRS at 37 °C. Thus, statistical power was likely limited in our experiment but our results nevertheless imply that even if $\boldsymbol{I}$ remains male-biased and increases with stress, this may foremost reflect an inflation of environmental variance. If so, decreasing heritabilities would result under stress, a trend that has been observed in wild bird populations (Charmantier & Garant, 2005; but see Husby *et al.*, 2011) and for a variety of traits exposed to hot temperatures (reviewed in: Angilletta, 2009; Berger *et al.*, 2013), and are consistent with our estimates of heritability (Fig. S1). As a consequence, purging of deleterious alleles through sexual selection on males could be significantly hampered under higher temperatures.

GEI:s dominated genetic variance for juvenile survival. However, these interactions were the result of differences in the relative ranking of genotypes across environments, rather than an overall inflation of genetic variance under stress as predicted by fitness

landscape theory (compare Fig. 1 with Fig. 4a, c). This suggests that balancing selection mediated by environmental heterogeneity may be responsible for maintaining a substantial fraction of standing genetic variation in juvenile survival. Moreover, these interactions also showed significant sex specificity (Table 2), indicating that the way in which the studied genotypes are affected by various larval conditions differ between the sexes. This observed sex specificity may be considered somewhat surprising given that selection is predicted to be more aligned in juvenile males and females compared to selection in the adult stage (Rice & Chippindale, 2001). However, sex-specific selection in the adult stage can enforce differential selection on male and female juvenile growth trajectories and resource intake as a means to achieve adult sexual dimorphisms (Badyaev, 2002), in line with the observed sex specificity in GEI:s being more pronounced across host species than temperatures, and pronounced sexual dimorphism in this population of *C. maculatus* (Berger *et al.* 2016).

For sexual selection to purge mutation load on population fitness, selection has to act concordantly across the sexes. Conversely, sexually antagonistic selection, benefitting different alleles at the same locus in males and females, could diminish any potential population benefits of sexual selection, as stronger selection on males could lead to the fixation of alleles decreasing female fecundity (Rice & Chippindale, 2001; Bonduriansky & Chenoweth, 2009). However, selection in males and females is predicted to align under stress and adaptation towards new phenotypic optima, reducing sexual antagonism (Long *et al.*, 2012; Berger *et al.*, 2014; Connallon & Clark, 2014; but see Delcourt, 2009; Punzalan *et al.*, 2014). Sex-specific GEI:s, as observed in this study, are implicit in such a reduction in sexual antagonism as it involves a sex-specific reshuffling of the fitness ranking of genotypes across environments. A previous study using all of the 41 available isofemale lines from this population did indeed find evidence for reduced sexual antagonism under temperature stress, signified by the intersexual genetic correlation for LRS shifting from being significantly negative at benign temperature to becoming positive under temperature stress (Berger *et al.*, 2014). Our study used only 14 of these isofemale lines and was thus not designed to estimate genetic correlations, but in line with these previous results we found that variance in LRS was composed of an, albeit marginally nonsignificant, sex by temperature and isofemale line interaction variance (Table 2). In contrast, sex-specific LRS showed no host specificity. A *post hoc* inspection of line scores for LRS instead indicated that the intersexual genetic correlations for LRS across hosts were overall negative, implying pronounced sexual antagonism in the adult stage and a limit to the population benefits of sexual selection. One possible explanation for this is that survival selection in the juvenile stage under host stress may have depleted condition-dependent (sexually concordant) genetic variation, leaving mostly sexually antagonistic genetic variation to be measured for adult LRS, which is in line with the observation that adults surviving on the most stressful host (adzuki beans) showed no decline in LRS. In any case, together with the observed differences in how the two environmental stressors affected life stage-specific fitness components (Fig. 2), these observations further highlight the possibility for selection in early life stages to modify the opportunity for selection in subsequent life stages and that this process may vary unpredictably across different environments.

Theoretical predictions of responses to selection under environmental change typically assume constant selection surfaces with only changing phenotypic optima (e.g. Burger & Lynch, 1995; Chevin, 2011; Walters *et al.*, 2012). However, this assumption remains largely untested in studies of genotype-by-environment interaction in general (Agrawal & Whitlock, 2010) and in studies of sexual selection in particular (Ingleby *et al.*, 2014; Kolluru, 2014). It is difficult to predict how the strength of selection on the two sexes will be affected by an abrupt environmental change that modifies the entire composition of phenotypes in the population because, in contrast to fecundity selection that may to a large extent be independent of processes involving intrasexual competition and corresponds to hard selection, sexual selection is affected by frequency-dependent processes and likely corresponds to soft selection. Thus, because variance in fitness was here measured among individuals competed against a nonstressed reference population, and not references experiencing the same conditions as the focal genotypes, our results are sensitive to changes in phenotype composition that would come about by abrupt and pronounced environmental change and should thus be interpreted with some caution.

## Summary

We measured sex- and life stage-specific selection and GEI:s in individuals of *C. maculatus* exposed to two different environmental stressors. Our results proved consistent with several straightforward predictions from a Gaussian fitness landscape assuming stronger selection in males, implying that sexual selection could efficiently purge maladaptive alleles under stress at low demographic costs by leaving females relatively spared of the cost of adaptation. Also according to predictions, genetic variance in fitness increased with stress. However, this increase was only modest, leading to seemingly reduced heritabilities, especially in males, which would compromise responses to sexual selection in new environments. GEI:s were generally not explained by increased variance in stressful conditions only, but also

by shifts in genotype ranking across environments. Moreover, these shifts showed high sex- and life stage specificity, which also differed qualitatively across the two stress gradients, suggesting that novel environments may result in idiosyncratic evolutionary responses in males and females. Future studies incorporating more environments, applied to a wider set of organisms, are needed to further evaluate the predictions and empirical patterns reported here, given that GEI:s are widespread and can be more complex than the view provided by fitness landscape theory applying unidimensional and constant selection surfaces.

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## Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:
**Table S1** Effect of sex and temperature on survival, LRS and total fitness.
**Table S2** Effect of sex and host plant on survival, LRS and total fitness.
**Table S3** Comparison of mean-standardized and absolute variances in survival and LRS.
**Figure S1** Sex-specific genetic variance and heritabilities for survival, LRS and total fitness.

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