doi:10.1111/evo.12439

INTRALOCUS SEXUAL CONFLICT AND ENVIRONMENTAL STRESS

David Berger,[1,2] Karl Grieshop,[1] Martin I. Lind,[1] Julieta Goenaga,[1] Alexei A. Maklakov,[1] and Göran Arnqvist[1]

[1]*Animal Ecology at Department of Ecology and Genetics, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, SE-75236 Uppsala, Sweden*

[2]*E-mail: david.berger@ebc.uu.se*

Received November 1, 2013
Accepted April 10, 2014

Intralocus sexual conflict (IaSC) occurs when selection at a given locus favors different alleles in males and females, placing a fundamental constraint on adaptation. However, the relative impact of IaSC on adaptation may become reduced in stressful environments that expose conditionally deleterious mutations to selection. The genetic correlation for fitness between males and females (r_{MF}) provides a quantification of IaSC across the genome. We compared IaSC at a benign (29°C) and a stressful (36°C) temperature by estimating r_{MF}s in two natural populations of the seed beetle *Callosobruchus maculatus* using isofemale lines. In one population, we found substantial IaSC under benign conditions signified by a negative r_{MF} (−0.51) and, as predicted, a significant reduction of IaSC under stress signified by a reversed and positive r_{MF} (0.21). The other population displayed low IaSC at both temperatures (r_{MF}: 0.38; 0.40). In both populations, isofemale lines harboring alleles beneficial to males but detrimental to females at benign conditions tended to show overall low fitness under stress. These results offer support for low IaSC under stress and suggest that environmentally sensitive and conditionally deleterious alleles that are sexually selected in males mediate changes in IaSC. We discuss implications for adaptive evolution in sexually reproducing populations.

KEY WORDS: **Adaptation, condition dependence, genetic quality, sexual selection, sexually antagonistic, temperature.**

Males and females share much of the same genome, but selection is often distinct in the two sexes. This leads to genetic conflict over sex-specific phenotypic optima where allele frequency changes at loci conferring a fitness advantage to one sex may bear costs to the other (Lande 1980; Rice 1984; Arnqvist and Rowe 2005; Bonduriansky and Chenoweth 2009). Such sexually antagonistic (SA) loci may thus place an ultimate limit on adaptation (Rice 1992; Chippindale et al. 2001; Arnqvist and Tuda 2010). This intralocus sexual conflict (IaSC) is predicted to affect a range of fundamental evolutionary processes, such as the maintenance of genetic variation and mutation load (Kidwell et al. 1977; Connallon et al. 2010; Fry 2010; Arnqvist 2011), population differentiation (Connallon and Clark 2012; Hesketh et al. 2013), and adaptation to environmental change (Whitlock and Agrawal 2009).

The extent to which IaSC will limit adaptation within natural populations is determined primarily by the amount of genetic variation at SA loci relative to those having sexually concordant fitness effects (Rowe and Houle 1996; Hunt et al. 2004). As a corollary, the relative amount of SA variation for fitness determines whether the net effect of sexual selection will increase or decrease the rate of adaptation (Agrawal 2001; Lorch et al. 2003; Radwan 2004; Morrow et al. 2008; Whitlock and Agrawal 2009; Arnqvist and Tuda 2010). If mutations have concordant effects across the sexes, then strong sexual selection eliminating males of poor genetic quality from the mating pool can decrease the mutation load at the population level without discernible demographic costs (Manning 1984; Agrawal 2001). On the other hand, if alleles have opposing fitness effects in the sexes then sexual selection in males would tend to increase the frequency of alleles having deleterious effects in females, imposing a potentially sizeable gender load on fitness (Chippindale et al. 2001; Bonduriansky and Chenoweth 2009; Arnqvist and Tuda 2010; Connallon et al. 2010). The relative contribution of SA loci to standing genetic variance in fitness thus has important implications for the rate of adaptation (Lorch et al. 2003; Whitlock and Agrawal 2009; Long et al. 2012).

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INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION

IaSC can be estimated through the intersexual genetic correlation for fitness (r_{MF}), using either quantitative genetic breeding designs or pedigree-based inferences. Estimates from standing genetic variation in laboratory *Drosophila* populations have shown negative r_{MF}s, demonstrating IaSC (e.g., Chippindale et al. 2001; Pischedda and Chippindale 2006; Delcourt et al. 2012) and data from wild populations of vertebrates seem to agree with these results (e.g., Brommer et al. 2007; Foerster et al. 2007; Svensson et al. 2009). However, because mutations with concordant effects in the sexes should be eliminated (or fixed) by selection while those with opposing effects may not be (Kidwell et al. 1977; Connallon et al. 2010; Fry 2010), allelic variation at SA loci should be maintained at relatively high equilibrium frequencies in well-adapted populations (Whitlock and Agrawal 2009; Connallon et al. 2010; Arnqvist 2011). Therefore, inferences based on standing genetic variation could be biased toward overestimating the impeding effect of IaSC on adaptation from new mutation. In support of this expectation, empirical evidence in *Drosophila* suggests that the majority of new mutations have deleterious effects across both sexes (e.g., Morrow et al. 2008; Sharp and Agrawal 2013).

Along the same line, estimates of r_{MF}s under benign equilibrium conditions may overestimate the negative impact of IaSC on adaptation from standing genetic variation in novel or stressful environments. This is because allelic variation with conditional effects might become more apparent under environmental stress, where it may dominate genetic variance for fitness (Hoffmann and Merilä 1999; Tomkins et al. 2004; Martin and Lenormand 2006; Long et al. 2013), thus reducing the relative contribution of SA genetic variation (Whitlock and Agrawal 2009; Long et al. 2012). Only a few studies have addressed changes in r_{MF}s and the relative prevalence of IaSC across different environmental conditions. Long et al. (2012) found, as expected, that well-adapted *D. melanogaster* populations had higher relative amounts of SA genetic variation compared to populations that had experienced an influx of foreign alleles. In contrast, *D. serrata* seems to show little consistency in terms of IaSC across a range of novel food sources, although differences between environments were not statistically certified (Delcourt et al. 2009; Punzalan et al. 2014). A possible explanation for these seemingly incongruent results is that novel environments not only expose previously neutral alleles to selection, but often change the direction and strength of selection on alleles with important fitness effects also in the ancestral environment (Martin and Lenormand 2006; Agrawal and Whitlock 2010; Long et al. 2013). Thus, while theory generally predicts a reduction of IaSC in stressful environments through increased sexually concordant directional selection for overall genetic quality and stress-resistant phenotypes, it is nevertheless possible that certain novel environmental conditions may instead intensify IaSC by changes in SA selection.

Here, we investigate effects of environmental stress on IaSC by estimating r_{MF} at a benign (29°C) and a stressful (36°C) temperature, using isofemale lines isolated from two natural populations of the seed beetle *Callosobruchus maculatus* (Bruchidae). Using temperature to induce environmental stress is motivated by its well-known effects on ectotherm physiology through thermodynamic constraints on metabolism (Gillooly et al. 2001; Hochachka and Somero 2002) and by the current interest and relevance in the face of global climate change. Beyond a certain limit, warm temperatures decrease fitness and induce stress responses in both sexes (see Parsons and Hoffmann 1991; Hochacka and Somero 2002; Angilletta 2009). We predicted that a stressful thermal regime would reduce IaSC (signified by r_{MF}s becoming more positive) by aligning selection in males and females through increased selection for overall genetic quality and stress-resistant phenotypes. We tested whether genetic variance for fitness was elevated at 36°C compared to 29°C, as might be expected if genetic variation with conditional fitness effects is exposed to increased selection under stress. We also estimated both genetic and overall variance in relative fitness across sexes and temperatures as measures of the opportunity for selection (Crow 1958), to assess if selection had stronger potential to act in males than in females, and if this putative sex difference was affected by temperature.

To further describe the dynamics of IaSC we repartitioned genetic variance for male and female fitness into a sexually concordant component, describing genetic variation with identical fitness effects in males and females, and an antagonistic component, describing genetic variation with opposing fitness effects in the sexes. Using these components of genetic variance, we tested two explicit predictions. First, we expected positive cross-environment genetic covariance for sexually concordant fitness, signifying variation for overall genetic quality. Second, because sexual selection for increased investment into costly secondary sexual traits is often stronger in males and is expected to trade-off against somatic maintenance, males should be more sensitive to environmental stress (Sheldon et al. 1998; Brooks 2000; Tomkins et al. 2004; Bussiere et al. 2008; Kwan et al. 2008; Bellamy et al. 2013; Sharp and Agrawal 2013). We thus predicted that SA genetic variance encoding high male but low female fitness at benign conditions would tend to show negative genetic covariance with fitness in both sexes under temperature stress.

Methods

STUDY POPULATIONS

Callosobruchus maculatus is a pest of leguminous crops that has colonized most of the tropical and subtropical regions of the world. Females start laying eggs on the day of adult eclosion. These beetles are capital breeders and lay most of their eggs

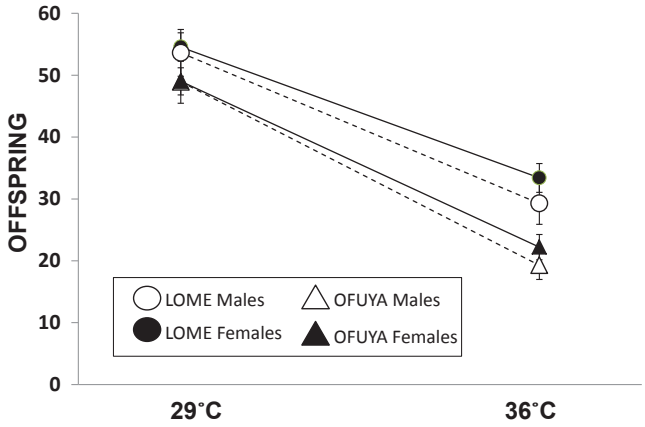

Figure 1. Mean number of offspring produced per individual in the female and male fitness assays under benign (29°C) and stressful (36°C) temperatures.

(80–90%) during the first few days of their life. Hatching success of eggs under benign laboratory conditions is typically above 95% and larval survival rates are typically above 90% (e.g., Fricke and Arnqvist 2004; Fox et al. 2011). The eggs are glued onto the surface of dry beans and hatched larvae bore into the beans, where they complete their juvenile phase in about three weeks at 29°C (e.g., Fox et al. 2011; Rogell et al. 2014). Although both sexes will mate on their first day of adulthood and then repeatedly throughout life, males will do so at much higher potential frequencies. Females are thus often seen resisting male mating attempts by displaying various resistance behaviors, such as kicking with the hind legs to thwart harassing males. Nevertheless, females typically mate multiply, introducing postcopulatory sexual selection on males in this species (e.g., Eady 1991; Maklakov and Arnqvist 2009). This species is facultatively aphagous, that is, adults do not require food or water to reproduce at high rates (Fox 1993). Demographic modeling suggests that *C. maculatus* colonized human grain stores during early Holocene (around 12,000 years ago; Kebe et al., unpubl. ms). Thus, they have adapted to conditions very similar to laboratory settings for several thousands of generations making them suitable as a laboratory model system (Fox et al. 2003; Messina et al. 2009). A temperature of 29°C is considered optimal for this species, whereas 36°C is clearly suboptimal with signs of reduced juvenile survival and female fecundity (Giga and Smith 1983; Fox and Stillwell 2009; Rogell et al. 2014; see also Fig. 1).

The two study populations were isolated from *Vigna unguiculata* seed pods collected in the field during October and November 2010. The "Lome" population was collected at a small scale agricultural field close to Lomé, Togo (06°10′N 01°13′E), whereas the "Ofuya" population was collected at an agricultural field in the Maiduguri area of Borno State, Nigeria (11°50′N 13°09′E). Average annual temperatures at these locations are 26.6°C (Lome) and 27.5°C (Ofuya) (http://www.worldclimate.com). Annual thermal fluctuations are higher at the Ofuya location: daily high temperatures regularly reach above 36°C during four months of the year here (March–June), something that is very rare at the Lome location. Seed pods were stripped in the laboratory and beans isolated individually. Virgin males and female hatching out of these beans were paired randomly and each pair founded an isofemale line. In total, 41 Lome and 32 Ofuya lines were established, each of which thus derived from a single maternal and a single paternal genome. Lines were immediately expanded (using all F1 offspring produced by the founders of each line) to a population size of approximately 2–300 adults that were then kept on *V. unguiculata* seeds at 29°C, 50% RH, and a 12L:12D light cycle, for 15 generations prior to the experiments.

FITNESS ASSAYS

To derive relevant sex- and temperature-specific estimates of each isofemale line's genetic values for fitness, as well as estimates of r_{MF}s at both temperatures, we setup replicated assays of male and female lifetime reproductive success. Three generations prior to the start of these assays, we created an outbred reference population each for the Lome and Ofuya population by taking 10–20 individuals from each isofemale line and letting them mate at random within each population. Individuals from these reference populations were then allowed to compete against and mate with the focal beetles originating from the isofemale lines (see below). The generation before an experimental block, each isofemale line, kept at 29°C, was provided with ca. 600 *V. unguiculata* beans. After 36–48 h of egg laying, we isolated 48 randomly selected beans individually from each line and assigned half of these to each of the two experimental temperatures (29°C or 36°C). Twenty to thirty days later, virgin beetles started emerging and these were immediately used in the assays. Similarly, for the reference populations, we provided each population, consisting of ca. 600 beetles, with approximately 1500 beans and isolated and assigned these to either 29°C or 36°C in the same manner.

To estimate male fitness, a single virgin focal male from an isofemale line was introduced together with two sterilized virgin males and three virgin females from the reference population. These six individuals were placed together in a Petri dish (90 mm ø) containing a surplus of *V. unguiculata* beans and kept there for their entire life. Reference males were sterilized by irradiating them with a 100 Gy dose from a cesium-137 source. This sterilization technique has been shown to cause lasting sterility in male seed beetles while not compromising male copulation ability and sperm competitive ability (Eady 1991; Maklakov and Arnqvist 2009). Although males will mate with more than three females if given the chance, we note that repeated mating with the same female also elevates male reproductive success in the face of sperm competition in this species. Our protocol therefore captures

variation in both male premating and postmating reproductive success. For the female fitness assays, a single virgin focal female was placed in a Petri dish with a surplus of beans along with two (nonirradiated) virgin reference males for their entire life, ensuring that females could remate at will. We used two males to reduce the risk of variation in female offspring production due to random variation in fertility among reference males. Using two males also ensures some male harassment such that a female's ability to resist male persistence forms an element of her fitness, as male interference is known to reduce female reproductive success in seed beetles (e.g., Yanagi and Miyatake 2003; Maklakov and Arnqvist 2009). Although it is impossible to capture all aspects of fitness variation in any system, our estimates should be highly relevant in this species. We further note that although male and female fitness assays differ in the numbers and ratio of same and opposite sex individuals, this is unlikely to bias our estimates of variance in temperature- and sex-specific fitness.

Fitness assays were kept at the experimental temperature for a total of 35 days after which replicates were frozen at −20°C. This ensures that all F1 offspring had emerged. Our measure of male and female lifetime reproductive success is the total number of adult beetles (i.e., offspring) hatching from each replicate. We note that the complete effects of treatment temperature (29°C or 36°C) on the whole life cycle are included in these estimates through thermal effects during juvenile development and subsequent adult performance in the parental generation (focal individuals) as well as any effects on juvenile survival in their F1 offspring.

Split evenly among the two experimental temperatures, we scored in total 1036 female and 993 male assays for the Lome population, and 975 female and 1042 male assays for the Ofuya population. Each sex × temperature combination was setup over five consecutive generations in the laboratory, with on average 12–13 and 14–18 individuals scored per line and combination for Lome and Ofuya, respectively. Sex- and temperature-specific sample sizes for each isofemale line are reported in Table S3.

ISOFEMALE LINE HERITABILITY AND r_{MF}s

Additive genetic variance for fitness can be approximated as twice the variance between isofemale lines, and the heritability of fitness is then estimated as (Hoffmann and Parsons 1988):

$$h_w^2 = \frac{2}{\frac{1}{t} - \frac{1}{2}}, \quad (1)$$

where t is the intraclass correlation across isofemale lines (i.e., $V_{\text{line}} / [V_{\text{line}} + V_{\text{error}}]$). The intersexual genetic correlation for fitness (r_{MF}) is then

$$r_{\text{MF}} = \frac{\text{COV}_{\text{MF}}}{\sqrt{[V_{\text{M}} \times V_{\text{F}}]}}, \quad (2)$$

where COV_{MF} is the genetic covariance between male and female fitness, and V_{M} and V_{F} are the sex-specific genetic variances. We setup replicate fitness assays for all lines over five consecutive generations, which should minimize any parental and common environment effects that could otherwise inflate our estimates of genetic (co)variance. Given this, our estimates are unbiased under the assumptions (i) that inbreeding after isofemale line expansion was negligible and (ii) that dominance variance is negligible. Although both inbreeding and dominance can lead to overestimation of heritabilities, the facts that we maintained our isofemale lines at a large population size and that the heritability from an isofemale line analysis well approximates the narrow-sense heritability over a wide range of dominance values (Hoffmann and Parsons 1988; David et al. 2005) suggest that our estimates are not significantly biased. We note here that our estimates of heritability (see below) were, if anything, lower than those reported earlier from both wild (Messina 1993; half-sib breeding design) and laboratory (Bilde et al. 2008; diallel cross design) populations of *C. maculatus*.

OPPORTUNITY FOR SELECTION

The total opportunity for (or intensity of) selection (I), defined as the variance in relative fitness, gives an upper boundary for the efficacy of genetic selection (Crow 1958) and is often predicted to be greater for males as a result of sexual selection (Bateman 1948; Wade 1979). To complement our estimates of genetic variance in fitness, which had rather low statistical power (see below), we also calculated I to assess whether the opportunity for selection was greater in males than in females and greater at stressful temperature, conditions that would imply strong potential for sexual selection to aid adaptation to temperature stress. Following Crow (1958):

$$I = \frac{V}{\overline{W}^2}, \quad (3)$$

where V equals variance in the number of offspring produced per focal parent and $\overline{W}$ equals the mean number of offspring produced per focal parent (Wade 1979). We note that this, along with all other derived metrics (Table 1), is based on log-transformed data. However, we are here interested in the comparisons across sexes and temperatures and performing the same calculations on the raw data gave the same qualitative results (not shown here).

SEXUALLY ANTAGONISTIC AND CONCORDANT GENETIC VARIANCE FOR FITNESS

A relatively simple reassignment of genetic variance in sex-specific fitness can greatly improve our understanding of the dynamics of IaSC under different environmental conditions. In the two-dimensional space made up by standardized scores of fitness of male and female genotypes, an axis with a slope of one will describe sexually concordant genetic variation. A second

Table 1. Genetic components of temperature-specific male and female fitness.

Pop	Effect	χ^2	df	*P*	Group	V_G	V_E	h^2	*I*
Lome	*Line*	3.41	1	0.065	*29F*	0.056	0.14	0.29	0.21 (0.18–0.24)
	Line:sex	11.45	1	**0.003**	*29M*	0.018	0.56	0.03	0.58 (0.52–0.66)
	Line:temp	0.88	1	0.348	*36F*	0.042	0.40	0.10	0.47 (0.40–0.51)
	Line:temp:sex	4.21	1	**0.040**	*36M*	0.090	0.81	0.10	0.93 (0.81–1.04)
Ofuya	*Line*	18.41	1	**<0.001**	*29F*	0.032	0.23	0.12	0.28 (0.24–0.31)
	Line:sex	6.12	1	**0.047**	*29M*	0.083	0.50	0.14	0.63 (0.53–0.68)
	Line:temp	6.96	1	**0.008**	*36F*	0.120	0.65	0.16	0.80 (0.70–0.92)
	Line:temp:sex	0.83	1	0.363	*36M*	0.042	0.92	0.04	0.99 (0.87–1.11)

V_G = genetic variance; V_E = environmental variance, h^2 = heritability, *I* = total opportunity for selection (95% credibility interval).
The left panel shows significance tests of random effects using REML model comparisons and a type-II SS approach. The right part shows variance estimates per sex and temperature from the Bayesian analyses.

axis that is orthogonal to the first axis will describe SA genetic variation. By projecting each genotype on these two axes, one can convert line scores of male and female fitness to line scores of sexually concordant and SA fitness (see Fig. 3A, B). We achieved this by, for each temperature and population separately, rotating the two-dimensional Cartesian coordinate system describing male and female genotypes clockwise by 45°:

$$x' = x\cos(\theta) - y\sin(\theta), \quad (4a)$$

$$y' = x\sin(\theta) + y\cos(\theta), \quad (4b)$$

where x' and y' are the values of SA and concordant fitness, x and y are male and female fitness, and θ is the angle by which the coordinate system has been rotated (i.e., 45°). This conversion was performed on zero-centered and unit variance standardized data, making the two derived variables analogous to principal components with the difference being that they are predefined to capture sexually concordant and antagonistic genetic variation, rather than the major (PC1) and minor (PC2) axis of variation in the original data. Note that no variance is lost during this procedure.

We first compared the amount of SA and concordant genetic variation at each temperature, given by the estimated variance between isofemale lines along these two dimensions. We then calculated correlations of line scores for sexually concordant and antagonistic variation across the two temperatures to ask (i) whether line scores on the concordant axis at the benign temperature were positively correlated to the concordant scores at the stressful temperature, suggesting variation in overall genetic quality, and (ii) if lines with high male-benefit scores on the antagonistic fitness axis at 29°C showed low concordant fitness scores at 36°C, as would be predicted if SA alleles encoding successful males at benign temperatures represent less stress-resistant genotypes.

STATISTICAL RATIONALE

To estimate genetic (co)variance matrices and test for significant differences in r_{MF}s between environments, we ran general linear mixed models using restricted maximum-likelihood (REML) implemented in the lme4 package, version 0.999999–2 (Bates et al. 2011) and the asreml-R package, version 3.0 (Butler 2009), available for the statistical software R, version 3.0.0 (R Core Team 2013). To calculate *P*-values we compared log-likelihoods between models where r_{MF}s either were constrained to be equal across environments or estimated in each environment, or between models where random effects of interest were either excluded or included.

To first validate the results of the REML analyses, we used Bayesian statistics using Markov Chain Monte Carlo resampling of the data, implemented in the MCMCglmm package (Hadfield 2010) for R. This approach also provides Bayesian *P*-values and 95% credible intervals (the Bayesian equivalent of confidence intervals) for variance components and correlations. These could then be used to quantify differences in SA and concordant genetic variance, as well as the total opportunity for selection and genetic variance, across sexes and temperatures. We set uniform priors for the correlations according to recommendations in Hadfield (2010). We ran 4,000,000 simulations preceded by a 400,000 burn-in phase and stored every 4000th iteration to produce 1000 uncorrelated posterior estimates of the genetic (co)variance matrix from which 95% credible intervals were calculated (Table S1 for details).

To confirm that 36°C was indeed a stressful environment compared to 29°C, we tested for main effects of the temperature treatment on fitness in linear mixed models with temperature, sex, generation, and their interaction as fixed factors. As random factors, we here included line crossed by temperature and sex, and temperature- and sex-specific effects of setup date.

To estimate temperature- and sex-specific genetic variance for fitness and test the main prediction that r_{MF}s should become

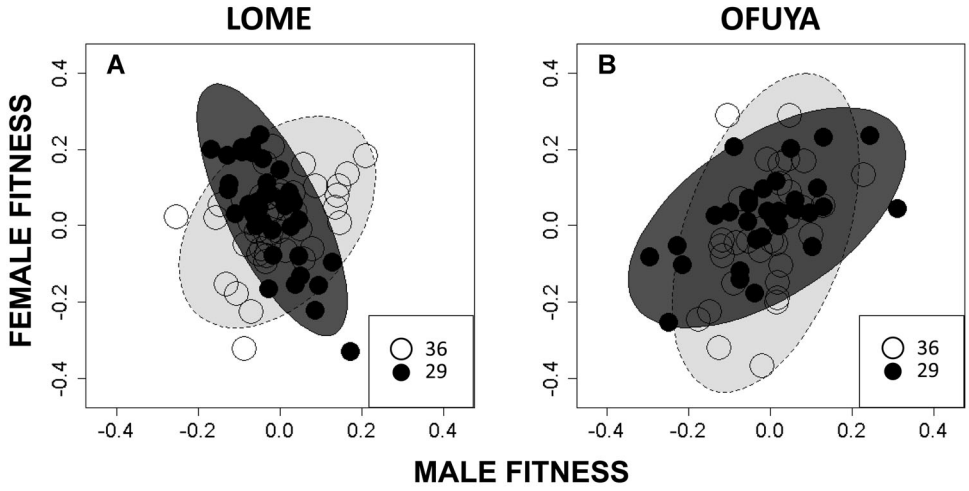

Figure 2. Intersexual genetic correlations (r_{MF}s) for fitness at the benign (29°C) and stressful (36°C) temperature, based on the best posterior estimates from the Bayesian mixed model analyses. Ellipses depict 95% of the predicted distribution of isofemale line scores for male and female fitness at each temperature.

more positive at 36°C, we first calculated relative fitness per sex and temperature for each experimental generation. Relative fitness was log-transformed to improve model fit. The model intercept was included as the only fixed effect and as random effects we included line crossed by temperature and sex (the statistical unit for estimates of genetic (co)variances), and temperature- and sex-specific effects of setup date.

Results

EFFECT OF TEMPERATURE ON FITNESS

Relative to 29°C, fitness at 36°C was reduced by 42% in the Lome population ($\chi^2 = 16.27$, df = 1, $P < 0.001$) and 57% in the Ofuya population ($\chi^2 = 36.95$, df = 1, $P < 0.001$). This effect did not differ significantly between male and female assays in either population (Lome: $\chi^2 = 0.028$, df = 1, $P = 0.87$; Ofuya: $\chi^2 = 0.35$, $P = 0.56$), confirming that 36°C indeed generally presented a stressful environment (Fig. 1).

CHANGES IN r_{MF}s

We first tested if the sex- and temperature-specific genetic architectures of the two particular populations used here were different by analyzing the whole dataset with population incorporated as a fixed effect that was crossed by the random terms (isofemale lines crossed by temperature and sex). Indeed, there was a significant difference in genetic architecture between the populations ($\chi^2 = 22.9$, df = 10, $P = 0.011$) that could mostly be ascribed to differences in sex-specific genetic architecture at 29°C (Table 1, Fig. 2). Hence, in the following analyses, the two populations were analyzed separately.

In the Lome population, we found evidence for a significant sex-by-temperature interaction for genetic variance in fitness ($P = 0.04$, Table 1). A direct test for a change in r_{MF}s was performed by comparing log-likelihoods of a model allowing for different r_{MF}s across temperatures, and an alternative model constraining these correlations to be equal. This showed that the r_{MF} changed significantly across environments ($\chi^2 = 5.18$, df = 1, $P = 0.023$), with a negative r_{MF} at 29°C and a positive r_{MF} at 36°C, thus providing evidence for a reversal of the intersexual genetic correlation for fitness across temperatures (Fig. 2A). The negative r_{MF} at 29°C was significantly different from zero ($\chi^2 = 3.90$, df = 1, $P = 0.048$), whereas the positive correlation at 36°C was not ($\chi^2 = 0.23$, df = 1, $P = 0.63$). In the Ofuya population, there was no significant sex-by-temperature interaction for genetic variance in fitness ($P = 0.36$, Table 1), and no change in r_{MF} across temperatures ($\chi^2 = 0.001$, df = 1, $P = 0.98$). The r_{MF}s were positive at both temperatures (Fig. 2B). These correlations were not significantly different from zero on their own (29°C: $\chi^2 = 2.67$, df = 1, $P = 0.10$; 36°C: $\chi^2 = 0.997$, df = 1, $P = 0.32$) but a pooled estimate across both temperatures showed evidence for a significant positive intersexual genetic correlation for fitness in the Ofuya population ($\chi^2 = 3.82$, df = 1, $P = 0.05$).

The total opportunity for selection was higher in males and increased under temperature stress in both populations, as predicted (Table 1). However, we found no support for a higher absolute level of genetic variance for fitness in males, or a general increase in genetic (co)variance under stress (Table 1, raw covariance matrices in Table S1). Additive genetic variance and heritability of fitness are typically low and thus notoriously difficult to estimate (e.g., Teplitsky et al. 2009) and our study was no exception (Tables 1 and S1). In particular, difficulties in partitioning variance

in male fitness among the genetic and environmental component resulted in low statistical power in estimates of genetic correlations across environments in males. As a result, we could not attain statistical support for sex differences in cross-environment genetic correlations (Lome: $\chi^2 = 0.28$, df $= 1$, $P = 0.59$, Ofuya: $\chi^2 = 0.20$, df $= 1$, $P = 0.66$) despite these being seemingly different in the sexes and significantly positive in females (Tables S1 and S2).

To assess whether low genetic variance in male fitness affected our results regarding differences in r_{MF}s, we used two complementary methods for comparing correlations. First, we performed a Bayesian analysis using Markov Chain Monte Carlo simulations to resample the data and estimate credible limits for model parameters. Second, we calculated temperature- and sex-specific arithmetic line means on the raw data and compared the r_{MF} across temperatures using ANCOVA with line identity as a random error term. Reassuringly, both of these methods yielded results that were qualitatively identical to those from the REML analysis. The P-value for a difference in r_{MF} across temperatures from the ANCOVA was again significant for Lome ($F_{1,38} = 9.69$, $P = 0.004$) and nonsignificant for Ofuya ($F_{1,29} = 0.03$, $P = 0.55$). The Bayesian estimates of correlations and their 95% credible limits showed a more negative r_{MF} at 29°C ($r = -0.51$, CI: -0.77; 0.05) compared to 36°C ($r = 0.21$, CI: -0.38; 0.66) for Lome, and no difference between correlations at 29°C ($r = 0.38$, CI: -0.14; 0.76) and 36°C ($r = 0.40$, CI: -0.25; 0.85) for Ofuya (Fig. 2, Tables S1 and S2).

SEXUALLY ANTAGONISTIC AND CONCORDANT GENETIC VARIATION IN FITNESS

Bayesian analyses of predicted isofemale line means for sexually concordant and SA fitness (Fig. 3) validated the analyses of changes in r_{MF}s. In the Lome population, the proportion of total genetic variance in fitness that was SA was reduced from 76% (CI: 48; 89) at 29°C to 41% (CI: 16; 68) at 36°C. In the Ofuya population, a much smaller fraction of fitness variation was SA both at 29°C (37%, CI: 12; 52) and 36°C (30%, CI: 8; 62).

In the Lome population, the cross-temperature correlation for sexually concordant genetic variation was weak (0.05, CI: -0.38; 0.54, $P = 0.62$) (Fig. 3A). In contrast, there was a positive, albeit nonsignificant, correlation across temperatures in the Ofuya population (0.51, CI: -0.03; 0.83, $P = 0.11$) (Fig. 3B).

Interestingly, the SA axis of genetic variance for fitness at 29°C was correlated to the concordant axis at 36°C: alleles beneficial to males and detrimental to females at 29°C were associated with overall low fitness in both sexes at the stressful 36°C. This correlation was significant in the Lome population (-0.58, CI: -0.81; -0.04, $P = 0.05$, Fig. 3A) and consistent in sign and magnitude in the Ofuya population (-0.46, CI: -0.70; 0.19, $P = 0.32$, Fig. 3B), although the latter was not statistically significant in isolation. We note that the Ofuya population showed a lower amount of SA genetic variation and was represented by fewer isofemale lines (32 for Ofuya vs. 41 for Lome), lowering the statistical power for this test. There was no difference in this correlation between the populations ($P = 0.53$) and pooling them to run the same Bayesian analysis on the full set of 73 isofemale lines yielded strong support for a consistent correlation across the populations (-0.57, CI: -0.76; -0.11, $P = 0.018$).

Discussion

Allelic variation at loci with SA effects on fitness should be maintained at relatively high frequencies under mutation-selection balance. Therefore, we predict that a large proportion of the standing genetic variation in fitness will have opposing effects in males and females in well-adapted populations (Kidwell et al. 1977; Rice 1984; Connallon et al. 2010; Arnqvist 2011; Long et al. 2012). However, stressful conditions will push populations off their equilibria: stress may change selection on SA loci and increase selection on mutations with conditional fitness effects, thereby lowering the relative contribution of SA loci to variance in fitness and reducing the impeding effects of IaSC on adaptation (Whitlock and Agrawal 2009; Long et al. 2012). Our study provides explicit experimental support for this prediction. In the Lome population, the genetic architecture of fitness at the benign temperature showed clear evidence for IaSC, signified by a negative intersexual genetic correlation for fitness. As predicted, this correlation changed sign and became significantly more positive under temperature stress. In the Ofuya population, SA genetic variation for fitness was much lower. Here, the genetic architecture of fitness instead seemed to be dominated by variation in overall genetic quality, as revealed by positive genetic correlations for fitness across sexes and temperatures. Nevertheless, the fact that IaSC was also low under temperature stress in Ofuya is consistent with the general hypothesis. Furthermore, despite the differences in sex-specific genetic architecture found between the two populations, our results show that SA alleles beneficial to males but detrimental to females under benign conditions were generally detrimental to both sexes under stressful conditions (Fig. 3C, D), implying a common mechanism modulating the environmental sensitivity of IaSC.

The significant difference in sex-specific genetic architecture between the two populations is interesting and likely reflects differences in evolutionary histories (Bonduriansky and Chenoweth 2009; Connallon and Clark 2012). One possible explanation for the higher level of sexually concordant genetic variation at 29°C in the Ofuya population could be that the more fluctuating climate at this geographical site acts to maintain such variation (Hedrick 1986). Alternatively, marked differences in the strength of sexual selection across natural populations have been documented

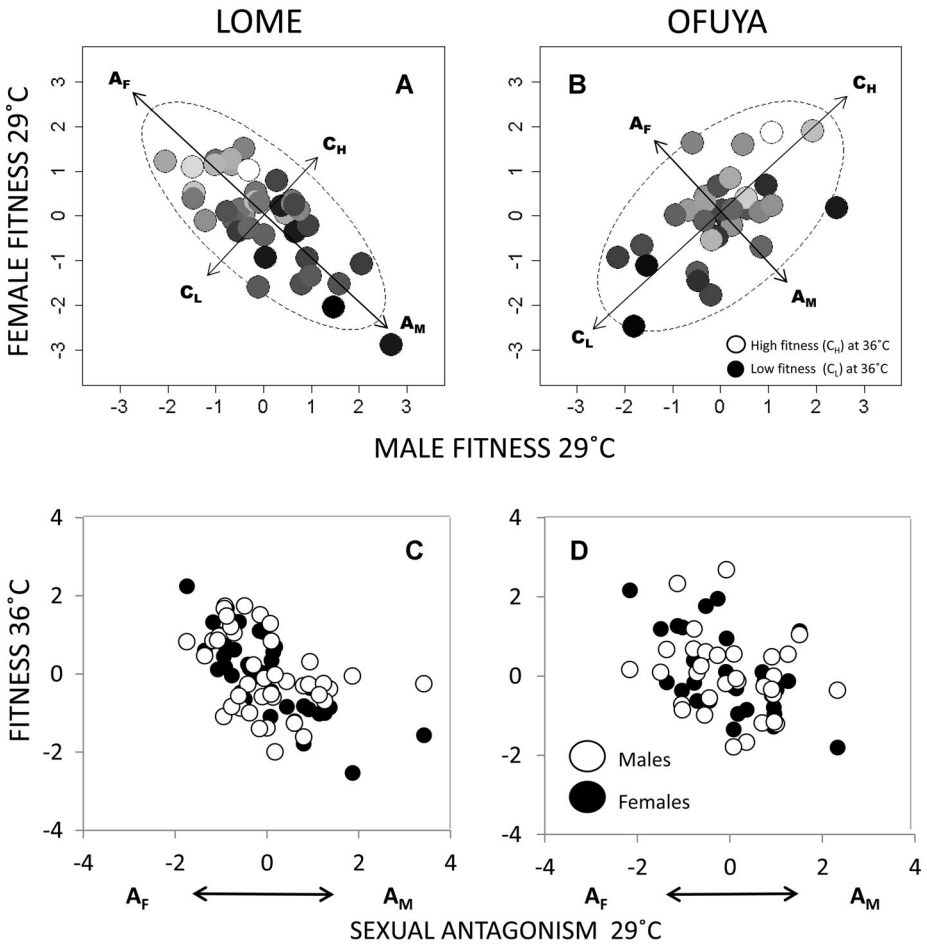

Figure 3. **Genotypes with a male bias along the axis of sexually antagonistic genetic variation under benign conditions showed lowest overall fitness under thermal stress. Shown in panels (A) and (B) are standardized Bayesian posterior estimates of sex-specific fitness ordinated in the two-dimensional space of isofemale line scores for fitness at 29°C. Line scores along the axis of sexually concordant genetic variance for fitness at 36°C are given as color intensity. Dark colors indicate a low score and light color indicates a high score for fitness at 36°C. Arrows depict the axes of sexually concordant (C) and antagonistic (A) fitness at 29°C. A_F and A_M denote female- and male-biased fitness scores along the antagonistic axis and C_H and C_L indicate high and low sexually concordant fitness scores. In Lome, there was low concordant variation at 29°C and a weak correlation between concordant fitness scores across temperatures. In Ofuya, lines that did overall well at 29°C also tended to do well under stress. Generally, lines that harbored SA alleles with beneficial effects in males but detrimental effects in females at 29°C had low sexually concordant fitness at 36°C, with both male and female genotypes doing poorly. This effect is illustrated in panels (C) and (D).**

in other insect species (e.g., Arnqvist 1992; Blanckenhorn et al. 1999) motivating the possibility that sexual selection may generally be weaker in the Ofuya population. Although the exact reasons remain unknown, our results highlight that IaSC and the effect of environmental stress on r_{MF}s may differ substantially among natural populations. Specifically, in populations like Ofuya, where the genetic architecture of fitness is already dominated by variation for overall genetic quality, increased stress may have little effect on the sign of the r_{MF}. In populations like Lome on the other hand, that exhibit less genetic variance for overall genetic quality under benign conditions, induced stress may have a greater effect on the r_{MF}.

Sexual and viability selection should align if the expression of sexually selected traits has an underlying condition-dependent component (Rowe and Houle 1996), such that genotypes with high breeding values for male reproductive success also show high breeding values for female lifetime fecundity. However, selection in males for traits such as persistence, activity rate, and ejaculate characteristics may act to increase IaSC if genetic variance for these traits is encoded for by alleles regulating allocation to reproductive effort rather than having an underlying basis that reflects overall genetic quality and resource acquisition potential (Hunt et al. 2004; Tomkins et al. 2004). We found little variance in overall genetic quality and instead significant IaSC in the Lome

population at 29°C. At 36°C stress may have exposed genetic variation with conditional effects on genetic quality (Hoffmann and Merilä 1999), as suggested by the increase in genetic variance in fitness in Lome males (Table 1). Although this is unlikely to alone explain the reversal of the r_{MF} (see below), it effectively would act to align viability and sexual selection, and to reduce IaSC.

The opportunity for selection is expected to be greater in males than in females in polygamous species (Wade 1979) like *C. maculatus*, and genetic variance in fitness is expected to increase in stressful environments (Martin and Lenormand 2006; Agrawal and Whitlock 2010). The total opportunity for selection was indeed greater in males and also increased under thermal stress in our populations (*I* in Table 1), indicating potential for strong sexual selection on males to aid thermal adaptation in this species (Whitlock and Agrawal 2009). However, we found no consistent differences in the genetic variance in fitness (Table 1), suggesting that the observed changes in the total opportunity for selection were mainly driven by the environmental variance component.

The fact that there was no general support (across sexes and populations) for an increase in genetic variance for fitness in the stressful thermal environment suggests that increased contribution to variance in fitness via alleles underlying genetic quality is not solely responsible for reduced IaSC in the Lome population. We suggest that selection on loci with SA effects on fitness at the benign 29°C may have changed and become more sexually concordant at stressful 36°C. Traits that may underlie such a change are, for example, genetically integrated sexually dimorphic life-history components. Previous studies have shown that female *C. maculatus* have a larger body size, longer life span, lower locomotor activity, and a lower metabolic rate than males (Fox et al. 2006; Arnqvist and Tuda 2010; Burgevin et al. 2013), and these traits have been implicated in IaSC under conditions similar to those of our benign environment (Bilde et al. 2009a,b; Arnqvist and Tuda 2010; Berg and Maklakov 2012). Plastic and genetic responses in these traits to hot temperature show some sex specificity (Hallsson and Björklund 2012; Rogell et al. 2014), in line with the fact that the genetic architecture of these traits is partly private in males and females in this species (Fox et al. 2006; Bilde et al. 2009b; Fox and Stillwell 2009, Hallsson and Björklund 2012). However, male and female responses tend to be in the same direction. These facts suggest that important life-history components may experience SA selection under benign conditions but sexually concordant selection at stressful temperatures. Similar environment-dependent changes in the relative strengths of natural and sexual selection may be common across taxa (e.g., Delph et al. 2011; Robinson et al. 2012), as many of the potential mechanisms offering stress-resistance act on traits such as body size and resource allocation to maintenance (Parsons and Hoffmann 1991; Blanckenhorn 2000; Clarke 2003) that often experience SA selection at benign conditions (Rice and Chippindale 2001; Wedell et al. 2006).

Theory predicts that in mating systems where males compete intensely over matings, male life-history strategies will be optimized by high investment into early reproduction and can be described by a "live-fast-die-young" strategy relative to females (Trivers 1972; Clutton-Brock and Parker 1992; Bonduriansky et al. 2008; Maklakov and Lummaa 2013). If so, we may expect males to be more sensitive to environmental stress (Sheldon et al. 1998; Brooks 2000; Tomkins et al. 2004; Bussiere et al. 2008; Kwan et al. 2008; Bellamy et al. 2013). This offers an explanation for why selection on important fitness components may converge in the sexes in stressful environments. The hypothesis is particularly likely to apply to temperature stress in ectotherms, as high temperatures increase metabolic rates deterministically to levels that eventually become detrimental (Huey and Kingsolver 1989; Brown et al. 2004; Angilletta 2009). In *C. maculatus*, males have higher activity levels and mass-specific metabolic rate than females and fast metabolism is associated with high fitness in males and low fitness in females at benign temperatures (Berg et al., unpubl. ms), well aligned with the fact that we found that SA alleles conferring a benefit to males at benign 29°C were detrimental to both sexes at stressful 36°C.

A substantial amount of research, mainly using laboratory evolution experiments comparing presence and removal of sexual selection, has aimed at assessing the net effect of sexual selection on rates of adaptation (e.g., Holland 2002; Martin and Hosken 2003; Rundle et al. 2006; Fricke and Arnqvist 2007; Hollis et al. 2008; Maklakov et al. 2009, 2010; Hollis and Houle 2011; McGuigan et al. 2011; Arbuthnott and Rundle 2012). The results are, however, mixed. One explanation for these discrepancies could be inherent to the approach; treatments allowing the potential for sexual selection and mate choice to aid adaptation may at the same time confer negative effects on female fitness from male harassment, making the net effect of sexual selection to some extent specific to the mating system studied (Whitlock and Agrawal 2009; Arbuthnott and Rundle 2012; Pennell and Morrow 2013). The mixed results are also consistent with the fact that although SA selection is common, estimates are variable across traits and species (Cox and Calsbeek 2009), and part of the explanation for this apparent lack of consistency could be that the relative amount of SA genetic variation varies across environments and populations, as documented in this study.

There are several reasons for why making universal statements about how environmental change will affect IaSC may be difficult, especially if environmental change is not so much stressful as it is novel. First, as illustrated by our studied populations, differences in genetic architecture due to evolutionary history are likely to make environmental effects on IaSC to some extent

population specific. Second, idiosyncrasies rooted in species-specific ecology may affect the manner by which novel conditions change sex-specific selection (Kwan et al. 2008; Agrawal and Whitlock 2010). Third, different types of environments may affect sex-specific selection in distinct ways (Agrawal and Whitlock 2010) and it is possible that some are more likely than others to increase SA selection, as has been suggested for evolution under high compared to low population density (Brommer et al. 2011; but see Sharp and Agrawal 2008). Fourth, SA genetic variation may increase in novel environments, if conditionally deleterious mutations expressed only under the novel conditions target developmental pathways regulating sexual differentiation. This could lead to the failure of sex-specific expression of SA loci, resulting in reduced sexual dimorphism (Aalberg-Haugen et al. 2012; Pavlicev and Wagner 2012) and elevated IaSC.

To predict IaSC under novel conditions, it may therefore be necessary to understand both the nature of sex-specific selection on different key fitness components and how and why these change with particular environmental conditions. Although IaSC over specific traits under SA selection have been convincingly identified in a number of species (e.g., locomotor activity in fruit flies [Long and Rice 2007], dietary preference in field crickets [Maklakov et al. 2008], longevity/metabolic rate in seed beetles [Bilde et al. 2009b; Berg and Maklakov 2012; Berg et al., unpubl. ms], testosterone levels in bank voles [Mills et al. 2012], longevity/development time in the Indian meal moth [Lewis et al. 2011], and wing length in great reed warblers [Tarka et al. 2014]), we still lack a detailed understanding of the mechanistic basis and dynamics of IaSC in any system. We know of only two other studies apart from ours that have directly compared IaSC across environments. Delcourt et al. (2009) and Punzalan et al. (2014) estimated the r_{MF} for fitness in a population of *D. serrata* reared on an ancestral and a range of novel food sources, but the authors found no consistent change in IaSC across environments. However, statistical power was low for these comparisons, making a direct comparison with our study difficult.

Quantitative genetic studies estimating fitness are often hampered by problems associated with low statistical power. To overcome this obstacle, we employed isofemale lines. Because isofemale lines are founded following one generation of full-sib mating, dominance variance might be somewhat inflated. However, we note that isofemale line analyses generally produce unbiased results over a wide range of dominance values, especially for rare alleles (Hoffmann and Parsons 1988), and that much more severe inbreeding is needed to produce noticeable sex-specific effects in this species (Bilde et al. 2009b). Further, such effects would need to be sex-, temperature-, and population-specific in a manner aligned with our main hypothesis to contribute to our results.

Conclusion

We provide experimental support for the prediction that natural populations containing high levels of SA variation should have this IaSC reduced under environmental stress. Our data suggest that a main cause for the observed low IaSC under stress was that SA alleles that conferred a sexual selection advantage to males under benign conditions were particularly sensitive to stress, while at the same time, SA alleles beneficial to females at benign conditions encode stress-resistant phenotypes. Several hypotheses that relate to the maintenance and expression of genetic variance for fitness across environmental gradients have been proposed to predict IaSC under environmental stress, but very few empirical studies have actually examined SA genetic variation across environments and populations with different evolutionary histories. More are needed.

ACKNOWLEDGMENTS

We thank J. Rönn and L. Shen for invaluable help with logistics; A. Husby and B. Rogell provided statistical advice; B. Stenerlöw at the Division of Biomedical Radiation Sciences, Uppsala University, provided access to the caesium source; T. Ofuya and I. A. Glitho kindly provided us with field collected seed pods. This research was made possible by generous financial support to DB and MIL from the Swedish Research Council, JG from the Wenner-Gren Foundation, AAM from the European Research Council (Starting Grant 2010 AGINGSEXDIFF), and GA from the European Research Council (AdG-294333) and the Swedish Research Council (621–2010–5266).

DATA ARCHIVING

The doi for our data is 10.5061/dryad.m06s2.

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Associate Editor: A. Chippindale

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Summary of Bayesian (MCMCglmm) analyses of genetic (co)variance matrices.
Table S2. Genetic correlation matrices based on arithmetic line means.
Table S3. Sample sizes per temperature and sex for all isofemale lines used.