



Genetic correlations and sex-specific adaptation in changing environments

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Females and males have conflicting evolutionary interests. Selection favors the evolution of different phenotypes within each sex, yet divergence between the sexes is constrained by the shared genetic basis of female and male traits. Current theory predicts that such “sexual antagonism” should be common: manifesting rapidly during the process of adaptation, and slow in its resolution. However, these predictions apply in temporally stable environments. Environmental change has been shown empirically to realign the direction of selection acting on shared traits and thereby alleviate signals of sexually antagonistic selection. Yet there remains no theory for how common sexual antagonism should be in changing environments. Here, we analyze models of sex-specific evolutionary divergence under directional and cyclic environmental change, and consider the impact of genetic correlations on long-run patterns of sex-specific adaptation. We find that environmental change often aligns directional selection between the sexes, even when they have divergent phenotypic optima. Nevertheless, some forms of environmental change generate persistent sexually antagonistic selection that is difficult to resolve. Our results reinforce recent empirical observations that changing environmental conditions alleviate conflict between males and females. They also generate new predictions regarding the scope for sexually antagonistic selection and its resolution in changing environments.

KEY WORDS: Adaptation, fitness, models/simulations, sex, sexual conflict, trade-offs.

Owing to the unique strategies that each sex employs in reproduction, selection often favors the evolution of different phenotypes in males and females (e.g., Andersson 1994). Yet the traits that each sex expresses are encoded in a shared genome (Pennell and Morrow 2013), and most phenotypes exhibit strong and positive additive genetic correlations between the sexes (hereafter r_{mf} ; see Poissant et al. 2010; Griffin et al. 2013)). Although a positive between-sex genetic correlation ($r_{mf} > 0$) promotes adaptation when directional selection aligns between the sexes, it reduces adaptation in each sex when selection is sexually antagonistic (Bonduriansky and Chenoweth 2009), giving rise to a form of evolutionary constraint known as intralocus sexual conflict (or sexual antagonism; see Rice 1992; Rice and Chippindale 2001; Bonduriansky and Chenoweth 2009; van Doorn 2009). Such constraints manifest in patterns of opposing directional selection between the sexes and genetic trade-offs between male and female fitness (Lande 1980; Connallon and Clark 2014)—patterns that have now been documented in several animal and plant populations (Chippindale et al. 2001; Foerster et al. 2007; Cox and

Calsbeek 2009; Delph et al. 2011; Long et al. 2012; Berger et al. 2014).

But what happens to these constraints, and the evolutionary potential for sexual antagonism, when a variable environment forces male and female fitness optima to change over time? Several recent empirical studies have shown that variation in environmental conditions can alter empirical signals of sexually antagonistic selection, such as sex-specific directional selection gradients and genetic correlations between female and male fitness components (Delcourt et al. 2009; Delph et al. 2011; Long et al. 2012; Berger et al. 2014; Punzalan et al. 2014). In *Drosophila* and in seed beetles, for example, exposure to novel lab conditions increases the genetic correlation between female and male fitness, relative to populations that have adapted to stable lab conditions (Long et al. 2012; Berger et al. 2014). Conversely, stable or benign lab conditions often show relatively pronounced signals of sexually antagonistic selection (Rice and Chippindale 2001; Innocenti and Morrow 2010; Long et al. 2012; Berger et al. 2014), although there are notable exceptions to this rule (Delcourt et al.

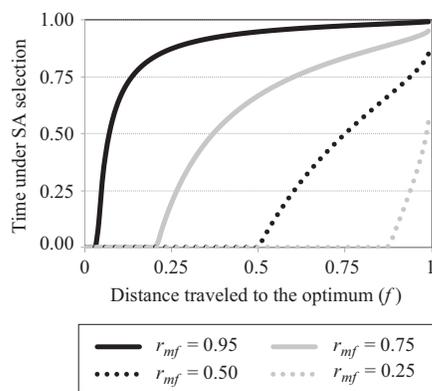


Figure 1. Strong genetic correlations between the sexes lead to pervasive sexually antagonistic (SA) selection during adaptation to stable environmental conditions. The figure quantifies the fraction of time in which an adapting population evolves under sexually antagonistic selection, as defined by the fraction of generations during the adaptive walk in which selection gradients have opposite signs (i.e., $\beta_f \beta_m < 0$, where β_f and β_m represent the directional selection gradients of females and males, respectively). The x-axis shows the fraction of distance the population has evolved to optimum sexual dimorphism ($f = 0$ before any evolution has occurred; $f \sim 1$ near optimum). Most notably, strong r_{mf} values lead to persistent sexual conflict, even when both sexes are relatively close to their respective optima; whereas weak r_{mf} values allow conflict to be resolved even when male and females are still diverging. The model is based on the univariate (single-trait) version of Lande's (1980) influential model for the evolution of sexual dimorphism (for details of the model, see Appendix 1 of the Supplementary Material, which follows from eqs. 16a, b of Lande 1980). Results show the case where males and females have the fixed optima: $\theta_m = 0.5$ and $\theta_f = -0.5$. The initial population is sexually monomorphic, with mean trait expression of $\bar{z}_f = \bar{z}_m = 2$ (thus, selection in each sex is initially in the same direction), and results are shown for the range $0 \leq f < 1$. The genetic and phenotypic variance is assumed to be equal between the sexes, as is the strength of stabilizing selection.

2009; Collet et al. 2016). All in all, these recent empirical studies suggest that changes in environmental conditions may often align the direction of selection in females and males, and thereby alleviate evolutionary constraints associated with sexually antagonistic selection (Long et al. 2012; Berger et al. 2014).

In contrast, a well-developed theory of adaptation to stable environmental conditions predicts that sexually antagonistic selection should arise rapidly during the process of adaptation toward sex-specific phenotypic optima, and persist across long evolutionary timescales (see Fig. 1). In Lande's (1980) original treatment of this scenario, sexual antagonism rapidly escalates during the early evolution of sexual dimorphism, in which the average phenotype of each sex evolves rapidly to a compromised position between the female and male fitness optima (i.e. the "fast phase" of evolutionary change). Sexual dimorphism evolves on a

much slower timescale, particularly when male and female traits are strongly genetically correlated, leading to a protracted period of sexually antagonistic selection (i.e., the "slow phase"). Over time, the mean phenotypes of each sex can eventually evolve to their respective optima, yet the slow evolutionary pace of sexual dimorphism gives rise to sexual antagonism over a large fraction of time during adaptation (Fig. 1). Opposing directional selection between the sexes may therefore represent the norm rather than the exception during bouts of adaptation towards sex-specific phenotypic optima.

Such predictions now seem at odds with the broad spectrum of sex-specific selection patterns that have been observed among populations, between localities within a species' range, or across gradients of environmental stress (i.e., from benign to harsh, see Cox and Calsbeek 2009; Delph et al. 2011; Long et al. 2012; Punzalan et al. 2014; Berger et al. 2014). These empirical observations suggest a potential role for environmental change in mediating patterns of sex-specific selection, as well as the conditions under which sexual antagonism should arise. Although this possibility is intriguing, it lacks a firm theoretical foundation, as current theory predominantly focuses on the evolutionary dynamics of sex-specific adaptation within temporally stable environmental conditions (e.g., Lande 1980; Connallon and Clark 2014; Connallon 2015).

This gap in theory is perhaps surprising, as natural selection in the wild is expected to exhibit considerable temporal variation, with fitness optima varying with changes in seasonal conditions, common pathogens, or predators, or other biotic and abiotic factors (e.g., Kingsolver 1995; Siepielski et al. 2009; Morrissey and Hadfield 2012; Siepielski et al. 2013; Brockhurst et al. 2014; but also see Morrissey and Hadfield 2012; Chevin et al. 2015). Indeed, there has been much theoretical attention given to the adaptation of multivariate traits in response to environmental change, with a focus on the evolutionary consequences of genetic correlations among traits that are expressed by single individuals (Walsh and Blows 2009; Kirkpatrick 2009; Kopp and Matuszewski 2014). This theory demonstrates that genetic correlations between traits can either hinder or enhance adaptation, depending on the degree of alignment between multivariate orientations of natural selection and the multivariate axes of phenotypic space that harbor high genetic variability (Gomulkiewicz and Houle 2009; Duputié et al. 2012; Chevin 2013; Kopp and Matuszewski 2014). Rarely, however, has the same theoretical approach been applied in the context of sex-specific adaptation (e.g., Lande 1980, 1987; Kirkpatrick 2009), despite inherent mathematical similarities between constraints that arise from between-trait versus between-sex genetic correlations.

A formal theoretical treatment of genetic correlations within the context of sex-specific adaptation can shed light on several key questions that theories of multivariate evolution have not yet

addressed. For example, what are the genetic and environmental conditions that are likely to generate sexually antagonistic selection? What conditions align directional selection between the sexes? Is there an optimal genetic correlation between male and female traits—a genetic correlation that maximizes long-term adaptation within each sex? Is the optimal genetic correlation the same or does it differ with respect to long-run adaptation of females versus males? More importantly, an explicit theoretical treatment of sex-specific adaptation under environmental change should provide insight into the possible links between environmental change and the scope for sexual antagonism, as implied by recent empirical research.

To this end, we develop simple models of sex-specific adaptation under two scenarios of environmental change—directional and cyclic changes over time—that each mediates selection on a trait that is expressed by both sexes. For each model, we ask how the between-sex additive genetic correlation for the trait (i.e., r_{mf}) influences sex-specific adaptation and the long-run displacement of each sex from its optimum. We show that genetic correlations that promote adaptation within one sex can simultaneously retard adaptation in the other, leading to a context-dependent relationship between r_{mf} and long-run adaptation in females versus males. Central to this relationship is the concept of sexually antagonistic selection, and its sensitivity to the dynamics of environmental change. While antagonistic selection can persist indefinitely under some conditions, continuous change in the environment will often resolve it, leading to sexually concordant patterns of directional selection to track moving trait optima. We discuss the scope for sexual antagonism and the role of evolutionary constraints in the context of species-specific drivers of environmental variability, including environmental cycles driven by parasites and predators that fluctuate predictably in time.

The Model

Following the framework of Lande and Shannon (1996), we consider temporal variation in a single environmental variable, and evolutionary change in a single trait that is expressed by both sexes. As in Lande and Shannon (1996), we assume that selection is sufficiently weak that we can approximate the dynamics of our three key variables—environmental state, and mean trait expression within each sex—using a continuous time model. Given the assumption of weak selection, continuous time dynamics will be indistinguishable from those of a discrete-time model.

GENERAL MODEL OF EVOLUTIONARY CHANGE IN A QUANTITATIVE TRAIT

We consider a simple model of evolution under sex-specific selection toward sex-specific phenotypic optima that change over

time. We assume that sex-specific fitness is a Gaussian function of trait expression within each sex. For a member of the j th sex ($j = \{f, m\}$), expressing phenotype z_j , fitness in a given generation follows the function:

$$W_j(z_j) \propto \exp\left(-\frac{(z_j - \theta_j)^2}{2\omega_j^2}\right), \tag{1}$$

where θ_j is the trait optimum, and ω_j determines the width of the fitness function. Here, the expected fitness of an individual is a function of both the difference between their trait value and the optimum phenotype ($z_j - \theta_j$) and the intensity of selection ($1/\omega_j^2$), which determines the width of the fitness function. Assuming that the trait is normally distributed within each sex, mean fitness will be:

$$\bar{W}_j \propto \frac{\sqrt{\omega_j^2}}{\sqrt{\omega_j^2 + \sigma_j^2}} \exp\left(-\frac{(\theta_j - \bar{z}_j)^2}{2\omega_j^2 + 2\sigma_j^2}\right), \tag{2}$$

where σ_j^2 is the total variance of the trait within sex j ; averages are denoted by an overbar.

Mean fitness can be used to quantify the strength of directional selection on the trait (Lande 1976; Lande and Arnold 1983). The selection gradient for sex j is:

$$\beta_j = \frac{\partial \ln(\bar{W}_j)}{\partial \bar{z}_j} = \gamma_j(\theta_j - \bar{z}_j), \tag{3a}$$

where $\gamma_j = 1/(\omega_j^2 + \sigma_j^2)$ is the strength of stabilizing selection and $(\theta_j - \bar{z}_j)$ is the evolutionary distance (i.e., the “lag”) between the mean trait value in sex j and its optimum. Following standard quantitative genetics theory of evolutionary change in a species with separate sexes, the rate of change in mean female and male trait expression will be:

$$\frac{\partial \bar{z}_f}{\partial t} = \frac{G_f \gamma_f (\theta_f - \bar{z}_f) + r_{mf} \sqrt{G_f G_m} \gamma_m (\theta_m - \bar{z}_m)}{2} \tag{4a}$$

and

$$\frac{\partial \bar{z}_m}{\partial t} = \frac{G_m \gamma_m (\theta_m - \bar{z}_m) + r_{mf} \sqrt{G_f G_m} \gamma_f (\theta_f - \bar{z}_f)}{2}, \tag{4b}$$

(see Lande 1980; Lande and Shannon 1996; Wyman et al. 2013), where G_j is the additive genetic variance in the j th sex, and r_{mf} is the genetic correlation between the sexes. Note that these rates of change are similar to those for a system of two traits that are genetically coupled through pleiotropy (see Lande 1979). In this case, the evolutionary change in a trait that is expressed by the j th sex is due to direct selection within that sex, and indirect selection through the other sex; the factor of $1/2$ in equation (4) reflects the equal genetic contributions of females and males to offspring (see Lande 1980, p. 294).

Sex differences in selection on a trait can potentially arise within contexts of natural or sexual selection, as males and females

often have different roles and costs associated with reproductive investment. Our model can readily accommodate selection with respect to viability or reproductive success. For example, if there is strong alignment between general viability and mating success (see Whitlock and Agrawal 2009), then effects of sexual selection are simply subsumed into the parameter γ_j . If sexual selection alters the net optimum trait value for either sex, as occurs when natural selection and sexual selection individually favor different phenotypes, then selection gradients can be partitioned to reveal the effects of viability and sexual selection on total selection on the trait. Following Lande (1980; see also Reeve and Fairbairn 2001), the net selection gradient becomes:

$$\beta_j = \gamma_j(\theta_{Vj} - \bar{z}_j) + S_j, \tag{5}$$

where θ_{Vj} represents the trait optimum under natural selection (i.e., based on viability), and S_j depicts the direction and strength of sexual selection (which, importantly, may be frequency dependent). From Lande (1980), the net optimum for each sex is then:

$$\theta_f = \theta_{Vf} + S_f/\gamma_f, \tag{6a}$$

and

$$\theta_m = \theta_{Vm} + S_m/\gamma_m. \tag{6b}$$

As described in Lande (1980, see p. 297) within the context of a temporally stable environment (in which $\theta_{Vj} + S_j/\gamma_j$ remain constant in time), the mean trait values for females and males will eventually evolve to the optima in equations (6a, b), provided the genetic correlation between the sexes is imperfect ($|r_{mf}| < 1$). When environmental conditions shift (as in cases that we consider below), the net optimum for each sex will change over time. Though our primary focus throughout will be on the effects of environmental change on the this net optimum, it is clear from the partitioning of selection components (as described above) that any shift in the net optimum for a given sex can potentially be due to changes in either θ_{Vj} or S_j . Therefore, our model can accommodate the effects of environmental change on natural selection or sexual selection.

ENVIRONMENTAL VARIATION AND LONG-TERM EVOLUTIONARY DYNAMICS

We model the optimum trait value for each sex as a simple function of an environmental variable that changes gradually over time. Let ϵ_t represent the state of the environment at time t . The phenotypic optimum for females and males (respectively) is a linear function of the environmental state:

$$\theta_{ft} = B_f \epsilon_t \tag{7a}$$

and

$$\theta_{mt} = B_m \epsilon_t, \tag{7b}$$

where B_f and B_m are constants that describe the direction and magnitude of changes to male and female optima that occur with changes in the environmental state, ϵ . Note that B_j can take positive or negative values, depending on how the optimal trait values of each sex change over time.

At an arbitrary time t , the degree of maladaptation of each sex and the direction of sex-specific selection are each functions of the “lag” between the optimum and mean phenotype ($\theta_{jt} - \bar{z}_{jt}$ for sex j). Below, we quantify sex-specific lags that arise after many generations have passed, and where the lag for each sex eventually approaches a steady-state value (as in models of directional change in an optimum over time), or a steady-state cycle (as in deterministic models of environmental fluctuation over time), as per previous theory (Lynch and Lande 1993; Lande and Shannon 1996; Chevin et al. 2010; Chevin 2013; Cotto and Ronce 2014). We consider both scenarios below, beginning with the simplest scenario of a linear, directional change in the environment.

KEY ASSUMPTIONS OF THE MODELS

The primary goal of our model is to relax the assumption of environmental constancy, as used in previous theory of sex-specific selection (Lande 1980), in order to address whether and when environmental change can resolve sexual conflicts (or rather, prevent them from arising). We retain several core assumptions from previous theories of both sex-specific adaptation and evolutionary change in quantitative traits under environmental change. Following influential models of adaptation under environmental change (e.g., Lynch and Lande 1993; Bürger and Lynch 1995; Lande and Shannon 1996; Gomulkiewicz and Houle 2009; Chevin et al. 2010), we assume that trait optima may change over time, whereas the curvatures of male and female fitness landscapes remain constant. Likewise, we assume that the additive genetic variances within each sex, and the covariance between them (G_j and r_{mf} in our model), remain stable across generations.

Although absolute constancy of genetic variances and covariance cannot strictly be true (e.g., given, at minimum, the action of genetic drift), the assumption is nevertheless reasonable when phenotypic variation is attributable to a large number of loci with individually small effects (i.e., the “infinitesimal model,” Fisher 1918). First, snapshots of genetic correlations within single populations and under single environmental contexts reveal that virtually all quantitative traits exhibit a strong and positive r_{mf} ($r_{mf} > 0.8$ for most of the traits compiled by Poissant et al. 2010), with the exception of fitness components (longevity, reproductive success, total fitness). Second, in some instances, snapshots of r_{mf} in a single population actually predict long-term capacity

for divergence between the sexes (Griffin et al. 2013; Innocenti and Chenoweth 2013), which implies some degree of stability for r_{mf} . Third, long-run predictions about sexual conflict from prior theory, which also assumes a constant r_{mf} (e.g., Lande 1980), appear to hold qualitatively in models that specify the mutational architecture underlying the genetic correlations between male and female traits (see Connallon and Clark 2014).

However, while we assume that r_{mf} between male and female traits is constant—an assumption that can potentially be relaxed in future studies—we note that the genetic correlation between male and female fitness is permitted to change rapidly in our models. Such changes mirror the more extensive empirical examples of a highly variable r_{mf} in fitness or fitness components (Delcourt et al. 2009; Punzalan et al. 2014; Berger et al. 2014; Collet et al. 2016).

Results

SEX-SPECIFIC ADAPTATION UNDER DIRECTIONAL ENVIRONMENTAL CHANGE

In the simplest model of environmental change, a single environmental variable changes as a linear function of time (Lynch and Lande 1993)—a scenario that we refer to as “directional” environmental change due to the trend of change in a single direction. Let the environmental state at time t be $\epsilon_t = vt$, where v represents the rate of change in the environment. Using equations (7a–b), the optimum in the j th sex at time t is $\theta_{jt} = B_j vt$, which changes at a constant rate ($d\theta_{jt}/dt = B_j v$). Over time the population eventually evolves toward a steady-state equilibrium lag (see Appendix 2 of the Supplementary Material), with sex-specific directional selection in females and males given by:

$$\tilde{\beta}_f = \frac{2B_f v(1 - r_{mf}\alpha)}{G_f(1 - r_{mf}^2)}, \tag{8a}$$

and

$$\tilde{\beta}_m = \frac{2B_m v(1 - r_{mf}/\alpha)}{G_m(1 - r_{mf}^2)}, \tag{8b}$$

where $\alpha = B_m \sqrt{G_f} / (B_f \sqrt{G_m})$ is a compound parameter that reflects both the similarity in direction of change in female and male optima (B_f vs. B_m), and the relative magnitude of additive genetic variances for the trait in females and males (G_f vs. G_m). Equality of additive genetic variances and equal rates and directions of change in the female and male optima correspond to $\alpha = 1$. Sexual dimorphism in environmental sensitivity ($B_f \neq B_m$) or genetic variance ($G_f \neq G_m$) can lead to $\alpha \neq 1$, which gives rise to sex differences in selection, and mediates opportunities for sexually antagonistic selection. Note that α is positive when the female and male optima shift in the same direction ($\alpha > 0$ when $B_f B_m > 0$), and negative when they shift in opposite directions ($\alpha < 0$ when $B_f B_m < 0$).

As in prior theory (Lynch and Lande 1993; Chevin et al. 2010), constant and directional changes in the trait optima over time ($d\theta_{jt}/dt \neq 0$, where j refers to the j th sex) give rise to sustained disparities between the mean expression values of male and female traits and their respective optima. Equations (8a, 8b) quantify the magnitude and fitness consequences of these disparities. A displacement from the optimum leads to a nonzero value of $\tilde{\beta}_j$, and the degree of maladaptation scales positively with the absolute magnitude of $\tilde{\beta}_j$, with mean fitness decreasing with the magnitude of the selection gradient.

OPTIMAL GENETIC CORRELATIONS UNDER DIRECTIONAL ENVIRONMENTAL CHANGE

From equations (8a, b), we can define the specific values of the between-sex genetic correlation that maximize long-run adaptation within each sex (see Appendix 2 of the Supplementary Material). We first consider values of the genetic correlation that cause steady-state maladaptation to become sex-limited—with one sex perfectly tracking its fitness optimum, and the other experiencing sustained directional selection and a permanent lag from its optimum. When $r_{mf} = 1/\alpha$, maladaptation is confined to males ($\tilde{\beta}_m = 2B_m v/G_m$; $\tilde{\beta}_f = 0$), whereas when $r_{mf} = \alpha$, maladaptation is female-limited ($\tilde{\beta}_f = 2B_f v/G_f$; $\tilde{\beta}_m = 0$). In these cases, the maladapted sex bears the full cost of directional selection; the other sex perfectly tracks its optimum through a genetically correlated evolutionary response to selection in the maladapted sex. This extra burden of selection on the maladapted sex is not trivial. Consider, as a point of contrast, a baseline of directional selection in which there are no sex differences in environmental sensitivity or genetic variability (i.e., $B_f = B_m$, $G_f = G_m$, $r_{mf} = 1$), and the equilibrium selection gradients reduce to $\tilde{\beta}_f = B_f v/G_f$ and $\tilde{\beta}_m = B_m v/G_m$. Comparing this baseline strength of directional selection to those that arise in the case of sex-limited maladaptation (i.e., for $r_{mf} = 1/\alpha$ or $r_{mf} = \alpha$) it is clear that the removal of directional selection in one sex generates a doubling of the strength of selection in the other (i.e., a twofold cost to the maladapted sex).

For the remaining values of α (i.e., $\alpha \neq r_{mf}, 1/r_{mf}$), both sexes experience sustained directional selection at steady state, with the strength and direction of sex-specific selection a function of both r_{mf} and α . In such cases, there will be an optimal genetic correlation that maximizes adaptation within each sex (i.e., minimizes the magnitude of the selection gradient). Interestingly, this optimal genetic correlation often differs between the sexes. The optimal correlation for females is:

$$\hat{r}_{mf}(f) = \begin{cases} \frac{1}{\alpha} (1 - \sqrt{1 - \alpha^2}) & \text{for } |\alpha| < 1 \\ \frac{1}{\alpha} & \text{for } |\alpha| > 1 \end{cases}, \tag{9a}$$

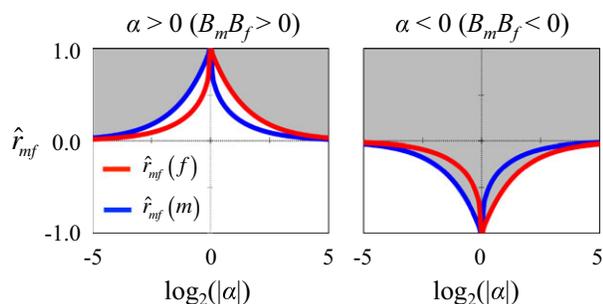


Figure 2. Optimal genetic correlations and zones of conflict under directional change in the environment. The red and blue curves are based on equations (9a, 9b), but with $|\alpha|$ presented in \log_2 scale so that one unit represents a doubling in the relative responses of males and females to changes in the environment (e.g., with $G_f = G_m$, positive values of $\log_2(|\alpha|)$ occur when optima shift faster in males, negative when faster in females). In the left panel, environmental changes cause male and female optima to shift in the same direction ($B_f B_m > 0$); in the right panel, the optima shift in opposite directions ($B_f B_m < 0$). Shaded regions of parameter space lead to persistent sexually antagonistic selection at steady state (therefore $\beta_f \beta_m < 0$); unshaded regions correspond to the parameter space where selection is sexually concordant (therefore $\beta_f \beta_m > 0$).

whereas the optimal correlation for males is:

$$\hat{r}_{mf}(m) = \begin{cases} \alpha & \text{for } |\alpha| < 1 \\ \alpha \left(1 - \sqrt{1 - \frac{1}{\alpha^2}}\right) & \text{for } |\alpha| > 1 \end{cases} \quad (9b)$$

Note the symmetric roles that α and $1/\alpha$ play in equations (9a, b). Intuitively, these expressions reduce to $\hat{r}_{mf}(f) = \hat{r}_{mf}(m) = 1$ in the absence of sexual dimorphism in genetic variance or sex differences in environmental sensitivity (i.e., when $G_f = G_m$, $B_f = B_m$, and thus, $\alpha = 1$). In this limiting case, a perfect genetic correlation maximizes the adaptive evolutionary responses of both sexes to directional selection, with females and males benefitting equally from sexually concordant directional selection.

When $|\alpha| \neq 1$, the optimal r_{mf} diverges between the sexes (see Fig. 2). Two broad patterns are apparent. First, as expected intuitively, the optimal r_{mf} is positive when female and male optima shift in the same direction ($\alpha > 0$ requires that $B_m/B_f > 0$; Fig. 2, left panel), and negative when they shift in opposing directions ($\alpha < 0$ when $B_m/B_f < 0$; Fig. 2, right panel). Second, when $|\alpha| > 1$, females benefit more from a strong genetic correlation than males do, whereas males benefit more from a large $|r_{mf}|$ when $|\alpha| < 1$. This pattern has a simple underlying basis: when $|\alpha| > 1$, a strong genetic correlation is more likely to facilitate adaptation in females than males, as males bear the brunt of the cost of selection (the opposite is true when $|\alpha| < 1$). These effects are most intuitive when the sexes exhibit similar amounts of genetic variation (Wyman and Rowe 2014). For example, when $\alpha = B_m/B_f > 1$, both optima shift in the same direction, with the more

rapid rate of change in the male optimum generating stronger directional selection in males than females. Females benefit from a strong positive genetic correlation, as the correlated response to selection in males helps females to closely track their changing optimum; males benefit the least from a strong genetic correlation as weaker directional selection in females may slow the male response to directional selection.

CRITERIA FOR UNRESOLVED SEXUALLY ANTAGONISTIC SELECTION

Prior theory predicts that sexually antagonistic selection will arise early during the process of sex-specific adaptation, and then persist over a long-time interval before eventually becoming resolved as both sexes reach their optimum (Fig. 1 herein; Lande 1980, 1987). Empirical estimates of sex-specific adaptation, however, have revealed a wide range of sex-specific selection patterns, including both sexually antagonistic and sexually concordant directional selection (see Cox and Calsbeek 2009). As both outcomes are possible in the context of a continuously changing environment, identifying the conditions for which sexual antagonism can persist indefinitely (and without eventual resolution), or alternatively, when directional selection is in agreement between the sexes, can help resolve the mismatch between theory and the single (temporal) snapshots from empirical studies.

By further evaluating equations (8a, 8b), it is straightforward to find criteria for unresolved sexually antagonistic selection, where females and males experience sustained directional selection in opposing directions. Criteria for sexual antagonism at steady-state are:

$$r_{mf} > \begin{cases} 1/\alpha & \text{for } |\alpha| > 1 \\ \alpha & \text{for } |\alpha| < 1 \end{cases}, \quad (10)$$

which correspond to shaded regions of parameter space in Figure 2. Interestingly, the boundary between sexually antagonistic and sexually concordant selection corresponds to r_{mf} values that maximize adaptation in one of the sexes (i.e., $\tilde{\beta}_f = 0$ when $r_{mf} = 1/\alpha$; $\tilde{\beta}_m = 0$ when $r_{mf} = \alpha$). Sexual antagonism is least likely to arise when α is close to one, and thus levels of genetic variance are similar in each sex and trait optima shift at similar rates (i.e., when $G_m \approx G_f$, $B_m \approx B_f$, shown as $\log_2(|\alpha|) = 0$ in Fig. 2). In this case, sexually antagonistic selection can persist only if the genetic correlation is perfect ($r_{mf} = 1$). Sexually dimorphic genetic variance and/or dimorphic rates of change in the optima greatly relax criteria for conflicting selection between the sexes: large deviations of α from one (i.e., $\min(\alpha, 1/\alpha) \ll 1$) can give rise to persistent conflict, even when r_{mf} is weakly positive. In such cases, a strongly positive genetic correlation guarantees unresolved sexual antagonism.

SEX-SPECIFIC SELECTION AND ADAPTATION UNDER CYCLIC ENVIRONMENTAL CHANGE

The results above apply to processes of sex-specific adaptation under directional environmental change. Here, we contrast these results with the comparatively complex dynamics of sex-specific adaptation under cyclic environmental change. We model cyclic change in the environmental state using a sine function, $\epsilon_t = v\sin(ct)$, where v is the amplitude and c is the period of each cycle (each cycle has a duration of $\tau = 2\pi/c$). The optimum in the j th sex varies following the function: $\theta_{jt} = B_j v\sin(ct)$. We assume for simplicity that genetic variance and stabilizing selection parameters are roughly equal between the sexes ($G = G_f = G_m, \gamma = \gamma_f = \gamma_m$). In this case, the selection gradients will eventually converge, over time, to the following steady state cycle:

$$\tilde{\beta}_j(t) = a_j \sin(ct) + b_j \cos(ct) \tag{11}$$

(i.e., for the j th sex), where:

$$a_m = \frac{2v(B_f + B_m)\gamma c^2}{(G\gamma(1 + r_{mf}))^2 + 4c^2} + \frac{2v(B_m - B_f)\gamma c^2}{(G\gamma(1 - r_{mf}))^2 + 4c^2},$$

$$b_m = \frac{vG\gamma^2 c(B_f + B_m)(1 + r_{mf})}{(G\gamma(1 + r_{mf}))^2 + 4c^2} + \frac{vG\gamma^2 c(B_m - B_f)(1 - r_{mf})}{(G\gamma(1 - r_{mf}))^2 + 4c^2},$$

$$a_f = \frac{2v(B_f + B_m)\gamma c^2}{(G\gamma(1 + r_{mf}))^2 + 4c^2} - \frac{2v(B_m - B_f)\gamma c^2}{(G\gamma(1 - r_{mf}))^2 + 4c^2},$$

and

$$b_f = \frac{vG\gamma^2 c(B_f + B_m)(1 + r_{mf})}{(G\gamma(1 + r_{mf}))^2 + 4c^2} - \frac{vG\gamma^2 c(B_m - B_f)(1 - r_{mf})}{(G\gamma(1 - r_{mf}))^2 + 4c^2}.$$

At steady state, the average selection gradient is zero, whereas the variance of selection gradients within each sex, and covariance between sexes, are given by:

$$\text{var}[\tilde{\beta}_j(t)] = E[\tilde{\beta}_j^2(t)] = \int_0^{2\pi/c} \frac{\tilde{\beta}_j^2(t)}{2\pi/c} dt = \frac{1}{2}(a_j^2 + b_j^2), \tag{12}$$

and

$$\text{cov}[\tilde{\beta}_f(t), \tilde{\beta}_m(t)] = E[\tilde{\beta}_f(t)\tilde{\beta}_m(t)] = \int_0^{2\pi/c} \frac{\tilde{\beta}_f(t)\tilde{\beta}_m(t)}{2\pi/c} dt$$

$$= \frac{1}{2}(a_f a_m + b_f b_m). \tag{13}$$

Equation (12) can be used to quantify the degree of adaptation in each sex, with relatively small values of $\text{var}[\tilde{\beta}_j(t)]$ corresponding to weak directional selection, on average, within sex j . Likewise, equation (13) can be used to define criteria in which selection is primarily sexually concordant ($\text{cov}[\tilde{\beta}_f(t), \tilde{\beta}_m(t)] > 0$), and criteria in which selection is primarily sexually antagonistic selection ($\text{cov}[\tilde{\beta}_f(t), \tilde{\beta}_m(t)] < 0$). While equations (12 and 13) are quite

general, and they provide an excellent match to deterministic simulations carried out over a wide range of the parameter space (i.e., for $c, v, G, \gamma, B_f, B_m, r_{mf}$), they are rather cumbersome, and not easily interpretable. We therefore make sense of these results by identifying approximations, which are presented below, for two extremes of cyclic change: slow cycles and fast cycles. These special cases illustrate the key features of sex-specific adaptation under cyclic environmental change.

ADAPTATION UNDER SLOW CYCLES OF CHANGE

When the duration of environmental cycles is long relative to the amount of genetic variability in the population (specifically, when $G\gamma(1 - r_{mf})$ and $G\gamma(1 + r_{mf})$ are both large compared to c), we can approximate the evolutionary dynamics using a Taylor Series expansion to 2nd order in c (and ignoring terms of c^4 and higher; see Appendix 3 of the Supplementary Material). The results of the expansion reveal striking parallels between sex-specific adaptation under directional and slow cycles of environmental change. The variances of the sex-specific selection gradients are proportional to the equilibrium gradients in the directional environmental change model (i.e., eqs. 8a, b). Consequently, the conditions in which sexually antagonistic selection predominates under slow cycles ($\text{cov}[\tilde{\beta}_f(t), \tilde{\beta}_m(t)] < 0$) correspond to the criteria for sexual antagonism under directional environmental change (i.e., eq. 10). Accordingly, adaptation of females and males remains highly sensitive to the genetic correlation between the sexes; r_{mf} values that maximize long-run fitness under directional environmental change (in eqs. 9a, b) similarly maximize fitness under slow environmental cycles (refer to Fig. 2).

ADAPTATION UNDER FAST CYCLES OF CHANGE

When cycles become sufficiently rapid that c is much larger than $G\gamma$, we can approximate the steady state variance and covariance of the selection gradients using the Taylor Series expansion (given $\gamma \ll c$):

$$\text{var}[\tilde{\beta}_f(t)] = \frac{(B_f \gamma v)^2}{2} \left[1 - \left(\frac{G\gamma}{2c} \right)^2 ((1 + \alpha r_{mf})^2 + 2(1 - \alpha^2)r_{mf}^2) \right] + O(\gamma^6), \tag{14a}$$

$$\text{var}[\tilde{\beta}_m(t)] = \frac{(B_m \gamma v)^2}{2} \left[1 - \left(\frac{G\gamma}{2c} \right)^2 ((1 + r_{mf}/\alpha)^2 + 2(1 - 1/\alpha^2)r_{mf}^2) \right] + O(\gamma^6), \tag{14b}$$

and

$$\text{cov}[\tilde{\beta}_f(t), \tilde{\beta}_m(t)] = \frac{(\gamma v)^2 B_f B_m}{2} \left[1 - \left(\frac{G\gamma}{2c} \right)^2 \frac{(B_f r_{mf} + B_m)(B_m r_{mf} + B_f)}{B_f B_m} \right] + O(\gamma^6). \tag{14c}$$

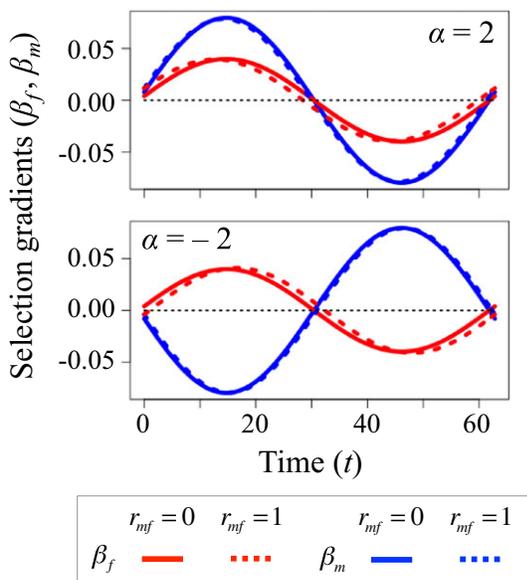


Figure 3. Sex-specific selection and adaptation are relatively insensitive to r_{mf} when environmental cycles are rapid. Note that the marginal difference between the broken lines (representing results for $r_{mf} = 1$) and continuous curves (where $r_{mf} = 0$). The top panel shows a complete steady-state cycle, with environmental sensitivity in males twice as strong as sensitivity of females, and male and female optima shifting in the same direction with change in the environment ($\alpha = B_m/B_f = 2$). The bottom panel shows a complete cycle, with environmental sensitivity in males twice as strong as sensitivity of females, and male and female optima shifting in opposite directions ($\alpha = B_m/B_f = -2$). Results are based on equation (11), with parameters $c = 0.1$, $G = 0.5$, $\gamma = 1/25$, $v = 1$, and $B_f = 1$.

Interestingly, when compared to the patterns of adaptation under slow cycles of change, r_{mf} only factors into the variances and covariances in equations (14a, c) through terms of order γ^4 and higher, and r_{mf} has little influence on sex-specific patterns of adaptation over time (shown in Fig. 3). Thus, when cycles of environmental change are sufficiently rapid (i.e., when $G\gamma/2c$ is small enough that terms of order γ^4 can be ignored), the strengths and relative orientations of sex-specific selection are largely determined by the amplitude of environmental cycles (v), the strength of stabilizing selection (γ), and the rate and direction of change in male and female optima (terms B_m and B_f , respectively).

CRITERIA FOR UNRESOLVED SEXUALLY ANTAGONISTIC SELECTION

Cyclic environmental variation modifies the parameter space for unresolved sexually antagonistic selection, but only when environmental change occurs under fast cycles (Fig. 4). The convergence between directional and cyclic change models (in the limit of long environmental cycles, or small c) makes intuitive sense, as changes in environmental state become approximately linear for

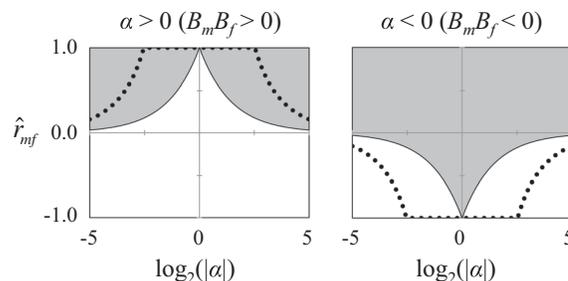


Figure 4. Cyclic environmental variation modifies the parameter space for sexually antagonistic selection. Dotted lines shows the transition point between antagonistic and concordant selection under rapid cycles of change (when $c/G\gamma = 1$), while shaded regions depict parameter zones of sexually antagonistic selection (i.e., where $cov(\beta_m, \beta_f) < 0$) under slow cycles of environmental change ($c/G\gamma \rightarrow 0$); these shaded areas are identical to those of Figure 2. As environmental cycles become increasingly rapid (as $c/G\gamma$ further increases), parameter space for sexually concordant selection (area below the dotted line) expands when female and male optima shift in the same direction ($\alpha > 0$, on the left), and parameter space for sexually antagonistic selection (area above the dotted line) expands when female and male optima shift opposite directions ($\alpha < 0$, on the right). In short, cyclic environmental changes cause the transition point between selection regimes to expand outward in both directions away from $\log_2(|\alpha|) = 0$ (i.e., away from $|\alpha| = 1$). Theoretical curves are based on a numerical analysis of the exact equations for the variance and covariance of selection gradients under cyclic change: equations (12-13). See also Fig. S1 in the Supplementary Material.

local time slices of the cyclic change model, provided the duration of each cycle is long. Stated another way, when the timescale of the approach to steady state is fast relative to duration of each environmental cycle, the dynamics of sex-specific selection remain qualitatively similar to those under directional change (compare shaded areas in Fig. 2 and Fig. 4).

In contrast, fast cycles substantially modify the parameter space of sexually antagonistic and sexually concordant selection (Fig. 4; Fig S1 of the Supplementary Material). When male and female optima shift in similar directions ($B_m B_f > 0$), then fast cycles restrict the parameter space leading to sexual antagonism and expand the parameter space for sexually concordant selection (see Fig. 4, left panel). In contrast, when male and female optima shift in opposite directions ($B_m B_f < 0$), sexual antagonism predominates across an expanded parameter space, and conditions for sexually concordant selection are restrictive (see Fig. 4, right panel). Further increases in cycle speed (i.e., the limit $c/G\gamma \rightarrow \infty$) would lead to sexual antagonism occurring across most values of r_{mf} and $\alpha < 0$; and conversely, sexually concordant selection across most values of r_{mf} and $\alpha > 0$. In this limit, evolution has a negligible influence on sex-specific selection, sexual dimorphism remains roughly constant over time, and adaptation

is almost entirely determined by the temporal dynamics of the male and female optima.

Discussion

Theories of sex-specific adaptation predict that sexual antagonism should manifest early during the evolution of sexual dimorphism, and persist over long evolutionary timescales (see Fig. 1 herein, and Lande 1980; Connallon and Clark 2014), particularly when additive genetic correlations between the sexes are strong and positive (which they typically are; Bonduriansky and Chenoweth 2009; Poissant et al. 2010; Griffin et al. 2013). Yet these predictions apply in environments that are relatively stable over time. Here, we address this gap in theory, and develop new predictions for the relationship between environmental change and sexual antagonism. We show that whether directional selection within one sex reinforces or conflicts with selection in the other sex (i.e., $\beta_f\beta_m > 0$ or $\beta_f\beta_m < 0$, respectively) ultimately depends upon the interaction between trait genetic architecture (including the strength of genetic correlations that link male and female traits), environmental change dynamics (e.g., directional or cyclic in time), and the relative sensitivities of female and male optima to environmental variation (described by parameters B_f and B_m in our model). We find that there is typically a critical strength of the genetic correlation that maximizes long-run adaptation in one sex (i.e., minimizes the magnitude of the selection gradient), though this critical r_{mf} may result in suboptimal adaptation in the other (and vice versa). Simply put, when male and female trait optima change at different rates over time, one sex will generally benefit more from a high genetic correlation than the other.

Our models support the intuition that environmental change should often align the direction of selection between the sexes, even when males and females have distinct trait optima. Sexually concordant selection is expected when environmental change causes the optima for male and female traits to shift in similar directions (e.g., B_f and B_m are similar in magnitude and sign), and conditions for sexually concordant selection are particularly promising when between-sex genetic correlations are low or when cycles of environmental change are rapid. Yet, in contrast to theory for the evolution of sexual dimorphism in stable environments, where conflict is eventually resolved (Pennell et al. 2016), we show that sexually antagonistic selection can potentially persist indefinitely within continuously changing environments. Such unresolved conflict is most permissible under directional environmental change (or slow environmental cycles), and when genetic correlations between the sexes are strong and positive. We discuss these findings in light of the types of environmental change that could lead to ongoing conflict in natural populations, the potential implications these changes have for population dynamics, and the inherent parallels with multivariate adaptation under pleiotropy.

SEX-SPECIFIC SELECTION AND ENVIRONMENTAL CHANGE IN NATURAL POPULATIONS

The new theory provides strong motivation to empirically explore not only the changes in sex-specific selection that can occur in novel environments (e.g., Berger et al. 2014), but also the form of change that occurs over time. For most organisms, a range of biotic and abiotic conditions will vary from generation to generation, potentially driving continual shifts in male and female optima in a variety of ways, from continuous directional change, to slow or rapid cyclic change. While several studies have quantified variation in selection over time (e.g., Siepielski et al. 2009; Morrissey and Hadfield 2012; Chevin et al. 2015), there has been much less emphasis on temporal variation in sex-specific selection. Cox and Calsbeek's (2009) synthesis of sex-specific selection gradients reveals much unexplained variation in selection across traits and taxa, though the underlying causes of this variability remain unknown. Environmental variability, which may uniquely impact different taxa and traits, can potentially account for some of the diverse forms of sex-specific selection observed in nature.

Directional and slow cyclical changes, along with corresponding changes in female and male optima, may often arise from exposure to novel biotic or abiotic variables, including modification of environmental conditions by human intervention, and other forms of environmental change that vary predictably over time. In many fish species, for example, sudden increases in eutrophication and turbidity have been associated with directional change in the visual systems underlying mate choice, and a change in the preferred mate phenotype (Seehausen et al. 1997; Candolin 2004; Järvenpää and Lindström 2004; Candolin et al. 2007). Changes in thermal conditions are another example of sustained directional change. Reductions in body size, for example, have been suggested as an almost universal response to climate warming (but see Gardner et al. 2011), with empirical support arising from latitudinal clines, fossil records, and experimental comparisons (Hunt and Roy 2006; Gardner et al. 2009; Sheridan and Bickford 2011). While these forms of environmental change may often lead to concordant directional selection between the sexes, they also provide some scope for persistent sexual antagonism, particularly among traits with high genetic correlations between the sexes.

In contrast, rapid cycles of environmental change are most likely to mask signals of conflicting selection between the sexes, at least as long as male and female optima shift in parallel directions ($B_f, B_m > 0$ or $B_f, B_m < 0$). Biotic conflicts, such as predator-prey or host-pathogen interactions, are a potentially powerful and widespread source of this type of environmental change (e.g., Brockhurst et al. 2014). In the context of predation, for example, sex-specific patterns of survival are well-documented in species where the elaborate ornamentation of males makes them more conspicuous to predators (Endler 1988; Magnhagen 1991).

Likewise, pathogens are also predicted to be a persistent source of selection in sexually dimorphic species (Hamilton 1980; Hamilton and Zuk 1982; Hamilton et al. 1990), and may often differentially impact selection and fitness within each sex (Sharp and Vincent 2015; discussed in Gipson and Hall 2016). Key to unraveling the persistence of sexually antagonism under biotic conflict will be the rate (c vs. $G\gamma$) and direction (B_f , B_m) of male and female optima shifts. Although our models predict that the temporal dynamics between predator and prey, or pathogen and host, should dampen the potential for sexual antagonism, and decrease empirical signals of genetic constraints, sexual antagonism over shared traits may nevertheless be common (Svensson et al. 2009; Vincent and Sharp 2014) if shifts in male and female optima are not concordant, or each sex differentially allocates resources to traits under selection (see Gipson and Hall 2016).

SEX-SPECIFIC ADAPTATION AND ITS IMPLICATIONS FOR POPULATION DYNAMICS

Adaptation is central to each species' capacity to persist, with genetic correlations potentially mediating adaptation, population growth, and the probability of extinction under systemic environmental change (Chevin 2013; Kopp and Matuszewski 2014). Our results highlight that different causes of environmental change may have distinct consequences for the long-term adaptation of sexually dimorphic populations. A simple expectation would be that the genetic and environmental conditions that maximize adaptation in females should also maximize the likelihood of population persistence. Under directional or slow cyclic change, therefore, genetic correlations that maximize how well females can track their moving optimum should facilitate population persistence. In contrast, when cyclic change is rapid, genetic correlations matter less for female maladaptation as the evolutionary responses within each cycle are modest and easily overwhelmed by the severity (i.e., amplitude) of environmental change. These simple expectations stem from the fact that the opportunity for population growth is often more closely tied to female than to male fitness (a scenario referred to as “female demographic dominance”; Crowley 2000; Harts et al. 2014)—a consequence of the typically higher parental investment by females in their offspring, and minimal investment by males.

On the other hand, there are a variety of situations in which males will directly influence demography (Rankin and Kokko 2007; Boyle et al. 2014). Female-biased sex ratios, including those leading to Allee effects in low-density populations, will lead to male-dependent population growth (e.g., pollen limitation in plants, Petry et al. 2016). Likewise, population persistence should depend on the long-run fitness of both sexes in species with significant parental investment by males, and those characterized by cooperative breeding (e.g., biparental care in birds, Møller 2000). In many cases, therefore, maximum population growth could

represent a compromise between the long-run mean fitness of males and females, particularly when environmental cycles are slow or change is directional. Overall, while we usually expect a greater effect of female fitness on population demography, the above scenarios touch on the complexity of the relationship between environmental change and maladaptation within each sex. Given the complexity of sex-specific adaptation for population persistence, a formal treatment of these dynamics will be presented elsewhere.

PARALLELS WITH MULTIVARIATE ADAPTATION UNDER PLEIOTROPY

We have focused on the emergence of sexually antagonistic selection in the face of strong between-sex genetic correlations for homologous female and male traits. This scenario bears many conceptual parallels to cases of adaptation and constraint during the evolution of multiple characters that are genetically correlated through pleiotropy, and are expressed by the same individual. Several studies have considered multivariate selection and adaptation under a directional change in the environment (Hansen and Houle 2008; Walsh and Blows 2009; Chevin 2013; Kopp and Matuszewski 2014). These studies show that the evolutionary trajectory of multivariate trait means tends to initially diverge away from the direction of change of the multivariate phenotypic optimum (i.e., following the direction of greatest genetic variance, Schluter 1996), and thereafter change in parallel to the optimum, giving rise to a “flying kite effect” (Jones et al. 2004; but see Fig. 2 of Kopp and Matuszewski 2014 for a clear visual representation). Arising from our model is that directional changes in the optima of each sex can potentially generate a similar effect, where the phenotype of the sex with the slower changing optimum is dragged above its optimal expression due to a strong correlated response to selection in the other sex (i.e., the sex with a more rapidly changing optimum).

A second parallel with models of multivariate evolution pertains to the adaptive consequences of the genetic correlations themselves, and the question of whether genetic correlations between traits tend to help or to hinder the process of adaptation. Genetic correlations are as likely to promote as to constrain adaptation within multivariate contexts when there is independence between the structure of the G matrix and the average orientation of multivariate selection (Hansen and Houle 2008; Kirkpatrick 2009). In contrast, genetic correlations generally promote adaptation if the direction of multivariate selection tends to align with phenotypic orientations that harbor high levels of genetic variation (Chevin 2013). Likewise, the evolutionary consequences of positive genetic correlations between the sexes ultimately depend on the relative sensitivity of female and male fitness landscapes to changes in the environment. While both sexes are likely to benefit when female and male optima shift in tandem with one

another, genetic correlations may impose unresolvable constraints to sex-specific adaptation when there is sexual dimorphism in the temporal dynamics of female and male optima.

Conclusion

Environmental conditions are clearly important in shaping patterns of selection on male and female traits, yet the relationship between environmental variability and sex-specific selection has only recently begun to motivate research on the ecological underpinnings of sexual antagonism. This recent work has raised interesting questions about: (1) the potential relationship between population adaptation and empirical signals of sexual conflict (Long et al. 2012; Connallon and Clark 2014), (2) the constancy of sex-specific selection across time and geographic space (Delph et al. 2011; Connallon 2015), and among environmental regimes of diet and temperature (Delcourt et al. 2009; Punzalan et al. 2014; Berger et al. 2014), and (3) the role of resource competition as a driver of sexually antagonistic selection (Slatkin 1984; Shine 1989; Hall et al. 2009; de Lisle and Rowe 2015). It is our hope that the current study helps to motivate further research on sex-specific selection, sexual antagonism, and the emergence of evolutionary genetic constraints in contexts of environmental change. The interactions between these evolutionary concepts may indeed be central to the process of adaptation in species with separate sexes.

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Supporting Information

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

Appendix 1: Sexual antagonism during adaptation to stable sex-specific optima.

Appendix 2: Steady-state selection gradients under directional environmental change.

Appendix 3: Taylor series approximations for the slow cyclic change model.

Figure S1. Optimal genetic correlations and zones of conflict under cyclic environmental change and arbitrary cycle length.