The geography of sex-specific selection, local adaptation, and sexual dimorphism

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Received February 5, 2015
Accepted July 15, 2015

Local adaptation and sexual dimorphism are iconic evolutionary scenarios of intraspecific adaptive differentiation in the face of gene flow. Although theory has traditionally considered local adaptation and sexual dimorphism as conceptually distinct processes, emerging data suggest that they often act concurrently during evolutionary diversification. Here, I merge theories of local adaptation in space and sex-specific adaptation over time, and show that their confluence yields several new predictions about the roles of context-specific selection, migration, and genetic correlations, in adaptive diversification. I specifically revisit two influential predictions from classical studies of clinal adaptation and sexual dimorphism: (1) that local adaptation should decrease with distance from the species’ range center and (2) that opposing directional selection between the sexes (sexual antagonism) should inevitably accompany the evolution of sexual dimorphism. I show that both predictions can break down under clinally varying selection. First, the geography of local adaptation can be sexually dimorphic, with locations of relatively high local adaptation differing profoundly between the sexes. Second, the intensity of sexual antagonism varies across the species’ range, with subpopulations near the range center representing hotspots for antagonistic selection. The results highlight the context-dependent roles of migration versus sexual conflict as primary constraints to adaptive diversification.

**Key Words:** Adaptation, clines, gene flow, sexual antagonism, sexual dimorphism.

Evolutionary theory has traditionally considered local adaptation and the evolution of sexual dimorphism as distinct phenomena, with little conceptual overlap. Nevertheless, the two processes have much in common. One shared element is the importance of gene flow as an evolutionary constraint to either adaptive genetic differentiation between geographic subpopulations of a species, or to divergence between the male and female halves of a population. Realized adaptive differentiation among geographic subpopulations reflects a tension between local selection, which favors evolutionary diversification in space, and migration, which erodes it (Haldane 1930; Wright 1931; Lenormand 2002). Likewise, the enforced transmission of genetic material from male and female parents to opposite-sex offspring establishes an analogous tension between sex-differential selection, which favors the evolution of sexual dimorphism, and genetic mixing between the sexes, which limits phenotypic divergence between them (Fisher 1930; Lande 1980, 1987; Bonduriansky and Chenoweth 2009).

Emerging data suggest that local adaptation and sex-specific selection may often interact during the process of adaptation. Direct phenotypic selection estimates across multiple environmental contexts demonstrate extensive temporal and spatial variability in the strength and orientation of selection (Siepielski et al. 2013). This includes environmentally heterogeneous patterns of selection on the components of male and female reproductive success (Gosden and Svensson 2008; Rundle et al. 2008; Bussière et al. 2008; Siepielski et al. 2011; Miller and Svensson 2014), and context-dependent patterns of sex-specific selection (Delph et al. 2011). Sex-specific genetic variance and between-sex covariance for fitness—which reflect sex differences in phenotypic selection—are also sensitive to environmental variables that commonly vary over space, such as food resources and temperature (Delcort et al. 2009; Long et al. 2012; Punzalan et al. 2014; Berger et al. 2014). Finally, the degree of sexual dimorphism often varies across species’
ranges (Fairbairn et al. 2007; Chenoweth et al. 2008; Gosden and Svensson 2008; Miller and Svensson 2014). In the same sense that phenotypic clines reflect spatially variable selection and local adaptation (Haldane 1948; Endler 1977; Mullen and Hoekstra 2008), historical interactions among migration, sex-specific selection, and environmental change may give rise to commonly observed patterns of clinal sexual dimorphism, reflecting sex-specific local adaptation (e.g., Blanckenhorn et al. 2006).

Theories of local adaptation and sexual dimorphism are individually well developed, yet few models have merged these evolutionary scenarios to examine the more general case of sex-specific local adaptation across a spatially variable environment (Owen 1986; Nagylaki 1996; Day 2000; Harts et al. 2014; Holman and Kokko 2014). The absence of a general theory of sex-specific local adaptation raises three issues that future theory needs to account for. First, despite good evidence for spatially variable sexual dimorphism, we currently lack a theoretical framework for interpreting spatial patterns of sex-specific phenotypic diversity, including genetically based clines in sexually dimorphic traits (e.g., Blanckenhorn et al. 2006; Fairbairn et al. 2007). Second, this lack of theory leads to a deficit of predictions about what we should expect to observe (but perhaps have not yet looked for), if spatial heterogeneity of sex-specific selection is indeed widespread in nature. Finally, by expanding and merging theories of local adaptation and sexual dimorphism, we raise the possibility that some of their key, individual predictions will break down when sex-specific phenotypic optima exhibit clinal variation. Local adaptation in males becomes partially decoupled from that of females, leading to variable — yet qualitatively predictable — patterns of sex-specific directional selection across the species’ range. The model predicts that genetic and demographic features that promote local adaptation simultaneously increase the likelihood of sexual antagonism during the evolution of sexual dimorphism. In particular, the model predicts that sexually antagonistic selection should predominate toward species’ range centers, whereas sexually concordant selection predominates at range boundaries.

Model
I consider the simplest possible model of a single quantitative genetic character with shifting male and female trait optima over a one-dimensional spatial gradient. Specific model assumptions (as outlined below) are chosen to facilitate direct contrasts with foundational theoretical studies of clinal selection and sexual dimorphism of quantitative traits. Given the general dearth of spatially explicit population and quantitative genetic models of sexual dimorphism and sex-specific selection, there is ample ground for future theoretical exploration, including models that address more complex genetic and demographic scenarios—a point that I return to in the Discussion.

The major model assumptions are as follows. Phenotypic and genetic variances and between-sex covariance are assumed to be stable over time and space (e.g., following Lande 1980; Pease et al. 1989; García-Ramos and Kirkpatrick 1997; Kirkpatrick and Barton 1997; Duputié et al. 2012). Population density is stable and subject to strong external density regulation (i.e., selection is “soft”; see Christiansen 1975; Owen 1986; Nagylaki 1996; García-Ramos and Kirkpatrick 1997; Day 2000). Generations are discrete, phenotypes and breeding values are normally distributed, selection and migration are weak, and population size is sufficiently large for genetic drift to be ignored (these follow standard quantitative genetics assumptions in similar models; Pease et al. 1989; Falconer and Mackay 1996; García-Ramos and Kirkpatrick 1997). Fitness landscapes of each sex follow Gaussian functions, with optimal trait values in each sex defined as linear functions of geographic location along a continuous environmental gradient (García-Ramos and Kirkpatrick 1997; see below). Following Day (2000), males and females exhibit the same distribution of dispersal distances. Although we acknowledge the occurrence of sex-biased dispersal in many species (e.g., Pusey 1987), an analysis of dispersal dimorphism is beyond the scope of the current study.

The population is spread across a one-dimensional spatial gradient, with the location along the gradient represented by x, and the range center occurring at x = 0. Population density is
distributed symmetrically in both directions away from the center of the gradient. Following prior work (García-Ramos and Kirkpatrick 1997; Day 2000), I examine two idealized density functions over space: (1) a uniform density function, with constant density between gradient boundaries, \( x = x^* \) and \( x = -x^* \), and a density of zero elsewhere; and (2) a Gaussian density function, proportional to \( n(x) \propto \exp(-x^2/2) \), which represents one form of the “abundant center” model (Brown 1984; Sagarin and Gaines 2002; Eckert et al. 2008). These density models represent two extremes of migration. In the uniform density model, migration is relatively symmetrical between the range center and range edges, and this promotes local adaptation along the environmental gradient. In the abundant center model, migration is asymmetrical, with the biased flow of migrants from the range center to the edges constraining local adaptation away from the center (see García-Ramos and Kirkpatrick 1997). As we shall see below, the opportunity for local adaptation is the primary predictor of the directional selection gradients. The first two terms on the right side of each equation describe the homogenizing effect of dispersal on male or female trait means, whereas the third term describes the local response to selection (see Pease et al. 1989; García-Ramos and Kirkpatrick 1997). The evolutionary response to selection gives equal weight to selection in females and males, which reflects the equal genetic contributions of each sex to the offspring (see Lande 1980; Day 2000). Note that equations (1a) and (1b) have a structure similar to single-sex multivariate models of clinal selection (Duputié et al. 2012; see also Hendry et al. 2001; Guillaune 2011). Thus, the general model easily accommodates sex-specific multivariate selection, as a potential topic for future work.

Let fitness in each sex follow the general Gaussian function, 
\[
    w_j(x) = \exp(-\omega_j(\theta_j(x) - \bar{z}_j(x))^2),
\]
where \( \theta_j(x) \) is the trait optimum at location \( x \) for the \( j \)th sex (\( j = \{m,f\} \)) and \( \omega_j \) is a positive constant that determines the strength of stabilizing selection. Following Lande (1976; also see Chevin and Haller 2014), the selection gradient in the \( j \)th sex is
\[
    \beta_j(x) = \frac{d\ln E[w_j(x)]}{d\bar{z}_j(x)} = S_j(\theta_j(x) - \bar{z}_j(x)),
\]
where \( S_j = 2\omega_j(1 + 2\omega_j P_j) \) accounts for sex-specific concavity of the fitness landscape \( \omega_0 \) and the total phenotypic variance \( P_j \). The fitness optimum for each sex varies as a linear function of location along the environmental gradient:
\[
    \theta_j(x) = b_j x - a
\]
and
\[
    \theta_m(x) = b_m x + a,
\]
where \( b_j \) represents the slope of the optimum in the \( j \)th sex, and \( a \) is a constant that reflects the amount of sexual dimorphism favored at the range center (i.e., optimal sexual dimorphism at the center is \( \theta_m(0) - \theta_f(0) = 2a \)). Note that, if \( b_f = b_m \neq 0 \), then the fitness optima change over space, but the difference between male and female optima remains constant. With differences between \( b_f \) and \( b_m \) the optimal amount of sexual dimorphism varies across the species’ range.

**Analysis of the Model**

Equilibrium phenotypic clines were obtained by solving equations (1a) and (1b), after setting the left side of each to zero. For the uniform density model, we assume that range boundaries are reflecting (at \( x = x^* \) and \( x = -x^* \)), which means that individuals do not migrate across boundaries; therefore we have boundary states: \( d\bar{z}_j^+(x^*)/dx = d\bar{z}_j^-(x^*)/dx = 0 \) (this assumption follows relevant cline papers by García-Ramos and Kirkpatrick 1997 and Day 2000). We additionally assume that...
the initial population has completely undifferentiated males and females, and therefore, no sexual dimorphism is able to evolve when \( r = 1 \). All analytical results, as well as the general model (eqs. (1a) and 1b), permit genetic correlations in the interval: \(-1 \leq r \leq 1\). Nevertheless, in analyzing and presenting the results, I focus on the parameter range in which \( r \) is positive. This focus is biologically inspired, as empirically estimated genetic correlations are overwhelmingly positive for virtually all traits measured to date (with the exception of some life-history traits and total fitness; see Poissant et al. 2010; Griffin et al. 2013).

I primarily focus below on the simplest scenario of clinal variation of female and male traits, by assuming that the curvature of the fitness landscape and the components of phenotypic variance are equal between females and males (i.e., \( G = G_f = G_m \) and \( S = S_f = S_m \)). These results closely parallel Lande’s (1980) influential analysis of the evolutionary dynamics of sexual dimorphism under temporally and spatially homogeneous selection (see p. 299 of Lande 1980; also see Lande 1987), with which the new results are contrasted. As subsequently shown, this idealized model yields results that are representative of the more general model (with \( G_f \neq G_m \) and/or \( S_f \neq S_m \)).

For the idealized case (\( G = G_f = G_m; S = S_f = S_m \)), we can rewrite equations (1a) and (1b) in terms of the sex-averaged phenotype, \( \bar{z}_{avg}(x) = (\bar{z}_m(x) + \bar{z}_f(x)) / 2 \), and of sexual dimorphism, \( \bar{z}_{SD}(x) = \bar{z}_m(x) - \bar{z}_f(x) \). The evolutionary dynamics are now described by the following partial differential equations:

\[
\frac{\partial \bar{z}_{avg}}{\partial t} = \frac{1}{2} \left[ \frac{\partial^2 \bar{z}_{avg}}{\partial x^2} + \frac{\partial^2 \bar{z}_{avg}}{\partial x \partial t} \right] = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}_{avg}}{\partial x^2} + \frac{\sigma^2}{2} \frac{\partial \ln(n(x))}{\partial x} \frac{\partial \bar{z}_{avg}}{\partial x} + \frac{G \omega (1 + r)}{1 + 2 \omega} \left[ \frac{b_m + b_f}{2} x - \bar{z}_{avg}(x) \right] \tag{4a}
\]

and

\[
\frac{\partial \bar{z}_{SD}(x)}{\partial t} = \frac{\partial \bar{z}_m(x) - \partial \bar{z}_f(x)}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}_{SD}}{\partial x^2} + \frac{\sigma^2}{2} \frac{\partial \ln(n(x))}{\partial x} \frac{\partial \bar{z}_{SD}}{\partial x} + \frac{G \omega (1 - r)}{1 + 2 \omega} \left[ (b_m - b_f) x + 2 \omega - \bar{z}_{SD}(x) \right] \tag{4b}
\]

Note that the sex-averaged phenotype and the degree of sexual dimorphism evolve independently. A similar result, for the case of spatially homogeneous selection, was previously noted by Lande (1980; i.e., compare eqs. 4a and 4b, presented here, to Lande’s eqs. 16a and 16b).

Results

EQUILIBRIUM CLINES UNDER SEX-SPECIFIC LOCAL ADAPTATION

Under spatially variable sex-specific selection, there are two relevant equilibrium clines: (1) a cline for the sex-averaged phenotype, described by \( \bar{z}_{avg}(x) = \frac{1}{2}(\bar{z}_m(x) + \bar{z}_f(x)) \), and (2) a cline for the magnitude of sexual dimorphism, described by \( \bar{z}_{SD}(x) = \bar{z}_m(x) - \bar{z}_f(x) \). Under the symmetric model \( (G = G_f = G_m \) and \( S = S_f = S_m \)), equilibrium clines reduce to relatively simple functions of the parameters of selection, dispersal, and genetic and phenotypic variance (see Table 1). With a perfect genetic correlation between the sexes (\( r = 1 \)) and identical male and female optima \( (a = 0, b = b) \), there is no sexual dimorphism at equilibrium, and the cline for \( \bar{z}_{avg}(x) \) simplifies to the standard result for a single trait cline (see eqs. 6 and 12 from García-Ramos and Kirkpatrick 1997). Likewise, if sex-specific optima are constant over space \( (b_m = b_f = 0) \) and the genetic correlation between the sexes is imperfect \( (r < 1) \), then the mean male and female trait values at equilibrium correspond exactly with their respective trait optima. Thus, sexual conflict is resolved at equilibrium, as predicted in Lande’s (1980) model for the evolution of sexual dimorphism.

With sexually dimorphic clines in the optima (again, with \( r < 1 \)), the population eventually evolves sexually dimorphic trait clines: male and female trait means are given by \( \bar{z}_m(x) = \bar{z}_{avg}(x) + \bar{z}_{SD}(x) / 2 \) and \( \bar{z}_f(x) = \bar{z}_{avg}(x) - \bar{z}_{SD}(x) / 2 \), with appropriate expressions for \( \bar{z}_{avg}(x) \) and \( \bar{z}_{SD}(x) \) in Table 1 (also see the Supporting Information). Under both population density models, sex-specific adaptation is predicted to be perfect at the range center, where the equilibrium selection gradients are \( b_f(x = 0) = b_m(x = 0) = 0 \).

If male and female optima change in parallel \( (b_m = b_f, b_{SD} = 0) \) and sex-specific selection is weak \( (S_f = S_m = 0) \), equilibrium sexual dimorphism remains constant across the species’ range, and both sexes exhibit identical patterns of directional selection across the spatial gradient (i.e., \( \beta_{m(x)} = \beta_{f(x)} \) for all \( x \). With sex-specific slopes \( (b_{SD} > 0) \), sexual dimorphism will vary across the species range (provided \( r < 1 \)), equilibrium directional selection becomes asymmetric away from the range center, and the sex with the greater cline slope is under stronger selection at equilibrium (Fig. 1; e.g., when \( b_m > b_f, |\beta_{m(x)}| > |\beta_{f(x)}| \)). With similar rates of change for the sex-specific optima (i.e., \( |b_{avg}| / |b_{SD}| \) large, where \( b_{avg} = (b_f + b_m)/2 \)), directional selection remains concordant between the sexes \( (|\beta_{f(x)}|/|\beta_{m(x)}| > 0) \), and selection in each sex reinforces adaptation in the other. As differences between the optimum functions increase \( (|b_{avg}| / |b_{SD}| \) decreases), equilibrium sexual antagonism becomes more prevalent. Sufficiently large differences between \( b_m \) and \( b_f \) can even give rise to countergradients between the trait cline of one sex and the cline of its optimum (e.g., \( b_f > 0 \) and \( (d \bar{z}_f(x)/dx)_{x=0} < 0 \);
**Table 1.** Equilibrium clines of female and male traits under the idealized model of stabilizing selection and genetic variance ($S = S_f = S_m$, $G = G_f = G_m$; see Supporting Information).

<table>
<thead>
<tr>
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<th>Abundant-center density model</th>
<th>Uniform density model</th>
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<tbody>
<tr>
<td>$z_{avg}(x)$</td>
<td>$b_{avg}x + \frac{\lambda_{avg}}{1 + \lambda_{avg}}$</td>
<td>$b_{avg}x - \frac{\sinh(x\sqrt{2\lambda_{avg}})}{2\lambda_{avg}\cosh(x\sqrt{2\lambda_{avg}})}$</td>
</tr>
<tr>
<td>$z_{SD}(x)$</td>
<td>$2a + b_{SD}x + \frac{\lambda_{SD}}{1 + \lambda_{SD}}$</td>
<td>$2a + b_{SD}x - \frac{\sinh(x\sqrt{2\lambda_{SD}})}{2\lambda_{SD}\cosh(x\sqrt{2\lambda_{SD}})}$</td>
</tr>
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Parameters: $b_{avg} = (b_f + b_m)/2$, $b_{SD} = (b_m - b_f)$; $\lambda_{avg} = SG(1 + r)/(2\sigma^2)$, $\lambda_{SD} = SG(1 - r)/(2\sigma^2)$.

Figure 1. Equilibrium trait clines and patterns of sex-specific selection. Equilibrium clines and patterns of selection were obtained using the equations in Table 1 ($G = G_f = G_m$ and $S = S_f = S_m$). Results for both density models use the parameters: $SG/\sigma^2 = 1$, $b_{avg} = (b_f + b_m)/2 = 1.5$, $b_{SD} = (b_m - b_f) = 1$, $r = 0.8$, and $a = 1.5$.

The potential for unresolved sexually antagonistic selection at equilibrium increases with the disparity between the optimum cline slopes of each sex (i.e., when $|b_{avg}/b_{SD}|$ decreases, it increases the likelihood that $\beta_f(x)/\beta_m(x) < 0$). The specific threshold condition for sexual antagonism depends on geographic location ($x$), the population density distribution across the species gradient ($n(x)$), the genetic correlation between the sexes ($r$), and the compound parameter $SG/\sigma^2$, which reflects the species’ capacity for local adaptation (see García-Ramos and Kirkpatrick 1997). In the abundant-center density model, equilibrium trait clines and selection gradients are linear across the gradient. Consequently, the specific form of sex-specific selection (i.e., sexually antagonistic or sexually concordant) is invariant across the species range.

Equilibrium sexually antagonistic selection (for all $x \neq 0$) requires that

$$\frac{b_{avg}}{b_{SD}} < \frac{1 + \lambda_{avg}}{2(1 + \lambda_{SD})},$$

where $\lambda_{avg} = SG(1 + r)/(2\sigma^2)$ and $\lambda_{SD} = SG(1 - r)/(2\sigma^2)$. Otherwise selection will be concordant between the sexes (Fig. 2). The right-hand term of equation (5) sets an upper limit for $|b_{avg}/b_{SD}|$ that gives rise to unresolved sexual antagonism. When the genetic correlation between the sexes is weak ($r << 1$), persistent sexually antagonistic selection requires that $|b_{avg}/b_{SD}| < \frac{1}{2}$. Parameter conditions that facilitate local adaptation (i.e., large values of $r$ and $SG/\sigma^2$; large $\lambda_{avg}$) increase the likelihood of sexual antagonism at equilibrium.
Figure 2. Equilibrium patterns of sexually antagonistic and sexually concordant selection across the species’ range. Under the uniform density model, with solid curves based on equations (6) and (7), the parameter space leads to three mutually exclusive forms of sex-specific selection: (I) sexually concordant selection throughout the species’ range, (II) sexual antagonism near the range center (0 < |x| << x∗) and sexually concordant selection at range boundaries (|x| = x∗), and (III) sexual antagonism throughout the species’ range, for all 0 < |x|. The “abundant center” model divides the parameter space into two selection regimes, delineated by the dotted line (based on eq. 5). Below the dotted line, sexual antagonism occurs throughout the species’ range, and sexually concordant selection occurs above it.

In the uniform population density model, the criteria for unresolved sexual antagonism vary with distance from the range center. When range size is very large (large x∗), males and females closely track their respective optima over most of the range, and in the limit of an infinite habitat (x∗ → ∞), sex-specific adaptation is perfect. With finite range boundaries, antagonism is most permissible near the range center (0 < |x| << x∗), where antagonism persists whenever:

\[
\left| \frac{b_{avg}}{b_{SD}} \right| < \frac{\cosh (x^* \sqrt{2/\lambda_{avg}})}{2 \cosh (x^* \sqrt{2/\lambda_{SD}})}
\]  

(6)

Criteria for sexually antagonistic selection are more stringent at the edges of the species’ range (x = x∗ and x = −x∗), with sexual antagonism requiring that

\[
\left| \frac{b_{avg}}{b_{SD}} \right| < \frac{\tanh (x^* \sqrt{2/\lambda_{avg}})}{1 - r \tanh (x^* \sqrt{2/\lambda_{avg}})}
\]  

(7)

As with the abundant-center density model, |b_{avg}/b_{SD}| = \frac{1}{2} represents the threshold for antagonistic selection when the between-sex correlation is weak (r << 1). This threshold increases with increasing λ_{avg} (with r and SG/σ2). From equations (6) and (7) in the uniform density model, sexual antagonism must always be less likely at range edges, leading to three mutually exclusive forms of sex-specific selection at equilibrium: (1) sexually concordant selection across the entire species’ range (region I of Fig. 2), (2) concordant selection at the range boundaries, and sexual antagonism toward the range center (region II), and (3) unresolved antagonism throughout the species’ range (region III). Although equilibrium sexual antagonism is particularly common away from the range boundaries in the uniform density model, the magnitude of antagonistic selection is likely to be weak when it is confined to the interior of the species’ range (region II of Fig. 2). In such cases, the degree of local adaptation is generally strong within both sexes, and directional selection gradients in both will be small (e.g., the right panels in Fig. 1).

Under both density models, equilibrium adaptation is optimized for one sex near the range center, with increased maladaptation toward the range boundaries (as in traditional cline theory; see García-Ramos and Kirkpatrick 1997). For the other sex, local adaptation remains high at the range center, and potentially at other locations along the species’ range. At the threshold between sexually antagonistic and concordant selection (e.g., |b_{avg}/b_{SD}| = (1 + λ_{avg}x)/2λ_{avg} SD in the abundant center model, eq. 7 in the uniform model), only one sex is maladapted away from the range center, whereas the other will be perfectly adapted at one or more locations toward the range boundaries. More generally, the relationship between local adaptation and the distance from the range center is expected to be weaker for the sex with the shallower optimum cline (the sex with lower b0). Most of the adaptive constraint that arises from migration is thereby imposed upon the sex with the steepest cline slope.

TRANSIENT EVOLUTIONARY DYNAMICS

All results thus far predict equilibrium cline shapes for male and female traits, and equilibrium patterns of sex-specific selection. However, the time scale for the evolution of sexual dimorphism—the number of generations required for a population to reach equilibrium—can be exceedingly long, particularly when the genetic correlation between the sexes is strong and positive, as is typical for most traits (see Lande 1980; Poissant et al. 2010; Griffin et al. 2013). It is therefore worth asking how patterns of sex-specific directional selection should manifest in nonequilibrium populations, and across different regions of the species range.

As previously noted by Lande (1980, 1987), when the between-sex genetic correlation is large (i.e., r near unity), then the sex-averaged phenotype (z_{avg}(x)) converges to equilibrium rapidly relative to the timescale of evolutionary divergence between the sexes. Noting the comparatively rapid rate of change in z_{avg}(x), relative to the evolutionary rate of z_{SD}(x) (from eqs. 4a and 4b, \frac{\partial z_{avg}(x)}{\partial t} is proportional to 1 + r, whereas \frac{\partial z_{SD}(x)}{\partial t} is proportional to 1 − r), we can approximate conditions of sexually antagonistic selection during the initial stages of adaptation to sex-specific optima. With r strong and positive (as in Lande 1980), the population rapidly approaches the equilibrium cline for z_{avg}(x), and slowly approaches the equilibrium for z_{SD}(x). Consequently, the evolving population initially approaches a state
in which \( \xi_m(x) \approx \xi_f(x) \approx \xi_{\text{avg}}(x) \) and \( \xi_{\text{SD}}(x) \approx 0 \). In this case, we can approximate directional selection gradients during the earliest stages of divergence as \( \beta_m(x) \approx S(0_m(x) - \xi_{\text{avg}}(x)) \) and \( \beta_f(x) \approx S(0_f(x) - \xi_{\text{avg}}(x)) \).

In the absence of spatial variation in the optima \((b_m = b_f = 0, \theta_m(x) = -\theta_f(x) = \alpha)\); as in Lande’s [1980] model, the system quickly evolves so that selection in males is opposed by equally strong counterselection in females \((\beta_m(x) \approx -\beta_f(x))\)—a pattern of opposing selection that persists until sexual dimorphism is complete (Lande 1980, 1987). When sex-specific optima vary in space \((b_m \neq 0 \text{ and/or } b_f \neq 0)\), subpopulations near the range center evolve a similar pattern of symmetrically strong and opposing directional selection in each sex: \( \beta_m(x = 0) = -\beta_f(x = 0) = 5a \). Thus, the early stages of adaptation at the range center yield sex-specific selection patterns that mimic exactly those of an unstructured population with distinct male and female optima (Lande 1980, 1987).

In subpopulations away from the range center, there is no guarantee that sexual antagonism will ever emerge during the evolution of sexual dimorphism. Following an initially rapid convergence to equilibrium for the sex-averaged phenotypic cline \((\xi_m(x) \approx \xi_f(x) \approx \xi_{\text{avg}}(x))\), we can predict the geographic limits of sexually antagonistic selection during the evolution of sexual dimorphism. For the abundant center model, sexual antagonism manifests between the following two critical points within the species’ range:

\[
x_{\text{crit}} = \begin{cases} \frac{-2a(1 + \lambda_{\text{avg}})}{-2b_{\text{avg}} + b_{\text{SD}}(1 + \lambda_{\text{avg}})} & \text{if } b_{\text{SD}} > 0 \\ \frac{2a(1 + \lambda_{\text{avg}})}{2b_{\text{avg}} - b_{\text{SD}}(1 + \lambda_{\text{avg}})} & \text{if } b_{\text{SD}} < 0 \end{cases}
\]

(8)

Opportunities for sexually antagonistic selection decrease with the distance from the range center (symmetrically so when \( b_{\text{SD}} = 0 \)). The geographic range of antagonistic selection increases with \( \lambda_{\text{avg}} \) (i.e., with \( S \sigma^2 / a^2 \)) and \( r \) and with the distance between male and female optima \((a)\). The range breadth of antagonistic selection decreases as \( \theta_{\text{avg}} / \sigma_{\text{SD}} \) increases. This maximal extent of sexual antagonism furthermore shrinks over time and is eventually limited to regions around the range center (Fig. 3). As in prior theory (Lande 1980, 1987), the temporal duration of sexual antagonism may be long when the between-sex genetic correlation is strong \((r \approx 1, \text{Fig. 3})\). With clinally variable selection, the temporal and spatial extent of sexual antagonism contracts as the between-sex genetic correlation decreases (see Fig. 3).

Uniform population density expands the geographic breadth of sexual antagonism during the transient phase of adaptation. For example, in the simplest case of parallel cline slopes of the optima \((b_{\text{SD}} = 0)\), transitions from sexually antagonistic to sexually concordant selection occur at the following critical locations within the species’ range:

\[
x_{\text{crit}} = \pm \frac{1}{\sqrt{2} \lambda_{\text{avg}} \cosh(x)} \left( \frac{\lambda_{\text{avg}}}{\sqrt{2} \lambda_{\text{avg}}} \arcsinh \left( \frac{\sqrt{2} \lambda_{\text{avg}}}{\lambda_{\text{avg}}} \right) \right)
\]

(9)

where \( \arcsinh(y) \) is the inverse hyperbolic sine function. Transitions between selection regimes require that values of \( x_{\text{crit}} \) occur within the range boundaries; \(-x < x_{\text{crit}} < x\); otherwise, sexually antagonistic selection initially occurs across the entire species’ range. As before, conditions that favor strong local adaptation (i.e., large \( \lambda_{\text{avg}} \)) shift the transition points away from the range center, and extend the fraction of the species’ range in which sexual antagonism occurs during the transient phase of evolution.

In the limit of low adaptability \((\lambda_{\text{avg}} \to 0)\), the transition points for both population density models converge (eqs. 8 and 9 reduce to \( x_{\text{crit}} \approx \pm a / \lambda_{\text{avg}} \)). With modest to large values of \( \lambda_{\text{avg}} \) the two density models diverge substantially, with transitions to sexually concordant selection occurring closer to the range midpoint under the abundant center model (Fig. 4).

In addition to defining the geographic boundaries between sexually antagonistic and sexually concordant selection regimes, equations (8) and (9) identify sites of maximal local adaptation for each sex during the initial stages of evolutionary divergence (i.e., locations where the displacement from the optimum is relatively small). In the absence of sexually dimorphic fitness optima \((a = 0)\), both sexes will be perfectly adapted at the range center and minimally adapted at range boundaries (as in previous...
theory: García-Ramos and Kirkpatrick 1997). Dimorphic fitness landscapes shift the points of maximal local adaptation away from the range center (\(|x_{c,1}| > 0\) when \(|\alpha| > 0\), and in opposite directions for each sex. When sexual antagonism extends across the species’ range (i.e., \(|x_{c,1}| > x^*\)), each range boundary represents a point of maximal local adaptation for one sex, and a point of minimal local adaptation for the other.

**SEXUAL DIMORPHISM OF VARIANCE COMPONENTS AND STRENGTHS OF STABILIZING SELECTION**

The above results apply when genetic variances \((G_f \text{ and } G_m)\) and the strengths of stabilizing selection \((S_f \text{ and } S_m)\) are approximately equal between the sexes. The former assumption may typically be valid, at least on average (Wyman and Rowe 2014), yet the latter may be systematically violated if total phenotypic variability \((P)\), see eq. 2) and/or the curvature of the fitness landscape \((m)\) are typically larger within one of the sexes (e.g., males; see Whitlock and Agrawal 2009; Wyman and Rowe 2014).

To assess how sexually dimorphic variances and fitness landscape parameters affect the above results, I carried out additional analyses of equations (1a) and (1b), focusing on the analytically tractable abundant center model (see the Supporting Information). For arbitrary \(S_m\), \(S_f\), \(G_m\), and \(G_f\), the criterion for sexual antagonism at equilibrium becomes

\[
\frac{b_{avg}}{b_{SD}} \leq \frac{2\sigma^2 + S_fG_f\left(1 + r\sqrt{G_f/G_i}\right)}{2\left(2\sigma^2 + S_fG_f\left(1 - r\sqrt{G_f/G_i}\right)\right)}, \tag{10}
\]

where \(i\) refers to the sex with the steeper cline slope for its optimum \((|b_i/b_f| > 1)\) when \(S = S_m = S_f \text{ and } G = G_m = G_f\), note that eq. (10) reduces to eq. (5)). From equation (10), and assuming a positive genetic correlation between the sexes \((r > 0)\; \text{see Poissant et al. 2010; Griffin et al. 2013}\), opportunities for antagonism at equilibrium increase under the following two conditions. The likelihood of antagonism increases when genetic variance is higher in the sex with the weaker cline slope \((G_m/G_f < 1 \text{ and } |b_m/b_f| > 1 \text{ or } G_m/G_f > 1 \text{ and } |b_m/b_f| < 1\), and second, when selection is stronger within the sex with the stronger cline slope \((S_m/S_f > 1 \text{ and } |b_m/b_f| > 1 \text{ or } S_m/S_f < 1 \text{ and } |b_m/b_f| < 1\). Both factors increase the likelihood that the sex with the shallower slope overshoots its fitness optimum, thereby giving rise to sexually antagonistic selection. However, the overall effect of sexual dimorphism in genetic variance or stabilizing selection is small as long as the magnitude of sexual dimorphism in \(G\) or \(S\) is small, or when \(SG/\sigma^2\) is modest (see Fig. 5).

The transient dynamics of sex-specific selection and adaptation remain qualitatively similar when variance and selection parameters differ between the sexes. As before, antagonism during the evolution of sexual dimorphism is more pervasive near the range center than the range edges (provided \(b_{avg}/b_{SD}\) is large). The specific locations along the species’ range in which sexually antagonistic selection transitions to sexual concordance depend on four factors: (1) the opportunity for local adaptation, with larger values of \(S_fG_f/\sigma^2\) and \(S_mG_m/\sigma^2\) inflating the initial range breadth of antagonism; (2) the slopes of the trait optima, with large ratios of \(b_{avg}/b_{SD}\) increasing symmetry of transition points about the range center, and decreasing the distance between the

**Figure 4.** Sex-specific local adaptation following the “fast phase” of evolutionary divergence, with parallel rates of change in male and female optima \((b_{SD} = b_m - b_f = 0)\). The selection gradients are represented by solid curves (gray = male, black = female). Results are based on fast-phase approximations, obtained using the equations in Table 1 \((G = G_f = G_m \text{ and } S = S_f = S_m)\), and as described in the “transient dynamics” section of the results. The dashed lines show the transition points between sexually antagonistic (between the lines) and sexually concordant selection. These are based on equations (8) and (9). Results are for the parameters: \(SG/\sigma^2 = 1\), \(b_{avg} = (b_f + b_m)/2 = 1.5\), \(b_{SD} = 0\), and \(r = 0.9\).
transition points; (3) the amount of sexual dimorphism favored (a); and (4) the presence of dimorphic selection and variance parameters, with asymmetries between $G_f$/$S_f$ and $G_m$/$S_m$ modulating the transition points (in either direction) relative to the range center.

Discussion

Two forms of evolutionary conflict come into play during sex-specific adaptation to a spatially variable environment. The conflict between migration and local selection determines the amount of spatial differentiation that can evolve among subpopulations of a widespread species (García-Ramos and Kirkpatrick 1997; Lenormand 2002). Conflict between male versus female adaptation arises from opposing directional selection within each sex, and a positive between-sex genetic correlation for the traits that they each express (Lande 1980, 1987). As demonstrated here, genetic and demographic factors that facilitate local adaptation also increase the likelihood of sexual antagonism.

Populations near the range center generally exhibit the highest degree of local adaptation to clinally variable selection. Migration does not greatly constrain adaptation at the range center, and consequently, residual maladaptation within each sex can be attributable to divergent selection toward sex-specific fitness optima. Local adaptation generally deteriorates away from the range center, leading to maladaptation by way of gene flow and sexual antagonism. When sex-specific optima change rapidly relative to the population’s evolutionary capacity for local adaptation (i.e., when $p_{avg}$ is large relative to $SG/\sigma^2$), migration serves as the primary constraint to sex-specific adaptation near range boundaries. Migration constrains both sexes similarly, and therefore tends to align the direction of selection in each sex. This relationship between local adaptation and sexual antagonism also accounts for the differential manifestation of sexual antagonism between population density scenarios. As emphasized by prior theory (García-Ramos and Kirkpatrick 1997), uniform population density promotes local adaptation by minimizing the flow of maladapted alleles from the range center to the boundaries. This expands the geographic breadth of sexual antagonism during the evolution of sexual dimorphism (as in Fig. 4), and increases the probability of sexual antagonism in equilibrium populations (as in Fig. 2).

These new results differ in two important ways from classical theories of clinal adaptation and sexual dimorphism, which traditionally focus on each evolutionary scenario in isolation. First, in contrast to cline theory, which predicts that subpopulations near range margins should experience the greatest degree of maladaptation (García-Ramos and Kirkpatrick 1997), maladaptation in dioecious (two-sex) systems need not be equally distributed between the sexes. At least one sex will generally be displaced from its local optimum near the range margin, whereas the other sex may be relatively well adapted at the same location. This finding raises an interesting empirical consideration. Sex-specific fitness assays near range boundaries, or in novel environments, may reveal substantial sex-asymmetries in performance, competitive ability, or other fitness components that are expressed by both sexes. Studies to test for such asymmetries might be feasible through mark–release–recapture experiments in animals, or transplant studies on dioecious plants. Second, although sexual antagonism is expected to accompany the evolution of sexual dimorphism, and eventually become resolved under spatio-temporally uniform selection (Lande 1980, 1987; Reeve and Fairbairn 2001; Connallon and Clark 2014), such expectations are easily violated in spatially complex environments. Concordant selection can dominate locally (although not globally), during the evolution of sexual dimorphism, particularly in subpopulations that are highly constrained by gene flow. During the transient dynamics, sexual antagonism is, at minimum, expected near the range center. Antagonism can potentially persist along the species’ range, even at equilibrium, when male and female optima exhibit different rates of change in space. Such dimorphic clines in male and female optima are implied from the
genetically based clines in phenotypic sexual dimorphism that
are observed in many species (see Blanckenhorn et al. 2006).

Joint consideration of local and sex-specific adaptation re-
valse a complex interplay among sex-specific selection, spatial
environmental change, and migration across a species’ range.
The simple model presented here illustrates, by proof-of-concept
(see Servedio et al. 2014), that sex-specific selection is important
during local adaptation, and worthy of future empirical and the-
oretical research. For example, the current model sets the stage
for several worthwhile theoretical extensions. First, it would be
worth incorporating hard selection into the model, and examin-
ing the impact of sex-specific selection on population growth
in space (e.g., Pease et al. 1989). A recent simulation study
(Harts et al. 2014) showed that hard selection can favor female
adaptation when population growth is tied to female fitness.
Although hard selection is unlikely to alter the qualitative results
of the current model, it may quantitatively bias equilibrium trait
clines in favor of local adaptation in females, and at a cost to
local adaptation in males. Moreover, by including hard selection
into the analysis, it should be possible to analyze species’ range
evolution in the context of sex-specific selection (Kirkpatrick and
Barton 1997; Duputié et al. 2012). Second, it would be worth ex-
ploring sex-specific selection and local adaptation within a gen-
eralized multivariate context, which should expand the arena for
evolutionary constraint and genetic trade-offs among traits, fitness
components, or sexes (e.g., Lande 1980; Orr 1998, 2000; Duputié
et al. 2012; Connallon and Clark 2014). Third, incorporating an
explicit genetic architecture for quantitative traits will permit a
full population genetic analysis, with genetic drift and spatial
divergence in r and G incorporated into the theory (e.g., Barton
1999; Reeve and Fairbairn 2001; Alleaume-Benharira et al. 2006).
Fourth, although the current model assumes linear, clinal change
in male and female optima, nonlinear spatial functions are also
biologically possible. For example, parabolic and sigmoid-shaped
trait functions are occasionally observed in life-history traits, and
these presumably reflect unknown trait optima that change non-
linearly in space (e.g., Hoffmann and Weeks 2007; Sgro et al.
2013).

The theory provides a strong motivation to increase empirical
focus on the spatial ecology of sex-specific selection and sexual
dimorphism. This spatial perspective is currently underdeveloped,
despite evidence that interactions between sexual selection and
environmental heterogeneity could be widespread (Miller and
Svensson 2014). Spatially explicit studies of sexual antagonism
are particularly rare, although a recent study using the dioecious
plant, Silene latifolia, supports the notion that concordant and
antagonistic selection regimes coexist within a single species’
rance (see Delph et al. 2011). When interpreted within the context
of the above models, a combination of high-resolution genetic
clines (e.g., clines in sex-specific body size; Blanckenhorn et al.
2006), and genetic variance and covariance estimates for male
and female traits (e.g., Poissant et al. 2010; Williams et al. 2012;
Gosden and Chenoweth 2014), should help establish whether
conditions for sexually antagonistic selection commonly arise
within natural populations.

The theoretical results suggest several additional predictions
regarding the types of species, traits, and ecological contexts in
which we might expect to observe sexually antagonistic selec-
tion. As mentioned, conflict may be more likely away from the
range boundaries, particularly when populations have yet to reach
equilibrium. Equilibrium sexual antagonism is facilitated by rela-
tively uniform density distributions, yet selection in this case may
be weak—and difficult to detect empirically—because both sexes
are expected to be relatively well-adapted across the gradient (e.g.,
Fig. 1). Directional selection near range boundaries may be both
sexually concordant and relatively strong, and hence, more de-
tectable. Second, some species-specific demographic properties,
such as high dispersal rates (e.g., birds, flying insects), should
reduce opportunities for local adaptation, and align directional se-
lection between the sexes. It would be interesting to ask whether
species with high migration rates exhibit weaker signs of sexual
antagonism. Third, certain types of traits might show heightened
signals of antagonistic selection. Prime candidate traits include
those with sex-specific optimum functions that are strongly di-
formic (a is large, |b$_{avg}$/b$_{SD}$| is small), those with a high capacity
for local adaptation (large G), and those with a strong genetic
correlation between the sexes (large r).

The new theory fits within a larger framework for sex-specific
adaptation, and may help to explain some of the currently observed
variability in sex-specific selection patterns among environmental
contexts and study systems. The general prediction—that
moderate- to well-adapted populations should manifest stronger
signals of sexually antagonistic selection—is grounded in theory
(Connallon and Clark 2014, the current study), and has received
recent empirical support (Long et al. 2012; Berger et al. 2014; but
see Delcourt et al. 2009; Punzalan et al. 2014). A population’s
state of adaptedness to its local environment may therefore serve
as a predictor of sexually antagonistic selection. Several studies
have estimated sex-specific variance and between-sex covariance
for fitness (or fitness components; e.g., Chippindale et al. 2001;
Fedorka and Mousseau 2004; Foerster et al. 2007; Mokkonen
et al. 2011), and directional selection on male and female traits
(e.g., Cox and Calsbeek 2009; Lewis et al. 2011, Stearns et al.
2012; Gosden et al. 2012). Patterns of selection in males rela-
tive to females vary considerably between these studies, and it
remains unclear why this should be so. The current model sug-
gests that information about gene flow and the geography of study
populations might be useful for predicting the degree of concor-
dance between male and female selection orientations. Environ-
mental heterogeneity and gene flow may play an important role in
aligning directional selection in males and females, perhaps in experimental populations that are poorly adapted to the environment in which fitness and selection are estimated.

ACKNOWLEDGMENTS
I am grateful for suggestions from and discussion with D. Dowling, T. Gosden, C. Jordan, C. Lasne, C. Sgrò, and A. Usuigi. Comments from D. Roze and two anonymous reviewers greatly improved the manuscript. This research was supported by a grant from the Australian Research Council, and funds from the School of Biological Sciences at Monash University.

LITERATURE CITED


Associate Editor: Dr. Denis Roze
Handling Editor: Dr. Maria Servedio
SUPPLEMENTARY MATERIAL

Equilibrium clines (Table 1), with $G = G_f = G_m$ and $S = S_f = S_m$

Under the uniform density model, at equilibrium, we have:

$$0 = \frac{\partial^2 \bar{z}_{avg}(x)}{\partial x^2} + \frac{SG(1+r)}{\sigma^2} \left( b_{avg} x - \bar{z}_{avg}(x) \right)$$

and

$$0 = \frac{\partial^2 \bar{z}_{SD}(x)}{\partial x^2} + \frac{SG(1-r)}{\sigma^2} \left( b_{SD} x + 2a - \bar{z}_{SD}(x) \right)$$

Recalling that boundaries ($x^*$ and $-x^*$) are reflecting, then the solutions to these equations are:

$$\bar{z}_{avg}(x) = \frac{(b_m + b_f)}{2} \left( x - \frac{\sinh \left( x \sqrt{\frac{SG(1+r)}{\sigma^2}} \right)}{\sqrt{\frac{SG(1+r)}{\sigma^2}} \cosh \left( x^* \sqrt{\frac{SG(1+r)}{\sigma^2}} \right)} \right)$$

and:

$$\bar{z}_{SD}(x) = 2a + \left( b_m - b_f \right) \left( x - \frac{\sinh \left( x \sqrt{\frac{SG(1-r)}{\sigma^2}} \right)}{\sqrt{\frac{SG(1-r)}{\sigma^2}} \cosh \left( x^* \sqrt{\frac{SG(1-r)}{\sigma^2}} \right)} \right)$$

which simplify to the results in Table 1.

Following García-Ramos and Kirkpatrick (1997), with normally distributed population density (and thus, $\partial \ln[n(x)]/\partial x = -x$), the equilibrium clines are linear, leading to:

$$0 = -x \sigma^2 \frac{\partial \bar{z}_{avg}(x)}{\partial x} + \frac{SG(1+r)}{2} b_{avg} x - \frac{SG(1+r)}{2} \bar{z}_{avg}(x)$$

and
\[ 0 = -x\sigma^2 \frac{\partial \pi_{SD}(x)}{\partial x} + \frac{SG(1-r)}{2} b_{SD} x + \frac{SG(1-r)}{2} 2a - \frac{SG(1-r)}{2} \pi_{SD}(x) \]

At equilibrium, we have:

\[ \pi_{avg}(x) = \frac{SG(1+r)b_{avg}x}{SG(1+r) + 2\sigma^2} \]

and

\[ \pi_{SD}(x) = \frac{SG(1-r)}{2\sigma^2 + SG(1-r)} b_{SD} x + 2a \]

which simplify to the results in Table 1.

**Evolution of counter-gradients**

When the optimum cline slopes differ strongly between the sexes, it is possible for the slope of the trait cline in one sex to have an opposite sign to the slope of its optimum. For example, consider in the abundant center density model, with symmetrical variance and selection parameters between the sexes \((G = G_f = G_m\) and \(S = S_f = S_m\)). At equilibrium, the clines for males and females are:

\[ \pi_f(x) = \pi_{avg}(x) - \frac{\pi_{SD}(x)}{2} = \left( \frac{2\lambda_{avg} b_{avg} - \lambda_{SD} b_{SD}}{1 + \lambda_{avg}} \right) x - a \]

and

\[ \pi_m(x) = \pi_{avg}(x) + \frac{\pi_{SD}(x)}{2} = \left( \frac{2\lambda_{avg} b_{avg} + \lambda_{SD} b_{SD}}{1 + \lambda_{avg}} \right) x + a \]

Therefore, the trait cline slopes are:

\[ \frac{d\pi_f(x)}{dx} = \frac{1}{2} \left( \frac{2\lambda_{avg} b_{avg} - \lambda_{SD} b_{SD}}{1 + \lambda_{avg}} \right) \]

\[ \frac{d\pi_m(x)}{dx} = \frac{1}{2} \left( \frac{2\lambda_{avg} b_{avg} + \lambda_{SD} b_{SD}}{1 + \lambda_{avg}} \right) \]
and

\[
\frac{d\tau_m(x)}{dx} = \frac{1}{2} \left( \frac{2\lambda_{avg} b_{avg} + \lambda_{SD} b_{SD}}{1 + \lambda_{avg}} + \frac{\lambda_{SD} b_{SD}}{1 + \lambda_{SD}} \right)
\]

Counter-gradients arise when:

\[
\left( \frac{d\tau_f(x)}{dx} \right)_{b_f} = \frac{2\lambda_{avg} b_{avg} - \lambda_{SD}}{1 + \lambda_{avg} b_{SD} + \lambda_{SD}} < 0
\]

or

\[
\left( \frac{d\tau_m(x)}{dx} \right)_{b_m} = \frac{2\lambda_{avg} b_{avg} + \lambda_{SD}}{1 + \lambda_{avg} b_{SD} + \lambda_{SD}} < 0
\]

From these, it becomes clear that a counter-gradient will arise when:

\[
\left| \frac{b_{avg}}{b_{SD}} \right| \left( \frac{1 - r}{2(1 + r)(1 + \lambda_{SD})} \right) < 0
\]

**Abundant center equilibrium for arbitrary \(G_f, G_m, S_f,\) and \(S_m\)**

With linear clines at equilibrium, and normally distributed population density about \(x = 0\), then at equilibrium we have:

\[
\frac{\partial \tau_f(x)}{\partial x} = \frac{1}{2\sigma^2} \left( G_f \beta_f(x) + r\sqrt{G_f G_m} \beta_m(x) \right)
\]

and

\[
\frac{\partial \tau_m(x)}{\partial x} = \frac{1}{2\sigma^2} \left( G_m \beta_m(x) + r\sqrt{G_f G_m} \beta_f(x) \right)
\]

At equilibrium directional selection gradients follow the form:
\[\beta_f(x) = S_f \left( b_f x - a - \bar{z}_f(x) \right) = S_f \left( b_f - \frac{\partial \bar{z}_f(x)}{\partial x} \right)\]

and

\[\beta_m(x) = S_m \left( b_m x + a - \bar{z}_m(x) \right) = S_m \left( b_m - \frac{\partial \bar{z}_m(x)}{\partial x} \right)\]

and trait functions must follow the form:

\[\bar{z}_f(x) = \frac{\partial \bar{z}_f(x)}{\partial x} x - a\]

and

\[\bar{z}_m(x) = \frac{\partial \bar{z}_m(x)}{\partial x} x + a\]

Therefore:

\[S_f \left( b_f - \frac{\partial \bar{z}_f(x)}{\partial x} \right) = \beta_f(x) = \frac{S_f}{2\sigma^2} \left( G_f \beta_f(x) + r_{G_f G_m} \beta_m(x) \right) + S_f b_f x\]

and

\[S_m \left( b_m - \frac{\partial \bar{z}_m(x)}{\partial x} \right) = \beta_m(x) = \frac{S_m}{2\sigma^2} \left( G_m \beta_m(x) + r_{G_f G_m} \beta_f(x) \right) + S_m b_m x\]

which yield the following solutions for the female and male selection gradients:

\[\beta_f(x) = 2\sigma^2 S_f x \frac{b_f \left( 2\sigma^2 + S_m G_m \right) - S_m b_m r_{G_f G_m}}{\left( 2\sigma^2 + S_m G_m \right) \left( 2\sigma^2 + S_f G_f \right) - S_f S_m r^2 G_f G_m}\]

and

\[\beta_m(x) = 2\sigma^2 S_m x \frac{b_m \left( 2\sigma^2 + S_f G_f \right) - S_f b_f r_{G_f G_m}}{\left( 2\sigma^2 + S_m G_m \right) \left( 2\sigma^2 + S_f G_f \right) - S_f S_m r^2 G_f G_m}\]

When \( S = S_m = S_f, G = G_m = G_f \), these results simplify to:
\[ \beta_f(x) = \frac{S}{2} \left( \frac{2b_{avg}x}{SG(1+r)} - \frac{b_{3D}x}{SG(1-r)} \right) \]

and

\[ \beta_m(x) = \frac{S}{2} \left( \frac{2b_{avg}x}{SG(1+r)} + \frac{b_{3D}x}{SG(1-r)} \right) \]

Further, when \( r = 1 \), and \( b = b_m = b_f \), we obtain:

\[ \beta(x) = \frac{Sbx}{1 + SG/\sigma^2} \]

which is equivalent to eq. (8) from Garcia-Ramos and Kirkpatrick (where they focused on the selection gradient at the range boundary: at \( x = 3 \))