

Environmental Changes and Sexually Antagonistic Selection

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Advanced article

Article Contents

- What Is Sexually Antagonistic Selection?
- Proximate Environmental Causes of Sexually Antagonistic Selection
- Sexually Antagonistic Selection and Rates of Adaptation
- Sexually Antagonistic Selection during Adaptation in a Novel Environment
- Sexually Antagonistic Selection during Adaptation in Continuously Changing Environments
- Conclusions and Future Directions

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Sexually antagonistic selection (SAS) occurs when the direction of natural selection on a trait, or a combination of traits, differs between the sexes. For example, the different roles of females and males in reproduction, along with different interactions between each sex and the environment, can generate selection for larger body size in one sex and smaller body size in the other – a pattern of selection that may eventually lead to the evolution of sexual size dimorphism. SAS has been documented in several animal and plant populations and is thought to constrain adaptation and reduce population fitness. Recent research has emphasised that the intensity of SAS depends, in part, on environmental conditions of the population, which may vary over time or across each species' geographic range. Theory predicts that SAS should be more common in stable compared to changing environments. These predictions have some experimental support, though the general manner with which environmental changes affect SAS remains an open question.

What Is Sexually Antagonistic Selection?

Many species are comprised of phenotypically distinct sexes – females and males – that largely express the same traits, yet they express them to different degrees: a phenomenon

known as sexual dimorphism (Andersson, 1994). For example, in mammals, the average body size of a male is typically greater than the average size of a female, whereas the opposite is true in most other species (reviewed in Fairbairn *et al.*, 2007). Sexual dimorphisms in morphology (e.g. antlers), physiology (e.g. thermal tolerance) and behaviour (e.g. locomotor activity) are widely observed among animals and plants (Darwin, 1871; Andersson, 1994; Barrett and Hough, 2012). These sex differences in trait expression imply that natural selection affects the sexes differently and is the driving force that that leads to the evolution of sexual dimorphism in female and male phenotypes (Trivers, 1972; Lande, 1980).

'Sexually antagonistic selection' (SAS) refers to differences in the direction of selection between males and females, which ultimately favour evolutionary differentiation between the sexes (Lande, 1980; Cox and Calsbeek, 2009). For a single trait that is expressed by both sexes, SAS occurs when the direction of selection in females is opposite to the direction of selection in males. For example, consider a single trait, such as height, where the optimal trait expression, in terms of fitness, differs between the sexes (**Figure 1**). Here, the optimal trait value for males (O_m in **Figure 1**) differs from the optimal value for females (O_f in **Figure 1**), and the female and male trait distributions are intermediate between the optima (e.g. $O_f < \bar{z}_f, \bar{z}_m < O_m$ in **Figure 1**, where $\bar{z}_f$ and $\bar{z}_m$ are the trait averages for females and males, respectively). The resulting direction of selection is sexually antagonistic as small individuals have the highest fitness among females, and large individuals have the highest fitness among males.

SAS on single traits can be experimentally tested by estimating linear associations between trait expression and fitness for each sex, and then testing whether the signs of the linear associations differ between the sexes (reviewed in Cox and Calsbeek, 2009; Morrissey, 2016). A 'selection gradient', which is the slope of the regression of mean-standardised fitness on trait expression, is commonly used to quantify the strength and direction of selection (Lande and Arnold, 1983). For the scenario shown in **Figure 1**, female and male selection gradients are:

$$\beta_f = \gamma_f(O_f - \bar{z}_f) \quad (1a)$$

$$\beta_m = \gamma_m(O_m - \bar{z}_m) \quad (1b)$$

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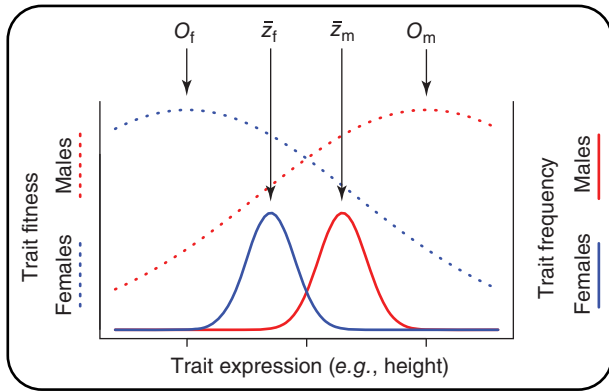


Figure 1 Sexually antagonistic selection (SAS) in a single trait. The solid blue and red curves show the frequency distributions for the trait within females and males, respectively; $\bar{z}_f$ and $\bar{z}_m$ refer to the average of the female and male trait distributions. The broken curves show female (blue) and male (red) relative fitness as a function of trait expression, with the optimum for each sex corresponding to the maximum of the function (O_f and O_m are the female and male trait expression optima). Since the female trait mean is above the female optimum, and the male mean is below the male optimum, directional selection on this trait is sexually antagonistic.

where γ_f and γ_m are positive constants that refer to the strength of selection near the female or male optimum. The example from **Figure 1** shows that there is negative directional selection on the trait in females ($\beta_f < 0$ because $O_f < \bar{z}_f$) and positive directional selection on the trait in males ($\beta_m > 0$ because $O_m > \bar{z}_m$). Female and male selection gradients thus have opposite signs ($\beta_f \beta_m < 0$), signifying SAS. This form of SAS has been documented in contemporary human populations as well as many other nonhuman taxa (i.e. SAS for human height; Sanjak *et al.*, 2017; examples of SAS in other species are reviewed in Cox and Calsbeek, 2009). Indeed, a recent meta-analysis of female and male selection gradient estimates suggests that SAS occurs for roughly 20% of traits where data is available (Morrissey, 2016).

In some cases, researchers have measured selection on more than one trait within a population, which allows for estimates of directional selection in multiple trait dimensions (Lewis *et al.*, 2011; Gosden *et al.*, 2012; Stearns *et al.*, 2012; Poissant *et al.*, 2016). Each trait is associated with a directional selection gradient (e.g. $\beta_{f,i}$ representing the female selection gradient for the i th in a set of n traits), and SAS is now defined by differences in the overall direction of selection between the sexes in multi-trait combinations. The orientations of directional selection on female versus male traits can be quantified by the angle (θ) between female and the male vectors of directional selection gradients:

$$\theta = \cos^{-1} \left(\frac{\sum_{i=1}^n \beta_{f,i} \beta_{m,i}}{\sqrt{\left(\sum_{i=1}^n \beta_{f,i}^2 \right) \left(\sum_{i=1}^n \beta_{m,i}^2 \right)}} \right) \quad (2)$$

where $\cos^{-1}(\cdot)$ refers to the inverse cosine (Gosden *et al.*, 2012). Directional selection is identical between the sexes when all of

their selection gradients are the same (i.e. $\theta = 0$). SAS occurs when the selection gradients are negatively correlated between the sexes, in which case, the angle between selection vectors falls within the range: $90^\circ < \theta < 180^\circ$. **Figure 2** provides examples of divergent directions of female and male selection in two trait dimensions. In the left-hand panel (**Figure 2a**), SAS is absent because the angle is less than 90° ($0^\circ < \theta < 90^\circ$), which signifies a positive correlation between female and male selection gradients across the set of traits. In the right-hand panel (**Figure 2b**), SAS is present.

Compared to single traits studies, empirical tests of SAS in multiple trait dimensions are relatively uncommon. Two studies using insect populations reported evidence of SAS in multiple trait dimensions ($90^\circ < \theta < 180^\circ$) in populations of the Indian meal moth (Lewis *et al.*, 2011) and the fly *Drosophila serata* (Gosden *et al.*, 2012). Two studies reported orthogonal patterns of female and male selection, which is right at the cusp of SAS ($\theta \approx 90^\circ$), in a contemporary human population (Stearns *et al.*, 2012), and a wild bird population (Poissant *et al.*, 2016).

Proximate Environmental Causes of Sexually Antagonistic Selection

Sex differences in selection can arise from two distinct sources – as a result of sexual selection driven by interactions between the sexes over mating opportunities, or from differences in how each sex interacts with the environment (Darwin, 1871; Lande, 1980; Slatkin, 1984; note that these sources are not necessarily mutually exclusive). Given the elaborate sexual signals that are widespread across the animal kingdom, not surprisingly, considerable effort has been directed at understanding how intrasexual contests for mates (e.g. male–male competition) or intersexual mating preferences (e.g. female choice) can give rise to SAS, favouring the evolution of conspicuous sexual dimorphisms (Andersson, 1994). Ecological sources of SAS that arise purely from males and females interacting differently with their environment are often more difficult to establish (Shine, 1989; Hedrick and Temeles, 1989), but provide important ways in which SAS can be maintained in changing environments, even if sexual selection is the original cause of any divergence.

Slatkin (1984) suggested three processes by which the ecology of an organism can give rise to SAS. The sexes may: (1) have dimorphic ecological niches as a consequence of their different ecological or social roles; (2) exhibit bimodal niches, whereby two or more fitness optima exist for both sexes simultaneously; or (3) experience competitive displacement, where competition between the sexes for a limited resource pool favours sexual dimorphism and niche partitioning. Of the three processes, the bimodal niche scenario is least likely to be a common source of SAS. It proposes that SAS occurs because males and females are part of a single multi-peaked fitness landscape where each sex could be selected towards a different fitness optimum. However, the conditions under which this form of SAS is predicted to arise are limited (Slatkin, 1984). Moreover, there is little empirical support for males and females sharing multiple fitness optima, though this scenario is admittedly difficult to test.

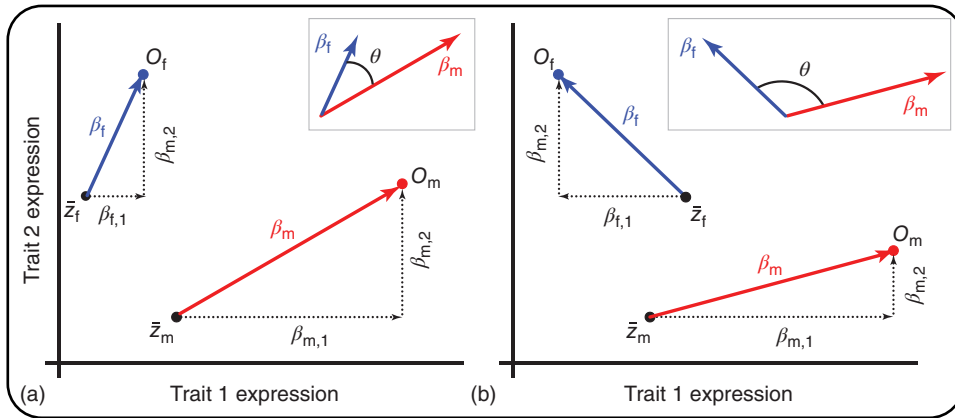


Figure 2 Sex-specific directional selection in two dimensions of trait variability. SAS is absent in panel a, whereas SAS is present on panel b. Within each panel, the dashed arrows show the selection gradients for each trait and sex (horizontal arrows depict the selection gradients for 'trait 1'; vertical arrows depict selection gradients for 'trait 2'). The solid arrows show the net directions of selection, as represented by vectors of selection gradients ($\beta_f = (\beta_{f,1}, \beta_{f,2})$ and $\beta_m = (\beta_{m,1}, \beta_{m,2})$ for females and males, respectively, which each point towards a trait optimum: O_f or O_m). In Panel b, the angle between the vectors, θ , is less than 90° , which denotes a partial alignment between female and male directional selection (and, thus, SAS is absent). In Panel b, the angle between the vectors, θ , is greater than 90° , which denotes a misalignment between female and male directional selection (and, thus, SAS is present).

The concepts of dimorphic niches and competitive displacement are intuitive, empirically testable and supported by evidence. Males and females often have distinct roles in reproduction, social interactions, or the ways they interact with the environment, including sex differences in habitat use, exposure to pathogens and predators, and dispersal (Andersson, 1994). These different niches and roles give rise to SAS; examples include the selection that often favours larger body sizes in females than in males, due to a significant female fecundity advantage of large size (Fairbairn *et al.*, 2007) and sex differences in selection on feeding morphology or behaviour as a consequence of sex-specific nutritional requirements (Shine, 1989). Competition between males and females for some limited resource is also expected to be common in the wild. A shared resource (e.g. a critical food resource) can also lead to divergence in morphological traits related to feeding because individuals with similar trait values are more limited in their ability to acquire resources, due to stronger competition from members of the opposite sex (Slatkin, 1984; Bolnick and Doebeli, 2003). For example, recent work by De Lisle and Rowe (2015, 2017) has demonstrated both SAS and the evolution of sexual dimorphism arising from inter-sexual resource competition in aquatic salamanders.

Sexually Antagonistic Selection and Rates of Adaptation

A population's short-term rate of adaptation depends on the degree of genetic variation in traits under selection (Walsh and Blows, 2009) (see also: **Quantitative Genetics**). Most genetic variation similarly affects female and male trait expression (Poissant *et al.*, 2010; Griffin *et al.*, 2013). For example, genetic variants that increase female height also tend to increase male height (Sanjak *et al.*, 2017). This shared inheritance can limit the

potential for SAS to drive evolution of different phenotypes in each sex. The extent to which the genetic basis of trait variation is shared between the sexes can be quantified by the cross-sex genetic correlation (r_{mf}) between traits expressed in both males and females. Quantitative genetics experiments have shown that, for most traits, r_{mf} is positive and typically strong (e.g. $0 < r_{mf} < 1$ for most traits, with r_{mf} near one for most morphological traits; see Poissant *et al.*, 2010; Griffin *et al.*, 2013).

The cross-sex correlation of a trait influences the evolutionary response of each sex to selection, with positive genetic correlations leading to correlated evolutionary changes in female and male traits (Lande, 1980; Stewart and Rice, 2018). For example, consider a trait with a similar amount of genetic variation within each sex, where G represents the additive genetic variance for the trait (for cases where G differs between the sexes, see Wyman and Rowe, 2014). The evolutionary change in the trait mean of each sex ($\Delta \bar{z}_f$ and $\Delta \bar{z}_m$), following one generation of selection, will be:

$$\Delta \bar{z}_f = \frac{G}{2}(\beta_f + r_{mf}\beta_m) \quad (3a)$$

$$\Delta \bar{z}_m = \frac{G}{2}(\beta_m + r_{mf}\beta_f) \quad (3b)$$

(Lande, 1980). These expressions illustrate that a positive genetic correlation increases the rate of evolution of both sexes as long as the direction of selection is the same. If β_f and β_m are both positive, for example, then a positive r_{mf} increases the rate of evolutionary change in the trait means, $\bar{z}_f$ and $\bar{z}_m$. On the other hand, when selection is sexually antagonistic – (one of β_f and β_m is positive and the other is negative –), a positive genetic correlation reduces the rate of evolution of both sexes. With strong r_{mf} values, the relative strengths of β_f and β_m also become increasingly important, as it is also possible for one sex to force

the other to evolve away from its optimum, leading to an increase in maladaptation for that sex. **See also: Sexual Conflict**

These predictions for the evolutionary consequences of cross-sex genetic correlations have been validated by laboratory evolution experiments that impose artificial selection on female and male traits (Lande, 1980; Stewart and Rice, 2018). Stewart and Rice (2018), for example used populations of the fruit fly *Drosophila melanogaster* to experimentally evolve male and female body size under conditions that mimic when SAS might be absent or present. Their results show that directional selection to either increase or to decrease body size leads to strong, correlated evolutionary responses of both sexes when the direction of selection is the same in each sex (i.e. SAS absent). However, evolutionary responses were negligible when females and males were selected in opposite directions (i.e. SAS present). The meagre evolutionary response to SAS was due to a strong cross-sex genetic correlation for body size, for which r_{mf} is close to one.

Sexually Antagonistic Selection during Adaptation in a Novel Environment

Directional selection implies a mismatch between the traits that individuals of a population express and the optimal expression of those traits. In other words, directional selection reflects maladaptation of the population to its current environment (**see also: Genetic Load**). The deviation between the trait optimum and the mean trait value of a population is the driver of directional selection, which intensifies with the magnitude of the deviation (Kopp and Matuszewski, 2014). SAS arises from a specific form of this maladaptation, in which both sexes are displaced from their optima, and their displacements occur in opposite directions away from the optima (Lande, 1980; Cox and Calsbeek, 2009). Returning to **Figure 1**, for example, SAS for height occurs when the trait mean for one sex is above its optimum and the trait mean for the other sex is below its optimum. Maladaptation arises because males and females have yet to evolve (or are unable to evolve) heights that would maximise individual fitness, leaving potential fitness gains unrealised.

In stable environments, maladaptation is predicted to be fleeting. Given time and genetic variation, populations are expected to adapt and ultimately evolve the traits that are favoured in their environments. SAS can similarly become resolved once evolutionary divergence between females and males allows members of both sexes to eventually express traits that match the sex-specific optima (i.e. the population eventually evolves until $\bar{z}_f = O_f$ and $\bar{z}_m = O_m$, provided r_{mf} is less than one; see Lande, 1980). An important feature of evolution in species with separate sexes, however, is that SAS is predicted to arise and persist for much of the timescale of adaptation when the sexes have sexually dimorphic optima (Lande, 1980; Connallon and Hall, 2016).

Consider, for example a population encountering a new environment, either because the environment of the population has recently been altered, or the population has colonised a new habitat. The novel environment poses new challenges that the

population must adapt to, and both sexes are initially expected to be maladapted to biotic and/or abiotic conditions within the new environment. If, in the new environment, the female and male trait optima have shifted in similar directions, then directional selection in females and males become aligned, potentially reducing or eliminating SAS. Such a scenario is depicted in **Figure 3**, where $\bar{z}_0$ represents the initial trait mean for both sexes, and the initial angle between selection vectors is modest ($\theta_0 < 90^\circ$, corresponding to a partial alignment of female and male directional selection). Yet despite its initial absence, SAS is nevertheless likely to emerge during the course of adaptation towards the trait optima, given that male and female traits are rarely genetically independent (**Figure 3**) (Lande, 1980; Connallon and Clark, 2014).

Genetic correlations play a key role in generating SAS during adaptation (**Figure 3**). When the traits responding to selection have strong and positive genetic correlations ($r_{mf} \gg 0$), evolutionary changes in female and male traits will be strongly correlated during the initial phase of adaptation (**Figure 3b**) (Lande, 1980; Connallon and Clark, 2014). Although SAS is initially absent, the genetic correlation causes both sexes to evolve rapidly towards an intermediate position between the female and male optima, leading to strong SAS following this initial phase of evolutionary divergence (**Figure 3a**). Once the population has evolved towards this intermediate state between the optima, females and males then slowly diverge towards their optima. This second phase of adaptation can eventually lead to pronounced sexual dimorphism, yet the process may take a long time – particularly when the genetic correlation is strong – which leads to an extended period of SAS during evolutionary divergence between the sexes (Lande, 1980; Connallon and Hall, 2016). If instead there was no genetic correlation between the sexes, evolution of each sex could proceed directly towards its optimum and SAS need not arise during the process of sex-specific adaptation (**Figure 3b**).

The theory summarised earlier predicts that the process of adaptation is likely to generate SAS, particularly when traits responding to selection have high cross-sex genetic correlations (as they typically do; Poissant *et al.*, 2010; Griffin *et al.*, 2013). In contrast, exposure to a novel environment may reset the directions of selection on each sex and thereby reduce or eliminate SAS. Several lab experiments have tested whether SAS is reduced in populations exposed to novel or stressful environmental conditions (Delcourt *et al.*, 2009; Long *et al.*, 2012; Berger *et al.*, 2014; Punzalan *et al.*, 2014; Holman and Jacomb, 2017; Martinossi-Allibert *et al.*, 2018). Some studies documented a decreased signal of SAS in the altered environment, consistent with the theory (Long *et al.*, 2012; Berger *et al.*, 2014), whereas others found no effect of the environmental manipulation on the signal of SAS (Holman and Jacomb, 2017; Martinossi-Allibert *et al.*, 2018). In a minority of cases, strong SAS was observed in the novel environment (Delcourt *et al.*, 2009; Punzalan *et al.*, 2014). Thus, tests of the theory are currently mixed, and further studies of this nature will be needed to resolve how often abrupt changes in the environment will mitigate the intensity of SAS. These studies also raise the question of how SAS will be affected by other forms of environmental change – a topic that we turn to in the following section.

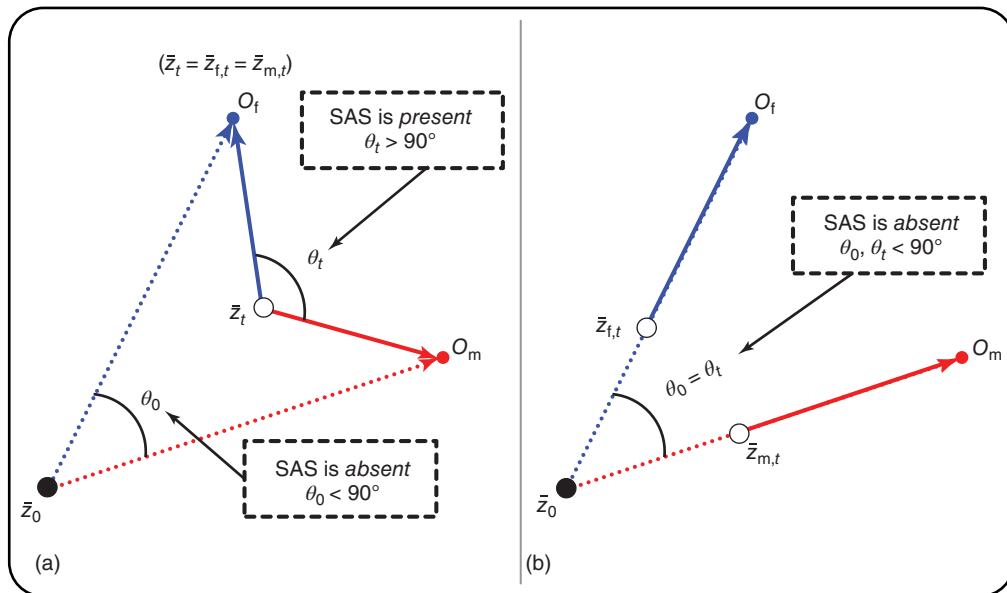


Figure 3 Genetic correlations and the emergence of SAS during adaptation. The broken arrows show the initial vectors of directional selection towards the female and male optima. The average trait expression is initially the same in each sex ($\bar{z}_0$ in both sexes at time '0'). The solid arrows show the vectors of selection after some time has passed and the population has partially adapted to the environment. Note that SAS is initially absent in both figure panels, as the initial angle between female and male selection gradient vectors is less than 90° . Panel a: A strong genetic correlation leads to rapid and correlated evolutionary divergence of female and male traits when direction of selection in each sex is aligned (i.e. from the initial condition where SAS is absent). However, adaptation of the population causes selection to become sexually antagonistic: following t generations of evolution, selection vectors point in opposing directions. Panel b: When there is no genetic correlation between the sexes ($r_{mf} = 0$), evolutionary divergence of each sex can proceed towards its optimum, without modifying the angle between female and male selection vectors (in the case shown, SAS is initially absent and remains absent). This example assumes that the two different traits genetically vary independently of one another.

Sexually Antagonistic Selection during Adaptation in Continuously Changing Environments

In natural populations, fitness optima are expected to be highly variable as a biotic and abiotic conditions change due to seasonal conditions, global change or even the influx of different pathogens or predators (Siepielski *et al.*, 2017). In such continuously changing environments, populations remain perpetually maladapted to the current environment, and must constantly evolve to match ever-changing conditions (Kopp and Matuszewski, 2014). As discussed in the previous section, maladaptation caused by abrupt environmental change may cause directional selection in females and males to become aligned, leading to a reduction or elimination of SAS. By logical extension, continuously changing conditions that lead to sustained maladaptation of the population over time may cause directional selection on each sex to become perpetually aligned. Consequently, SAS may be less common in populations in rapidly changing environments, relative to populations within comparatively stable conditions. Yet as we discuss below, this conclusion depends entirely on the how male and female fitness optima change through space or time.

Theoretical models have shown that environmental change across geographic space can indeed mitigate SAS, but not

necessarily across all regions of a species distribution. For example, changing environmental conditions across a species' range can lead to variation in SAS among different subpopulations in the range (Connallon, 2015). When the key environmental variables affecting selection change monotonically across the range (e.g. average temperatures change directionally across a latitudinal gradient), SAS is more likely to occur near the range centre, where local adaptation is relatively high, than near the range boundaries, where local adaptation is most limited. Although these theoretical predictions still need to be tested in a broad range of systems, some recent studies provide tentative support. Delph *et al.* (2011), for example demonstrated that SAS was confined to a fraction of subpopulations within the range of the dioecious plant, *Silene latifolia*. A recent meta-analysis of selection gradients in animals by De Lisle *et al.* (2018) showed that a population's position within the species' range was correlated with sex differences in the strength and direction of local natural selection, with selection becoming more similar between the sexes in populations near range margins.

Continuously changing environments over time can also eliminate SAS, despite differences between female and male trait optima, but again some scenarios of change can lead to perpetual SAS (Connallon and Hall, 2016). SAS is likely to occur when environmental changes cause female and male trait optima to shift in different directions, or when change is gradual and the optima shift at different rates. SAS is least likely to occur when

environmental changes are rapid or cyclic and these changes cause the sex-specific optima to shift in the same directions. De Lisle *et al.* (2018) recently showed that temporal fluctuations in micro-climatic variables were associated with broad-scale patterns of sex-specific selection, with seasonally variable environments associated with increased similarity between female and male selection gradients. These results suggest that environmental drivers of temporally fluctuating natural selection may similarly impact female and male optima, though further empirical study is needed to validate this possibility.

Conclusions and Future Directions

A population's environment determines the form with which natural selection affects its members. From this perspective, sex differences in selection, including SAS, only make sense in light of the environmental conditions to which populations or species with separate sexes are exposed. While studies of SAS and its evolutionary consequences have spiked over the last two decades (Rice and Chippindale, 2001; Bonduriansky and Chenoweth, 2009; Rowe *et al.*, 2018), much less effort has been directed towards understanding the dependency of SAS upon on the environment (Miller and Svensson, 2014; Connallon *et al.*, 2018).

Current data suggest that the interplay between environmental change and adaptation to new conditions can mediate the expression of SAS within a population. Nevertheless, we currently know little about the specific environmental factors that are most and least likely to be associated with SAS and its resolution. Although this represents a gap in our understanding, it also points towards exceptional opportunities for new empirical research that establishes closer links between ecological complexity and processes of female and male adaptive evolution (Yun *et al.*, 2018). Whether or not these links impact population dynamics and extinction susceptibility also warrants future attention (Kokko and Brooks, 2003; Gomulkiewicz and Houle, 2009).

Glossary

Additive genetic variance A measure of genetic variability of a trait. The rate of evolutionary change of a trait and the degree to which relatives resemble one another each depend on the additive genetic variance.

Cross-sex genetic correlation A measure of the extent to which genetic variation affecting a trait has similar effects on the trait's expression in females versus males. A large and positive cross-sex genetic correlation implies that genetic variants typically have similar effects on female and male trait expression.

Selection gradient A measure of the strength and direction of selection on a trait. The selection gradient is based on the covariance between trait expression and fitness among individuals of a population.

Sexual dimorphism Statistical difference in trait expression between the sexes. Sexual dimorphism usually refers to sex differences in the average expression of a trait.

Sexual selection A form of natural selection that specifically arises from competition for mates. The outcome of sexual

selection may depend on direct competition between the members of the same sex (e.g. combat) or indirect competition mediated by the mate preferences of the opposite sex.

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