

# Predicting Multivariate Responses of Sexual Dimorphism to Direct and Indirect Selection

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**ABSTRACT:** Sexual dimorphism is often assumed to result from balancing the strength of antagonistic selection in favor of dimorphism against the degree of constraint imposed by the shared genome of the sexes, reflected in the **B** matrix of genetic intersexual covariances. To investigate the totality of forces shaping dimorphism, we reparameterized the Lande equation to predict changes in trait averages and trait differences between the sexes. As genetic constraints on the evolution of dimorphism in response to antagonistic selection become larger, dimorphism will tend to respond more rapidly to concordant selection (which favors the same direction of change in male and female traits) than to antagonistic selection. When we apply this theory to four empirical estimates of **B** in *Drosophila melanogaster*, the indirect responses of dimorphism to concordant selection are of comparable or larger magnitude than the direct responses of dimorphism to antagonistic selection in two suites of traits with typical levels of intersex correlation. Antagonistic selection is more important in two suites of traits where the intersex correlations are unusually low. This suggests that the evolution of sexual dimorphism may sometimes be dominated by concordant selection rather than antagonistic selection.

**Keywords:** sexual dimorphism, **G** matrix, **B** matrix, sexual conflict.

## Introduction

Males and females are frequently subjected to very different selection pressures (Parker 1979; Arnqvist and Rowe 2005). If the fitness surface remains constant for many generations, the result is some combination of sexual dimorphism and sexual conflict (e.g., fig. 1 in Cox and Calsbeek 2009). When the fitness optimum differs between the

sexes, sexual dimorphism should evolve. Sexual conflict occurs when the current sexual dimorphism does not match the optimum level of dimorphism. Thus, sexual conflict can be transitory as sexual dimorphism evolves toward the optimum level or persistent if some other factor constrains dimorphism from reaching its optimum. On the other hand, many previous authors have emphasized that the current level of dimorphism and sexual conflict have no necessary relationship (Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009; Ingleby et al. 2015), as constrained traits can be subject to persistent conflict without evolving dimorphism.

The usual explanation for the constraints that lead to sexual conflict is that there are genotype-by-sex interactions for fitness, such that a genotype that functions well in a female would perform poorly in a male and vice versa (Lande 1980, 1987; Rice 1984; Halliday and Arnold 1987; Arnqvist and Rowe 2005), resulting in “intra-locus” sexual conflict. Intra-locus sexual conflict provides a compelling explanation for the negative correlation of adult fitnesses in *Drosophila melanogaster* (Chippindale et al. 2001; Innocenti and Morrow 2010). At least some of the responses to altered strength of sexual selection (e.g., Holland and Rice 1999) are due to the resolution of intra-locus conflicts (Prasad et al. 2007; Hollis et al. 2014). Despite this evidence, there are only a handful of examples of specific loci that are proven to be undergoing sexually conflicting selection (Rowe et al. 2018).

A quantitative genetic framework is useful to capture the ability of variation to allow or constrain alterations in the level of sexual dimorphism because it allows the incorporation of the response in many traits simultaneously (Lande 1980). The variances and covariances among male- and female-expressed traits are summarized in a matrix, **G**, with a row and column corresponding to each male and female trait. Lande (1980) highlighted the role of cross-sex covariances—collected in **B**, which is a submatrix of **G**—in shaping the response of shared traits to selection in each sex.

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In practice, most analyses of constraints on the evolution of sexual dimorphism have focused on a single pair of homologous traits rather than the  $\mathbf{B}$  matrix as a whole. In this simple univariate case, the  $\mathbf{B}$  matrix consists of a single covariance, which can be well summarized by a single genetic correlation,  $r_{MF}$ . It is easy to understand the evolutionary effects of  $r_{MF}$  using the familiar reasoning that the rate of response to antagonistic selection on male and female traits will be slower the more positive the correlation between them is.

Previous work makes it clear that there is more to the prediction of sexual dimorphism than  $r_{MF}$ . First, sexual dimorphism can change if male and female traits evolve at different rates arising from quantitative asymmetries in either selection or genetic variation (Fisher 1930; Lande 1980, 1987; Leutenegger and Cheverud 1982; Cheverud et al. 1985; Lynch and Walsh 1998, chap. 24; Bonduriansky and Chenoweth 2009; Wyman et al. 2013; Connallon and Clark 2014). Second, selection on traits other than the focal trait can affect the evolution of dimorphism as well (Blows and Hoffmann 2005; Hansen and Houle 2008; Walsh and Blows 2009). This is particularly clear in the case of gene expression, where we can measure the genetic variances and covariances among tens of thousands of genes and the expression of many of these genes is highly correlated (Ayroles et al. 2009; Houle and Cheng 2020a). In addition, Gosden et al. (2012) pointed out that asymmetry of  $\mathbf{B}$ , resulting from inequalities of cross-sex, cross-trait covariances, will actually promote the evolution of dimorphism. A recent crop of empirical studies has begun to address the effects of the  $\mathbf{B}$  matrix as a whole on responses to selection, a topic we return to in the discussion section.

In this contribution, we consider the short-term evolution of sexual dimorphism in the multivariate case. Previous analyses have been undertaken in what we will call the “male/female space,” where each male and female trait defines an axis of variation. Following the implicit approach of Lande (1980), we choose to work in the “concordant/antagonistic space,” where the averages of and differences between male and female phenotypes each define an axis of variation. This change of view from the male/female space to the concordant/antagonistic space makes it easier to understand the importance of all of the factors that affect the rate of change in sexual dimorphism. We then apply our theoretical findings to several quantitative genetic data sets from *D. melanogaster*.

### Theory: What Influences the Rate of Evolution of Sexual Dimorphism?

Lande (1979) formulated the now widely known quantitative genetic prediction equation

$$\Delta\bar{z} = \mathbf{G}\beta, \quad (1)$$

which predicts a vector of responses to selection,  $\Delta\bar{z}$ , from a measure of selection,  $\beta$ , a vector of partial regression coefficients of fitness on trait, and  $\mathbf{G}$ , the additive genetic covariance matrix.

Lande (1980) then generalized this to consider  $k$  traits with values in each sex using

$$\begin{bmatrix} \Delta\bar{z}_m \\ \Delta\bar{z}_f \end{bmatrix} = \frac{1}{2} \mathbf{G}_{mf} \cdot \beta_{mf}, \quad (2)$$

where

$$\mathbf{G}_{mf} = \begin{bmatrix} \mathbf{G}_m & \mathbf{B} \\ \mathbf{B}^T & \mathbf{G}_f \end{bmatrix}, \quad \beta_{mf} = \begin{bmatrix} \beta_m \\ \beta_f \end{bmatrix},$$

and the subscripts  $\mathbf{m}$  and  $\mathbf{f}$  index male and female response vectors,  $\mathbf{G}$  matrices, and selection gradient vectors. The constant 1/2 is appropriate for gonochoristic species where each parent experiences selection as either a male or a female. There are  $k$  pairs of quantitative traits with phenotypic values in the two sexes:  $z_{m1}, z_{m2}, \dots, z_{mk}$ , and  $z_{f1}, z_{f2}, \dots, z_{fk}$ . Individual elements of the sex-specific  $k \times k$  symmetrical  $\mathbf{G}$  matrices will be written  $m_{ij}$  and  $f_{ij}$ , where  $1 \leq i$  and  $j \leq k$ . The  $k \times k$  matrix  $\mathbf{B}$  contains the covariances between traits expressed in the other sex, with  $b_{ij}$  denoting the covariance of the  $i$ th trait in males with the  $j$ th trait in females. The diagonal of  $\mathbf{B}$  consists of the covariances between homologous traits in different sexes, while the off-diagonal elements are the covariances among nonhomologous traits between sexes. In contrast to the  $\mathbf{G}_m$  and  $\mathbf{G}_f$  matrices, the matrix  $\mathbf{B}$  can be asymmetrical, that is to say,  $b_{ij}$  need not equal  $b_{ji}$ .

To work in the space of concordant and antagonistic changes, we introduce a dimorphism transformation,

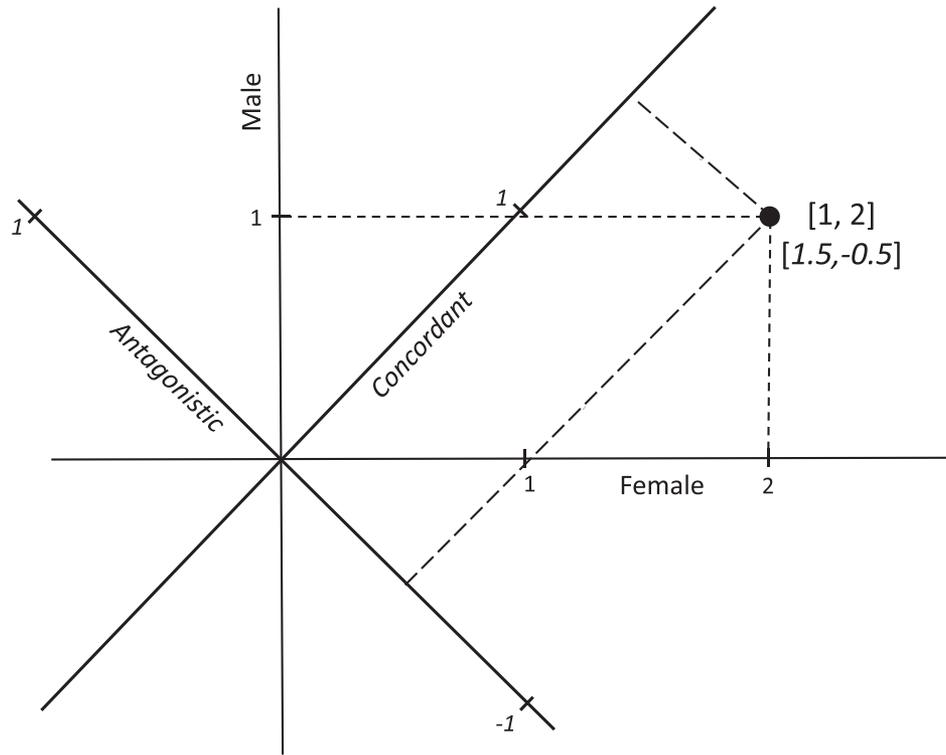
$$\mathbf{Q}_{mf \rightarrow ca}: \text{male/female space} \rightarrow \text{concordant/antagonistic space},$$

that maps the male and female traits in the male/female space to concordant and antagonistic traits in the concordant/antagonistic space. We implement the transformation as the matrix

$$\mathbf{Q}_{mf \rightarrow ca} = \frac{1}{2} \begin{bmatrix} \mathbf{I} & \mathbf{I} \\ \mathbf{I} & -\mathbf{I} \end{bmatrix},$$

where  $\mathbf{I}$  is the  $k \times k$  identity matrix. The transformation  $\mathbf{Q}_{mf \rightarrow ca}$  defines new variables that are functions of the means of the male and female traits and the mean differences between male and female traits.

Figure 1 shows the transformation of a vector in male/female space into a vector in concordant/antagonistic space. Note that this transformation implicitly defines dimorphism relative to the trait mean over sexes. Many



**Figure 1:** Conversion from male/female space to concordant/antagonistic space when  $k = 1$ . The male/female space has coordinates that are the values of the male and female. The black circle represents the vector  $[1 \ 2]$  in male/female space and  $[1.5 \ -0.5]$  in concordant/antagonistic space. These values could represent any relevant vector, for example, the mean male and female phenotype  $\bar{z}^T$  or the transpose of a selection gradient vector,  $\beta^T$ . The  $\mathbf{Q}_{mf \rightarrow ca}$  matrix rotates the coordinate vectors  $45^\circ$ , flips the sign of the antagonistic axis, and scales the axes to make the values in concordant/antagonistic space correspond to averages in male/female space. If the male and female values were equal, the point would fall on the concordant axis. The distance from the concordant axis expresses dimorphism as the male value minus the average of the male and female values. Alternatively, one could define dimorphism as the female value minus the average or scale the axes differently. For example, defining  $\mathbf{Q}_{mf \rightarrow ca}$  to use  $1/\sqrt{2}$  instead of  $1/2$  preserves the lengths of vectors and the size of the  $\mathbf{G}$  matrix. All results in this article scale using  $1/2$ .

previous estimates of sexual dimorphism express it as the difference between the sexes. The constant  $1/2$  in the equation scales the strength of selection in concordant/antagonistic space to be the averages of those in male/female space.

The matrix  $\mathbf{Q}_{mf \rightarrow ca}$  relates the  $\mathbf{G}$  matrix in concordant/antagonistic space to that in male/female space:

$$\mathbf{G}_{ca} = \mathbf{Q}_{mf \rightarrow ca} \mathbf{G}_{mf} \mathbf{Q}_{mf \rightarrow ca}^T = \mathbf{Q}_{mf \rightarrow ca} \mathbf{G}_{mf} \mathbf{Q}_{mf \rightarrow ca},$$

as  $\mathbf{Q}_{mf \rightarrow ca}$  is symmetric and  $\mathbf{Q}_{mf \rightarrow ca} = \mathbf{Q}_{mf \rightarrow ca}^T$ . The matrix

$$(\mathbf{Q}_{mf \rightarrow ca}^T)^{-1} = 2\mathbf{Q}_{mf \rightarrow ca}$$

represents the transformation that maps the selection gradient vectors,  $(1/2)\beta_{mf}$ , of male/female space to

$$\beta_{ca} = 2\mathbf{Q}_{mf \rightarrow ca} \cdot (1/2)\beta_{mf} = \mathbf{Q}_{mf \rightarrow ca} \cdot \beta_{mf}$$

of concordant/antagonistic space.

Lande's equation (1) is invariant after the dimorphism transformation:

$$\begin{array}{l} \text{concordant/} \\ \text{antagonistic space} \end{array} \quad \begin{array}{l} \text{male/female space} \\ \Delta \bar{z}_{ca} = \mathbf{Q}_{mf \rightarrow ca} \Delta \bar{z}_{mf}, \\ \mathbf{G}_{ca} = \mathbf{Q}_{mf \rightarrow ca} \mathbf{G}_{mf} \mathbf{Q}_{mf \rightarrow ca}, \\ \beta_{ca} = \mathbf{Q}_{mf \rightarrow ca} \beta_{mf}, \\ \Delta \bar{z}_{ca} = \mathbf{G}_{ca} \beta_{ca} \Leftrightarrow \Delta \bar{z}_{mf} = \frac{1}{2} \mathbf{G}_{mf} \cdot \beta_{mf}. \end{array} \quad (3)$$

We can then predict the response to selection in concordant and antagonistic subspaces using

$$\begin{bmatrix} \Delta \bar{z}_c \\ \Delta \bar{z}_a \end{bmatrix} = \begin{bmatrix} \mathbf{G}_c & \mathbf{B}_{ca} \\ \mathbf{B}_{ca}^T & \mathbf{G}_a \end{bmatrix} \begin{bmatrix} \beta_c \\ \beta_a \end{bmatrix}. \quad (4)$$

The matrix  $\mathbf{G}_c$  is the genetic variation in the concordant subspace. It allows male and female traits to respond at the same rate and direction to selection. The matrix  $\mathbf{G}_a$  is the genetic variation in the antagonistic subspace that

allows male and female traits to respond in opposite directions to selection. The matrix  $\mathbf{B}_{ca}$  is the genetic covariation that leads to indirect responses to selection in the other subspace, for example, an indirect antagonistic response to concordant selection.

*Two-Trait Case*

We will return to the general case of multiple traits when  $k$  is large below, but first we build intuition about the meaning of these terms by first considering the two-trait case,  $k = 2$ . The additive genetic covariance matrix is

$$\mathbf{G} = \begin{bmatrix} m_{11} & m_{12} & b_{11} & b_{12} \\ m_{21} & m_{22} & b_{21} & b_{22} \\ b_{11} & b_{21} & f_{11} & f_{12} \\ b_{12} & b_{22} & f_{21} & f_{22} \end{bmatrix},$$

where the subscripts index the traits involved. The familiar quantities  $r_{MF-i} = b_{ii} \cdot m_{ii}^{-1/2} \cdot f_{ii}^{-1/2}$  involve the diagonal elements of the submatrices  $\mathbf{G}_m$ ,  $\mathbf{G}_f$ , and  $\mathbf{B}$ .

For  $k = 2$ , the transformation matrix is

$$\mathbf{Q}_{mf \rightarrow ca} = \frac{1}{2} \begin{bmatrix} 1 & 0 & 1 & 0 \\ 0 & 1 & 0 & 1 \\ 1 & 0 & -1 & 0 \\ 0 & 1 & 0 & -1 \end{bmatrix}.$$

The genetic submatrices in equation (4) are then

$$\begin{aligned} \mathbf{G}_c &= \frac{1}{4} \begin{bmatrix} (m_{11} + f_{11}) + 2b_{11} & (m_{12} + f_{12}) + (b_{12} + b_{21}) \\ (m_{12} + f_{12}) + (b_{12} + b_{21}) & (m_{22} + f_{22}) + 2b_{22} \end{bmatrix}, \\ \mathbf{G}_a &= \frac{1}{4} \begin{bmatrix} (m_{11} + f_{11}) - 2b_{11} & (m_{12} + f_{12}) - (b_{12} + b_{21}) \\ (m_{12} + f_{12}) - (b_{12} + b_{21}) & (m_{22} + f_{22}) - 2b_{22} \end{bmatrix}, \\ \mathbf{B}_{ca} &= \frac{1}{4} \begin{bmatrix} (m_{11} - f_{11}) & (m_{12} - f_{12}) + (b_{21} - b_{12}) \\ (m_{12} - f_{12}) + (b_{12} - b_{21}) & (m_{22} - f_{22}) \end{bmatrix}. \end{aligned}$$

Note that  $\mathbf{B}_{ca}$  is composed of differences in (co)variances in the two sexes and the asymmetries of the off-diagonal elements of  $\mathbf{B}$ . The diagonal elements of  $\mathbf{B}$  are absent from  $\mathbf{B}_{ca}$ , and thus  $r_{MF}$  values cannot affect the indirect responses to concordant or antagonistic selection.

We can also use  $\mathbf{Q}_{mf \rightarrow ca}$  to cast the selection vector into the concordant/antagonistic space, as shown in equation (3). Any selection gradient vector that imposes equal selection on each pair of homologous male and female traits  $z_{mi}$  and  $z_{fi}$  falls entirely within the concordant subspace. For example, the selection gradient

$$\beta_{mf}^T = [\beta_{m1} \ \beta_{m2} \ \beta_{f1} \ \beta_{f2}] = [1 \ 0 \ 1 \ 0]$$

gives rise to the concordant and antagonistic selection gradients

$$\begin{cases} \beta_c^T = [1 \ 0], \\ \beta_a^T = [0 \ 0]. \end{cases}$$

The selection gradient

$$\beta^T = [2 \ 1 \ 2 \ 1]$$

maps to

$$\begin{cases} \beta_c^T = [2 \ 1], \\ \beta_a^T = [0 \ 0]. \end{cases}$$

Similarly, selection can be purely antagonistic only when the strength of selection on all traits is precisely balanced by opposing selection in the other sex.

When selection is entirely in the concordant subspace, there will be an indirect response in the antagonistic subspace whenever  $\mathbf{B}_{ca} \neq 0$ . For example, the concordant selection gradient  $\beta_c^T = [1 \ 0]$  generates a set of indirect responses in the two dimorphism traits of

$$\begin{aligned} \Delta \bar{z}_a &= \begin{bmatrix} \Delta \bar{z}_{m1} - \Delta \bar{z}_{f1} \\ \Delta \bar{z}_{m2} - \Delta \bar{z}_{f2} \end{bmatrix} \\ &= \frac{1}{4} \begin{bmatrix} (m_{11} - f_{11}) \\ (m_{12} - f_{12}) + (b_{12} - b_{21}) \end{bmatrix}. \end{aligned}$$

The indirect response of dimorphism in  $z_1$  to selection on  $\bar{z}_1$  depends on the asymmetry in genetic variances ( $m_{11} - f_{11}$ ), as it would in the  $k = 1$  case. The indirect response of dimorphism in the other trait,  $z_2$ , depends on both the asymmetry in the within-sex covariances  $m_{12}$  and  $f_{12}$  and the asymmetry of the cross-sex, cross-trait covariances  $b_{12}$  and  $b_{21}$ , which are omitted in the  $k = 1$  case.

In general, most selection gradients will be somewhat asymmetrical and generate selection in both the concordant subspace and the antagonistic subspace. For example,

$$\beta^T = [\beta_{m1} \ \beta_{m2} \ \beta_{f1} \ \beta_{f2}] = [2 \ 1 \ 1 \ 2]$$

maps to

$$\begin{cases} \beta_c^T = [3/2 \ 3/2], \\ \beta_a^T = [1/2 \ -1/2]. \end{cases}$$

This translates to equal selection to increase  $\bar{z}_1$  and  $\bar{z}_2$  but also to selection to increase  $z_{m1}$  while decreasing  $z_{f1}$  and to selection to decrease  $z_{m2}$  while increasing  $z_{f2}$ . The total strength of selection in each subspace is the length of the corresponding vector. In this example, the strength of concordant selection is 2.12, three times the strength of antagonistic selection.

*General Case*

With just  $k = 2$  traits under selection, we can imagine that the direct responses to selection will tend to swamp indirect ones. In nature, the number of traits that are potentially selected simultaneously is very large, so the

response to selection of any one trait will include a very large number of indirect responses when many traits are under directional selection.

The matrix  $\mathbf{G}_{ca}$  is related to that in the male/female space by

$$\begin{aligned} \mathbf{G}_{ca} &= \begin{bmatrix} \mathbf{G}_c & \mathbf{B}_{ca} \\ \mathbf{B}_{ca}^T & \mathbf{G}_a \end{bmatrix} \\ &= \frac{1}{4} \begin{bmatrix} (\mathbf{G}_m + \mathbf{G}_f) + (\mathbf{B} + \mathbf{B}^T) & (\mathbf{G}_m - \mathbf{G}_f) + (\mathbf{B} - \mathbf{B}^T) \\ (\mathbf{G}_m - \mathbf{G}_f) - (\mathbf{B} - \mathbf{B}^T) & (\mathbf{G}_m + \mathbf{G}_f) - (\mathbf{B} + \mathbf{B}^T) \end{bmatrix}. \end{aligned}$$

The matrix  $\mathbf{G}_{ca}$  can also be expressed in terms of four different  $k \times k$  matrices:

$$\begin{cases} \bar{\mathbf{G}} = \frac{\mathbf{G}_m + \mathbf{G}_f}{2}, \text{ average genetic variance matrix;} \\ \dot{\mathbf{G}} = \frac{\mathbf{G}_m - \mathbf{G}_f}{2}, \text{ differences between male and female matrices;} \\ \bar{\mathbf{B}} = \frac{\mathbf{B} + \mathbf{B}^T}{2}, \text{ symmetrical component of the B matrix;} \\ \dot{\mathbf{B}} = \frac{\mathbf{B} - \mathbf{B}^T}{2}, \text{ asymmetrical component of the B matrix.} \end{cases}$$

Putting all of these together,

$$\mathbf{G}_{ca} = \begin{bmatrix} \mathbf{G}_c & \mathbf{B}_{ca} \\ \mathbf{B}_{ca}^T & \mathbf{G}_a \end{bmatrix} = \frac{1}{2} \begin{bmatrix} \bar{\mathbf{G}} + \bar{\mathbf{B}} & \dot{\mathbf{G}} + \dot{\mathbf{B}} \\ \dot{\mathbf{G}} - \dot{\mathbf{B}} & \bar{\mathbf{G}} - \bar{\mathbf{B}} \end{bmatrix}. \quad (5)$$

The rate of change in sexual dimorphism is  $\Delta\bar{\mathbf{z}}_a = (1/2)(\Delta\bar{\mathbf{z}}_m - \Delta\bar{\mathbf{z}}_f)$ . We can further decompose changes in dimorphism into that caused by selection in the concordant versus antagonistic subspaces

$$\Delta\bar{\mathbf{z}}_a = \mathbf{G}_a\beta_a + \mathbf{B}_{ca}\beta_c.$$

To quantify the magnitude of change in overall sexual dimorphism in  $n$  traits, we use its Euclidean norm,  $\|\Delta\bar{\mathbf{z}}_a\| = (\Delta\bar{\mathbf{z}}_a^T \Delta\bar{\mathbf{z}}_a)^{1/2}$ .

Any selection response can be decomposed into a concordant and an antagonistic component that sum to the total response. Thus, without loss of generality we can consider two extreme selection scenarios: antagonistic selection ( $\beta_a = \beta$ ,  $\beta_c = 0$ ) and concordant selection ( $\beta_a = 0$ ,  $\beta_c = \beta$ ).

In supplement S1 (supplements S1–S3 are available online in the supplemental PDF), we show that under antagonistic selection, the maximum change of overall sexual dimorphism is

$$\max_{\|\beta\|=1} \|\Delta\bar{\mathbf{z}}_a\| \leq \|\mathbf{G}_a\|, \quad (6)$$

where  $\|\mathbf{G}_a\| = \{\sum_i \lambda_i^2(\mathbf{G}_a)\}^{-1/2}$  is the Frobenius norm, a common measure of matrix size that generalizes the Euclidean norm to matrices, and  $\lambda_i(\mathbf{G}_a)$  are the eigenvalues of the matrix  $\mathbf{G}_a$ . On the other hand, under concordant selection,  $\|\mathbf{B}_{ca}\|$  limits the maximum change of overall sexual dimorphism under concordant selection:

$$\max_{\|\beta\|=1} \|\Delta\bar{\mathbf{z}}_a\| \leq \|\mathbf{B}_{ca}\|. \quad (7)$$

The expected change in sexual dimorphism due to direct selection depends on the respondability of  $\mathbf{G}_a$  and the indirect respondability through  $\mathbf{B}_{ca}$ . Hansen and Houle (2008) showed that the Frobenius norm is an upper bound on the average respondability of a  $\mathbf{G}$  matrix and developed a more accurate approximation that applies to the whole  $\mathbf{G}$  matrix. It is unclear whether a similar approximation applies to  $\mathbf{B}_{ca}$ .

Supplement S1 also shows that if we assume that traits are subject to randomly fluctuating selection gradients drawn from a multivariate normal distribution, the sizes of the matrices  $\mathbf{G}_a$  and  $\mathbf{B}_{ca}$  measured by their Frobenius norms ( $\|\mathbf{G}_a\|$  and  $\|\mathbf{B}_{ca}\|$ ) control the average rate of change in dimorphism under antagonistic selection and concordant selection. Furthermore, we also show that the relative sizes of  $\|\mathbf{G}_a\|$  to  $\|\mathbf{G}_c\|$  informs the size of  $\|\mathbf{B}_{ca}\|$ . In particular,

$$\begin{aligned} \|\mathbf{B}_{ca}\| &\geq \|\mathbf{G}_a\| \quad \text{if } \|\mathbf{G}_a\| \ll \|\mathbf{G}_c\|, \\ \|\mathbf{B}_{ca}\| &< \|\mathbf{G}_a\| \quad \text{if } \|\mathbf{G}_a\| > \|\mathbf{G}_c\|. \end{aligned} \quad (8)$$

Combining these results with equations (6) and (7) shows that we can infer the relative contribution of direct and indirect responses to the evolution of sexual dimorphism by comparing the sizes of matrices  $\mathbf{G}_c$  and  $\mathbf{G}_a$  as well as  $\mathbf{G}_a$  and  $\mathbf{B}_{ca}$ .

In supplement S2, we show that  $r_{MF}$  plays a counter-intuitive role as a predictor of the responses to selection. As shown in the  $k = 1$  case, high  $r_{MF}$  values restrict the direct response to antagonistic selection. However, high  $r_{MF}$  values must also reflect the fact that  $\mathbf{G}_m$  and  $\mathbf{G}_f$  will be highly correlated, creating the necessary condition for a small  $\mathbf{G}_a$  relative to  $\mathbf{B}_{ca}$  and thus relatively large indirect responses of dimorphism to concordant selection.

#### Response to Selection When $\mathbf{G}_m$ and $\mathbf{G}_f$ Are Similar

In an ancestral population with no sexual dimorphism, we expect that  $\mathbf{G}_m \approx \mathbf{G}_f$  and that there are near-perfect correlations between the sexes. In supplement S3, we show that in the initial stage of divergence  $\|\mathbf{G}_a\| \approx 0$  and  $\|\mathbf{B}_{ca}\| > \|\mathbf{G}_a\|$ . Therefore, indirect responses to concordant selection will dominate the evolution of sexual dimorphism. Conversely, when  $\mathbf{G}_m$  and  $\mathbf{G}_f$  are so dissimilar that  $\|\mathbf{G}_a\| > \|\mathbf{G}_c\|$  and  $\|\mathbf{B}_{ca}\| < \|\mathbf{G}_a\|$ , the direct responses to antagonistic selection will dominate the evolution of dimorphism.

### Application to G Matrices: Methods

#### Application to G Matrix Estimates

To demonstrate how to apply the above theoretical results, we predicted changes in sexual dimorphism based

on  $\mathbf{G}$  matrices estimated from four different suites of traits in *Drosophila melanogaster*.

First, we predict changes in sexual dimorphism for linear combinations of gene expression traits based on data gathered by Ayroles et al. (2009). Houle and Cheng (2020a) estimated a broad-sense  $\mathbf{G}$  matrix from these data, defining traits on the basis of a principal component analysis of relatively unbiased genes, resulting in  $k = 4$  linear combinations of expression traits. Second, we used the  $\mathbf{G}$  matrix estimated by Sztepanacz and Houle (2019) from  $k = 20$  wing shape traits gathered by Mezey and Houle (2005). Finally, we used two  $\mathbf{G}$  matrices for cuticular hydrocarbon (CHC) expression that Ingleby et al. (2014) estimated in a subset of the genotypes first studied by Innocenti and Morrow (2010). We extracted the  $\mathbf{G}$  matrix for the  $k = 4$  CHCs that were least sexually dimorphic in their expression from Ingleby et al.'s (2014) table 3 and the  $\mathbf{G}$  matrix ( $k = 4$ ) for the most dimorphic CHCs from their table 5. The least sexually dimorphic CHC matrix was multiplied by 100 before analysis, while values in the most dimorphic matrix CHC were multiplied by 1,000.

#### Responsability

To test how much of the response to concordant and antagonistic selection falls within concordant and antagonistic subspaces, we calculated responsibilities (Hansen and Houle 2008) to random skewers (Cheverud 1996; Cheverud and Marroig 2007) constrained to fall in either the concordant subspace or the antagonistic subspace. Responsibility is the total length of a vector of responses to selection to a unit length vector. To probe a matrix of dimension  $k$  per sex, we formed a  $\beta$  vector of length  $k$  with elements sampled from a standard normal distribution and then standardized the length of  $\beta$  to 1. For response to selection in the concordant or antagonistic subspaces, we calculated

$$\Delta\bar{z}_c = \mathbf{G}_{ca} \begin{bmatrix} \beta \\ 0 \end{bmatrix}, \quad \Delta\bar{z}_a = \mathbf{G}_{ca} \begin{bmatrix} 0 \\ \beta \end{bmatrix}.$$

Responsability in the concordant (antagonistic) subspace is the length (2-norm) of the first (last)  $k$  elements of  $\Delta\bar{z}$ .

We estimated confidence intervals for evolvabilities and responsibilities for the gene expression and wing shape data sets using the restricted maximum likelihood multivariate normal (REML-MVN) method (Meyer and Houle 2013; Houle and Meyer 2015). We do not have estimates of sampling error in the predictions for the two CHC data sets. For reasons noted in the discussion section, we expect that sampling error in submatrices will tend to bias responsibilities upward and that this bias will be larger for smaller submatrices than larger ones, minimizing the differences among submatrices.

The compiled data and the SAS (SAS Institute 2016) code to produce the results have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2280gb5pb>; Houle and Cheng 2020b).

#### Measuring the Similarity of Two Matrices

To interpret the matrix estimates, it is useful to have a scalar measure of matrix similarity that generalizes the notion of vector correlation to matrices. The similarity, denoted as  $\mathbb{S}$ , between two matrices/vectors  $\mathbf{F}$  and  $\mathbf{M}$  is defined as

$$\mathbb{S}_{\mathbf{F},\mathbf{M}} = \frac{\text{tr}(\mathbf{F}^T\mathbf{M})}{\|\mathbf{F}\|\|\mathbf{M}\|}, \quad (9)$$

where  $\text{tr}()$  is the trace and  $\|\cdot\|$  is the Frobenius norm. Similarity,  $\mathbb{S}_{\mathbf{F},\mathbf{M}}$ , is constrained to fall between  $-1$  and  $1$ , where  $1$  corresponds to a perfect positive relationship,  $0$  to no similarity, and  $-1$  to a perfect negative relationship.

#### Application to $\mathbf{G}$ Matrices: Results

##### Predicting Evolution of Dimorphism: Gene Expression

To illustrate application of our theory, we first present a detailed analysis of a  $\mathbf{G}$  matrix for whole-body expression of  $k = 4$  linear combinations of genes with relatively unbiased expression in males and females (Houle and Cheng 2020a). The  $\mathbf{G}_{mf}$  matrix in familiar male-female space is shown in table 1. The intersexual correlations for these traits,  $r_{MF}$ , shown in boldface and italic type along the diagonal of the upper right submatrix, average 0.82, similar to the average value of 0.75 found in previous studies (Poissant et al. 2010).

Transformed submatrices relevant to predicting response in concordant/antagonistic space for the gene expression data are shown in table 2. The upper set of matrices shown in table 2 are the average,  $\bar{\mathbf{G}}$ , and differences,  $\mathbf{G}$ , between the male- and female-specific matrices  $\mathbf{G}_m$  and  $\mathbf{G}_f$  (see eq. [5]). Inspection of these matrices reveals that  $\mathbf{G}_m$  and  $\mathbf{G}_f$  are strikingly asymmetrical in the variances and covariances for trait UB1 and modestly so for the other three traits.

Scalar measures of the genetic variation in concordant/antagonistic space are shown in the upper set of measurements in figure 2. From figure 2, we can see that the median similarity of  $\mathbf{G}_m$  and  $\mathbf{G}_f$  measured by  $\mathbb{S}_{mf}$  is just 0.72, which is actually less than the similarity of  $\mathbf{B}$  to  $\mathbf{G}_m$  ( $\mathbb{S}_{b,m} = 0.89$ ) or to  $\mathbf{G}_f$  ( $\mathbb{S}_{b,f} = 0.76$ ). In addition, the median norm of  $\mathbf{G}_f$  is 43% larger than that of  $\mathbf{G}_m$  ( $\|\mathbf{G}_m\| = 92$ ,  $\|\mathbf{G}_f\| = 132$ ). The median difference between replicate estimates of  $\|\mathbf{G}_m\|$  and  $\|\mathbf{G}_f\|$  is 38.5, which is just significantly greater than zero (95% confidence limits: 0.2, 85.5).

**Table 1:** Genetic correlation and covariance matrices for  $k = 4$  linear combinations of gene expression traits

	Male expression				Female expression			
	UB1	UB2	UB3	UB4	UB1	UB2	UB3	UB4
	<b>G<sub>m</sub></b>				<b>B</b>			
Male expression:								
UB1	<b>21.4</b> (5.0)	.01 (.16)	-.15 (.16)	-.15 (.17)	<b>.60</b> (.11)	.16 (.16)	-.14 (.17)	-.32 (.15)
UB2	.3 (5.5)	<b>53.7</b> (12.4)	.05 (.16)	-.10 (.17)	-.37 (.14)	<b>.87</b> (.05)	-.14 (.16)	.08 (.17)
UB3	-4.6 (5.0)	2.3 (7.9)	<b>42.2</b> (10.0)	.09 (.17)	-.14 (.16)	-.00 (.17)	<b>.93</b> (.03)	-.03 (.17)
UB4	-4.1 (4.6)	-4.1 (7.2)	3.4 (6.5)	<b>34.5</b> (8.4)	-.02 (.17)	-.13 (.17)	.08 (.17)	<b>.85</b> (.06)
	<b>B</b>				<b>G<sub>f</sub></b>			
Female expression:								
UB1	<b>28.2</b> (8.9)	-27.6 (12.9)	-9.4 (11.0)	-.9 (10.0)	<b>103.5</b> (23.8)	.00 (.17)	.09 (.17)	.03 (.17)
UB2	4.3 (4.5)	<b>36.8</b> (9.1)	-.1 (6.3)	-4.3 (5.8)	.2 (9.8)	<b>33.4</b> (8.1)	-.11 (.17)	.14 (.17)
UB3	-3.9 (4.8)	-6.5 (7.6)	<b>37.2</b> (8.9)	3.0 (6.2)	5.6 (10.5)	-4.0 (6.1)	<b>38.1</b> (9.2)	-.01 (.17)
UB4	-9.3 (5.1)	3.7 (7.8)	-1.1 (7.0)	<b>31.6</b> (8.1)	1.7 (10.8)	5.3 (6.3)	-.2 (6.7)	<b>39.9</b> (9.7)

Source: Cheng and Houle 2020a.

Note: Genetic variances are shown in boldface type on the main diagonal. Genetic correlations are above the main diagonal, and genetic covariances are below. Sampling standard errors are shown in parentheses on the line below the estimates. Cut-in heads outline the submatrices  $G_m$  (upper left),  $G_f$  (lower right), and  $B$  (off-diagonals). Diagonal elements of  $B$  are shown in boldface and italic type.

Inspection of the  $B$  matrix in table 1 shows that it is quite asymmetrical, resulting in a similarity of  $B$  and  $B^T$  of ( $S_{B,B^T} = 0.78$ ), which is likely to be significantly less than 1 given the confidence interval. A striking example of this is that male expression of UB2 is strongly negatively correlated with female expression of UB1 ( $r_{M2F1} = -0.37 \pm 0.14$ ), while female expression of UB2 is positively correlated with male expression of UB1 ( $r_{M1F2} = 0.16 \pm 0.16$ ). This asymmetry is apparent in the magnitude of the elements of the asymmetric component of the  $B$  matrix,  $\hat{B}$ , many of which are comparable to the sizes of the elements of  $\bar{B}$ , as shown in the second set of matrices in table 2.

The two matrices at the bottom of table 2,  $G_a$  and  $B_{ca}$ , allow us to predict the rate of evolution of dimorphism under antagonistic and concordant selection. The matrix  $G_a$  summarizes the genetic variances in the antagonistic subspace, where male and female expression evolve in opposite directions. The matrix  $B_{ca}$  summarizes the variation that can cause changes in dimorphism as an indirect response to selection in the concordant subspace. The median norm of  $G_a$  is  $\|G_a\| = 22$ , substantially smaller than  $\|B_{ca}\| = 27$ . The median size difference of  $-5.1$  (95% confidence interval:  $-12.2$  to  $1.1$ ) is not sig-

nificantly different from zero, but it clearly rejects the expectation that dimorphism should change much faster under antagonistic selection than concordant selection.

To test the impact of these matrices on the direct and indirect responses in each subspace, we calculated the respondabilities (Hansen and Houle 2008) to random selection gradients that were constrained to lie in either the concordant subspace or the antagonistic subspace, with results shown in table 3. Responses within the selected subspace are direct, while those in the other subspace are indirect. The direct responses in the concordant subspace to concordant selection are 4.6–5 times as large as the responses in the antagonistic subspace to antagonistic selection, roughly consistent with the 4.5 times greater norm of  $G_c$  compared with  $G_a$ . The indirect response to concordant selection in the antagonistic subspace is also larger than the direct response to antagonistic selection, by a factor of 1.2, close to the ratio of  $B_{ca}$  to  $G_a$ . Comparison of respondabilities calculated from the best estimate with those calculated from the sample of matrices consistent with the data are different in median and confidence quantiles. In particular, the broader confidence quantiles of the sample show that there is substantial estimation error for this matrix.

**Table 2:** Predictive matrices derived from the gene expression **G** matrix

UB1	UB2	UB3	UB4	UB1	UB2	UB3	UB4
<b><math>\bar{\mathbf{G}}</math></b>				<b><math>\hat{\mathbf{G}}</math></b>			
62.4 (39.5, 90.9)	.3 (-12.7, 13.2)	.5 (-12.7, 13.7)	-1.2 (-14.0, 13.3)	-41.1 (-40.5, -63.9)	.0 (-8.8, 9.4)	-5.1 (-14.9, 3.5)	-2.9 (-12.1, 6.2)
	43.5 (31.3, 70.2)	-.9 (-14.6, 10.5)	.6 (-11.5, 12.4)		10.2 (.6, 19.3)	3.2 (-2.2, 9.3)	-4.7 (-11.1, .5)
		40.2 (27.6, 65.2)	1.6 (-10.9, 13.2)			2.1 (-4.3, 10.2)	1.8 (-3.7, 7.2)
			37.2 (26.2, 57.8)				-2.7 (-10.0, 6.1)
<b><math>\bar{\mathbf{B}}</math></b>				<b><math>\hat{\mathbf{B}}</math></b>			
28.2 (11.9, 47.1)	-11.7 (-27.3, 2.9)	-6.7 (-21.3, 6.1)	-5.1 (-17.5, 7.34)	0	16.0 (5.6, 27.8)	2.7 (-6.5, 12.7)	-4.2 (-13.9, 4.0)
	36.8 (23.7, 62.4)	-3.3 (-17.1, 7.4)	-.3 (-12.6, 11.7)	-16.0 (-27.8, -5.6)	0	-3.2 (-9.5, 2.4)	4.0 (-1.8, 11.0)
		37.2 (23.3, 60.6)	.91 (-11.3, 13.3)	-2.7 (-12.7, 6.5)	3.2 (-2.4, 9.5)	0	-2.1 (-7.7, 3.4)
			31.6 (19.0, 51.0)	4.2 (-4.0, 13.9)	-4.0 (-11.0, 1.8)	2.1 (-3.4, 7.7)	0
<b><math>\mathbf{G}_a</math></b>				<b><math>\mathbf{B}_{ca}</math></b>			
17.9 (10.5, 26.5)	6.0 (2.9, 9.4)	3.6 (1.2, 6.2)	2.4 (-.5, 5.5)	-20.3 (-31.9, -9.7)	8.1 (-.1, 17.0)	-1.4 (-9.8, 7.7)	-3.6 (-12.1, 4.4)
	4.0 (2.1, 6.4)	1.4 (.2, 2.9)	.4 (-1.0, 1.8)	-8.1 (-13.6, -3.0)	4.9 (.3, 9.7)	.2 (-4.3, 4.6)	-5 (-4.8, 3.7)
		2.2 (1.0, 3.8)	.1 (-1.1, 1.2)	-4.0 (-8.3, -.2)	3.2 (-.4, 7.2)	1.4 (-2.1, 5.1)	-3 (-3.7, 3.1)
			3.6 (1.9, 5.8)	1.0 (-3.3, 5.5)	-4.8 (-9.8, -.6)	2.1 (-2.2, 6.7)	-1.0 (-5.0, 3.0)

Note: The pair of numbers in parentheses below the median estimate are the 95% confidence limits. Matrices on the left are predictive of responses in dimorphism to antagonistic selection, while matrices on the right are predictive of changes in dimorphism due to concordant selection. The matrices **G**,  **$\hat{\mathbf{G}}$** ,  **$\bar{\mathbf{B}}$** , and  **$\mathbf{G}_a$**  are symmetric, so we omit the elements below the diagonal. By construction, the diagonal of  **$\hat{\mathbf{B}}$**  is zero, and the corresponding elements on either side of the diagonal differ only in sign.

*Predicting Evolution of Dimorphism: Wing Shape*

Sztepanacz and Houle (2019) estimated  **$\mathbf{G}_{mr}$**  for  $k = 20$  wing shape traits. The scalar characteristics of this matrix are presented in the second set of estimates in figure 2. This  **$\mathbf{G}_{mr}$**  has an atypically large set of  $r_{MF}$  values, averaging 0.92 with a minimum of 0.86. As expected from this, the **B** matrix has a relatively large norm relative to  **$\mathbf{G}_m$**  and  **$\mathbf{G}_r$** ; there are near-perfect correlations between **B**,  **$\mathbf{G}_m$** , and  **$\mathbf{G}_r$** ; and very low asymmetry in **B**. Consequently, the norm of  **$\mathbf{G}_c$**  is much greater than the norm of  **$\mathbf{G}_a$** . The values in table 3 show that it is much easier to get a response in the concordant subspace than in the antagonistic subspace, regardless of what kind of selection is experienced. The ratio of the norms of  **$\mathbf{B}_{ca}$**  and  **$\mathbf{G}_a$**  is even larger than in the gene expression matrix, leading to predicted indirect responses in the antagonistic subspace 50% larger than the direct responses. Comparison of the confidence quantiles show that there is very little estimation error in this matrix.

*Predicting Evolution of Dimorphism: CHCs*

For contrast, we investigated two  **$\mathbf{G}_{mr}$**  that Ingleby et al. (2014) estimated for CHCs. They have much smaller  $r_{MF}$  values, averaging 0.24 in the least dimorphic CHC matrix and 0.04 in the most dimorphic CHC matrix, far less than the average of found in previous studies (Poissant et al. 2010). Results are shown in the last section of table 3. Each **B** matrix has a very small norm relative to  **$\mathbf{G}_m$**  and  **$\mathbf{G}_r$** . The matrices **B**,  **$\mathbf{G}_m$** , and  **$\mathbf{G}_r$**  are less correlated than in the more typical matrices. In the most dimorphic matrix, the **B** matrix is actually negatively correlated with  **$\mathbf{G}_m$**  and  **$\mathbf{G}_r$** . In both of these matrices, the norm of  **$\mathbf{G}_a$**  is large relative to the norm of  **$\mathbf{G}_c$** , and the norm of  **$\mathbf{B}_{ca}$**  is relatively small. As these values predict, respondabilities in table 3 show that antagonistic selection is very effective at promoting sexual dimorphism, and indirect responses are relatively small.

Ingleby et al. (2014) also estimated the form of selection on both sets of traits. For the most dimorphic traits,

Matrix	MF space				CA space	
	Sub-matrix	norm	Similarities ( $s$ )		Sub-matrix	norm
			$G_f$	$B$		
Gene expression	$G_m$	92 (71-119)	0.72 (0.58-0.85)	0.89 (0.78-0.96)	$G_c$	90.2 (71.7-113.0)
	$G_f$	132 (94-177)		0.76 (0.61-0.87)	$G_a$	21.9 (13.7-31.7)
	$B$	85 (65-110)		0.78 (0.57-0.93)	$B_{ca}$	27.1 (16.5-40.2)
Wing shape	$G_m$	92 (86-98)	0.97 (0.96-0.98)	0.99 (0.98-0.99)	$G_c$	86.9 (82.1-91.8)
	$G_f$	90 (85-96)		0.99 (0.98-0.99)	$G_a$	4.2 (3.5-5.0)
	$B$	84 (79-89)		0.98 (0.97-0.99)	$B_{ca}$	6.5 (5.6-7.8)
CHCs Least Dimorphic ( $\times 100$ )	$G_m$	100	0.81	0.62	$G_c$	67.2
	$G_f$	135		0.57	$G_a$	45.7
	$B$	35		0.12	$B_{ca}$	23.1
CHCs Most Dimorphic ( $\times 1000$ )	$G_m$	45	0.90	-0.13	$G_c$	23.1
	$G_f$	54		-0.37	$G_a$	26.3
	$B$	12		0.45	$B_{ca}$	6.8

**Figure 2:** Characteristics of four different *Drosophila melanogaster*  $G$  matrices in male/female (MF) and concordant/antagonistic (CA) spaces. For the gene expression and wing shape matrices, values shown are median and 2.5% and 97.5% quantiles (in parentheses) over a sample of 1,000 matrices drawn from the sampling distribution. For the cuticular hydrocarbon (CHC) matrices, values are calculated on the basis of the single estimate available.

the selection gradients for males and females for these traits are

$$\beta_m^T = [ 0.14 \quad 0.41 \quad 0.03 \quad 0.02 ],$$

$$\beta_f^T = [ -0.69 \quad 0.22 \quad -0.13 \quad 0.29 ],$$

in standard deviation units. Transformation into concordant/antagonistic space using equation (3) yields the selection gradients

$$\beta_c^T = [ -0.27 \quad 0.31 \quad -0.05 \quad 0.15 ],$$

$$\beta_a^T = [ 0.42 \quad 0.10 \quad 0.08 \quad -0.14 ].$$

The norms of these vectors show that selection in concordant and antagonistic subspaces is nearly equal ( $\|\beta_c\| \approx \|\beta_a\| \approx 0.45$ ). When applied to the  $G$  matrix, concordant selection is predicted to have 56% of the effect on dimorphism that antagonistic selection has. Selection on the least dimorphic traits is far more antagonistic than concordant ( $\|\beta_c\|/\|\beta_a\| \approx 0.13$ ), and concordant selection is predicted to have 24% of the effect on dimorphism that antagonistic selection has. For both sets of traits, the total concordant response is larger than the antagonistic re-

sponse—54% more for the most dimorphic traits, and 30% larger than in the least dimorphic traits.

## Discussion

We have analyzed the evolution of sexual dimorphism in response to a single generation of directional selection utilizing a partition of phenotype space that separates the genetic variation that promotes dimorphism when selection favors dimorphism from that which promotes dimorphism when selection acts in the same way on both sexes. This partition of phenotype space makes it easy to understand what portion of selection acts antagonistically, promoting dimorphism, and which part of selection acts concordantly, directly favoring changes in trait means. A novel result of our analyses is that concordant selection frequently leads to greater changes in sexual dimorphism than antagonistic selection, even when concordant and antagonistic selection are equally strong.

### Partitioning Phenotype Space

Previous quantitative genetic analyses of the evolution of sexual dimorphism have all been in the familiar phenotype

**Table 3:** Quantiles of responsibilities for dimorphism to random concordant and antagonistic selection gradients

Matrix, selected space <sup>a</sup>	Direct responsibility		Indirect responsibility	
	Best estimate <sup>b</sup>	Sample matrices <sup>c</sup>	Best estimate <sup>b</sup>	Sample matrices <sup>c</sup>
Gene expression:				
C	39.53 (33.85–47.95)	43.64 (26.95–66.53)	10.19 (2.26–22.69)	10.93 (2.67–28.20)
A	8.35 (1.37–18.73)	8.64 (1.80–22.49)	9.68 (2.37–22.46)	10.84 (2.69–27.95)
Wing shape:				
C	16.90 (7.66–31.11)	17.82 (7.69–32.83)	1.06 (.46–2.17)	1.29 (.60–2.66)
A	.73 (.29–1.43)	.84 (.34–1.70)	1.07 (.47–2.22)	1.30 (.60–2.66)
Least dimorphic CHCs:				
C	30.43 (14.74–52.74)		10.60 (4.56–18.71)	
A	20.77 (7.97–38.30)		10.51 (4.48–18.49)	
Most dimorphic CHCs:				
C	11.55 (7.35–14.66)		2.87 (1.04–5.86)	
A	11.64 (7.04–21.06)		2.80 (1.02–5.95)	

Note: Matrices are described in figure 2. Values shown are medians, with 2.5% and 97.5% quantiles in parentheses.

<sup>a</sup> C = selection gradient within the concordant subspace; A = selection gradients within the antagonistic subspace.

<sup>b</sup> Distribution over 1,000 random selection vectors for best-estimated matrix.

<sup>c</sup> Distribution over 10 random selection vectors applied to each of 1,000 sample estimates of matrices.

space of the measured male and female traits, which we call male/female space. In contrast, our analyses use a phenotype space consisting of a “concordant” space of sex-averaged trait values and an “antagonistic” space consisting of the differences between sex-averaged trait values. There is no loss of information when changing from the male/female space to the concordant/antagonistic space. The male/female space and the concordant/antagonistic space are equally valid systems in which to study the effects of selection on the sexes and the evolution of sexual dimorphism.

In both spaces, the selection and response vectors consist of two parts: in male/female space, there are male and female subvectors; in concordant/antagonistic space, there are concordant and antagonistic subvectors. Similarly, the two  $\mathbf{G}$  matrices,  $\mathbf{G}_{mf}$  and  $\mathbf{G}_{ca}$ , each consist of three submatrices. In male/female space, there is a male submatrix,  $\mathbf{G}_m$ ; a female submatrix,  $\mathbf{G}_f$ ; and a cross-sex covariance matrix  $\mathbf{B}$ . The matrices  $\mathbf{G}_m$  and  $\mathbf{G}_f$  predict the response in each sex of direct selection on that sex;  $\mathbf{B}$  predicts the indirect response of one sex to selection on the other sex. In concordant/antagonistic space, there is a concordant submatrix,  $\mathbf{G}_c$ ; an antagonistic submatrix,  $\mathbf{G}_a$ ; and a matrix of covariances between the concordant and antagonistic subspaces,  $\mathbf{B}_{ca}$ . The submatrix  $\mathbf{G}_c$  predicts responses to selection in the concordant subspace of average trait values,  $\mathbf{G}_a$  predicts responses to selection in the

antagonistic subspace of differences in trait values, and  $\mathbf{B}_{ca}$  predicts the indirect responses in the concordant subspace to selection in the antagonistic subspace and the indirect responses in the antagonistic subspace to selection in the concordant subspace.

The advantages of working in concordant/antagonistic space arise when one is primarily interested in the evolution of dimorphism rather than the specific trait values in each sex. Evolution of dimorphism in male/female space depends on the entire matrix  $\mathbf{G}_{mf}$ ; evolution of dimorphism in concordant/antagonistic space depends on the smaller matrix  $\mathbf{G}_a$  when selection is antagonistic and on the matrix  $\mathbf{B}_{ca}$  when selection is concordant. The elements of these matrices combine just the elements of  $\mathbf{G}_{mf}$  that affect the evolution of dimorphism. This makes it much easier to determine the totality of the factors that affect the evolution of dimorphism.

The matrix  $\mathbf{G}_a$  depends on the difference between the average male and female genetic variation and the symmetrical part of the  $\mathbf{B}$  matrix (eq. [5]). Thus, as the single-trait theory suggests, the diagonals of the  $\mathbf{B}$  matrix are important constraints to responses to antagonistic selection, as are the average off-diagonal elements of  $\mathbf{B}$ . The emphasis on  $r_{MF}$  in previous work is empirically justified by the observation that the off-diagonal correlations in  $\mathbf{B}$  are usually of lower magnitude than  $r_{MF}$ . However, the

matrix  $\mathbf{B}_{ca}$ , which determines the response of dimorphism to concordant selection, depends on the differences between male and female  $\mathbf{G}$  matrices and the asymmetries within  $\mathbf{B}$ . The diagonal elements of  $\mathbf{B}$ , the covariances summarized by  $r_{MF}$ , play no role.

We also showed that the overall magnitudes of responses in sexual dimorphism are correlated with the sizes of  $\mathbf{G}_a$  and  $\mathbf{B}_{ca}$ , as measured by their Frobenius norms. This is consistent with results from Hansen and Houle (2008) showing that the Frobenius norms slightly overestimate the respondabilities, the total length of the response to directional selection. Perhaps most importantly, when  $\mathbf{G}_m$  and  $\mathbf{G}_f$  are similar to each other, the norm of  $\mathbf{B}_{ca}$  is necessarily much larger than the norm of  $\mathbf{G}_a$ . When this is the case, dimorphism will have a larger response to concordant selection than to antagonistic selection of equal strength.

### Empirical Results

Until recently, empirical work on the genetics of sexual dimorphism has understandably focused on the case of a single homologous trait at a time. The degree of constraint that this imposes on that trait is well summarized by its standardized value as a genetic correlation,  $r_{MF}$ . Much empirical evidence shows that  $r_{MF}$  is generally positive. A meta-analysis of almost 400 estimates of  $r_{MF}$  suggests that the average value is around 0.75 (Poissant et al. 2010). This, in turn, suggests that the typical correlations between  $\mathbf{B}$ ,  $\mathbf{G}_m$ , and  $\mathbf{G}_f$  will be large, reducing the direct responses to antagonistic selection relative to the indirect responses to concordant selection.

The traditional emphasis on  $r_{MF}$  has recently been expanded, as a relatively large number of recent studies have provided new estimates of  $\mathbf{G}_{mf}$  matrices involving more than one trait (Steven et al. 2007; Barker et al. 2010; Campbell et al. 2011; Lewis et al. 2011; Gosden et al. 2012; Reddiex et al. 2013; Gosden and Chenoweth 2014; Ingleby et al. 2014; Walling et al. 2014; Cox et al. 2017; Holman and Jacomb 2017; Sztepanacz and Houle 2019; Houle and Cheng 2020a). Many of these studies investigated the effects of the estimated  $\mathbf{B}$  matrices on the response to either observed (e.g., Walling et al. 2014) or hypothesized selection gradients. The typical approach is to compare the predicted responses using the observed  $\mathbf{G}_{mf}$  matrix to predicted responses based on a  $\mathbf{G}_{mf}$  matrix in which  $\mathbf{B}$  has been altered in some way. The alterations include setting  $\mathbf{B} = 0$  (Lewis et al. 2011; Gosden et al. 2012; Ingleby et al. 2014); setting the intersex correlations to 1 (Cox et al. 2017); or forcing  $\mathbf{B}$  to be symmetrical (Sztepanacz and Houle 2019). Gosden et al. (2014) compared the rate of evolution in the sex-specific  $\mathbf{G}_{mf}$  matrices, the  $\mathbf{B}$  matrix, and the symmetrical and asymmetrical compo-

nents of  $\mathbf{B}$ . These approaches are excellent ways to understand the effect of  $\mathbf{B}$  on the evolution of male and female traits and, less directly, the effect of  $\mathbf{B}$  on the evolution of dimorphism, but they do not address the totality of genetic factors affecting dimorphism.

We predicted the evolution of dimorphism to equally strong antagonistic and concordant selection for four example  $\mathbf{G}$  matrices from *Drosophila melanogaster* populations with different average  $r_{MF}$  values. We predicted responses over a random set of directions in each subspace. The  $\mathbf{G}_{mf}$  matrix for gene expression data (Houle and Cheng 2020a) had a slightly higher than typical average  $r_{MF}$  value of 0.82. For this matrix, the predicted average indirect response of dimorphism to random concordant vectors was about 20% higher than the response to random antagonistic vectors. The wing shape  $\mathbf{G}_{mf}$  matrix (Sztepanacz and Houle 2019), in contrast, had a higher than average  $r_{MF}$  value of 0.92, and as predicted by our theory, the predicted average indirect response of dimorphism to random concordant vectors was 50% higher than the response to random antagonistic vectors. In contrast, we also made predictions for two  $\mathbf{G}_{mf}$  matrices for CHC expression (Ingleby et al. 2014) that had very low average  $r_{MF}$  values of 0.24 and 0.04. For these matrices, the direct responses are predicted to be double and quadruple the indirect responses to equal selection, respectively.

Taken at face value, these results suggest that the typical  $\mathbf{G}_{mf}$  matrix with large positive  $r_{MF}$  values will generate comparable indirect and direct responses in sexual dimorphism. These respondabilities, however, are averaged over all possible concordant and antagonistic vectors. The realized respondabilities of these populations to an actual set of selection gradients may be different. There are very few systems where both selection and genetic variation have been estimated for phenotypes in both sexes. A key question is whether the actual directions of selection covary with the available genetic variation that allows the evolution of dimorphism. Persistent patterns of selection can be expected to alter the genetic variance in selected directions, although theory shows that both increases and decreases are possible depending on the nature of selection (McGlothlin et al. 2019) and the interaction of allele frequency changes with epistasis (Carter et al. 2005).

A related concern is the possibility of estimation bias in both the Frobenius norms used to measure the sizes of the matrices and in the average respondabilities in response to simulated selection. The variance of eigenvalues is overestimated when matrices are measured with error (Hill and Thompson 1978), which will bias the Frobenius norm upward, as it is quadratic function of eigenvalues. It also results in measurable bias in respondabilities at small sample sizes (Grabowski and Porto 2017). Furthermore, it also suggests that the Frobenius norm and respondabilities of

submatrices with smaller norms might be more biased than those with larger norms. Consequently, we expect that the upward bias will be larger for small matrices, tending to minimize the differences between submatrices.

*Do These Results Challenge How We Understand the Evolution of Sexual Dimorphism?*

There is a canonical model for the evolution of sexual dimorphism in homologous traits (e.g., fig. 1 in Cox and Calsbeek 2009) that ascribes the evolution of dimorphism to sexually antagonistic selection on an initially monomorphic population. On the other hand, it has long been known that dimorphism can evolve whenever the rate of response to selection is different in the two sexes due to any kind of sex-by-genotype or sex-by-fitness interaction (Fisher 1930; Lande 1980, 1987; Leutenegger and Cheverud 1982; Cheverud et al. 1985; Lynch and Walsh 1998, chap. 24; Bonduriansky and Chenoweth 2009; Wyman et al. 2013; Connallon and Clark 2014).

Lande's (1980) original explication of the quantitative genetics of dimorphism clearly incorporated the likelihood that concordant selection would affect dimorphism. Lande chose to emphasize the effects of antagonistic selection for dimorphism on the basis of the assumption that evolution of sex-averaged means would be relatively unconstrained and rapidly achieve their optima, while evolution of optimal differences between the sexes would tend to be constrained and take a long time to reach their optima. This point is made explicit in the model of Connallon and Clark (2014), who show that the evolution of some dimorphism is almost inevitable whenever selection in any direction perturbs an initially monomorphic population. If  $\mathbf{G}$  matrices generally constrain responses to antagonistic selection more than responses to concordant selection, we will observe that sex-specific traits will tend to be under antagonistic selection more frequently than they are under concordant selection.

The relatively few direct studies of natural selection on sex-specific traits actually suggest that the opposite pattern holds. Morrissey (2016) reanalyzed 424 selection gradient estimates compiled by Cox and Calsbeek (2009) and estimated the distribution of estimates once sampling error was taken into account. Overall, antagonistic selection was less common than concordant selection. More importantly, the strength of antagonistic selection was dramatically lower than that of concordant selection.

Lande's (1980) argument that antagonistic selection will be more commonly observed is based on the assumption that selection regimes change infrequently, allowing the population to approach new concordant optima and leaving the slow-resolving sexual conflicts to be observed. An alternative world view is that changes in

selection are frequent rather than rare and that populations are rarely at selected optima, even for traits with high evolvability. This scenario is consistent with the pattern of sex-specific selection identified by Morrissey (2016) as well as with the frequent observation of very strong linear selection gradients (Kingsolver et al. 2001; Hereford et al. 2004) observed generally.

Thus, not only do our results suggest that the structure of  $\mathbf{G}$  matrices generally allows comparable rates of responses to antagonistic and concordant selection, but direct estimates of selection suggest that antagonistic selection may be rarer and weaker than concordant selection. If both of these conclusions hold, the evolution of sexual dimorphism in response to directional selection will be dominated by indirect responses to concordant selection, in contrast to the canonical model, in which dimorphism reflects a balance between antagonistic selection and constraints on the ability of populations to respond to that selection.

Even if the suggestion that concordant selection contributes to many cases of sexual dimorphism is correct, this does not mean that antagonistic selection is never responsible for sexual dimorphism. For example, the sexual dimorphisms for morphological traits in an introduced population of house finches (*Carpodacus mexicanus*) are well explained by a pattern of strong, statistically significant antagonistic selection on many of the dimorphic traits (Badyaev and Martin 2000). Several lines of evidence suggest that selection on sex-biased gene expression traits in *D. melanogaster* are subject to ongoing antagonistic selection (Innocenti and Morrow 2010; Griffin et al. 2013; Hollis et al. 2014). Innocenti and Morrow's (2010) data on selection are, however, also consistent with substantial concordant selection on expression. They treated significant sex-by-fitness interactions for transcription (their models used transcription as the dependent variable) as equivalent to sexually antagonistic selection. Such interactions ensure that there is an antagonistic component to selection. Unfortunately, Innocenti and Morrow (2010) did not report effect sizes, so the relative importance of concordant and antagonistic selection on gene expression traits in their experiment is unclear.

One possible way to rescue the primacy of the canonical model is to show that the available data on genetic variation and natural selection are not representative of natural populations. For example,  $\mathbf{G}$  is frequently estimated in a laboratory environment, where genotype-by-environment interactions may be incorporated into the estimates. This is certainly true for *D. melanogaster*, the species from which we drew all of our example  $\mathbf{G}$  matrices.

There are many reasons to suspect that estimates of selection in natural populations may be flawed (Kingsolver et al. 2001; Hereford et al. 2004; Morrissey et al. 2010;

Morrissey and Hadfield 2012). Estimates are often based on small samples and have large sampling errors (Morrissey and Hadfield 2012), often use less than ideal measures of fitness, and cannot always account for environmentally induced covariances between traits and fitness (Rauscher 1992; Stinchcombe et al. 2002; Winn 2004). The compilation of selection gradient estimates (Cox and Calsbeek 2009) that Morrissey (2016) reanalyzed included estimates from just 34 species and do not necessarily encompass a typical sample of traits.

These weaknesses in the available data certainly make our conclusion that concordant selection is more important than previously thought tentative. However, until data are able to confirm aspects of the canonical scenario, it should be treated with healthy skepticism. We look forward to further empirical work that will enable generalizations about the relative rates of direct and indirect evolution of sexual dimorphism.

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**Statement of Authorship**

The project was jointly conceptualized by C.C. and D.H. C.C. was responsible for the majority of the mathematical analysis. C.C. and D.H. assembled the data sets from the literature. D.H. carried out the data analyses. C.C. and D.H. jointly drafted the introduction. C.C. wrote the original draft of the theory section and the supplements. D.H. drafted the two-trait example and the methods, results, and discussion sections. C.C. and D.H. revised the initial drafts. D.H. obtained funding.

**APPENDIX**

**Table A1:** Frequently used symbols and abbreviations

Symbol	Meaning
<b>Boldface fonts</b>	Matrices and vectors
tr	Trace of a matrix (the sum of diagonal elements of the matrix)
Superscript T	Transpose of a matrix
$\ \cdot\ $	Frobenius norm for a matrix, Euclidean norm for a vector (the square root of the sum of squares of its elements)

**Table A1 (Continued)**

Symbol	Meaning
$\lambda(\mathbf{G})$	Eigenvalue of a matrix $\mathbf{G}$
$\mathbf{G}_{mf}$	$\mathbf{G}$ matrices in male/female space
$\mathbf{G}_m, \mathbf{G}_f, \mathbf{B}$	Submatrices of the $\mathbf{G}$ matrices in male/female space
$\bar{\mathbf{G}}$	Average of male $\mathbf{G}_m$ and female $\mathbf{G}_f$
$\hat{\mathbf{G}}$	Difference between male $\mathbf{G}_m$ and female $\mathbf{G}_f$
$\bar{\mathbf{B}}$	Symmetric part of $\mathbf{B}$
$\hat{\mathbf{B}}$	Antisymmetric part of $\mathbf{B}$
$\beta_m$	Selection in male space
$\beta_f$	Selection in female space
$\mathbf{z}_m$	Traits in male space
$\Delta\bar{\mathbf{z}}_m$	Change of traits in male space
$\mathbf{z}_f$	Traits in female space
$\Delta\bar{\mathbf{z}}_f$	Change of traits in female space
$\mathbf{G}_{ca}$	$\mathbf{G}$ matrices in concordant/antagonistic space
$\mathbf{G}_c, \mathbf{G}_a, \mathbf{B}_{ca}$	Submatrices of the matrix $\mathbf{G}_{ca}$
$\beta_c$	Selection in concordant space
$\beta_a$	Selection in antagonistic space
$\mathbf{z}_c$	Traits in concordant space
$\Delta\bar{\mathbf{z}}_c$	Change of traits in concordant space
$\mathbf{z}_a$	Traits in antagonistic space
$\Delta\bar{\mathbf{z}}_a$	Change of traits in antagonistic space
$\mathbf{Q}_{mf \rightarrow ca}$	Transformation matrix mapping male/female space to concordant/antagonistic space
$r_{MF}$	Intersexual genetic correlation
$\mathbb{S}_b$	Symmetry of $\mathbf{B}$ matrix (the similarity between $\mathbf{B}$ and its transpose $\mathbf{B}^T$ )
$\mathbb{S}$	Similarity between two matrices or two vectors
$\mathbb{S}_{m,f}$	Similarity between male $\mathbf{G}_m$ and female $\mathbf{G}_f$
$\mathbb{S}_{m,b}$	Similarity between male $\mathbf{G}_m$ and the matrix $\mathbf{B}$
$\mathbb{S}_{f,b}$	Similarity between male $\mathbf{G}_f$ and the matrix $\mathbf{B}$

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Male and female flame bowerbird (*Sericulus ardens*) courtship. The brightly colored male constructs a bower of small sticks, which attracts the dull-colored female. Once the female enters the bower, the male then performs an elaborate display dance while she watches. Photo credit: David Houle.