A TEST OF THE CONJECTURE THAT G-MATRICES ARE MORE STABLE THAN B-MATRICES

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The G-matrix occupies an important position in evolutionary biology both as a summary of the inheritance of quantitative traits and as an ingredient in predicting how those traits will respond to selection and drift. Consequently, the stability of G has an important bearing on the accuracy of predicted evolutionary trajectories. Furthermore, G should evolve in response to stable features of the adaptive landscape and their trajectories through time. Although the stability and evolution of G might be predicted from knowledge of selection in natural populations, most empirical comparisons of G-matrices have been made in the absence of such a priori predictions. We present a theoretical argument that within-sex G-matrices should be more stable than between-sex B-matrices because they are more powerfully exposed to multivariate stabilizing selection. We tested this conjecture by comparing estimates of B- and within-sex G-matrices among three populations of the garter snake *Thamnophis elegans.* Matrix comparisons using Flury's hierarchical approach revealed that within-sex G-matrices had four principal components in common (full CPC), whereas B-matrices had only a single principal component in common and eigenvalues that were more variable among populations. These results suggest that within-sex G is more stable than B, as predicted by our theoretical argument.

KEY WORDS: Flury hierarchy, genetic covariance matrix, sexual dimorphism, *Thamnophis elegans.*

The additive genetic variance–covariance matrix, or G-matrix, plays a central role in evolutionary theory in predicting deterministic responses to selection as well as the stochastic consequences of finite population size (Lande 1979). In particular, the deterministic evolution of the phenotypic mean is affected both by selection and the G-matrix. Unfortunately, however, we lack an analytical framework for predicting how **G** itself will evolve in response to selection in populations of finite size. Likewise, no equations have been derived that specify the stability of **G** in evolving populations. In the absence of an analytical framework, our knowledge of how **G** responds to selection and finite population size is based on simulation and empirical studies (Arnold et al. 2008).

Correlational selection should have profound consequences for G-matrix evolution and stability. Indeed, simulations have shown that **G** stability depends on trait-specific issues of mutation and selection, as well as on population size. As expected from theoretical considerations (Lande 1980a), the stability of the principal components of **G** (i.e., the angle of its eigenvectors) is enhanced by strong correlational selection, as well as by large population size (Jones et al. 2003, 2004, 2007; Revell 2007). In contrast, neutral or weakly selected characters with little or no genetic correlation in small populations will be especially prone to G-matrix fluctuation. High migration rates, such as those often seen at the intraspecific level, can also substantially affect the shape and orientation of **G** and its stability (Guillaume and

Whitlock 2007). Thus, even though we lack an extensive analytical framework, simulation studies have provided a set of predictions about selective effects that can be tested with data from natural populations (Arnold et al. 2008).

Empirical studies provide a complementary perspective on the evolution and stability of **G**. A recent review of comparisons of G-matrices sampled from experimental and natural populations showed that some conservation of eigenvectors is found in a majority of comparisons (Arnold et al. 2008). Such structural conservatism may reflect long persistent regimes of multivariate selection that confer G-matrix stability (Arnold et al. 2008). Nevertheless, in some studies the G-matrices of even closely related populations have been found to be strikingly different. Whether such differences represent stochastic variation or systematic differences in structure that reflect responses to differences in selection is an unresolved issue. In some cases, however, differences in **G** have been documented in samples from populations that are likely to experience differences in selection (Jernigan et al. 1994; Cano et al. 2004). In such cases, differences in **G** may very well represent responses to selection.

Because relatively few of these studies have formulated and tested predictions about how multivariate selection might affect the evolution and stability of the G-matrix, the primary aim of this article is to formulate such a prediction and test it with a comparison of G-matrices estimated in three populations of the garter snake *Thamnophis elegans*. At the crux of our comparison is the expectation that within-sex inheritance matrices should be more stable than their between-sex analogs.

In populations with separate sexes, quantitative characters may be differently expressed in the two sexes and possess different systems of inheritance (Steven et al. 2007). The genetic basis of variation in metrical characters, including sexual dimorphism, is usually polygenic (Lynch and Walsh 1998). However, the two sexes may be subject to different selective pressures in connection with their contrasting roles in reproduction (Darwin 1871). This sexual difference in selection can result in the accumulation of genes with different effects in males and females, causing a character to become sexually dimorphic (Fisher 1958). Lande (1980b) proposed a general model for character evolution in such populations. In this model, the G-matrix is partitioned into four sub-matrices that describe inheritance within males ($\mathbf{G_m}$), within females ($\mathbf{G_f}$), and between the sexes ($\mathbf{B}$ and its transpose $\mathbf{B^T}$). The B-matrix is the least familiar of these matrices. Its elements are the covariances between the additive effects of autosomal genes when expressed in males and females (Lande 1980b). The ij[th] element of this matrix (B_{ij}) represents the additive genetic covariance between the ith character expressed in males and the jth character expressed in females. Although B-matrices represent genetic covariance between the sexes arising from pleiotropy and linkage disequilibrium, these covariances are not expressed. For example, neglecting subscripts for simplicity, the genetic variance for a trait is expressed in the male populations as $\mathbf{G_m}$, and in the female population as $\mathbf{G_f}$, but the genetic covariance between the sexes in this trait, $\mathbf{B}$, is not expressed in any subset of individuals.

A crucial difference between G- and B-matrices emerges when we consider how they might be affected by nonlinear (stabilizing, disruptive, and correlational) selection. $\mathbf{G_m}$ and $\mathbf{G_f}$ are directly affected by these forms of selection each generation. In contrast, $\mathbf{B}$ is not actually expressed in any subset of individuals that is exposed to selection within a generation. Consequently, although $\mathbf{B}$ will experience indirect effects of selection acting within each sex, it is generally sheltered from the direct effects of selection (elaboration is provided in the Results section). Only under exceptional circumstances, which will be discussed later, is $\mathbf{B}$ directly pruned by stabilizing selection or torqued by correlational selection. This apparent difference in selection impact leads to the prediction that within-sex G-matrices should be more stable than between-sex B-matrices in population comparisons, a proposition that seems never to have been posed or tested.

Our past work on quantitative inheritance in the garter snake *T. elegans* provides an opportunity to test the proposition that within-sex **G** is more stable than **B**. This work involved scoring six meristic characters (scale counts) that are expressed in both sexes, with some showing strong sexual dimorphism (Arnold and Phillips 1999). The counts do not change during postnatal life and are strongly buffered against temperature effects during development (Arnold and Peterson 2002). Directional, stabilizing, and correlation selection on these counts has been detected in *T. elegans* and other garter snakes (Arnold 1988; Arnold and Bennett 1988; Manier et al. 2007; Hohenlohe and Arnold 2008). Most of these counts are moderately to strongly heritable with weak genetic correlations (Arnold and Phillips 1999; Phillips and Arnold 1999). A comparison of G-matrices from two populations from northern California showed conservation of structure in their G-matrices despite having divergent values for several of these meristic traits, as well as different foraging habits, and diet (Arnold and Phillips 1999; Phillips and Arnold 1999). Although those studies examined and compared matrices both within and between the sexes, the significance of those comparisons was not appreciated or discussed (but see Holloway et al. 1993; Guntrip et al. 1997; Ashman 2003; Jensen et al. 2003; Rolff et al. 2005; Steven et al. 2007).

The aims of this article are to examine the conjecture that within-sex **G** is more stable than **B** and to test that conjecture in natural populations of the garter snake *T. elegans*. To test this conjecture, we extend the sample used by Arnold and Phillips (1999) to include a third population of *T. elegans*. Using an equation that describes how multivariate selection should affect inheritance matrices in equilibrium populations within a generation, we find that our conjecture is supported on theoretical grounds. By surveying

the literature, we show that a condition favorable to our conjecture is often true; the elements of within-sex G-matrices are larger than the corresponding elements of B-matrices. We then use the Flury hierarchy to compare the within-sex G- and the B-matrices of our three populations and find that within-sex **G** is more stable in size, eccentricity, and orientation. These results suggest that selection is responsible for the greater stability of G-matrices.

Materials and Methods

SAMPLES OF SNAKES AND SCORING OF TRAITS

Samples

Newborn snakes were obtained from pregnant females collected at three localities in northern California in Humboldt, Lassen, and Sonoma counties. The Humboldt and Lassen sites are described in Phillips and Arnold (1999) and are 285 km apart. The Sonoma site (38.4367 lat, −123.1042 long) is located 290 km and 308 km from the Humboldt (40.930, −124.130) and Lassen sites (40.557, −120.784), respectively. After capture, females were transported to the laboratory, where they were maintained under uniform conditions until their litters were born (Arnold 1988). A total of 327 females from Humboldt ($n = 102$), Lassen ($n = 156$), and Sonoma ($n = 69$) counties gave birth to a total of 3115 offspring.

Trait scores

The following scale counts were made on ethanol-preserved mothers and their offspring: number of ventral scales (VENT); number of subcaudal scales (SUB); total number of infralabial (ILAB), supralabial (SLAB), postocular (POST) scales on the left and right sides; number of dorsal scale rows at midbody (MID). Conventions for making these counts and further details about scale count procedures are described in Arnold and Phillips (1999).

PARAMETER ESTIMATION

Because only mother and offspring phenotypes were available to us, additive genetic variances and covariances were estimated by regressing the mother's scores on the average scores of her offspring. We estimated the G_f-matrix (within-sex) by regressing the mother's score on the average score of her daughters and the B-matrix (between-sex) by regressing the mother's score on the average scores of her sons. Within-sex phenotypic variances and covariances (P_m- and P_f-matrices) were estimated as the sum of within and among family components of variance based on analysis of newborn offspring. Female environmental variances and covariances (E_f-matrix) were estimated as the difference between the P_f- and G_f-matrices. Additional details about estimation of variation parameters can be found in Arnold and Phillips (1999). The effect of multiple paternity on the interpretation of parameter estimates is discussed by Arnold and Phillips (1999) and

Manier et al. (2007). To assess statistical significance in hierarchical comparisons of inheritance matrices, we did bootstrap sampling across families (Phillips and Arnold 1999). Standard errors were calculated from the variances of the empirically derived error distributions after resampling 5000 times. All calculations of covariance component estimates were carried out using the software package *H2boot* (Phillips 1998). In particular, we used the following *H2boot* options: parent-offspring regression with full-sib analysis of variance, use of only families with complete data, multiple population analysis and comparison, and bending of nonpositive definite matrices.

We used two different procedures to estimate correlations. In the case of the phenotypic and environmental matrices correlation estimates, we used the means of the bootstrap distribution to estimate correlations. In the case of the within-sex G- and the B-matrices we used the median values of the bootstrap distributions to estimate correlations, because a few extreme outliers markedly affected the mean of the bootstrap distribution.

MATRIX COMPARISONS

Several alternative methodologies are available for comparison of G-matrices (e.g., Roff 2002; Cheverud and Marroig 2007; Hansen and Houle 2008). We chose the common principal component approach (Flury 1988; Phillips and Arnold 1999) because it is especially well suited to the issues we need to address in this study. In particular, this method enables us to test for the particular aspect of matrix stability (stability of eigenvectors) expected from a persistent pattern of stabilizing selection (Lande 1980a; Arnold et al. 2008) that is aligned with a predominant direction of peak movement in our garter snake system (Hohenlohe and Arnold 2008).

In the procedure described by Phillips and Arnold (1999), the testing hierarchy follows a progression from unrelated structure to partial common principal components (PCPC) to common principal components (CPC) to proportionality and finally to equality. The testing procedure compares all matrices simultaneously at each level of the hierarchy. We used the jump-up approach (Phillips and Arnold 1999) to determine the level in the hierarchy at which matrices could no longer be considered similar. Because of extremely low *P*-values, the statistics reported here are robust to corrections for multiple comparisons within a test (as can be a potential issue with the jump-up approach; Phillips and Arnold 1999). Covariance component matrices were compared using a randomization approach with the program *CPCrand* (Phillips and Arnold 1999).

We also used Krzanowski subspace analysis to compare the principal components of the within-sex ($\mathbf{G_f}$) and between-sex ($\mathbf{B}$) matrices between pairs of populations (Krzanowski 1979). The analysis is "subspace" in the sense that comparisons are necessarily restricted to no more than half the principal components of the

matrices, and consequently we focused on the first three principal components in our six-dimensional character space. Following the notation of Blows et al. (2004), let L and M represent the 6×3 matrices of principal component loadings (eigenvectors) for the 6×6 inheritance matrices from two of our populations (e.g., two B-matrices). We can solve for a 3×3 matrix $S = L^T M M^T L$ that has useful properties (Krzanowski 1979). The best possible alignment of principal components in this subspace for the population represented by L is given by the column vector $b_1 = La_1$, where a_1 is the first principal component of S, associated with its largest eigenvalue, λ_1. The column vector corresponding to the other population is $MM^T b_1$. The angle (in degrees) between these best-aligned vectors, given by $\cos^{-1}\{(\lambda_1)^{\frac{1}{2}})\}$, provides a measure of similarity between them that ranges from 0 deg (coincidence) to 90 deg (orthogonality). The same properties hold for the second and third pairs of vectors, associated with the second and third eigenvalues of S. The sum of the three eigenvalues provides an overall measure of similarity for the set of vectors, ranging in the present case from 3 (coincident vectors) to 0 (orthogonal vectors). Finally, the loadings of vectors La_1 and $MM^T b_1$ can be compared to determine which traits contribute to similarities and differences between populations. We also solved for the eigenvectors of Krzanowski's (1979) H matrix, which give a simultaneous solution for the vector closest to the principal components of all three populations. We compare this last solution to the Flury CPC solution for both within-sex (G_f) and between-sex (B) matrices. A spreadsheet showing the steps in these analyses is available on SJA's website.

Results

We begin with theoretical considerations that support the conjecture that within-sex G is more stable than B and then turn to empirical tests of this conjecture. Before presenting our theoretical results, we will briefly sketch the conceptual background for our argument.

The manner in which selection affects B and within-sex G-matrices is at the crux of our conjecture. These matrices are properties of populations and consequently, in the absence of group selection, they are not the actual units of selection. Instead, selection acts on the traits of individuals, and that selection has percolating effects on the statistical moments of trait distributions (Lande and Arnold 1983), including G_f, G_m, and B. We show below that these percolating effects are more direct in the case of within sex-G than in the case of B. Consequently, the impact of selection on within sex-G is stronger than on B. It is easy to understand how this difference in selective impact might arise.

Inheritance matrices are especially affected by nonlinear selection that changes variances (stabilizing and disruptive selection) and covariances (correlational selection). These kinds of

nonlinear selection act on individuals in the following sense. An individual's phenotype can be said to include squared trait values (e.g., body size $\times$ body size). The axis of those squared values captures the essence of stabilizing and disruptive selection; the farther along the axis an individual lies, the more it is affected by those kinds of selection. Likewise, individuals also possess phenotypic values that can be expressed as the products of the values of different traits (e.g., body size $\times$ head size). The axis of those product values captures the essential feature of correlational selection. The more an individual departs from the midpoint of this axis, the more it is affected by correlational selection. These considerations have an important bearing on the difference between selective effects on within-sex G and B. In the case of within-sex G, actual individuals in the population express the trait combinations (squared trait values and products of trait values). Consequently selection on those individuals (males or females) directly affects the corresponding within-sex G. In the case of the B-matrix, however, the relevant trait combinations (products of trait values, one of which is expressed in a male and the other in a female) are usually not represented in actual individuals or otherwise directly exposed to selection. Less obviously, B is indirectly affected by selection, because the nonlinear effects of selection on one sex will percolate from one sex to the other as a consequence of genetic correlations between the sexes. Thus, at issue is the sum of direct and indirect selection effects on the two kinds of matrices. We expect that the total effect of selection be stronger on within-sex G than on B. In the next section, we present a formal argument supporting this conjecture.

THEORETICAL SUPPORT FOR THE CONJECTURE THAT WITHIN-SEX G IS MORE STABLE THAN B

We can represent the overall additive genetic-variance covariance matrix as a partitioned matrix in which male-specific, female-specific, and cross-sex components are grouped separately in a block structure (in which the column and row trait labels are each repeated twice):

$$G = \begin{bmatrix} G_m & B \\ B^T & G_f \end{bmatrix}, \tag{1}$$

where G_m and G_f are, respectively, the within-sex matrices for males and females. We can describe the strength of nonlinear selection (stabilizing, disruptive, and correlational selection) operating on each trait using the nonlinear selection matrix (Lande and Arnold 1983), γ, which is partitioned in the same way as G:

$$\gamma = \begin{bmatrix} \gamma_m & 0 \\ 0 & \gamma_f \end{bmatrix}, \tag{2}$$

where γ_m and γ_f are matrices that measure sex-specific nonlinear selection on males and females. The diagonal elements in these

two matrices measure the strength of stabilizing (disruptive) selection within each sex, whereas their off-diagonal elements measure correlational selection within each sex. The off-diagonal zeros in the overall γ-matrix (2) represent matrices in which all elements are zero because no phenotypic selection operates directly on the cross-sex traits. If we assume that the population is at equilibrium (with nonzero genetic variation and covariation for sexually dimorphic traits), with no directional selection on any character such that $\beta = 0$, and that the traits are multivariate normal in distribution, the change in the G-matrix induced by selection within a generation is approximately

$$\Delta_s G = G \gamma G \qquad (3)$$

(Lande 1980a; Phillips and Arnold 1989). At equilibrium, this change in the G-matrix is balanced by a change of opposing sign resulting from mutation, recombination, and migration (Lande 1980a; Phillips and McGuigan 2006). Substituting (1) and (2) into (3), we find that the overall changes in the within-sex G-matrices and the B-matrix due to nonlinear selection is

$$\Delta_s G = \begin{bmatrix} \Delta_s G_m & \Delta_s B \\ \Delta_s B^T & \Delta_s G_f \end{bmatrix}$$

$$= \begin{bmatrix} G_m \gamma_m G_m + B \gamma_f B^T & G_m \gamma_m B + B \gamma_f G_f \\ B^T \gamma_m G_m + G_f \gamma_f B^T & G_f \gamma_f G_f + B^T \gamma_m B \end{bmatrix}. \qquad (4)$$

The $G_m \gamma_m G_m$ and $G_f \gamma_f G_f$ terms represent the direct effects of selection within a sex on the within-sex G-matrix of that same sex. The $B \gamma_f B^T$ and $B^T \gamma_m B$ terms represent selection acting within one sex and exerting indirect effects on the other sex via the B-matrix. Thus, nonlinear selection exerts both direct and indirect effects on the within-sex matrices. In contrast, both of the terms for change in B-matrix represent indirect effects.

Do we expect within-sex **G** or **B** to be more stable over time? We can address this question by asking which matrix is more likely to respond to stabilizing and correlational selection, forces that would be expected to stabilize the matrices against other factors such as mutational input and genetic drift (Arnold et al. 2008). Focusing first on the G_m-matrix for simplicity, a little algebra using (4) shows that the change induced in $\mathbf{G_f}$ by selection is greater than the change induced in **B**, $\Delta_s \mathbf{G_f} > \Delta_s \mathbf{B}$, when

$$\mathbf{G_f \gamma_f (G_f - B^T)} > \mathbf{B \gamma_m (G_m - B)}. \qquad (5)$$

In other words, an element in $\Delta_s \mathbf{G_f}$ is larger than the corresponding element in $\Delta_s \mathbf{B}$ when the inequality for corresponding elements in (5) holds. Given the multivariate nature of each of the elements in the matrices in (5), there are clearly many ways in which the inequality might be expected to hold—or to fail. We can simplify things by examining the special case in which the traits in males and females share the same genetic basis. In this

case, $\mathbf{G_m = G_f = G}$. If we further assume that the pattern of multivariate stabilizing selection is the same within each sex ($\gamma_m = \gamma_f$), then the condition expressed in (5) simplifies to within-sex $\mathbf{G > B}$. In other words, under these conditions, within-sex **G** is expected to be more stable than **B** whenever the elements of within-sex G-matrix are larger than the corresponding elements of the B-matrix. A priori, this condition is one that we would expect almost always to hold, because genetic correlations between the sexes are likely to be less than one. (Consider the situation for a single trait with $\mathbf{G_m = G_f = G}$, and let the covariance between the sexes be **B**. Then the genetic correlation between the sexes is **B/G** and it must be ≤ 1, so $\mathbf{G \geq B}$). Consequently under these assumptions, we would have a strong expectation that within-sex **G** should be more stable than **B** in equilibrium populations and perhaps over evolutionary time.

What happens when these assumptions are relaxed? There are clearly many possible complex sets of interactions between sex-specific gene expression and sex-specific selection that could lead to either greater stability of either within-sex **G** or **B**. The factors that are most likely to perturb the general expectation are very different patterns of sex-specific selection, as might be expected under sexual selection (Lande 1980b), and very different sex-specific genetic architectures, such that the patterns of within and between sex genetic covariance are different from one another. Lande's (1980a) model also assumes a bivariate normal distribution of allelic effects, which might be unlikely to hold under intense, prolonged directional selection (Barton and Turelli 1987; Turelli and Barton 1994). Nevertheless, these equations provide a conceptual framework that can be used to formulate empirical expectations.

EMPIRICAL SUPPORT FOR THE CONDITION WITHIN-SEX G > B

In the preceding section we found that, under some simplifying conditions, within-sex **G** is likely to be more stable than **B** if elements of within-sex **G** are larger than the elements of **B** (i.e., within-sex $\mathbf{G > B}$). We surveyed the empirical literature to determine how often the within-sex $\mathbf{G > B}$ condition is satisfied. We quickly discovered that relatively few studies have estimated both within sex G- and B-matrices so that comparisons can be made (Table 1). Furthermore, statistical tests comparing the sizes of within-sex **G** and **B** are complicated by the fact that corresponding elements in the two kinds of matrices are usually not independent (e.g., the same set of female parents might be used to estimate both $\mathbf{G_f}$ and **B**, as in our study). Devising a proper statistical analysis that takes the resulting sampling covariance into account is beyond the scope of this article. Nevertheless, when we compiled summary statistics for element-by-element comparisons of **B** and within-sex G-matrices in five study systems, a clear pattern emerged. In all five studies, the elements of within-sex **G**

Table 1. A summary of studies in which elements of within-sex (G) and between-sex (B) matrices can be compared. This table summarizes a total of 172 comparisons of corresponding elements in G- and B-matrices. Note: "morpho." indicates morphometric traits; "morpho.*" stands for morphometric and parasite resistance traits.

	Meagher (1999)	Steven et al. (2007)	Poissant et al. (2008)	Coltman et al. (2001)	Arnold and Phillips (1999) plus this study
Taxon	plant	plant	mammal	mammal	snake
Traits	morpho.	morpho.	morpho.	morpho.*	meristic
Number of traits	4	7	2	3	6
Within-sex G-matrices compared with B	G_f, G_m	G_f, G_m	G_f, G_m	G_f, G_m	G_f
Number of populations	2	1	1	1	3
Total number of element comparisons	40	56	6	6	64
Average of within-sex **G** elements (SE)	11.65 (8.44)	0.009 (0.003)	0.17 (0.03)	7.26 (4.27)	1.55 (0.53)
Average of **B** elements (SE)	4.81 (2.09)	0.005 (0.002)	0.06 (0.01)	2.91 (2.41)	1.30 (0.40)
Average of comparisons (within-sex **G-B**) (SE)	9.16 (7.76)	0.004 (0.002)	0.11 (0.02)	4.34 (2.58)	0.25 (0.19)

average larger than the elements of **B**, sometimes by a considerable margin (Table 1). We note that Poissant et al. (2009) have recently done an extensive survey of between-sex genetic correlations ($r_g = B/\sqrt{G_m G_f}$), finding that estimates are commonly larger than 0.80, but that is a separate issue from the one that concerns us here.

WITHIN- AND BETWEEN-SEX COMPARISONS IN *T. ELEGANS*

Sexual dimorphism and geographic variation in means

The six traits varied in degree of sexual dimorphism (Table 2). SUB was the most sexually dimorphic trait, with males show-

Table 2. Trait means for male and female offspring from the Sonoma population of *Thamnophis elegans.* Heritability estimates (±SE) are based on mother–daughter regressions. **$P<0.01$; *$P<0.05$; ns, nonsignificant.

Trait	Trait means		Heritability (h^2)
	Male n^1	Female n^2	Female litter $n=46$
VENT	157.752	152.547	0.384±0.236*
SUB	79.871	69.743	0.366±0.174*
MID	18.952	18.939	0.171±0.147 ns
ILAB	19.699	19.714	0.334±0.212*
SLAB	15.785	15.723	0.026±0.079 ns
POST	6.033	5.986	0.437±0.293**

[1]Sample sizes for the six traits are, in order, 331, 334, 334, 335, 335, 335.
[2] Sample sizes for the six traits are, in order, 362, 362, 362, 364, 364, 364.

ing an average of 10 more subcaudal scales than females, a 14% difference in means. VENT also showed appreciable sexual dimorphism, with males showing an average of five more ventral scales than females, a 3% difference in means. Sexual dimorphism in the other traits was less substantial (0–1%) and usually in the same direction, with males averaging higher counts than females. The overall pattern of sexual dimorphism is similar to that reported for two other populations of *T. elegans* (Arnold and Phillips 1999).

Focusing on within-sex comparisons, the Sonoma population most closely resembles Humboldt, another coastal population, showing lower scores in all scale counts than Lassen, an inland population; compare our Table 2 with Table 1 in Arnold and Phillips (1999).

Within- and between-sex matrices and heritabilities in the Sonoma population

In this section, we report matrices from just the Sonoma population. Matrices for the other two populations (Humboldt and Lassen), estimated in the same way, are reported in Arnold and Phillips (1999).

Both the P_m- and P_f-matrices were nearly diagonal in structure, with average correlations in the range of 0.06 and 0.09 (Table 3). Similarly, the E_f-matrices was almost diagonal in structure, with an average correlation of -0.12. In contrast, the G_f- and B-matrices showed more off-diagonal structure, with average correlations of 0.61 and 0.77. All of the traits showed some evidence of heritable variation (Table 2). SUB and VENT showed the highest heritabilities ($h^2 = 0.37$–0.38) and SLAB and MID showed the lowest ($h^2 = 0.03$–0.17).

Table 3. Within-sex phenotypic, genetic, and environmental and between-sex genetic variance–covariance matrices (±SE) for the Sonoma population of *Thamnophis elegans*.

Trait(s)	Within-sex P		Between-sex G	Within-sex G	Within-sex E
	P_m $n=46$	P_f $n=46$	B $n=46$	G_f $n=46$	E_f $n=46$
VENT	21.013±2.595	23.372±3.298	12.714±5.194	8.962±5.603	14.410±5.835
VENT, SUB	16.159±3.642	17.747±3.347	17.568±5.335	9.175±6.262	8.572±6.594
VENT, MID	−0.152±0.221	−0.097±0.228	0.469±0.440	0.846±0.486	−0.944±0.542
VENT, ILAB	0.242±0.332	0.141±0.331	0.446±0.358	0.285±0.482	−0.144±0.475
VENT, SLAB	0.302±0.231	0.876±0.771	−0.134±0.367	0.304±0.914	0.572±0.466
VENT, POST	0.077±0.128	0.107±0.223	−0.170±0.422	0.516±0.364	−0.409±0.436
SUB	46.272±7.153	45.598±8.813	22.987±7.280	16.200±7.273	29.398±10.927
SUB, MID	−0.379±0.219	−0.709±0.629	0.476±0.327	1.106±0.772	−1.815±1.291
SUB, ILAB	0.434±0.509	0.181±0.328	1.334±0.699	1.317±0.935	−1.136±0.977
SUB, SLAB	0.482±0.361	0.306±0.589	0.215±0.777	−0.681±0.583	0.987±0.732
SUB, POST	−0.062±0.205	0.337±0.300	0.688±0.531	0.550±0.493	−0.213±0.544
MID	0.308±0.104	0.432±0.091	0.009±0.158	0.075±0.067	0.357±0.916
MID, ILAB	−0.090±0.078	0.012±0.027	0.053±0.045	0.070±0.055	−0.058±0.058
MID, SLAB	−0.029±0.020	0.067±0.056	0.038±0.038	0.257±0.219	−0.190±0.235
MID, POST	−0.035±0.025	0.002±0.029	0.0002±0.034	−0.107±0.024	0.0132±0.038
ILAB	0.660±0.226	0.584±0.124	0.053±0.049	0.195±0.131	0.389±0.153
ILAB, SLAB	0.189±0.079	0.161±0.061	0.170±0.143	0.115±0.101	0.046±0.093
ILAB, POST	0.055±0.045	0.101±0.053	0.082±0.044	0.141±0.070	−0.040±0.438
SLAB	0.509±0.194	0.999±0.461	0.044±0.078	0.010±0.050	0.988±0.488
SLAB, POST	0.034±0.021	0.014±0.024	0.080±0.049	0.006±0.039	0.007±0.037
POST	0.173±0.043	0.314±0.073	0.101±0.103	0.136±0.095	0.177±0.101
Average correlation (r)	0.059	0.091	0.607	0.770	−0.124

Population comparisons of within- and between-sex matrices using the Flury hierarchy

For G_f-matrices we could reject the hypotheses that matrices were identical or proportional (Table 4). Proceeding to the next step in the hierarchy, we could not reject the hypothesis of common principal components. Thus, G_f-matrices had four principal components in common (full CPC). For B-matrices we could reject the hypotheses of identity, proportionality, as well as the hypotheses that the populations had 4, 3, or 2 common principal components. Thus, B-matrices had a single principal component in common. In contrast, for neither the P_m- nor the P_f-matrix could we reject the hypothesis of full CPC (Table 4). Thus, it would be hard to attribute the apparent instability of the B-matrix to a sexual difference in G-stability since the G_f- and G_m-matrices are so similar across populations. We have an estimate of the within-sex E-matrix only for females (E_f). Comparing that matrix across populations, we cannot reject the hypothesis of equality (Table 4). Thus, we cannot show that the eigenvalues of the within-sex E-matrix are different across populations. Likewise, despite minimal similarity between B-matrices, the E_f-matrices for Lassen, Humboldt, and Sonoma share principal component structure.

The principal component (eigenvector) structure of the G_f- and B-matrices yield some insight into what genetic CPC structure is maintained between the three populations. Separate CPC solutions for the G_f- and B-matrices are shown in Table 5. The first three eigenvectors of these solutions are strikingly similar. In both G_f- and B-matrices, the first eigenvector is a VENT and SUB sum, the second is a VENT and SUB contrast, the third is an ILAB and SLAB sum, and the fourth is a MID and POST contrast. The fifth and sixth eigenvectors are less similar between **G_f** and **B**. The fifth eigenvector is a MID and POST sum, and the sixth is an ILAB and SLAB contrast, although in both cases contributions from other traits tend to blur the similarities. The similarities between **G_f** and **B**, especially in the first four eigenvectors, suggest a tendency to maintain similar eigenstructure in both kinds of matrices, even though variation among populations in B-structure causes us to reject all varieties of common structure except CPC(1) (Table 4).

Eigenvalues of the CPC solutions for the G_f- and B-matrices are also compared in Table 5. The average eigenvalues of the two solutions are quite similar, reflecting in part the similarities in traits loading on each eigenvector. Variation among populations

Table 4. Tests of matrix similarity among three populations of *Thamnophis elegans* using the Flury hierarchy of comparisons (Phillips and Arnold 1999). The probability that a particular type of similarity can be rejected is indicated with a *P* value in each cell. Bold entries indicate the highest step in the hierarchy of hypotheses that cannot be rejected.

Step in hierarchy	Matrix comparison	
	B	G_f
Equal	0.000	0.000
Proportional	0.000	0.000
Full CPC	0.002	**0.304**
CPC (4)	0.002	0.321
CPC (3)	0.005	0.297
CPC (2)	0.005	0.351
CPC (1)	**0.414**	0.888
Step in hierarchy	P_m	P_f
Equal	0.000	0.000
Proportional	0.000	0.000
Full CPC	**0.161**	**0.073**
CPC (4)	0.138	0.068
CPC (3)	0.215	0.050
CPC (2)	0.487	0.095
CPC (1)	0.454	0.326
Step in hierarchy		E_f
Equal		**0.336**
Proportional		0.331
Full CPC		0.495
CPC (4)		0.450
CPC (3)		0.429
CPC (2)		0.593
CPC (1)		0.536

in eigenvalues is, however, distinctly different between the $\mathbf{G_f}$ and $\mathbf{B}$ solutions. In particular, the eigenvalues of the first two eigenvectors show much greater variation among populations in $\mathbf{B}$ than in $\mathbf{G_f}$. Among population variance in eigenvalues, an indicator of instability, is about 4–5 times greater in $\mathbf{B}$ than in $\mathbf{G_f}$, although the difference in coefficients of variation is less striking.

Population comparisons of within- and between-sex matrices using Krzanowski subspace analysis

A Krzanowski (1979) analysis confirms the result that G_f-matrices are more similar than B-matrices and provides more detail about the source of differences. Even though this analysis was restricted to comparing the first three principal components, these vectors did account for most of the genetic variation in our populations. The cumulative percent of variation explained in G_f-matrices ranged from 99.0 to 99.4%; in B-matrices it ranged from 92.9 to 100% (Table S1). We conducted three pairwise comparisons

with both G_f- and B-matrices (Sonoma vs. Lassen, Humboldt vs. Lassen, and Sonoma vs. Humboldt). Overall similarity among populations was stronger for G_f-matrices than for B-matrices (Table S2). The sum of eigenvalues for S-matrices, on a scale that ranged from 0 (orthogonal) to 3 (coincident), averaged 2.2 for G_f-matrices (2.0–2.6) but only 1.7 for B-matrices (1.4–1.9). The largest contribution to this similarity, in both kinds of matrices, came from the first two principal components of $\mathbf{S}$, which generally represented sums or contrasts in VENT and SUB. Nevertheless, both of these principal components showed stronger alignment in G_f-matrices (average vector angles $= 1.6°$ and $14.3°$) than in B-matrices (average vector angles $= 5.5°$ and $43.9°$). In contrast, the third principal components were poorly aligned in both kinds of matrices, averaging $63.6°$ $(31.0–89.2°)$ in G_f-matrices and $79.3°$ $(66.1–87.0°)$ in B-matrices. These low alignment angles reflected large differences in loading profiles in population comparisons. MID, ILAB, and SLAB tended to show high loadings on the third principal component, but sometimes VENT, SUB, and POST did as well. Comparing all three populations simultaneously yielded similar solutions for G_f- and B-matrices: the first eigenvector represented the sum of VENT and SUB, the second represented the contrast between VENT and SUB, and the third generally showed high loadings for MID, ILAB, and SLAB (Table S3).

Visualizing the within-sex G- and B-matrices

The structure of the G_f- and B-matrices can be visualized by displaying the pattern of covariance structure using 95% confidence ellipses (Arnold and Phillips 1999). Figure 1 shows these confidence ellipse representations for the VENT and SUB submatrices from each population. As can be seen in Table 5, it is this part of the matrix that is responsible for the similarity in eigenvectors between the G_f- and B-matrices, so not surprisingly the inclination of the ellipses is similar between rows in Figure 1. In contrast, the shapes of B-matrices appear to be more variable than the shapes of G_f-matrices, a difference that is substantiated in Table 5 (see values at bottom of first two columns). It is also apparent from Figure 1 that within populations, G- and B-matrices are similar in shape and size, as well as in inclination. Similarity in inclination is most apparent when matrices are cigar-shaped (Sonoma), rather than nearly circular (Humboldt). This last result is consistent with simulation studies that show that cigar-shaped G-matrices tend to be more stable than circular matrices (Jones et al. 2003).

Discussion

THEORETICAL SUPPORT FOR THE CONJECTURE THAT WITHIN-SEX G IS MORE STABLE THAN B

Applying Lande's (1980a) expression for the effects of nonlinear selection to within-sex G- and B-matrices, we showed that

Table 5. Separate common principal component solutions for the between-sex matrices, B, and the within-sex matrices, G_f, for the Lassen, Humboldt, and Sonoma populations. The eigenvectors represent the solutions for models constrained to have common principal components. The two traits with dominant loadings on each eigenvector are shown in bold.

Trait	Eigenvectors					
	1	2	3	4	5	6
CPC eigenvectors:						
Between-sex, **B**						
VENT	**0.589**	**0.789**	−0.064	0.007	−0.049	0.155
SUB	**0.807**	**−0.586**	−0.004	−0.018	0.02	−0.076
MID	0.02	0.114	0.177	**−0.648**	**0.639**	−0.357
ILAB	0.013	−0.06	**0.611**	0.226	0.421	**0.628**
SLAB	0.033	0.067	**0.76**	−0.138	**−0.543**	−0.321
POST	0.035	0.114	0.115	**0.714**	0.342	**−0.588**
Within-sex, **G_f**						
VENT	**0.619**	**0.77**	−0.067	0.02	0.004	−0.139
SUB	**0.78**	**−0.625**	−0.007	−0.002	−0.035	0.019
MID	0.032	0.013	0.163	**0.761**	**0.57**	0.261
ILAB	0.08	0.127	**0.572**	−0.252	−0.176	**0.745**
SLAB	−0.011	−0.031	**0.78**	0.162	−0.173	**−0.578**
POST	0.023	−0.019	0.182	**−0.575**	**0.783**	−0.149
CPC eigenvalues:						
Between-sex, **B**						
Lassen	10.111	6.331	0.466	0.648	0.636	0.749
Humboldt	7.722	3.404	0.887	0.326	0.105	0.001
Sonoma	32.801	0.431	1.061	0.849	0.776	0.846
Mean	16.878	3.389	0.805	0.608	0.506	0.532
Variance	191.583	8.703	0.094	0.07	0.125	0.214
Coefficient of variation	0.82	0.871	0.38	0.435	0.699	0.869
Within-sex, **G_f**						
Lassen	11.055	4.62	0.436	0.598	0.393	0.447
Humboldt	5.765	5.358	0.993	0.251	0.381	0.001
Sonoma	19.672	2.889	0.736	0.693	0.486	0.584
Mean	12.164	4.289	0.722	0.514	0.42	0.344
Variance	49.275	1.606	0.078	0.054	0.003	0.093
Coefficient of variation	0.577	0.295	0.386	0.453	0.136	0.886
Ratio of **B** to **G_f** variances	3.9	5.4	1.2	1.3	38.1	2.3

within-sex **G** is likely to be more stable than **B**. This result makes intuitive sense because whereas the elements of within-sex **G** are expressed within populations of males or females, the elements of **B** are not expressed in any real population that is directly exposed to selection. As a consequence the B-matrix only indirectly experiences the stability-conferring effects of stabilizing and correlational selection, whereas the within-sex G-matrix experiences those effects directly (4). Although we did find theoretical support for the conjecture that within-sex **G** is more stable than **B**, our proof relies on simplifying assumptions of sexual homogeneity ($G_m = G_f$, $\gamma_m = \gamma_f$) that could not be tested in our study system, but deserve to be tested in other systems. It seems likely that these conditions hold when sexual dimorphism is absent or only moderately developed, as in our study system. We did examine

a condition (within-sex **G** > **B**) that helps make within-sex **G** to be more stable than **B**. In our system and in four others, the elements of within-sex **G** do indeed average larger than the elements of **B** (Table 1). Although the within-sex **G** > **B** trend is strong in some studies and consistent across all studies, some element comparisons contradict this trend in every study.

TESTING THE ROLE OF SELECTION IN STABILIZING AND SHAPING THE G-MATRIX

We tested the conjecture that **G_f** is more stable than **B** using estimates from three populations of the garter snake *T. elegans*. We found that neither G_f- nor B-matrices are identical or proportional in population comparisons of *T. elegans*. Nevertheless, our G_f-matrices had a full CPC versus only one PC in common for
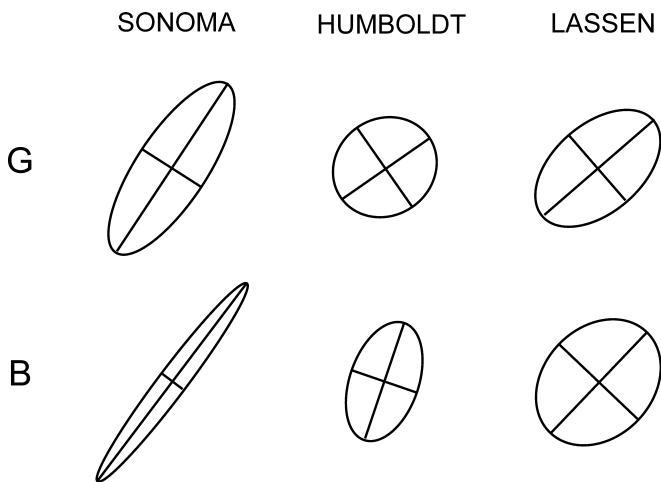
SONOMA   HUMBOLDT   LASSEN

Figure 1. Within-sex G- and B-matrices from the Sonoma, Humboldt, and Lassen populations of *Thamnophis elegans* represented as approximate 95% confidence ellipses. These ellipses illustrate the eigenvectors and eigenvalues of the VENT and SUB submatrices for each population. Eigenvectors are represented as axes within each ellipse. The distance from the center of each ellipse to the edge of the ellipse along each axis represents 1.96 times the square root of the corresponding eigenvalue. The estimated second eigenvalue for the Sonoma B-matrix was negative but is illustrated in the figure with reversed sign.

B-matrices. Thus, a primary difference between the two kinds of matrices is in stability of orientation. In other words, G_f-matrices were more stable in orientation than B-matrices.

   Selection is a leading candidate explanation for the difference in matrix stability that we observed, because B-matrices are likely to experience weaker multivariate stabilizing selection than G_f-matrices (see the theoretical section of Results). In support of this interpretation, we note that in simulation studies, multivariate stabilizing selection has been shown to promote the kind of stability that we observed (Arnold et al. 2008). Turning to the relevant empirical evidence, a variety of studies have indeed demonstrated stabilizing and/or correlational selection on scale counts, and especially on VENT and SUB, in *T. elegans* and related species (Arnold 1988; Arnold and Bennett 1988). Furthermore, a comparative study by Hohenlohe and Arnold (2008) indicates that peak movement during the radiation of *Thamnophis* species has been predominantly along a selective line of least resistance involving VENT and SUB. Such alignment of peak movement with the leading eigenvector of the adaptive landscape has been shown to stabilize the orientation of the G-matrix in simulation studies (Jones et al. 2004). Thus, abundant evidence supports the argument that the right kind of selection is both present in our study system and capable of promoting the eigenvector stability that we observed.

   Although the evidence that selection has helped produce differences between **B** and G_f is reasonably good in our system,

several limitations of our study should be borne in mind. In the first place, because our comparisons are limited to only three populations we cannot be completely certain that differences that we observed between **B** and G_f are truly systematic differences arising from a difference in selection. They might instead represent a chance difference among matrices that are stochastically fluctuating. Second, we sampled only one within- and one between-sex matrix from each population. In the ideal case one would compare both within-sex matrices (G_m and G_f) with both between-sex matrices (mother–son, father–daughter) and so make stronger tests than we did. A few studies have compared within-sex G-matrices (i.e., G_m and G_f) sampled from the same population. In some cases, these matrices differ significantly in eigenstructure (Jensen et al. 2003; Rolff et al. 2005; Steven et al. 2007), but not always (Ashman 2003). Steven et al. (2007) argue that these results, together with other differences between G_m and G_f reported by Holloway et al. (1993) and Guntrip et al. (1997), indicate that systematic differentiation of within-sex matrices is widespread, a possibility that we could not explore or take into account in our system. Finally, although several studies have detected multivariate stabilizing selection on the kinds of traits that we studied (see above), we do not have direct empirical confirmation of the theoretical result that the effects of multivariate selection are stronger on the G-matrix than on the B-matrix. Nor do we have population comparisons of selection. These limitations, however, are not unique to our study. Companion comparisons of inheritance matrices and selection surfaces across a series of populations are virtually nonexistent but would go a long way toward illuminating the role of selection in shaping within-sex **G** and **B**.

   Only a few other studies have attempted to test for a role of selection in comparisons of G-matrices. Furthermore, most comparative studies of **G** make comparisons without a priori expectations about how the matrices might differ. In a few instances, however, investigators have been able to approach the comparisons with stated a priori expectations. For example, Jernigan et al. (1994) compared genetic correlation matrices for sensory structures in amphipods (*Gammarus minus*) sampled for a surface and a cave population in each of two areas, i.e., in a total of four populations. Their sampling design permitted comparisons between habitats that are likely to experience similar selection regimes despite independent evolutionary histories. Focusing on pairs of traits most likely to respond differently to selection in the two habitats (i.e., eye-antennal correlations), they did find that genetic correlations were more similar within habitats than between clades. In another revealing study, Cano et al. (2004) compared the G-matrices of larval morphometric and developmental timing traits in two populations of frogs (*Rana temporaria*) reared under three experimental treatments (i.e., a total of 6 matrices in a 2×3 factorial design). The authors detected significant population differences in **G** which they attributed to differences in

selection. The argument that a population difference in selection caused the differences in **G** was bolstered by a Q_{ST}-F_{ST} analysis that showed the phenotypic traits had experienced a history of directional selection (i.e., more differentiation in phenotypic mean than expected under neutrality).

A second kind of test involves comparing the alignments of **G** and matrices that describe the pattern of multivariate stabilizing selection. The expectation of alignment is based on analytical and simulation results that predict alignment of eigenvectors when the adaptive landscape retains its configuration over long stretches of evolutionary time (Lande 1980a; Arnold et al. 2008). Only a few tests of this proposition have been conducted and they give conflicting results (Brodie 1989, 1992; Blows et al. 2004; Hunt et al. 2007; Hohenlohe and Arnold 2008).

SITUATIONS IN WHICH THE B-MATRIX MIGHT BE DIRECTLY AFFECTED BY SELECTION

Although we have argued that the B-matrix will ordinarily experience only indirect effects of selection, one can imagine circumstances in which the effects of selection would be direct. We first examine the possibility of such direct selection in garter snakes and then turn to the general case. We conclude that although direct selection on the B-matrix is conceivable in particular circumstances, it will generally be so weak that it can be ignored. The problem is that two factors will often act in combination to reduce the force of correlational selection acting across the sexes: the absence of strong assortative mating and the infrequency with which across-sex phenotypes are exposed to selection.

In garter snakes we need to consider a circumstance in which a phenotypic trait in males will be statistically associated with a phenotypic trait in females so that selection can act on the across trait combination and not just separately in the two sexes. Of the traits considered in this article, numbers of body and tail vertebrae (VENT and SUB) are probably the best candidates, because these two traits experience the strongest stabilizing and correlational selection within-sexes (Arnold 1988; Arnold and Bennett 1988). The best prospect for direct selection on, say, the combination of male BODY and female BODY values would appear to occur during mating, especially during intromission when the two sexes are bound together for an average of about 60 min (King et al. 2009; S. J. Arnold, pers. obs.). One can imagine that correlational selection might favor particular combinations of male BODY and female BODY, and that such selection might arise from mechanical advantages in transferring sperm, resisting the assaults of rival males, or by avoiding predation during tandem locomotion. Although such selection is conceivable its effects may be negligible for two reasons. First, assortative mating for BODY and other phenotypic traits is probably absent or weak in garter snakes. A multiyear study of *Thamnophis sirtalis* revealed weak assortative mating for body size ($r = 0.12$–0.30), a trait which is weakly correlated with BODY ($r = 0.28$) (Arnold and Bennett 1988; Shine et al. 2000a,b). In the absence of strong assortative mating, the phenotypic association between BODY across sexes is necessarily weak and so too is the statistical association between the product of those two variables and fitness. In contrast, the square of a trait expressed in one individual (i.e., $BODY^2$) is not subject to this kind of statistical depreciation, nor is the product of two different traits expressed in the same individual (e.g., BODY $\times$ VENT). Second, even if correlational viability selection did occur, its force must be devalued by the infrequency of its occurrence. Stabilizing viability selection on male BODY probably occurs throughout the active season, every year of the snake's life. Using life-history estimates for *T. elegans* (Bronikowski and Arnold 1999), life-long opportunity for selection translates into roughly an average of seven months per year times an average life expectancy of 5 years for a total of about 35 months or about 1.4 million min. In contrast, a male that matures at three years of age might over three breeding seasons engage in a total of six intromissions, lasting in total for 360 min. Just on the basis of the difference in temporal opportunity for viability selection, one would expect stabilizing selection on BODY in males to be as much as 4000 times stronger than correlational selection on the between-sex BODY combination. We conclude that even under the most favorable prospects for between-sex correlational selection its effects may be negligible in garter snakes.

Although the prospects for direct effects of selection on the B-matrix appear poor in garter snakes, they might be better in other organisms. In particular, strong assortative mating for particular traits coupled with a long period of copulation or mate association during which the mating pair flies or locomotes might provide a favorable circumstance for direct selection on male-female trait combinations. Indeed, in some insects (e.g., diptera, odonates, phasmids) copulation and mate guarding can last for hours or days, up to 79 days in one species of walkingstick (Thornhill and Alcock 1983). In these taxa the opportunity for selection associated with survival and sexual interference is correspondingly large. In the case of species with parasitic males (e.g., anglerfish) the sexual association can be very long, approaching the life span (Pietsch 1975), as it is in some truly monogamous birds with long-lasting pair bonds. All of these are circumstances that might place a selective premium on between-sex correlation in trait values. At the same time, one must consider the strength of assortative mating and the relative frequency of the events required for between-sex selection, which—as in the garter snake case—may often be so infrequent and short in duration as to make selective effects on the B-matrix trivial compared to selective effects on the sex-specific G-matrix. However, despite the plausibility of direct selective effects on the B-matrix in some kinds of special circumstances, the necessary measurements and estimates of correlational selection seem not to have been made.

COMPARISON OF FLURY HIERARCHY AND KRZANOWSKI SUBSPACE ANALYSES

Because these two kinds of analyses do not seem to have previously been conducted on the same dataset, we will compare the insights that they offered in our test case. In the first place, these analyses were in broad agreement that G_f-matrices were more similar than B-matrices across populations. Furthermore, the two leading eigenvectors in both analyses were similar for both G_f- and B-matrices. The difference between the two analyses emerges when we compare the third eigenvectors. In the Flury analysis, the third, fourth, and fifth eigenvectors of the CPC solution are very similar for both G_f- and B-matrices (Table 5). The third eigenvectors of the comparable solution in the Krzanowski (1979) analysis are also similar, but the analysis is limited to only three eigenvectors (Table S3). Comparing these third eigenvector solutions, we find high loadings for ILAB and SLAB in the CPC solutions, but overall high loadings for MID, ILAB, and SLAB in the Krzanowski solution. Apparently, the restriction of the Krzanowski analysis to just three eigenvectors resulted in a compromised solution for the third eigenvector. In contrast, the CPC analysis, with more degrees of freedom, was able to find additional common principal components that more finely represented the latent structure in the inheritance matrices. This greater flexibility was apparently responsible for the CPC conclusion that G_f-matrices had all six principal components in common, whereas the B-matrices had just one in common. The Krzanowski analysis did provide measures of matrix similarity (vector angles), but failed to give a full picture of overall similarity and differences. For additional comments of the limitations and value of the Krzanowski analysis see Flury (1988; pp. 65, 132, 144) and Blows et al. (2004).

Conclusions

The studies cited in the section before last and this study highlight a crucial missing ingredient in comparative studies of the G-matrix. We lack a theoretical framework that makes specific predictions that are useful in comparative empirical work. In the present study, we build such a framework, but its scope is limited to making the prediction that within-sex **G** should be more stable than **B**. Future theoretical work could be profitably focused on making other testable predictions of this kind. Alternatively, it may be possible to tailor simulations of **G** evolution (Arnold et al. 2008) so that they make specific predictions that are testable in particular case studies.

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Supporting Information

The following supporting information is available for this article:

Table S1. The first three eigenvectors for the within-sex ($\mathbf{G_f}$) and between-sex ($\mathbf{B}$) matrices for Sonoma, Lassen, and Humboldt.
Table S2. Krzanowski subspace analysis of population differences in within-sex ($\mathbf{G_f}$) and between-sex ($\mathbf{B}$) matrices.
Table S3. Krzanowski subspace analysis solutions for the eigenvectors closest to the subspaces of all three populations.

Supporting Information may be found in the online version of this article.

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