COMMENTARY

A cautionary tale of two matrices: the duality of multivariate abstraction

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'It was the best of times, it was the worst of times, it was the age of wisdom, it was the age of foolishness...' (Charles Dickens: *A Tale of Two Cities*)

The metaphorical Tale of Two Matrices reveals how combining the worlds of multivariate abstraction and empiricism can both illuminate and obfuscate biological questions. To be sure, there are many potential benefits to limiting the dimensionality in multivariate problems—greater statistical power and the ability to explore relationships among more than two traits simultaneously are chief among them. Conversely, the rotation of trait space into new orthogonal axes may lead us ever further from the biological realities and intuitions that underlie the questions we pursue. The seduction of generating increasingly complex ways to view selection and multivariate inheritance brings with it the cost of greater and greater abstraction as disparate biological forces are lumped into common summary statistics. The success of matrix diagonalization for examining selection and quantitative genetics will be determined by practitioners' ability to keep their eyes on the prize and use the techniques to inform experimental tests of the hypotheses they generate.

The power of any methodology is determined by its ability to help us answer the questions we want to ask. Evolutionary quantitative genetics (EQG) and related approaches became popular because they are quantitative and simple to apply, and because they offer a direct insight into fundamental questions in evolutionary biology. As is often the case with a new set of tools, the heyday of EQG was accompanied by a sometimes blind application to any and every system, without sufficient regard to the importance of conceptual context and the limitations of the techniques. Diagonalization of the important matrices in EQG gives us a new set of variables to examine, but we are still inherently bound by the same questions, constraints and pitfalls. Below, we offer our opinions on the key problems in selection and EQG and the ways in which matrix diagonalization may or may not move us forward on these fronts.

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What is the form of natural selection?

One of the most critical issues in evolutionary QG concerns the predominance of linear versus nonlinear forms of selection (Kingsolver *et al.*, 2001), a problem curiously ignored by Blows in his Tale of Two Matrices (Blows, 2007). Linear, or directional, selection (or β in the selection analysis parlance), is the form of selection that is expected to lead to adaptive change in mean phenotypes. Nonlinear selection (or γ) influences higher moments of distributions (primarily variances, covariances, and their multivariate corollaries, and perhaps skewness and kurtosis). Because nonlinear selection does not directly cause differences in the average traits among populations or species, many biologists who think in a broader comparative context do not consider it to lead to adaptation, but instead view it as a force of stasis. While γ matrix rotation helps us to examine the complexity of the relationship between fitness and combinations of multiple (i.e. more than two) traits, it ignores directional selection, which many consider the most important force of adaptation and evolutionary change. As Blows illustrates, significance tests on these canonical axes can reveal which trait combinations are experiencing selection. However, this approach does nothing to address the fundamental question of whether linear or nonlinear selection predominates. This is a question for model comparison, wherein we compare models and examine the goodness of fit as we add modes of selection. This is easily accomplished in a linear regression framework (e.g. Brodie, 1992) but it is not yet clear how we would combine linear and rotated nonlinear terms in a single model.

A corollary to this question concerns the form of nonlinear selection *per se*. For decades, it has been assumed that stabilizing selection is the primary form in nature, but we have little evidence to support this assertion (Endler, 1986; Travis, 1989; Kingsolver *et al.*, 2001; Hansen & Houle, 2004). In fact, the prevailing data suggest that linear selection is more common (though of course there are biases in what is studied and how easy it is to detect different forms), and that stabilizing selection tends to be relatively weak when it is detected (Kingsolver *et al.*, 2001). It has also been suggested that correlational selection may be the most common form of nonlinear selection, but studies that have attempted to measure it are scarce (Schluter & Nychka, 1994; Kingsolver *et al.*, 2001). One purported advantage of the rotation approach is that we can move past descriptors such as stabilizing, disruptive and correlational selection, because all curvature of the fitness surface is treated equally. All nonlinear selection may then be seen as selection affecting covariance, with correlational selection affecting a covariance among multiple traits and stabilizing/disruptive selection affecting the covariance of a trait with itself. Despite this statistical relationship, such a formulation obfuscates the more intuitive understand-

ing that most biologists have of stabilizing and disruptive selection as forces that reduce or increase variance of single traits, and correlational selection as a force that strengthens or reduces integration between traits (Lande & Arnold, 1983; Phillips & Arnold, 1989; Brodie *et al.*, 1995). Combining all three of these modes into a single descriptor affecting a canonical axis will not necessarily move us any closer to an understanding of what influences the evolution of trait distributions.

It is also worth noting that detection of selection is distinct from quantification and visualization and that each may serve its own purpose (Phillips & Arnold, 1989; Schluter & Nychka, 1994; Brodie *et al.*, 1995). One advantage of selection gradients obtained from linear regression is their direct relationship to the parameters in quantitative models of evolutionary change (Lande, 1979; Lande & Arnold, 1983; Phillips & Arnold, 1989). Combined with estimates of the covariance between phenotype and genotype, we may use selection gradients to predict changes in trait means, variances and covariances. Such predictions not only provide quantitative hypotheses to compare with empirical observation (Grant & Grant, 1995, 2002; Merilä *et al.*, 2001; Kruuk *et al.*, 2002) but also serve as heuristics for evaluating rates of phenotypic evolution (Reznick *et al.*, 1997; Hendry & Kinnison, 1999). Although canonical variates may provide more accurate descriptors of complex surfaces, is it unclear how they are directly interpretable in terms of models of evolutionary change.

How does selection influence trait integration?

Our need to visualize phenomena constrains most of us to view the world in two or perhaps (gasp) three dimensions at once. This limitation is probably what biases us to think about pairwise combinations of traits. The concept of trait integration, in both a genetic and functional sense (Olson & Miller, 1958; Cheverud, 1982, 1984; Brodie, 1989, 1992), has typically been evaluated in terms of pairwise correlations between traits, but not for any inherent biological reason. The need to think about more than two traits at a time is a problem for which matrix rotation might have significant benefits. As Blows highlights in his review and illustrates in other papers (Blows *et al.*, 2003; Blows & Brooks, 2003), if we rotate the selection surface to its canonical axes, nonlinear selection can be detected on combinations of multiple traits at once. This approach can lead to novel hypotheses of trait interaction (again, beyond the pairwise).

However, as with traditional approaches, this step only suggests which sets of traits interact to influence fitness, but cannot reveal how or why. The next step must be to translate the hypotheses revealed by selection analysis into experimental tests of functional integration and the causes of selection (Wade & Kalisz, 1990; Schluter &

Nychka, 1994; Brodie *et al.*, 1995). How to proceed may be clear with simple pairwise combinations of traits—for example, we may simply perform a 2×2 factorial experimental manipulation—but the situation is markedly less transparent when examining composites of three or more characters. The logistical problem then is how to move from a multivariate hypothesis of functional integration among many traits to empirical tests that manipulate phenotypes or context so that we can explicitly test the patterns revealed by selection analysis.

The eventual outcome of functional integration is predicted to be genetic integration (Olson & Miller, 1958; Cheverud, 1982, 1984; Brodie, 1989, 1992). Developmental morphologists and anatomists were early proponents of this idea, but it has percolated through other disciplines until it is now a keystone of thinking in physiology, performance and behaviour. In the two-trait world, there is a direct prediction of the translation—correlational selection that favours combinations of traits should alter the genetic covariance between them (Lande, 1980, 1984; Phillips & Arnold, 1989). The translation to multidimensional correlational selection (or nonlinear selection on a canonical variate) is not so clear. Do we expect changes in higher order moments of distributions such as skewness and kurtosis (Rice, 2002, 2004)? Or is the predicted outcome a change in the multivariate correlation pattern? Moreover, how do differences in the patterns of loadings of individual traits on a canonical variable alter these predictions? These are fundamental questions for the application of multidimensional analysis to the problem of phenotypic integration, but not reasons to avoid the approach. Indeed, resolution of these translations might lead us to new ways of thinking about and testing phenotypic integration on a grander scale.

How does selection affect patterns of inheritance?

Perhaps the most fundamental question in evolutionary genetics is whether selection alters genetic architecture or genetic architecture limits the response to natural selection. This question is almost certainly one of degree, and has an answer that is particular to a given population and set of phenotypes (Turelli, 1988; Arnold & Phillips, 1999). Empirical approaches to the problem range from comparing selection and inheritance within populations to the comparison of genetic architecture (as **G**-matrices) across populations or species. All of these approaches rely on the comparison of matrices and in particular the direct test of the null hypothesis of matrix identity. Despite the blossoming of several different approaches to this problem (common principal components, element-by-element, maximum likelihood and others; (Shaw, 1991; Shaw *et al.*, 1995; Phillips & Arnold, 1999; Roff, 2002; Steppan *et al.*, 2002; Baker & Wilkinson, 2003; Bégin & Roff, 2004), we still lack a consensus best way to compare

either genetic matrices among populations or selection and genetic matrices within populations. One of the major problems here remains how to simultaneously consider the many dimensions of a matrix and still test the proper null hypothesis. Matrix diagonalization offers some advantages here by reducing dimensionality, but we then must consider the problem of how to compare matrices that have been diagonalized independently and may have unique and incomparable canonical variates.

Comparing selection to the **G** matrix within a population is perhaps the most immediate way to ask whether selection is influencing genetic architecture. In other papers, Blows has outlined methods of matrix projection using diagonalized matrices that essentially ask whether the directions of greatest genetic variance align with the selection surface by comparing angles of the eigenvectors (Blows & Higgie, 2003; Blows et al., 2004; Blows & Hoffmann, 2005). This approach has the potential to allow us to evaluate the fundamental question of whether, and how, selection modifies genetic architecture within populations. Unfortunately, this is an area where the theoretical predictions are complex, and the appropriate comparisons are not transparent. For example, linear selection (β) on a canonical variable is predicted to reduce variance in the long term, but not necessarily the short term. As we can see from the within-generation equation for changes in **G**:

$$\Delta\mathbf{G} = \mathbf{G}(\gamma - \beta\beta^{\mathrm{T}})\mathbf{G}$$

(where T indicates matrix transposition) both nonlinear selection and linear selection will influence patterns of variance (Phillips & Arnold, 1989). The relative magnitudes of linear and nonlinear selection, as well as the combinations of traits experiencing linear selection, will affect the predicted changes. It may be possible to diagonalize the combined selection matrix in this equation [$\gamma - \beta\beta^{\mathrm{T}}$, which represents the curvature of the adaptive landscape (Phillips & Arnold, 1989)], but this would mask whether selection altering genetic covariances stems from linear selection on individual traits, or nonlinear selection on combinations of traits. Without considering all forms of selection simultaneously, we will remain unable to clearly test whether patterns of **G** reflect the patterns of selection. This is not a criticism of matrix diagonalization, but rather a call for further investigation of the conditions under which we expect the evolution of **G** in both the long and short term.

Due to the effects of recombination, mutation and other phenomena, it is difficult to predict changes in **G** across generations unless certain restrictive assumptions hold true (Tallis & Leppard, 1988; Turelli, 1988; Phillips & Arnold, 1989). Thus, how selection affects **G** over the empirical question. Although several studies have detected concordance between observed natural selection and patterns within **G** (Brodie, 1992; Conner & Via, 1993; Morgan & Conner, 2001; McGlothlin et al., 2005), such an approach fails to demonstrate the causal link between selection and genetic architecture. Artificial selection experiments are the key to directly testing how selection changes **G**. It has already been demonstrated that artificial directional selection may sometimes alter **G**, and that selection on trait combinations may alter the relationships among them (Wilkinson et al., 1990; Wilkinson, 1993; Shaw et al., 1995; Blows & Higgie, 2003; Conner, 2003; Phelan et al., 2003; Frankino et al., 2005). What has not been explored is how artificial nonlinear selection on multiple traits (i.e. correlational selection) affects **G**. It is this form of selection that is predicted to most directly influence the covariance structure among traits. Future studies should examine changes in **G** under various scenarios combining directional and nonlinear selection. The obvious place to start such experiments is by examining pairwise combinations of traits. Performing artificial selection on eigenvectors may allow us to incorporate more characters, but at the same time may make it difficult to generate predictions to test.

Do patterns of inheritance constrain response to selection?

G as a summary of constraint often comes under fire under the assumption that evolutionary change is not limited if the genetic correlation between traits is less than unity. The rationale is that if there is any available variance, then selection can push a phenotype in the direction of adaptation, however slowly. The problem with this characterization is that it assumes selection only moves phenotypes along the axis of an original trait or pair of traits. However, as Dickerson pointed out in the 1950s, response to selection can be prevented even if the average correlation among many traits is relatively weak (specifically, if the average correlation between pairs of n traits is $1/n$) (Dickerson, 1955). This observation is analogous to noting that if the **G**-matrix has any dimensions without variance (i.e. some eigenvalue of zero), no response to selection can occur in that direction (Blows & Hoffmann, 2005). Blows rightly points out that diagonalization can lead us to a direct assessment of the dimensionality of the **G** matrix, and this promises to improve our ability to assess constraints to adaptive evolution. There are, of course, statistical difficulties in the manifestation of the program, as well as the prevailing issue of translating back to original trait space, so the approach is not a panacea.

G itself is only an approximation of the truly important matrix in EQG, that which describes the covariance of breeding values and phenotypes, or $\mathbf{C}_{az}$ (Kirkpatrick & Lande, 1989; Arnold, 1994; Cheverud & Moore, 1994). Evolution proceeds via selection because changes in phenotypic distributions alter the underlying distributions of breeding values through the covariance between the two. In cases of simple Mendelian inheritance, $\mathbf{C}_{az}$ simplifies on average to **G** (Kirkpatrick & Lande, 1989).

However, a number of violations of the standard assumptions of EQG, as well as the presence of maternal effects or indirect genetic effects (IGEs), can render **G** a less useful description of the components of inheritance that are important (Kirkpatrick & Lande, 1989; Lande & Kirkpatrick, 1990; Cheverud & Moore, 1994; Wolf *et al.*, 1998). In extreme situations, the presence of IGEs can allow for evolution in dimensions that lack direct genetic variance (Cheverud & Moore, 1994; Wolf *et al.*, 1998). In such cases, the investigation of **G** for dimensions of zero eigenvalues would not necessarily reflect dimensions without potential for evolutionary response. Once again, this is not a problem with diagonalization *per se*, but rather the uncritical application of the **G** matrix to evolutionary problems. In all likelihood, the C_{az} matrix (or combinations of C_{az} and maternal effect or IGE matrices) could be explored in much the same way as Blows outlines for **G**, though it is not clear how we would then interpret a zero eigenvalue. Is the lack of evolutionarily important variance due to direct genetic effects (**G**), indirect effects (maternal effects or IGEs), or a combination of factors?

Cautions regarding diagonalization

One of the primary concerns over any multivariate summary is how the new axes relate to the original trait space and how we will interpret results based on the new axes. For the γ and **G** matrices, there are two main issues. First, do the new canonical variates summarize multivariate space in a biologically meaningful way? One of the common (and fair) criticisms of measuring selection on principal components is that selection does not necessarily target orthogonal axes of variation. Rotation of the γ matrix circumvents this difficulty because it is actually the selection surface that is being summarized (Phillips & Arnold, 1989; Schluter & Nychka, 1994). We are looking directly at axes that describe the shape of the selection surface, not merely dimensions of variance. On the other hand, rotation of the **G** matrix does lead us back to axes describing dimensions of variance without regard to their biological integration. As The Tale tells, this is an effective way of identifying dimensionality and singularity of the matrix, but it does not necessarily provide us variables that are analogous to the directions of selection, even in the rotated space.

The interpretation of canonical variates is always problematic. As biologists, we will want to understand these new axes in terms of the 'original traits', and therein lies the rub. If we examine selection on a set of six traits, each of six new variates will have loadings from each of the originals. The temptation is to look at the largest loadings and simplify interpretation in terms of those two or three variables, but the reality is that if this were accurate, rotation would not be necessary at all. If the canonical variate was really describable as the combination of A & B or the difference between C & D,

then an element-by-element analysis would suffice. Moreover, if we use loadings to evaluate correlational selection—for instance we find positive nonlinear selection on an axis for which D & E load positively—we would be tempted to conclude that there is correlational selection favouring positive combinations of these characters. In fact, other measured traits almost always contribute to the orientation of the axis, however weakly. This leads to difficulty in interpretation. Are weakly loaded traits F, G, H & I really creating the pattern that we see? Further, the loadings in any particular analysis are descriptors of a given dataset. Using them to evaluate the pattern of selection in general requires an assumption that even the smaller loadings (and how do we evaluate what is large and small?) are errorless estimates of relationships among traits as the affect fitness.

When we consider **G**, we see another kind of difficulty in interpreting diagonalized matrices. **G** is itself an abstraction of multiple genetic phenomena that allows us to simultaneously summarize the genetic architecture of many polygenic characters. Whether we refer to a genetic covariance between two traits, or the eigenvalue of a canonical variate describing the greatest genetic variance, we are abstracting the summation of a range of genetic phenomena—pleiotropy, linkage disequilibrium, etc.—that influence that value. The risks that are inherent in the abstraction to **G** are potentially magnified in its subsequent diagonalization.

The specific genetic phenomena that are responsible for a genetic covariance are quite different in their predicted effects on response to selection, genetic integration, and the stability and importance of **G**. Genetic covariances that arise from pleiotropy are predicted to be more stable across generations, and more difficult to generate from selection if only because they require the appropriate mutational variance to arise (Lande, 1980). Physical linkage disequilibrium may be more malleable, but depending on proximity on the map could be difficult to disrupt. Gametic phase disequilibrium, at the other end of the spectrum, is cheap (Tallis & Leppard, 1988; Wolf & Brodie, 1998). It is quickly generated through assortative mating and selection, and quickly eroded when those forces disappear. Even the frequency of alleles with major effect can have enormous effects on the magnitude and sign of covariances. If allele frequencies change quickly, such as during a selection episode, then the structure of **G** is predicted change quickly as well (Carriére & Roff, 1995; Agrawal *et al.*, 2001). All of these forces, distinct in their impact on stability and their influence by selection, contribute to the number we observe as a genetic covariance and are not recognizable in that summary. By diagonalizing **G**, we go even further from the underlying genetic phenomena, and will inevitably combine more and more disparate forces within a single summary value. Again, this is a risk inherent to **G**

or a diagonalized **G**, but one worth considering carefully before entering another level of abstraction.

Conclusion

The diagonalization approach offers us the opportunity to reduce a tangled bank of trait relationships into fewer dimensions, and with that reductionism promises to let us see patterns that are obscured when we view the world in a univariate or pairwise way. On the one hand, a canonical axis is no more arbitrary a trait than any other variable we chose to measure. All traits are defined by those who study them, and even characters as seemingly objective as bone length and call frequency can be argued to be abstractions of underlying variables. The difference is that most traits chosen for study are defined based on some biological intuition that grows out of observation and understanding of a particular system, rather than the simplification of set of variables based on patterns of orthogonal variance. In Dickens' Tale of Two Cities, he cautions us about the societal risks of excess as well as the dangerous backlash of overreaction. We should keep these lessons in mind and search for the valuable middle ground as we add matrix diagonalization to the EQG toolkit.

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