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COMMENTARY

Escape from flatland

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In 1884, midway in time between the widespread acceptance of Darwin's theory of natural selection and the rediscovery of Mendel, the English clergyman Edwin Abbott Abbott (writing under the apt pseudonym of A. Square) published his classic *Flatland, A Romance of Many Dimensions* (Abbott, 1884). The inhabitants of Flatland, a two dimensional space (essentially a sheet of paper) have distorted views of even two-dimensional objects (such as triangles), whose appearance changes as they change their orientation with respect to the viewer. Viewed from one perspective, they appear as a line, whereas seen from another angle they suggest a polygon. On rare occasions when visitors from spaceland (3-D space) appear, their appearance dynamically changes as well. A sphere passing through flatland starts as a point, becoming an ever-growing circle that reaches a maximal size and then shrinks again down to a point before disappearing. *Flatland* was a truly ground-breaking work (motivating later excursions into other spaces, such as Burger's *Sphereland*, Dewdeny's *The Planiverse* and Stewart's *Flatterland*), suggesting the inherent distortions and ambiguities when viewing a geometrical object from a lower-dimensional perspective.

On a cold winter night on the first of February in 1898, 14 years after *Flatland* appeared, Hermon Bumpus was collecting 136 house sparrows (*Passer domesticus*) stunned by a severe winter storm in Providence, Rhode Island. Only 64 of these survived, resulting in the famous Bumpus data set on multivariate morphological traits and survival (Bumpus, 1899), and leading in the future to many attempts to map a complex geometrical space onto lower dimensions. However, the geometrical complexities of this problem were largely unnoticed by biologists. It was not until 1917, when D'Arcy Wentworth Thompson published his classic *On Growth and Form*, that biologists started to think very seriously about geometry. Thompson's ideas lead to the field of morphometrics, whose practitioners routinely think in tensor spaces and all sorts of other delicious aspects of geometry.

Geometry has also played a key role in evolutionary theory. The year following Thompson's book, R. A. Fisher's classic 1918 paper appeared. Although widely recognized as starting the field of quantitative genetics, it is perhaps less appreciated that this paper was also heavily geometric, introducing the world to the orthogonal decomposition of components of variance (indeed, introducing the term variance itself). Fisher's 1930 model of the probability of a new mutation being advantageous was also heavily geometric, and the notion of Sewall Wright's genotypic fitness surfaces, which George Gaylord Simpson expressed as fitness given measures on phenotypic space, still dominates much of current evolutionary thinking.

Fast-forwarding in time we pass Dickerson (1955) who was among the first to suggest that univariate heritability estimates can give a very misleading picture of response to selection on an index of traits. Finally, we reach Lande (1979) and Lande & Arnold (1983) who left us with the legacy of genetic constraints through the **G** matrix of genetic variances and covariances, and the matrix γ of the quadratic partial regression coefficients as an estimate of the curvature of an individual fitness surface. Both of these matrices are compact representations of a complex geometric space.

Thus organismal and evolutionary biology has a rich (but under-appreciated) history of geometry. However, biology also has a Flatland history, in trying to consider complex high-dimensional spaces in simpler (lower-dimensional) terms. Just as a triangle can appear as either a line or a polygon in flatland, different projections into lower dimensional spaces can result in very different perspectives of the same complex geometrical object. Against this background appears the current Target Review from Mark Blows (Blows, 2007), whose lab has produced a number of remarkably interesting (and important) papers over the past few years. Blows correctly stresses that viewing the complex geometries inherent in the **G** and γ matrices from a Flatlandian element-by-element analysis gives a very distorted picture of their true nature.

To more fully see this, let us explore a couple of simple cases involving just two traits. Consider selection response first, with two students working on different traits in the same study organism. Student one finds that trait one has an additive genetic variance of 10 and a directional selection gradient of 2, suggesting an expected response of $R_1 = \sigma_A^2(1) \cdot \beta(1) = 20$. Likewise, the second student finds $\sigma_A^2(2) = 40$ and $\beta(2) = -1$, suggesting a response of -40 for trait two. In reality, suppose the **G** matrix is:

$$\mathbf{G} = \begin{pmatrix} 10 & 20 \\ 20 & 40 \end{pmatrix},$$

the resulting multivariate response to selection becomes:

$$\mathbf{R} = \mathbf{G}\boldsymbol{\beta} = \begin{pmatrix} 10 & 20 \\ 20 & 40 \end{pmatrix} \begin{pmatrix} 2 \\ -1 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \neq \begin{pmatrix} 20 \\ -40 \end{pmatrix}.$$

In this case, neither trait response to selection because the desired direction of response (β) is exactly along the direction where there is no genetic variation. In geometrical terms, β is in the same direction as an eigenvector of **G** that has an associated eigenvalue of zero. By not considering the full geometry, we are led to a very misleading view of selection response.

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Now, consider quadratic fitness surface estimation, with three different γ matrices, all with the same diagonal elements:

$$\gamma_1 = \begin{pmatrix} -1 & 0.25 \\ 0.25 & -1 \end{pmatrix}, \ \gamma_2 = \begin{pmatrix} -1 & 1.41 \\ 1.41 & -1 \end{pmatrix}, \ \gamma_3 = \begin{pmatrix} -1 & 4 \\ 4 & -1 \end{pmatrix}.$$

In all three cases, simply considering the γ_{ii} terms would suggest convex (i.e. potentially stabilizing) selection. However, by considering the full geometry (i.e. the eigenstructure) of these matrices, matrix one suggests convex selection on both axes (y_1,y_2) of a rotated fitness surface, with (ignoring any directional selection) an expected relative fitness of:

$$w = a - 2.05\,y_1^2 - 0.94\,y_2^2.$$

However, matrix two shows convex selection along one axis (y_1) and a ridge (no quadratic selection) along the other (y_2), with:

$$w = a - 3.00\,y_1^2.$$

Finally, matrix three shows a saddle point, with convex selection along one axis (y_1) and concave selection along the other (y_2):

$$w = a - 5.53\,y_1^2 + 2.53\,y_2^2.$$

Three very different views of the true nature of selection thus emerge from three matrices with identical diagonal elements when the off-diagonal elements are considered. Further note (as pointed out by Blows & Brooks, 2003) that by considering eigenvalues, the true strength of selection is stronger than suggested from the diagonal elements (for convex selection, −2.05, −3.00, and −5.53 vs. −1). The eigenvalues of γ provide the true picture of its geometry whereas its diagonal elements do not.

Thus, a Flatlandian view can easily lead us astray, even in the simplest case of just two traits. However, not all is bad about Flatland. Indeed, many apparently complex biological geometries may in fact have themselves a touch of Flatland, with most of their variation residing on a lower-dimensional (perhaps a very considerably lower dimensional) subspace. Indeed, Blows & Hofmann (2005) have correctly taken many authors to task (including this one) for the often unspoken assumption that there is essentially genetic variation for any trait measured. It is certainly true that almost all traits in outbred populations show nonzero heritabilities. However, as our first example suggests, single-trait variances are very misleading and indeed it may be the case that very little genetic variation exists along the direction that natural selection is trying to move the trait. Two striking examples of this, involving *Drosophila serrata* and the Australian rainbow fish (*Melanotaenia*), have recently come out of the Blows lab (Blows *et al.*, 2004; McGuigan *et al.*, 2005). It now becomes an open (and very interesting) question as to the general dimensionally of many **G** matrices. If, in general for n traits, most of the genetic variation residues on a subspace of dimension $\ll n$, then there are strong constraints on natural selection. Although one might initially dismiss this suggestion as requiring a pathological combination of genetic correlations to give eigenvalues of **G** very near zero, this is exactly what one might expect if a trait has been under consistent natural selection. Over time, usable genetic variation along the desired direction of response can become depleted, all the while considerable additive variation can exist when any single trait is considered in isolation.

As hinted in the last paragraph, a very positive aspect of Flatland is that a complex high-dimensional vector of traits may be a much simpler geometric object whose variation almost entirely lies on a much lower dimensional space. Analysis of the full dimensional space suggests the appropriate subspace to consider (the eigenvectors associated with the leading eigenvalues). Rescaling the data to these new axes results in transforming a problem of estimating $n(n-1)/2$ elements (genetic covariances for **G**, quadratic regression coefficients for γ) into a much simpler regression problem of estimating k parameters, corresponding to re-estimation of the leading k eigenvalues. This resulting lower-dimensional space is a much truer set of traits from a genetical (**G**) or ecological (γ) presective than the initial set of traits that the biologist had chosen to measure. A very interesting problem is that the lower-dimensional subspace for genetical constraints (**G**) and natural selection (γ) may be very different spaces for the same set of starting traits. In such cases, geometry again comes to the rescue, as one can consider the projection of one subspace into another, providing a measure for the amount of usable genetic variance in the genetic subspace with respect to the fitness subspace (Blows *et al.*, 2004).

As biologists (indeed as scientists) we all live in Flatland, trying to peer at highly complex problems from different perspectives to obtain some insight into their true nature. As biology continues to move to even higher-dimensional problems (and especially data sets), the simple lessons suggested by Abbott over 120 years ago are more relevant than ever.

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