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Variation, selection and evolution of function-valued traits

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Abstract

We describe an emerging framework for understanding variation, selection and evolution of phenotypic traits that are mathematical functions. We use one specific empirical example – thermal performance curves (TPCs) for growth rates of caterpillars – to demonstrate how models for function-valued traits are natural extensions of more familiar, multivariate models for correlated, quantitative traits. We emphasize three main points. First, because function-valued traits are continuous functions, there are important constraints on their patterns of variation that are not captured by multivariate models. Phenotypic and genetic variation in function-valued traits can be quantified in terms of variance-covariance functions and their associated eigenfunctions: we illustrate how these are estimated as well as their biological interpretations for TPCs. Second, selection on a function-valued trait is itself a function, defined in terms of selection gradient functions. For TPCs, the selection gradient describes how the relationship between an organism's performance and its fitness varies as a function of its temperature. We show how the form of the selection gradient function for TPCs relates to the frequency distribution of environmental states (caterpillar temperatures) during selection. Third, we can predict evolutionary responses of function-valued traits in terms of the genetic variance-covariance and the selection gradient functions. We illustrate how non-linear evolutionary responses of TPCs may occur even when the mean phenotype and the selection gradient are themselves linear functions of temperature. Finally, we discuss some of the methodological and empirical challenges for future studies of the evolution of function-valued traits.

Introduction

An important accomplishment of evolutionary ecology during the past quarter century has been our theoretical and empirical understanding of natural selection and evolution in action in populations in the wild. We now have an impressive set of case studies demonstrating selection and evolution of quantitative traits in natural populations (Grant, 1985; Endler, 1986; Thompson, 1998). There are well-developed theoretical models and statistical tools for assessing variation, selection and evolution of quantitative traits (Lande, 1976; Lande, 1979; Lande & Arnold, 1983). A recent review identified more than 2000 published estimates of the strength of natural or sexual selection in nature (Kingsolver et al., 2001). In the vast majority of cases, the phenotypic value of a given trait for an individual may be characterized by a single value: that is, an individual organism expresses a single value of that particular trait during the time period (e.g., an episode of selection) of interest. Often we can characterize the phenotype of the individual as a finite set of quantitative, perhaps correlated, traits. Lande, Arnold and others (Lande, 1979; Lande & Arnold, 1983; Arnold & Wade, 1984a; Arnold & Wade, 1984b) have provided a theoretical framework for modeling how patterns of phenotypic and genetic variation and selection in a population may lead to evolution of such sets of correlated quantitative traits.

By contrast, many features of an individual organism may vary continuously or discontinuously in some manner. For example, the size, shape and other

features of an individual may change with age. Rates of growth, development, feeding, locomotion, nutrient uptake, photosynthesis and other processes of an individual may vary with environmental conditions such as temperature, moisture and light intensity that may change during an individual's life. The position and force production of a limb during locomotion (e.g., during the wingbeat of a bird or insect) also varies continuously and cyclically. For these and many other features of an individual, the trait is naturally described as a mathematical function. How do we evaluate variation, selection and evolution of quantitative traits that are functions – what we term function-valued traits (Ramsay & Silverman, 1997; Pletcher & Geyer, 1999)?

In this paper we describe recent theoretical, statistical and empirical advances that provide a framework for analyzing and modeling the evolution of function-valued traits. Throughout the paper we will demonstrate how models for function-valued traits are a natural extension of the more familiar models of multivariate evolution developed by Lande & Arnold (1983). Our discussion will emphasize three main issues, and illustrate these using one particular example of a function-valued trait: the growth rate of a caterpillar as a function of its body temperature. First, what are the patterns of variation in function-valued traits in a population? We will discuss appropriate methods for quantifying phenotypic and genetic variation in function-valued traits, and why there are important constraints on the possible patterns of variation in such traits. Second, what is phenotypic selection on a function-valued trait? We will discuss how selection itself is a function, and describe how directional selection functions may be estimated in the field. We will also consider how the selection function may depend on the selective environment, and how one might evaluate the targets of selection on function-valued traits. Third, how do selection and variation combine to generate evolutionary change in a function-valued trait? We will emphasize how changes in the selective environment may alter the directions of evolution in function-valued traits, and how constraints on the patterns of phenotypic and genetic variation may preclude evolution in certain directions.

Variation in function-valued traits

Function-valued data

As noted above, many traits of organisms are naturally described as mathematical functions. Such traits have been given a variety of labels, including infinite-dimensional (Kirkpatrick & Heckman, 1989), longitudinal or repeated (Meyer & Hill, 1997), function-valued (Pletcher & Geyer, 1999), and functional (Ramsay & Silverman, 1997) traits. Here we shall use the term 'function-valued trait': a phenotypic trait whose value is a function of some continuous index (e.g., of age, environmental temperature, etc). The first class of function-valued traits to receive detailed attention was variation in a trait across ages of an organism, or ontogenetic trajectories. The most common ontogenetic trajectories examined have been growth curves, which describe the change in body mass as an organism ages (Kirkpatrick, Lofsvold & Bulmer, 1990; Kirkpatrick & Lofsvold, 1992; Meyer & Hill, 1997). Currently one of us (PAC) is examining ontogenetic trajectories of a behavioral trait (voluntary wheel running) in lines of mice that have been selected for that behavioral trait (Swallow, Carter & Garland, 1998) and in control lines. Figure 1 (Morgan and Carter, unpublished) shows the ontogenetic trajectories for wheel running in the four selected lines and the four control lines for the first 80 weeks of the lifespan of these mice.

Another general class of function-valued traits is continuous reaction norms, for which the trait varies as a function of some continuous environmental variable (Scheiner, 1993). One example of a continuous physiological reaction norm, which we shall develop in detail here, is a thermal performance curve (TPC), representing how the performance of an organism varies continuously with its body temperature (Huey & Stevenson, 1979; Huey & Kingsolver, 1989). For example, Figure 2 shows how mean, short-term mass-specific growth rate varies as a function of temperature for two species of caterpillars. TPCs for many aspects of organismal performance, including growth, have a similar overall form: at low temperatures, performance increases with increasing temperatures, reaches a maximum at intermediate temperatures, then declines rapidly with further increases in temperature (Huey & Kingsolver, 1989; Casey, 1993). For ectothermic organisms in natural environments, an individual may experience a wide range of temperature conditions during its life, and therefore will express a wide range of performance values: A TPC is naturally a function-valued trait. More generally, if z is some trait of interest and T is a continuous index, then $z(T)$ indicates the value of a function-valued trait when the index value is T. T may represent age, an environ-

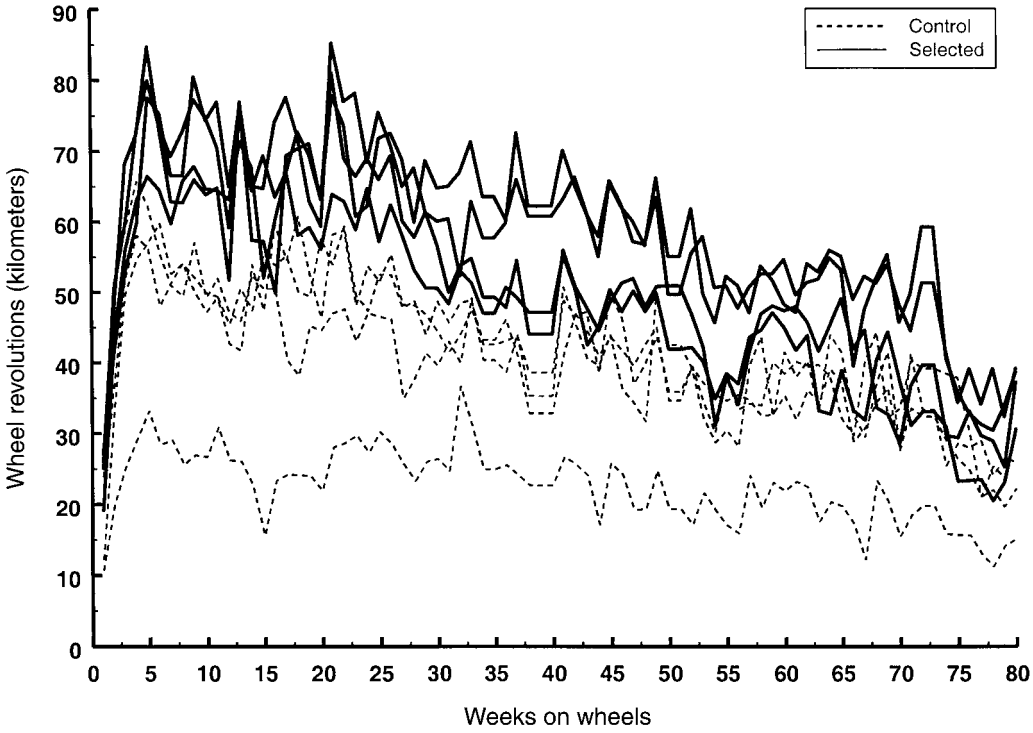

Figure 1. Mean wheel-running (km/w) as a function of age for four selected lines (solid lines) and four control lines (dashed lines) of mice. Data from Morgan and Carter (in prep).

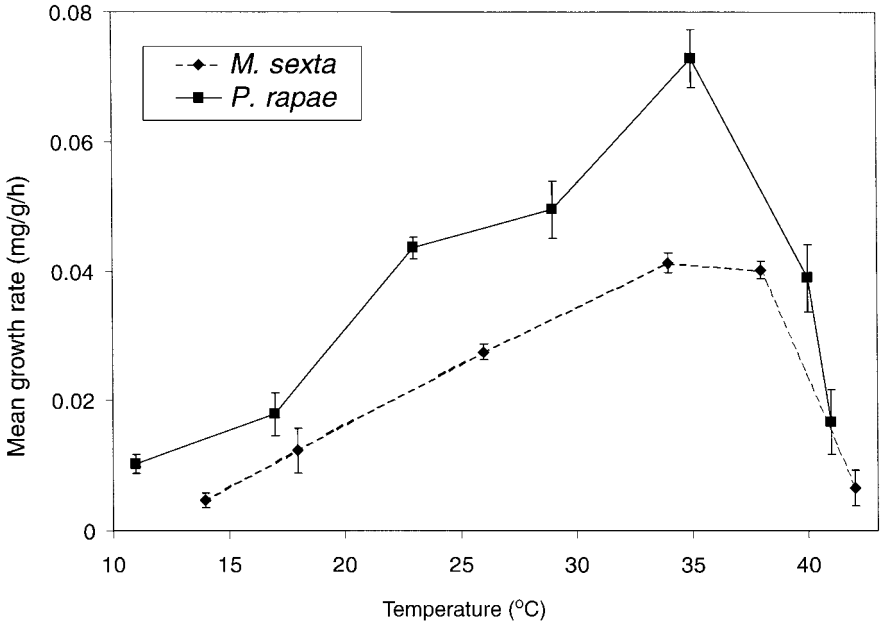

Figure 2. Mean(± 1 se) short-term relative growth rates (in mg/g/h) as a function of temperature for *Manduca sexta* (diamonds, dashed line) and *Pieris rapae* (squares, solid line) caterpillars. Data from Kingsolver and Woods (1997) and Kingsolver (2000).

mental variable such as temperature or light intensity, or some other appropriate index. Because T may take on an infinite number of values on an interval, an infinite number of values are needed to *fully* describe the trait z: for this reason function-valued traits can also be called 'infinite-dimensional' traits (Kirkpatrick & Lofsvold, 1988; Kirkpatrick, Lofsvold & Bulmer, 1990). Obviously, individuals and genotypes in a natural population may vary in $z(T)$ (see next section).

An important consideration is how best to describe the function-valued trait $z(T)$ mathematically, given a limited number of values of T at which z can actually be measured for each individual in a population or sample (Figures 1,2). One approach is to use parametric models that require specific assumptions about the form of the function $z(T)$, and to consider the estimated parameters in the model as the traits representing the phenotype of each individual (DeJong, 1990; Gibert et al., 1998). One advantage of a parametric model for $z(T)$ is that by constraining the form of the function, the statistical power for estimating parameters is often increased. However, the chosen model may not adequately reflect all of the possible patterns of variation in $z(T)$ in a population. This will be particularly problematic for function-valued traits that are non-linear and asymmetric, including TPCs. The parameter estimates for such models are sometimes highly correlated, and the biological interpretation of the parameters may be unclear. An alternative approach, which we will emphasize here, is to use non-parametric methods that make essentially no assumptions about the shape of the function $z(T)$, albeit at the potential price of additional parameters and reduced statistical power.

Quantifying phenotypic and genetic variation in function-valued traits

Suppose that we can measure the values of $z(T)$ at a (finite) series of values of T ($T = T_1, T_2, T_i ... T_n$) for each individual in a population as part of a breeding design study. The multivariate approach to these data, which has been widely used in studies of phenotypic plasticity (Via & Lande, 1985), is to represent the phenotype of each individual as a vector of distinct, correlated measures at each value T_i:{$z(T_1)$, $z(T_2)$,... $z(T_n)$}. Using these data, one can estimate the phenotypic (**P**) and genetic (**G**) variance-covariance matrices for the population (Lande, 1979).

For example, one of us (JGK) has measured TPCs for short-term growth rate in *P. rapae* caterpillars from Seattle WA (Kingsolver, 2000). In these studies, we raised 21 full-sib families of caterpillars from egg through 3rd instar on collard leaves in a fluctuating (10–30°C) temperature regime in an environmental chamber. Following molt into the 4th instar, we measured the short-term (2–12 h) relative growth rate (RGR = ln[final mass-initial mass]/time) of each caterpillar feeding on fresh collard leaves at a series of 5 temperatures: 11, 17, 23, 29 and 35°C (Figure 2); all measurements were completed within the 4th instar. We have used these data to obtain preliminary estimates of the phenotypic and broad-sense genetic variance-covariance matrices (Table 1). Values along the diagonal represent the estimated genetic variance in RGR at each of the five measurement temperatures; genetic variance in RGR clearly increases with increasing temperature. The off-diagonal elements represent the estimated covariance between RGR at pairs of temperatures; for example, the estimate of $G_{4,5}$ indicates a strong positive genetic covariance between RGR at 29°C and RGR at 35°C. This multivariate method has been widely used in studies of phenotypic plasticity (Via & Lande, 1985).

Table 1. Estimated broad-sense genetic variance-covariance matrix for short-term relative growth rate of 4th instar *Pieris rapae* caterpillars from Seattle, Washington, measured at 5 temperatures (Temp): 11, 17, 23, 29 and 35°C

Temp	11	17	23	29	35
11	1.255	−0.229	0.043	−1.027	−0.214
17	−0.229	3.156	−1.099	−1.026	0.735
23	0.043	−1.099	4.505	3.725	1.613
29	−1.027	−1.026	3.725	14.393	3.947
35	−0.214	0.735	1.613	3.947	23.094

Based on 21 full-sib families. Preliminary data based on Kingsolver (2000, 2001).

The problem with this approach is that it ignores the fact that TPCs and similar traits are continuous functions of the continuous variable temperature. Growth rate at temperature T_1 cannot be assumed to be independent of growth rate at temperature T_2: as T_2 - $T_1 \rightarrow 0$, the growth rate at the two temperatures must converge. This basic fact places important constraints on possible patterns of variation in TPCs and other function-valued traits (Kirkpatrick & Lofsvold, 1988; Kirkpatrick, Lofsvold & Bulmer, 1990; Gomulkiewicz & Kirkpatrick, 1992; Kirkpatrick & Lofsvold, 1992).

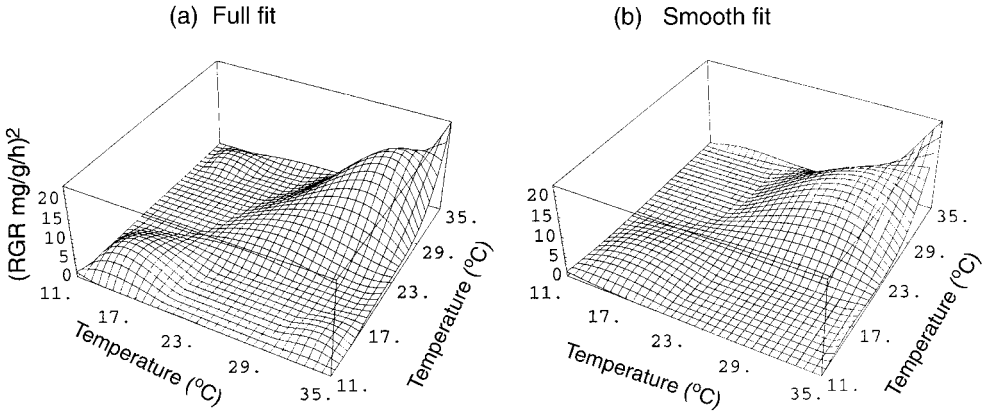

Figure 3. Estimated broad-sense genetic variance-covariance functions $[G(T,\theta)]$ for relative growth rates (RGR) of 4th instar *P. rapae* caterpillars from Seattle, Washington, USA. Based on individuals from 21 full-sib families (see text for details). Left panel: full fit (5th order) model; right panel: Smoothed fit (3rd order) model. $G(T,\theta)$ is in units of $(\text{mg/g/h})^2$, as functions of temperature (°C).

Note also that the multivariate method ignores the order of the data with respect to T: re-ordering the traits [e.g., {RGR(29°C), RGR(17°C), RGR(35°C), RGR(11°C), RGR(23°C)}], would have no effect on the estimated variances or covariances. It has been shown that methods that account for the natural order of traits have greater statistical power than multivariate methods (Kirkpatrick & Heckman, 1989). Finally, theoretical analyses demonstrate that the multivariate method of analysis seriously underestimates the magnitude of constraints on patterns of covariation when applied to function-valued traits (Gomulkiewicz & Kirkpatrick, 1992; Kirkpatrick & Lofsvold, 1992).

If we interpolate between the values in Table 1, we see that the entries of the genetic variance-covariance matrix **G** can be viewed as particular values of a genetic covariance function $G(T,\theta)$ that represents the genetic variances and covariances between pairs of temperatures T and θ for all (infinite) possible values of T and θ. (The phenotypic covariance function may be similarly defined.) The estimated genetic covariance function for the caterpillar TPC data is given in Figure 3(a–b). The estimated G function suggests that relative growth rates are positively correlated genetically across most temperatures, with the strongest correlations at higher temperatures (29–35°C).

Both parametric and nonparametric methods have been developed for estimating covariance functions. The most straightforward of these are the nonparametric least-squares methods developed by Kirkpatrick and coworkers (Kirkpatrick & Heckman, 1989; Kirkpatrick, Lofsvold & Bulmer, 1990; Kirkpatrick, Hill & Thompson, 1994). This involves using least-squares to fit the bivariate function, $G(T,\theta)$, to the estimated genetic covariance matrix **G** using a set of appropriate univariate functions, $b(T)$, called basis functions; Kirkpatrick and coworkers use orthogonal polynomials as the basis functions in their method. The covariance functions shown in Figure 3 were fit to the covariance matrix values in Table 1 using least squares. More recently, Meyer and Hill (Meyer & Hill, 1997) have developed a restricted maximum likelihood (REML) method for estimating genetic covariance functions directly from individual measurements without first estimating a genetic covariance matrix. These REML methods can have greater statistical power than least-squares and also guarantee estimated covariance functions to be positive semi-definite (e.g., constraining estimated variances to be non-negative).

It is always possible to fit a sufficiently complicated covariance function $G(T,\theta)$, to a given genetic covariance matrix **G** exactly in the sense that $G(T_i,\theta_j)$ is equal to the *ij*th component of the matrix **G**. Such a function is said to fully fit the data (e.g., Figure 3(a)). Because we expect observational data to involve observational error, fully fitting data is tantamount to 'over-fitting' it. Moreover, complicated covariance functions tend to exhibit meaningless fluctuations and usually require the estimation of a large number of parameters (which can compromise statistical power and computational efficiency). For these reasons, it is desirable to obtain a 'smoothed' estimate that more closely resembles the actual covariance function. Both least-squares and REML approaches

can be used to obtain not only smoothed estimates but also to compare the estimate with data and with more complicated covariance function estimates: for details, see (Kirkpatrick, Lofsvold & Bulmer, 1990; Kirkpatrick, Hill & Thompson, 1994; Meyer & Hill, 1997). Figure 3(b) shows an example of a smoothed covariance function estimated from the data in Table 1 using the least-squares approach. However, choosing the degree of smoothing with this method is subjective.

Three alternative approaches for obtaining smooth covariance function estimates have been proposed: random regression, cubic splines, and character process models. An important feature of these methods is that they do not limit the possible shapes of the mean function (i.e., the fixed effect). In random regression (Shaeffer & Dekkers, 1994; Meyer, 1998; Jones, White & Brotherstone, 1999), individual breeding values are modeled as relatively simple weighted sums of basis functions. Variances of the weights, and covariances between them, can be estimated using standard least-squares or REML methods. These variances and covariances can then be used to construct a genetic covariance function estimate. If the same basis functions are used in random regression and a least-squares approach, both methods will produce exactly the same covariance function estimate (Meyer, 1998). However, random regression requires one to choose *a priori* both the type and number of basis functions to be utilized in the analysis. The cubic splines approach is similar to random regression except that piecewise continuous polynomials are used to model individual breeding values (White, Thompson & Brotherstone, 1999). The degree of smoothness can be controlled by using a 'roughness penalty', which explicitly balances the degree of fit with the degree of roughness or curvature of the estimated function; the smoothing parameter is then determined objectively using the penalized likelihood (Ramsay & Silverman, 1997). Finally, Pletcher and Geyer (Pletcher & Geyer, 1999) have proposed a character process approach in which the covariance or correlation between observations at two different temperatures is assumed to depend only on the difference between the temperatures and not their absolute values. The methods described above are anything but the final word in genetic covariance function estimation, which is an active field of research. An informative discussion of the strengths and weaknesses of current methods can be found in Kirkpatrick and Bataillon (Kirkpatrick & Bataillon, 1999).

Identifying axes of variation in function-valued traits

For multivariate traits, it is often difficult to identify general patterns of variation and covariation by inspection of the phenotypic or genetic variance-covariance matrix. It is frequently more informative to perform a principal components (PC) analysis of the variance-covariance matrix. This analysis decomposes the matrix into a set of eigenvectors and associated eigenvalues. Each eigenvalue indicates the amount of variance explained by its associated eigenvector. Each eigenvector indicates an axis (principal component) in terms of the original set of traits; the eigenvector loading for each trait quantifies the trait's contribution to that eigenvector. PC analysis has been widely used to explore variation in sets of correlated morphometric traits; often the first eigenvector (that explaining the largest proportion of total variance) shows positive loadings for all morphometric traits, thus representing variation in overall size. The loadings of an eigenvector thus reflect patterns of covariation among the traits.

Table 2. Loadings for the first three eigenvectors (PC1, PC2, PC3) of the genetic variance-covariance matrix in Table 1

Temp(°C)	PC1	PC2	PC3
11	−0.029	0.084	−0.179
17	−0.001	0.175	0.614
23	0.039	−0.276	−0.705
29	0.166	−0.926	0.305
35	0.985	0.170	−0.029

For example, Table 2 gives the first three eigenvectors for the genetic variance-covariance matrix for TPCs of caterpillar growth rate. The first eigenvector, which explains 67% of the total genetic variance, has small (near zero) loadings at lower temperatures, and much larger loadings at the higher temperatures. For example, the strong positive loadings of RGR at 29 and at 35°C on this eigenvector indicate that most of the variation in overall RGR is associated with RGRs at high temperatures. The second and third eigenvectors, which explain 29% and 3% of the variance respectively, show more complex patterns of negative and positive loadings (see below).

As before, this principal components analysis of the variance-covariance matrix ignores the fact that temperature T may take on an infinite number of values for TPCs or other function-valued traits. Instead,

we can perform principal components analysis on the variance-covariance function: This analysis decomposes the variance-covariance function into a set of eigenfunctions and associated eigenvalues (Ramsay & Silverman, 1997). The eigenfunctions are the continuous counterparts of the eigenvectors: Indeed, we can view the loadings on an eigenvector as discrete points along the equivalent (continuous) eigenfunction.

What is the biological meaning of an eigenfunction? The key is to recognize how different patterns of variation in function-valued traits relate directly to the form of the eigenfunctions. To illustrate this, let's consider three different hypotheses about variation in TPCs: the Faster-Slower, the Hotter-Colder, and the Generalist-Specialist hypotheses (Figure 4) (Huey & Kingsolver, 1989). For simplicity, let all individuals in some hypothetical population have the same 'optimal' temperature for performance (the temperature at which performance is maximum). First (Faster-Slower hypothesis, Figure 4(a)), imagine a set of individuals or genotypes that vary in the overall height of the TPC, such that some individuals or genotypes have higher growth rates at all temperatures (light solid line), or have lower growth rates at all temperatures (dashed line), relative to the mean TPC for the population (heavy solid line). Alternatively (Hotter-Colder, Figure 4(b)), a set of individuals or genotypes might vary in the degree or direction of asymmetry of the TPC, such that some individuals or genotypes have higher growth rates at hotter temperatures but lower growth at colder temperatures (light solid line), whereas other individuals or genotypes have higher growth rates at colder temperatures but lower growth at hotter temperatures (dashed line), relative to the mean TPC for the population (heavy solid line). A third possibility (Generalist-Specialist, Figure 4(c)) is that a set of individuals or genotypes might vary in the width of the TPC, such that individuals or genotypes with higher growth rates at intermediate temperatures have lower growth rates at low and high temperatures (Specialists, light solid line), whereas individuals or genotypes with lower growth rates at intermediate temperatures have higher growth rates at low and high temperatures (Generalists, dashed line), relative to the mean TPC for the population (heavy solid line). We can think of these three different patterns – Faster-Slower, Hotter-Colder, and Generalist-Specialists – as different possible axes of variation in TPC within a population; of course real populations may contain mixtures of genotypes that may vary along these (and other possible) axes of variation.

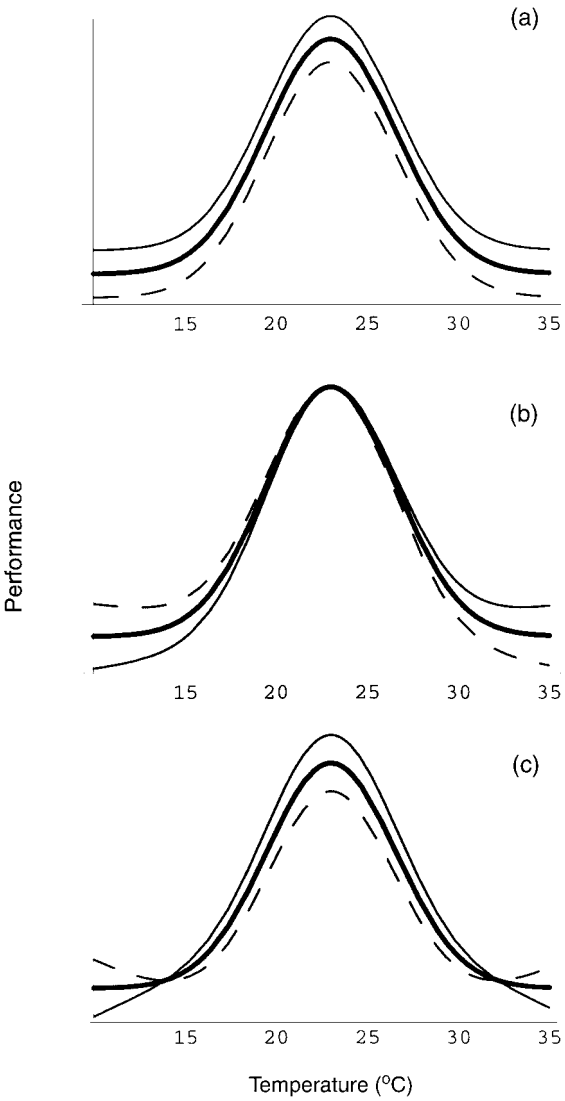

Figure 4. Hypothetical patterns of variation in thermal performance curves (TPCs). In each panel, the heavy solid line represents the population mean phenotype (TPC); the light solid and dashed lines represents variation about the mean TPC. See text for explanation (a) Faster-slower pattern. (b) Hotter-colder pattern. (c) Generalist-specialist pattern.

These different patterns or axes of variation among genotypes in TPCs will result in different eigenfunction shapes (Figure 5). Within the Faster-Slower axis of variation (Figure 5(a)) growth rate is positively correlated across all temperatures, so that the eigenfunction will take on positive values at all temperatures (or equivalently, negative values at all temperatures). This means selection for increased growth rate at one temperature would lead to an increase in growth rate at all temperatures (or *vice versa*). Within the Hotter-

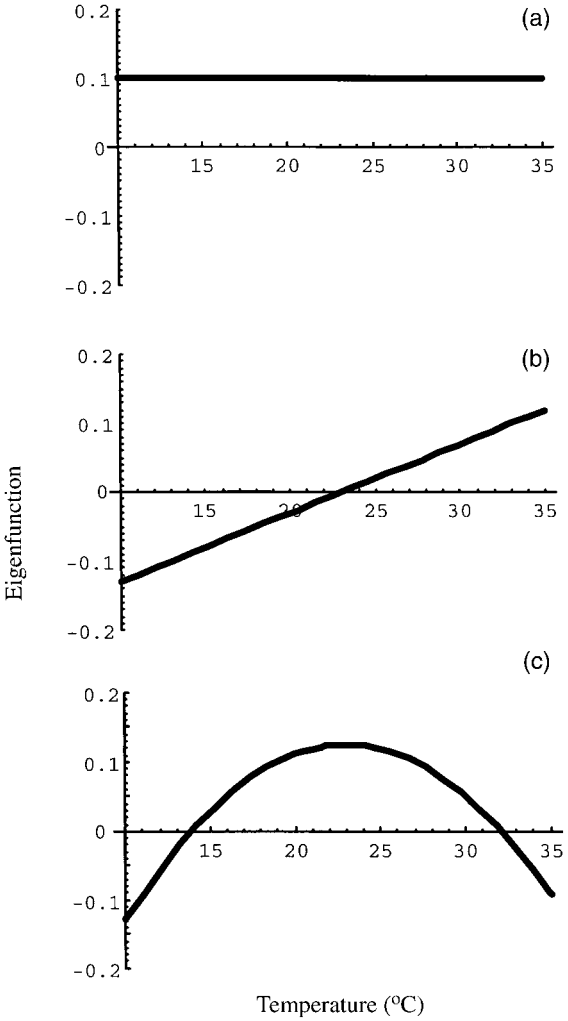

Figure 5. Eigenfunction associated with each pattern of TPC variation in Figure 4. See text for explanation. (a) Faster-slower axis. (b) Hotter-colder axis. (c) Generalist-specialist axis.

Colder axis of variation (Figure 5(b)), growth rate at lower temperatures is negatively correlated with growth at higher temperatures (and *vice versa*), so that the eigenfunction will be negative at low temperatures and positive at higher temperatures (or the reverse). This means that selection for increased growth rate at low temperature will lead to a decreased growth rate at high temperature (or *vice versa*). Within the Generalist-Specialist axis of variation (Figure 5(c)), growth rate at intermediate temperatures is negatively correlated with growth at extreme temperatures. This means that selection for increased growth rate at low or high temperatures will lead to a decreased growth rate at intermediate temperatures (or *vice versa*). (Interestingly, variation in the position [but not shape] of the TPC along the temperature axis leads to more complex patterns that cannot be fully described by a single eigenfunction: R. Gomulkiewicz, unpublished results.)

In this way, eigenfunction analyses of phenotypic and genetic variation can help us understand underlying patterns of variation in TPCs (Gomulkiewicz & Kirkpatrick, 1992; Kirkpatrick & Lofsvold, 1992). With this in mind, let's return to our analysis of genetic variation in TPCs of caterpillar growth. We have estimated eigenfunctions of the (broad-sense) genetic variance-covariance function of TPC growth rates in Figure 3. The first (leading) eigenfunction (Figure 6(a), solid lines), representing 62% of the total variance in TPCs, has loadings near zero for temperatures below ~20°C, and positive loadings for temperatures above ~20°C, with the largest loadings at the highest temperatures. Within this axis of variation, growth rate is positively correlated genetically across temperatures from 20 to 35°C, consistent with a 'Faster-Slower' pattern of variation across this temperature range. The small loadings on this eigenfunction at lower temperatures reflect the fact that, within this axis of variation, there is relatively little genetic variance in growth rate at low temperatures compared with higher temperatures (Figure 3). The second eigenfunction (Figure 6(a), dashed line), representing 21% of the total variance in TPCs, has positive loadings at intermediate (20–30°C) temperatures, and negative loadings at lower (<20°C) and higher (>30°C) temperatures. Within this axis of variation, growth rate at intermediate temperatures is negatively correlated genetically with growth rate at lower or higher temperatures, which is consistent with a 'Generalist-Specialist' pattern of variation. These preliminary analyses for *P. rapae* indicate that the dominant axis of genetic variation reflects overall variation in growth rates at higher temperatures, but also suggest the possibility of generalist-specialist tradeoffs in thermal sensitivity (Huey & Kingsolver, 1989; Gilchrist, 1996).

Eigenfunctions can, in principle, be estimated from any genetic covariance function. So far, only Kirkpatrick et al. (1990) has detailed a method for obtaining eigenfunctions from an estimated covariance function in a quantitative genetics context. In their least-squares approach, the coefficients of eigenfunctions with respect to designated basis functions are computed directly from the eigenvectors of the coefficient matrix that is used to describe the full or smoothed covariance function (rather than from the eigenvectors of the original covariance matrix **G**).

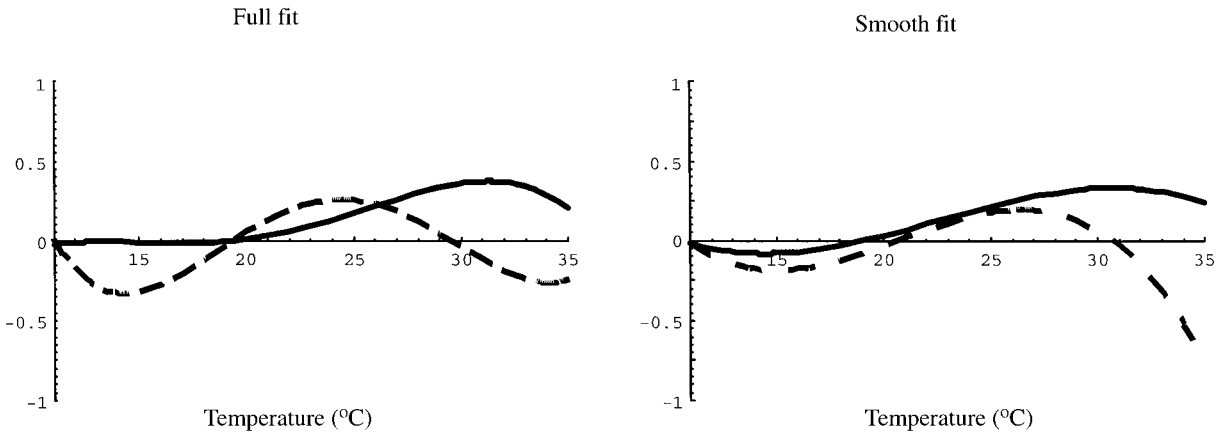

Figure 6. Leading (first) and second eigenfunctions estimated from the genetic variance-covariance function for TPCs of relative growth rate for *P. rapae* caterpillars given in Figure 3. Left panel: based on full fit (5th order) model; right panel: based on smoothed fit (3rd order) model.

In this case, a smoothed eigenfunction refers to an eigenfunction obtained from a smoothed covariance function estimate. The smoothed eigenfunctions of the (smoothed) broad-sense genetic variance-covariance function (Figure 3(b)) for the caterpillar TPC data are presented in Figure 6(b). Note that smoothing in this case has little effect on the qualitative shapes of the first (solid line) and second (dashed lines) eigenfunctions. Conceivably, the same methods used to obtain smooth covariance function estimates (such as REML and cubic splines) could be applied to eigenfunction smoothing. Although the problem of eigenfunction estimation has received relatively little attention so far, it is clearly important for understanding the evolution of function-valued traits and warrants further investigation.

Estimation of quantitative genetic parameters for multiple traits can require large sample sizes, in particular many sets of genetic relatives (Falconer & MacKay, 1996). For example, for N quantitative traits, $N(N+1)/2$ distinct elements of the genetic variance-covariance matrix **G** must be estimated. Note that for an equivalent function-valued trait $z(T)$ measured at N different values of the index T, the number of parameters estimated for the genetic variance-covariance function $G(T,\theta)$ is typically smaller than $N(N+1)/2$, except for the fully-fit model; and the greater the degree of smoothing employed, the smaller the number of parameters. In particular for character process models of function-valued traits, the number of model parameters may be greatly reduced, leading to considerably improved statistical power (Pletcher & Geyer, 1999). This increased statistical efficiency is an important but largely unrecognized advantage of the function-valued approach compared with the conventional multivariate method. However, estimation of confidence or support limits on genetic variance-covariance functions has received little attention, and requires further research.

Selection on function-valued traits

Estimating phenotypic selection

One standard way to quantify the strength of directional selection on a quantitative trait (z) is in terms of the linear selection gradient (β), which relates variation in the trait (in units of standard deviation of the trait) to variation in relative fitness, where mean fitness in a population or sample is defined as equal to 1, (Lande, 1979). For a set of traits, $z = \{z_1, z_2 ... z_n\}$, the selection gradient is a vector $\beta = \{\beta_1, \beta_2 \ldots \beta_n\}$, that represents the strength of direct directional selection on each trait (Lande & Arnold, 1983). The components of a selection gradient represent the direct strength of selection on each trait, adjusting for the phenotypic correlations among the traits; they can be readily estimated with partial regression analyses, in studies where both trait values and fitness com-

ponents are measured for a set of individuals in a population (Lande & Arnold, 1983; Arnold & Wade, 1984a; Arnold & Wade, 1984b). In addition, the selection gradients are directly relevant to models for the evolution of quantitative traits (see below).

This multivariate approach has been used to estimate selection on phenotypic plasticity by considering an individual's (or genotype's) phenotype in different environments (T_i) as distinct, correlated traits – that is, as a vector of distinct, correlated measures for each value T_i: $\{zT_1), z(T_2), \ldots z(T_n)\}$. The resulting selection gradient vector $\underline{\boldsymbol{\beta}}$ thus represents the strength of directional selection on the trait as expressed in each environment T_i . Returning to our caterpillar example, the TPC for relative growth rate (RGR) for each caterpillar is represented as the vector $\underline{z} = \{\text{RGR}(11°\text{C}), \text{RGR}(17°\text{C}), \text{RGR}(23°\text{C}), \text{RGR}(29°\text{C}), \text{RGR}(35°\text{C})\}$; the elements of the selection gradient vector represent directional selection on RGR at each measured temperature T_i. However, because temperature may take on an infinite number of values, we can view the elements of the selection gradient vector $\boldsymbol{\beta}$ as points along a selection gradient function, $\beta(T)$, that indicates the strength of directional selection on the function-valued trait $z(T)$ (Kirkpatrick & Lofsvold, 1988; Gomulkiewicz & Kirkpatrick, 1992; Kirkpatrick & Lofsvold, 1992).

To apply this analysis of selection to our example of TPCs for caterpillar growth rates, we must first consider the various ways that temperature effects on growth rate might influence fitness in *P. rapae*. First, temperatures above 38–40°C can directly reduce caterpillar survival (Kingsolver, 2000). Second, increased growth and development rates at higher temperatures reduce the time to pupation. Because *P. rapae* populations in Seattle have multiple generations per year, reducing the time to pupation can increase the effective number of generations per year and greatly increase the intrinsic rate of increase (Taylor, 1981). Third, increased growth and developmental rates decrease the time caterpillars are exposed to enemies, potentially increasing survival rates to pupation (Benrey & Denno, 1997). Fourth, higher temperatures can result in smaller pupal and adult size, which is correlated with reduced lifetime fecundity (Jones, Hart & Bull, 1982). Thus in our studies we have used estimates of larval survival, time to pupation and pupal mass as relevant aspects of fitness in the field.

As described above, we raised 250 *P. rapae* caterpillars from egg through 3rd instar on collard leaves in a fluctuating (10–30°C) temperature regime in an environmental chamber. Following molt into the 4th instar, we estimated short-term (2–12 h) RGR of each caterpillar at 11, 17, 23, 29 and 35°C. We then placed the caterpillars (now late 4th-instars) on individual collard plants in an experimental collard garden in Seattle in July 1999, and monitored survival and time to pupation and pupal mass for each caterpillar. The collard garden was covered with coarse-mesh, bridal veil netting to exclude social wasps and other large predators.

We can use these data to estimate the selection gradient functions that relate variation in relative growth rate as a function of temperature, as measured in the lab, to variation in survival, time to pupation, and pupal mass measured in the field (Figure 7). Our analyses of the selection gradients indicate no significant relationship between the TPCs for growth rate and larval survival or development time, but detected significant directional selection on TPCs for growth via effects on pupal mass, with positive selection at lower temperatures and negative selection at higher temperatures. If we consider temperatures individually, there was significant selection via pupal mass for increased growth rate at 11°C but not at any other temperature. These results suggest that caterpillars with relatively higher growth rates at low temperatures (11–17°C) had relatively greater pupal masses, whereas caterpillars with relatively higher growth rates at higher (29–35°C) temperatures had similar or relatively smaller pupal masses.

The selection gradient functions $\beta(T)$ in Figure 7 represent smooth interpolations between the elements of the selection gradient vectors $\boldsymbol{\beta}$. To date, only Kirkpatrick et al. (1990) have described methods for fitting selection gradient functions to fitness and phenotypic data. Theirs is again a non-parametric least-squares approach that fits univariate basis functions to estimated selection gradient vectors. One can obtain full or smoothed estimates of $\beta(T)$ using their methods. Presumably REML, spline-smoothing or other methods could also be used to estimate smoothed selection gradients (Ramsay & Silverman, 1997; White, Thompson & Brotherstone, 1999). The estimation of selection gradient functions represents another important unresolved statistical question for investigations of function-valued trait evolution.

Selection and environmental variation

For TPCs and other function-valued traits that are continuous functions of environmental conditions, one

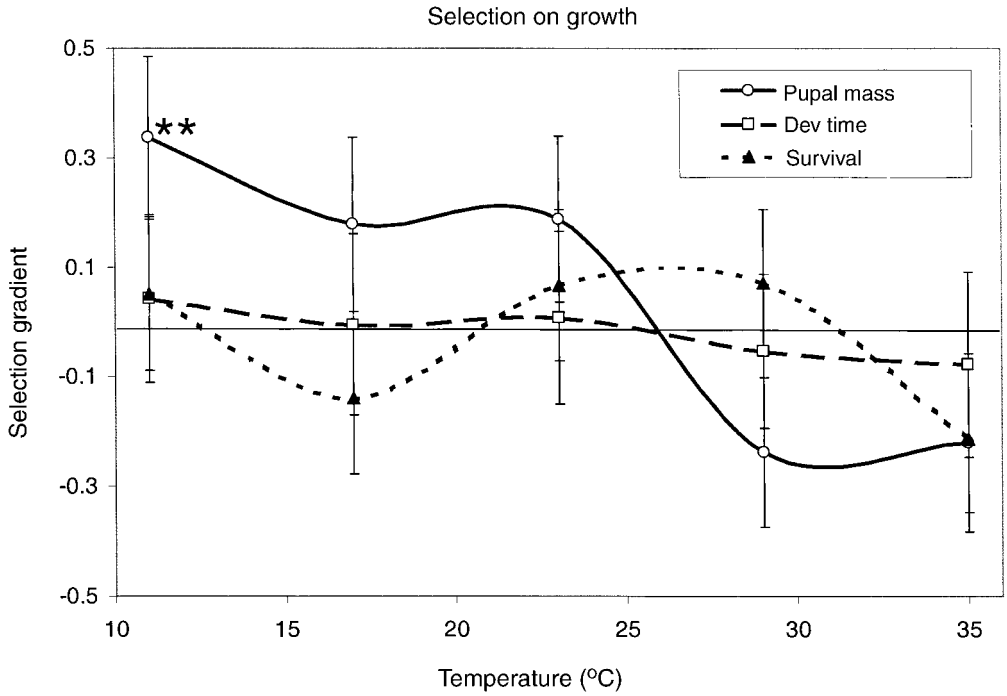

Figure 7. Estimated selection gradient functions for TPCs of relative growth rate for *P. rapae* caterpillars in an experimental collard garden in Seattle, Washington, 28 Jul-5 Aug 1999. Selection functions for three separate components of larval fitness: pupal mass (open circle, solid line); time to popation (squares, dashed line); and survival to pupation (triangles, dotted line). **Indicates that this selection function is significantly different from zero, and that the selection gradient value at 11°C is significantly different from zero. Data from Kingsolver (2001). See text.

would expect that the patterns of selection would depend on the environmental conditions experienced during the period in which selection is occurring. Theoretical models for reaction norms indicate that the selection gradient function will depend on the distribution of environmental states occurring during the selection episode (Gomulkiewicz & Kirkpatrick, 1992). In the present case, selection on the TPC for growth rate $[\beta(T)]$ should depend on the distribution of caterpillar temperatures $[f(T)]$.

How do we characterize the thermal environment of a caterpillar? Caterpillars of *P. rapae* and many other species are thermoconformers: they do not behaviorally orient to solar radiation or wind direction (except to avoid deleteriously high body temperatures), and do not use evaporative cooling or metabolic heat production to regulate body temperature (Casey, 1993). *P. rapae* caterpillars are cryptic green, and usually rest on the shady undersides of leaves, moving to the margins of the leaves to feed (Jones, 1977). Physical models of caterpillars can mimic the body temperatures of early 5th instar *P. rapae* caterpillars within 1–2°C, and thus provide a useful means of quantifying the thermal environment of caterpillars in the field (Kingsolver, 2000).

By placing an array of model caterpillars into the experimental collard garden and recording the mean temperature of each model every 5 min, we can estimate the frequency distribution of temperatures, $[f(T)]$, experienced by *P. rapae* caterpillars during the episode of selection described above (Kingsolver, 2000) (Figure 8). The distribution of operative caterpillar temperatures is bimodal, with modes near 15 and 25°C: indeed, bimodal temperature distributions are typical of many terrestrial environments, as a result of diurnal temperature variation. Mean operative temperatures ranged from 7 to only 29°C, and temperatures were below 23°C during 75% of the time period (yet another cloudy week in Seattle).

Comparing the pattern of selection, $\beta(T)$, (via pupal mass) on TPCs (Figure 7) with the distribution of temperatures, $[f(T)]$, during selection (Figure 8), we see that positive directional selection for increased growth appeared only at temperatures below ~23°C – the range of temperatures that dominated during selection in the field. This supports the idea that the

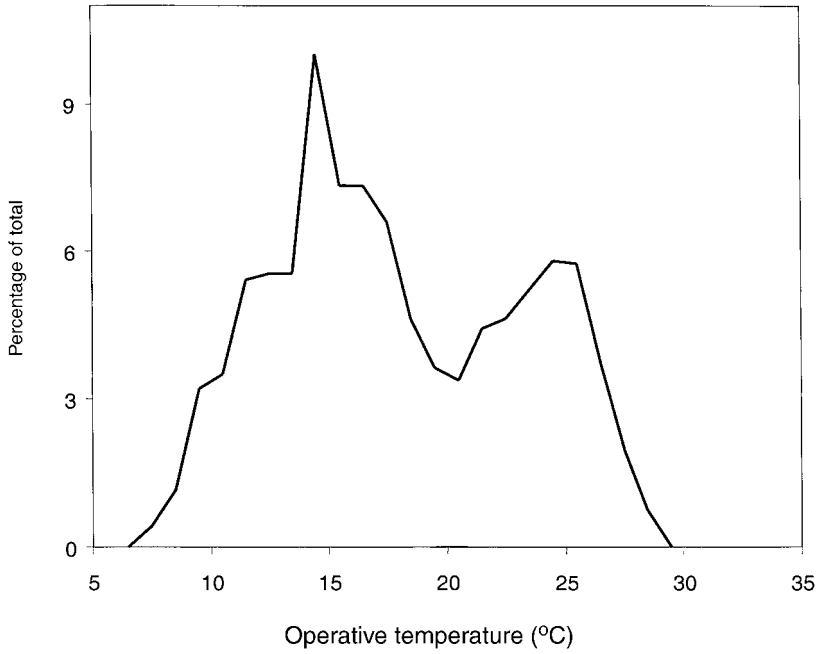

Figure 8. Frequency distribution (% of total time period) for spatial- averaged operative caterpillar temperatures in an experimental collard garden in Seattle, Washington, 28 Jul-5 Aug 1999, during the selection episode in Figure 7. Operative temperatures was measured using 20 physical models of *P. rapae* caterpillars (data and methods from Kingsolver, 2000).

selection gradient function should directly reflect the distribution of environmental conditions. Conversely, changes in thermal conditions will alter patterns of selection on TPC; and the frequency distribution of temperatures experienced by a population may vary substantially within seasons, seasonally, and annually with the vagaries of weather and climate. For example, at the time scale of the 5th larval instar of *P. rapae* (~1–2 weeks), during which more than 70% of all larval growth occurs, the distribution of caterpillar temperatures may vary dramatically within the summer, especially at higher temperatures (Kingsolver, 2000). As a consequence, temporal patterns of selection on TPCs may fluctuate in both predictable and unpredictable ways (Kingsolver & Huey, 1998).

Targets of selection

An important issue for the study of function-valued traits is identifying targets of selection. For thermal performance curves, does selection act primarily on performance at specific temperatures, or does it act primarily on some integrated aspect of performance over a range of temperatures or over the time period of selection (Hertz, Huey & Garland, 1988)? For example, if some aspect of performance (such as sprint speed) is important for escape from predators, selection might act primarily on performance at those temperatures during which predation risks are greatest. Alternatively, if performance (such as relative growth rate) is important for feeding, growth or development, selection might act primarily on total growth or development over some time interval (Beder & Gomulkiewicz, 1998). In the case of growth rate, total growth of an individual over some time interval will be determined by the integrated product of the individual's TPC for growth rate, $z(T)$, and the frequency distribution of temperatures experienced by the caterpillar, $[f(T)]$. Because growth rates of *P. rapae* caterpillars increase strongly with increasing temperatures between 5 and 35°C (Figure 2), growth rates at higher temperatures will have disproportionate effects on total growth: even infrequent periods at higher temperatures can contribute importantly to total growth (Kingsolver, 2000). This has important implications for selection on TPCs (Beder & Gomulkiewicz, 1998), because TPCs that enhance growth, especially at higher temperatures and even at the expense of growth at lower temperatures, could be favored over TPCs that (for example) enhance growth modestly across all temperatures.

Evolutionary reponses to selection

Predicting evolutionary responses in function-valued traits

Once an estimate of the genetic covariance function for a function-valued trait is available, it is not difficult to project the short-term evolutionary trajectory of the trait for estimated or hypothetical selection gradient functions. If $\bar{z}(T)$ is the current mean of a function-valued trait and $\bar{z}'(T)$ its mean in the next generation, then the between-generation change in the mean, $\Delta\bar{z}(T) = \bar{z}'(T) - \bar{z}(T)$ can be computed as

$$\Delta\bar{z}(T) = \int G(T,\theta)\beta(\theta)\,\mathrm{d}\theta,$$

where the partial integration is taken over the range of T (Beder & Gomulkiewicz, 1998; Kirkpatrick & Heckman, 1989). The inter-generational change in the mean $\Delta\bar{z}(T)$ is called the *evolutionary response* to selection. The equation makes clear that the evolutionary response depends on both the pattern of additive genetic variation underlying the function-valued trait, $G(T,\theta)$, and the form and strength of directional selection acting on the trait, $\beta(\theta)$. The integral equation is the infinite-dimensional extension of the more familiar $R = h^2 S$ for a single quantitative trait (S is the intra-generational change in the mean, h^2 is heritability, and R is the evolutionary response to selection: (Falconer & MacKay, 1996)) and $\Delta\bar{\mathbf{z}} = \mathbf{G}\beta$ for the evolutionary response of a multivariate trait z with additive genetic covariance matrix $\mathbf{G}$ and selection gradient vector $\boldsymbol{\beta}$ (Lande, 1979).

To demonstrate the computations, consider the short-term evolutionary response of the mean TPC for RGR to the selection indicated by the selection gradient function shown in Figure 7. The current mean is estimated to be a linear function

$$\hat{\bar{z}}(T) = -6.24 + 0.969T$$

and the estimated selection gradient function is also the linear function

$$\hat{\beta}(T) = 0.6464 - 0.0256T.$$

Note that the pattern of selection favors increased RGR below $T = 25.25$°C and reduced RGR above $T = 25.25$°C (see Figures 7 and 9). For the additive genetic covariance function, we used the smoothed, broad-sense genetic covariance function shown in Figure 3(b),

$$\begin{aligned}\hat{G}(T,\theta) \;=\; & 753 - 125T + 6.242T^2 - 0.0945T^3 \\ & -125\theta + 20.9T\theta - 1.05T^2\theta \\ & +0.0159T^3\theta + 6.24\theta^2 - 1.05T\theta^2 \\ & +0.0529T^2\theta^2 - 0.000807T^3\theta^2 \\ & -0.09460\theta^3 + 0.0160T\theta^3 \\ & -0.000807T^2\theta^3 + 0.0000124T^3\theta^3.\end{aligned}$$

(This requires the admittedly dubious assumptions of no epistasis, no dominance, and no environmental correlations between siblings.) Then the short-term evolutionary response to selection is

$$\begin{aligned}\Delta\hat{\bar{z}}(T) \;=\; & \int_{11}^{35} \hat{G}(T,\theta)\hat{\beta}(\theta)\,\mathrm{d}\theta = -93.0 \\ & +15.8T - 0.776T^2 + 0.0112T^3,\end{aligned}$$

which in turn gives the following prediction for the mean TPC for RGR in the next generation:

$$\begin{aligned}\hat{\bar{z}}'(T) \;=\; & \hat{\bar{z}}(T) + \Delta\hat{\bar{z}}(T) = -99.3 \\ & +16.7T - .776T^2 + 0.0112T^3.\end{aligned}$$

The results are displayed in Figure 9: Figure 9(a) shows the selection gradient function, $\beta(T)$; Figure 9(b) shows the predicted change in the mean phenotype function, and Figure 9(c) shows the mean phenotype function before selection (dashed line), and in the next generation after selection (solid line).

Even though the initial mean function $\hat{\bar{z}}(T)$ and selection gradient function $\hat{\beta}(T)$ are both linear, the mean TPC evolves to become nonlinear. This is a direct consequence of the patterns of genetic variation and covariation present in the genetic covariance function. We emphasize that if we had assumed that $z(T)$ was linear and had characterized variation in $z(T)$ in terms of variation in slopes and intercepts, this predicted nonlinear evolutionary response would have been precluded. This result clearly illustrates the potential problems with making *a priori* assumptions about the parametric form of function-valued traits, as discussed above. Another important point is that the predicted evolutionary response is quite large at higher temperatures; this occurs in part because the genetic variance in RGR increases with temperature (see Figure 3 and 6).

Notice that, as expected from the $\hat{\beta}(T)$ function (Figure 9(a)), the evolved TPC has higher RGR at lower temperatures and lower RGR at higher temperatures as expected given the overall pattern of selection (Figure 9(c)). However, on closer inspection, the

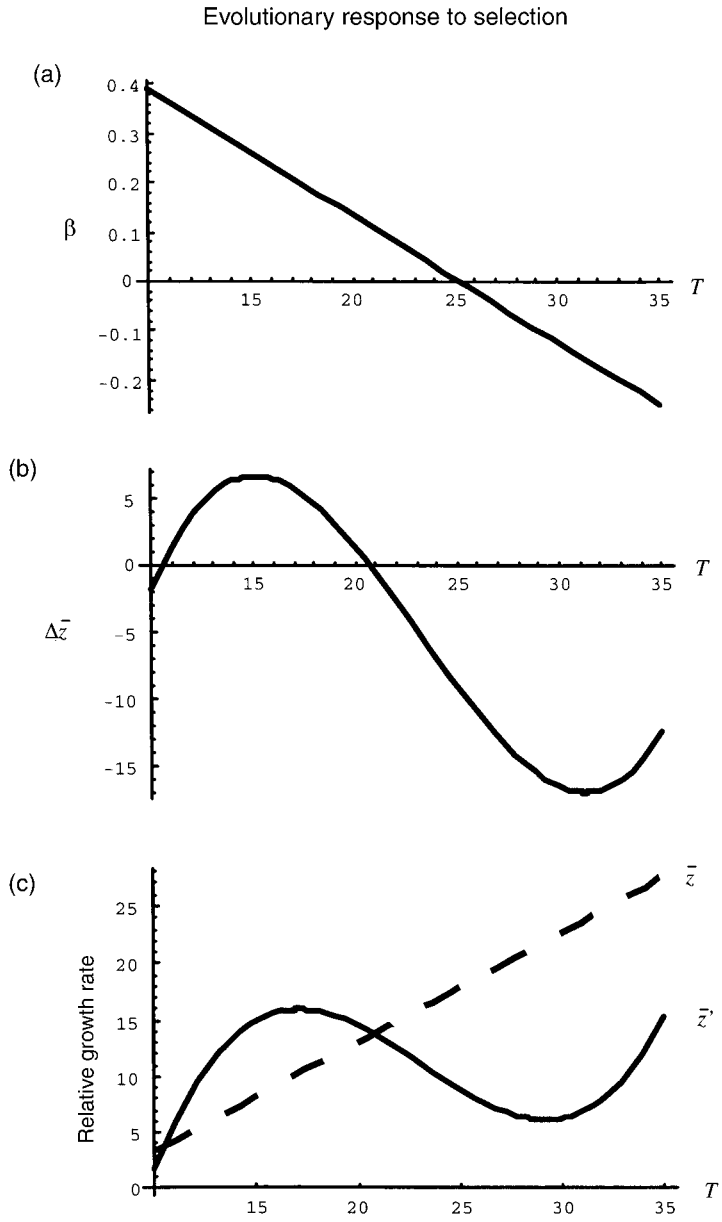

Figure 9. Predicted evolutionary response to selection growth TPCs of *P. rapae* caterpillars. Predictions based on estimates of mean phenotype function (Figure 2), smoothed genetic variance-covariance function (Figure 3(b)), and selection gradient function for pupal mass (Fig. 7). See text for details. (a) Selection gradient function, $\beta(T)$. (b) Predicted change in mean phenotype function. (c) Mean phenotype function before selection (dashed line), and in the next generation (solid line).

evolved TPC does not closely match the favored directions of selection indicated by $\hat{\beta}(T)$. In particular, the form of $\hat{B}(T)$ suggests that higher RGR is favored for all temperatures below, roughly, $T = 25°C$ (Figure 9(a)). Yet between $T \approx 21$ and $T \approx 25°C$ a lower RGR is predicted to evolve (Figure 9(b)). Notice also that, even though the strength of directional selection on RGR increases for temperatures increasingly distant from $T = 25°C$, the greatest responses to selection occur at intermediate temperatures, particularly near $T \approx 3°C$. However, discordance between what is favored by selection and what actually evolves is not unexpected given genetic covariation between RGR across temperatures. Patterns of heritable genetic cov-

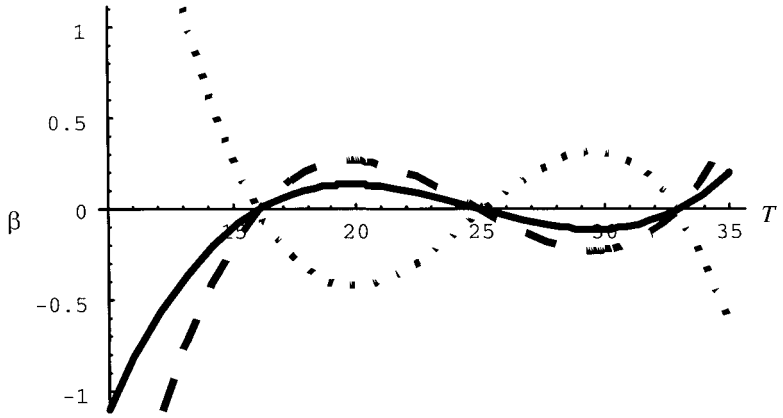

Figure 10. Constraints on evolutionary response to selection. Lines represent selection gradient functions that generate no evolutionary response to selection. Based on the broad-sense genetic variance-covariance function for growth TPCs of *P. rapae* caterpillars (Figure 3(b)).

ariation modify – often significantly – the directions of evolution favored by selection. This has been demonstrated numerous times for multivariate traits (Lande & Arnold, 1983), and the principle applies even more forcefully with function-valued traits (Gomulkiewicz & Kirkpatrick, 1992; Kirkpatrick & Lofsvold, 1992).

Although the general point about how patterns of genetic covariation affect adaptive evolution is clearly valid, the specific incongruities between selection and evolution identified above must be viewed with caution given high degree of uncertainty in the estimates of $\bar{z}$, G, and β. An important future task will be the development of prediction methods for function-valued traits that directly account for estimation error.

Constraints on evolutionary responses

The previous section showed that patterns of genetic covariation can hinder the evolutionary responses favored by selection. For some covariance functions, the patterns of genetic covariation can completely prevent evolutionary responses to particular selection gradients. These selection gradients target principal components for which no genetic variation is present. In fact, one can compute such selection gradient functions directly from the genetic covariance function itself: they are the eigenfunctions associated with a zero eigenvalue. Kirpatrick calls these eigenfunctions 'evolutionary constraints' – they represent directions of adaptation that are evolutionarily inaccessible in the population.

In the analysis of TPCs for RGR, the smallest eigenvalue of $G(T,\theta)$ using the four polynomial smoothed fit was $\hat{\lambda}_4 = 1.64$, which accounts for only about 1% of the total genetic variation. Assuming a modest amount sampling error, it is conceivable that the estimate $\hat{\lambda}_4 = 1.64$ is statistically indistinguishable from $\lambda = 0$, in which case its associated eigenfunction, $\varphi_4 = -6.98 + 0.926T - 0.0391T^2 + 0.000528T^3$, would represent the evolutionary constraints contained in $G(T,\theta)$. Any selection gradient function proportional to $\varphi_4(T)$ will produce no evolutionary response; that is, if $\beta(T) = k\varphi_4(T)$ for any positive or negative constant k, then $\Delta\bar{z}(T) = 0$. Three such examples are displayed in Figure 10. Note that in these examples, the lack of a short-term evolutionary response to selection requires a quite complex pattern of positive and negative selection across temperatures, as can be easily seen in the three $\beta(T)$ functions in Figure 10. It is worth emphasizing that the infinite-dimensional approach deduces evolutionary constraints from estimated patterns of genetic variation. This is in contrast with alternative parametric and 'optimization' approaches that have been used to study TPC evolution in that the latter require the *a priori* identification of evolutionary constraints (Gomulkiewicz, 1998). Of course the detection of zero eigenvalues and estimation of associated evolutionary constraints is a difficult and currently unresolved statistical problem. Still, the infinite-dimensional approach offers the important advantage of allowing evolutionary constraints to be inferred from data rather than be assumed *a priori*.

Prospects and challenges

In this paper we have described an emerging framework for understanding variation, selection and evolution of phenotypic traits that are functions. We have used one specific empirical example – thermal performance curves (TPCs) for growth rate of caterpillars – to demonstrate how models for function-valued traits are natural extensions of more familiar, multivariate models for correlated, quantitative traits. We believe the example illustrates some of the advantages of this framework for understanding the evolution of function-valued traits. First, the function-valued form of the trait can be estimated empirically from empirical data, without relying on *a priori* or *ad hoc* assumptions about the trait. Similarly, phenotypic and genetic variation in the function-valued trait can be quantified in terms of variance-covariance functions that are readily estimated (Figure 3). Second, a key theoretical result is that there may be important constraints on pattern of variation in function-valued traits because of their continuous nature. Such patterns of variation can be quantified in terms of eigenfunctions that are easily interpreted in biological terms; in the case of caterpillar TPCs, for example, eigenfunctions can be directly related to 'generalist-specialist' and 'faster-slower' axes of variation in thermal sensitivity (Figure 4–6).

Third, selection on a function-valued trait is itself a function defined in terms of selection gradient functions. For TPCs, the selection gradient describes how the relationship between an organism's performance and its fitness varies as a function of its temperature; for our preliminary data on caterpillar growth rate, there was positive selection for increased growth rates at lower but not at higher temperatures (Figure 7). The selection function should reflect the distribution of temperatures experienced during selection: for our caterpillar example, lower temperature dominated throughout the selection episode (Figure 8), generating positive selection on growth rates at those temperatures (Figure 7). Finally, we can predict evolutionary responses of function-valued traits in terms of the genetic variance-covariance and the selection gradient functions; one interesting result from our TPC example is that the evolutionary response may be a nonlinear function of temperature, even when the mean phenotype and the selection gradient are themselves linear functions of temperature. This highlights an important advantage of this method over parametric alternatives. For example, if we had described growth TPCs as linear functions and characterized each individual's TPC in terms of a slope and intercept (or equivalent parameters), non-linear evolutionary responses would have been precluded.

Although the framework appears promising, many challenges remain. For example, several different methods have been proposed for estimating genetic variance-covariance functions (Kirkpatrick & Heckman, 1989; Kirkpatrick, Lofsvold & Bulmer, 1990; Kirkpatrick, Hill & Thompson, 1994; Shaeffer & Dekkers, 1994; Meyer & Hill, 1997; Meyer, 1998; Jones, White & Brotherstone, 1999; Pletcher & Geyer, 1999; White, Thompson & Brotherstone, 1999). the relative merits of these methods for different datasets and questions have yet to be fully explored (Kirkpatrick & Bataillon, 1999; Pletcher & Geyer, 1999). In addition, it would be valuable to develop and test specific *a priori* hypotheses about the structure of the genetic variance-covariance function or its eigenfunctions, that are analogous to such tests for the structure of genetic variance-covariance matrices (Cowley & Atchley, 1990; Kingsolver & Wiernasz, 1991). Our hypotheses and associated eigenfunctions for TPCs (Figure 4–6) are a step in this direction, but explicit statistical tests (e.g., analogous to the Mantel test for matrices) are lacking.

Analyses of selection functions have received little attention: to our knowledge the caterpillar TPC example developed here is the first attempt to estimate selection functions from field studies (Kingsolver, 2001). Appropriate statistical methods for estimating and choosing selection functions are largely unexplored. Although we expect a relationship between the estimated selection function and the distribution of environmental states (such as temperature) during selection, it is not clear *a priori* what this relationship should be, nor how best to quantify the relationship. Nor is it clear how uncertainties in our estimates of genetic variance-covariance functions and selection functions should be combined in predicting evolutionary responses. These and other methodological issues all require attention.

A final task is empirical: choosing appropriate and informative study systems. The evolutionary study of function-valued traits requires repeated measurements on (at least) hundreds of individuals of known genetic relatedness, combined with field studies of the fitness consequences of those traits. Identifying systems and traits that are both logistically feasible and evolutionarily important should be an interesting but valuable challenge.

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