

A General Model of Functional Constraints on Phenotypic Evolution

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ABSTRACT: A general model of the functional constraints on the rate and direction of phenotypic evolution is developed using a decomposition of the Lande-Arnold model of multivariate phenotypic evolution. The important feature of the model is the **F** matrix of performance coefficients reflecting the causal relationship between morphophysiological (m-p) and functional performance traits. The structure of **F**, which reflects the functional architecture of the organism, constrains the shape of the adaptive landscape and thus the rate and direction of m-p trait evolution. The rate of m-p trait evolution is a function of the pattern of coefficients in a row of **F**. The sums and variances of these rows are related to current concepts of evolvability. The direction of m-p trait evolution through m-p trait space is a function of the functional covariances among m-p traits. The functional covariance between a pair of m-p traits is a measure of how much the traits function together and is computed as the covariance between rows of **F**. Finally, it is shown that genetic covariances between m-p traits and performance traits are a function of the **F** matrix, but a **G** matrix that includes these covariances cannot be used to model functional constraints effectively.

Keywords: functional integration, trade-offs, facilitations, evolvability, correlational selection, performance.

A major goal of evolutionary biology is the elucidation of the mechanisms that bias the rate and direction of phenotypic evolution. Addressing this goal raises two related questions. First, why do some phenotypic traits evolve rapidly and others slowly or not at all? Second, why do populations repeatedly evolve along preferred paths through phenotypic space, making certain regions of phenotypic space densely occupied but leaving other regions

sparse or even empty? Ever since Lande (1979; Lande and Arnold 1983), most of the effort in quantitatively modeling these biases, or constraints, on phenotypic evolution has focused on the **G** matrix of genetic variances and covariances among traits (Cheverud 1984, 1988; Lande 1986; Zeng 1988; Houle 1992; Schluter 1996; Hansen et al. 2003).

This article develops the idea that the pattern of selection itself is constrained, not by external features of the environment but by the internal features of functional systems, or functional architecture. More specifically, this article introduces a quantitative model of constraints on the rate and direction of phenotypic evolution due to the distribution of morphological and physiological (m-p) traits among multiple functional systems. While the model is new, the concepts it quantifies are old. For example, functional ecologists have long recognized that functional trade-offs limit adaptation within a niche by precluding the simultaneous optimization of two functional performances (functional performance traits are measures of the ability to perform some task, such as absorb light or run fast). Functional morphologists have advanced this concept by explicitly showing how a trait or trait complex that causally influences multiple performances has limited evolutionary capacity but that decoupling traits within a functional complex (Lauder 1981) or a single trait from multiple performances (Liem 1973) allows for the evolution of greater phenotypic diversity. Finally, evolutionary morphologists have appreciated at least since Stebbins (1950) and Olson and Miller (1958) that some combinations of traits augment function while other combinations compromise function and that this functional interdependency among traits influences the direction of phenotypic evolution (Endler 1995).

The word "constraint" has many usages in the literature, and a definition different from that intended here would lead to an incorrect reading of the model. For the purpose of this article, constraints are features of systems that bias the rate and direction of phenotypic evolution. Constraints on the rate of evolution make a trait more likely to evolve rapidly or slowly, while constraints on the direction of evolution make a phenotype more likely to evolve in some

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directions through the phenotypic trait space than others. “Constraint” as used here does not in any way mean that either rates or directions must occur as predicted by some model or that some rates or directions cannot occur. It only means that some rates and directions are more likely than others. A functional constraint, then, is a bias on the rate and direction of phenotypic evolution due to the distribution of m-p traits among multiple functional systems.

A quantitative model of functional constraints was recently developed to investigate the influence of functional architecture on the evolution of performance (Ghalambor et al. 2003). Here, the model is used to show how functional architecture biases the rate and direction of the evolution of the m-p traits themselves. A major result of the model is the demonstration that this constraint acts by biasing the pattern of selection available to morphological traits (my meaning of “availability” will become clearer further on). One consequence of this bias is that different m-p traits have different capacities to evolve. A second consequence of this bias is the presence of preferred directions of evolution through m-p trait space due to the influence of functional architecture on correlational selection. The preferred directions are determined by patterns of functional integration among the m-p traits. Indeed, the model offers a novel and clear definition of functional integration and shows how functional integration biases patterns of phenotypic variation among populations, species, and higher taxa.

Introduction to the Model

The focus on \mathbf{G} in studies of constraints on phenotypic evolution naturally follows the modeling of phenotypic evolution using the multivariate expansion of the breeder's equation

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

(Lande 1979; Lande and Arnold 1983), where $\Delta \bar{\mathbf{z}}$ is a vector of the standardized, generation-by-generation response (change in mean phenotype) of each trait and $\bar{\mathbf{b}}$ is the vector of mean selection coefficients on each trait (computed as the standard partial regression coefficients of fitness on morphology). The \mathbf{G} matrix is frequently interpreted as the source of constraints on phenotypic evolution, an interpretation that implies that selection coefficients in $\bar{\mathbf{b}}$ can have any combination of values and that each of these combinations is equally likely (the particular combination is simply a function of the environment inhabited by the population). In this view, selection is not a source of constraint. The functional constraint model developed below shows that this view of $\bar{\mathbf{b}}$ is not

a good model for natural selection in the wild because patterns of coefficients in $\bar{\mathbf{b}}$ are biased by functional architecture. That is, some patterns of $\bar{\mathbf{b}}$ are more available than others because of functional constraints.

The form of equation (1), which reflects a history of selective breeding and artificial selection experiments, effectively masks the influence of functional constraints on phenotypic evolution. Functional constraints are unmasked by the decomposition

$$\bar{\mathbf{b}} = \mathbf{F} \bar{\mathbf{w}} \quad (2)$$

(Ghalambor et al. 2003), where \mathbf{F} is a matrix in which each row (f_i) contains the standard partial regression coefficients of each performance on m-p trait i and $\bar{\mathbf{w}}$ is a vector of standard partial regression coefficients of fitness on each performance trait. Functional performance traits are measures of the maximum ability of an organism to perform some fitness-related task, such as run fast, jump high, or swim efficiently, and are critical measures for understanding how organismal design varies among an array of environments (Wainwright and Reilly 1994; Irschick and Garland 2001). The decomposition $\bar{\mathbf{b}} = \mathbf{F} \bar{\mathbf{w}}$ is simply the algebraic form of the familiar morphology \rightarrow performance \rightarrow fitness path model developed in Arnold (1983), which has been utilized primarily to measure performance as a proxy for fitness. The decomposition as developed here is more in the spirit of the verbal models of Liem, Lauder, Stebbins, and Endler, all of whom emphasized the evolutionary consequences of the ubiquity of m-p traits that contribute to multiple functions.

The structure of \mathbf{F} reflects the functional architecture of the m-p system. Within a row of \mathbf{F} , two performance coefficients of opposite sign indicate a functional trade-off between the two performances with respect to that m-p trait. Change in the m-p trait augments one performance at a cost (reduction) to the second performance (by “change” I mean the wholly theoretical idea of manipulating an individual m-p trait while leaving all other traits constant; I do not mean variation across individuals or evolutionary change over generations). The converse of a functional trade-off, when the two performance coefficients have like signs, is a functional facilitation. Net functional trade-offs and facilitations are a function of the similarity in the patterns of performance coefficients among columns of \mathbf{F} . These net functional trade-offs and facilitations are measured by the vector cross-products (the unstandardized vector correlation) among columns, which are conveniently captured in the off-diagonals of the matrix $\mathbf{F}^T \mathbf{F}$.

Trade-offs between life-history traits are sometimes called functional trade-offs, but a life-history trade-off is

somewhat different from the trade-offs among performance traits modeled here. Life-history trade-offs arise because of the variable allocation of limited resources among life-history traits, while performance trade-offs (functional trade-offs as defined here) result from the variable allocation of an m-p trait among performance traits. But the sense of “variable allocation” differs between the two. The allocation of resources among life-history traits can be modified with changes in resource acquisition (de Jong and van Noordwijk 1992), but the allocation of m-p traits among functional systems cannot. One could model life-history trade-offs by using the allocation function as an m-p trait and the life-history traits as performance traits, but alternative (and perhaps better) models of life-history trade-offs are available (Roff et al. 2002; Roff and Fairbairn 2007). By contrast, these alternative models are not sufficient for modeling either the functional trade-offs and facilitations envisioned here or the effects of these trade-offs and facilitations on m-p trait evolution.

The goal of this study is to use the decomposition of \mathbf{b} in equation (2) to demonstrate the presence of functional constraints on m-p trait evolution. Well-known problems with multiple regression estimates (Mitchell-Olds and Shaw (1987) are not relevant to this goal but are relevant to any empirical use of the model. Indeed, modeling functional constraints on m-p trait evolution is not dependent on a quantitative genetic model (eq. [1]) but could start from any model in which the selection function can be decomposed into performance-on-trait and fitness-on-performance components. This could allow, for example, the use of alternative genetic models of phenotypic evolution (Alfaro et al. 2004) combined with theoretical (rather than empirically estimated) models of functional performance (Marks and Lechowicz 2006).

Because functional architecture biases the pattern of selection on m-p traits, the remainder of this article focuses on \mathbf{b} and not $\Delta\bar{z}$. It is ultimately these biases on \mathbf{b} , however, that form the basis of functional constraints on m-p trait evolution ($\Delta\bar{z}$). The analysis does not ignore or discount genetic constraints on m-p trait evolution and most certainly does not suggest that patterns of \mathbf{G} (or $\bar{\mathbf{w}}$) cannot be found that oppose the biases determined by \mathbf{F} . Instead, the analysis simply demonstrates an additional source of constraints on the rate and direction of m-p trait evolution.

Functional Constraints on the Rate of Evolution of M-P Traits

Evolvability, or “the ability of particular features of systems to facilitate change” (West-Eberhard 1998, p. 8417), concerns differential rates of genotypic or phenotypic evolution. Modifications to functional architecture and the

subsequent consequences on the ability of the phenotype to evolve are major components of verbal models of functional constraints on evolvability (Liem 1973; Lauder 1981; Friel and Wainwright 1997). In these models, evolvability is increased following the acquisition of functional redundancy by either structural duplication or functional adoption. Structural duplication occurs when modifications in ontogeny increase the copy number of some m-p trait or trait complex, either by duplication of a developmental process (Hurley et al. 2005) or by the physical division of an initially single structure (Friel and Wainwright 1997). In functional adoption, an m-p trait or trait complex adopts a function that is redundant with that of another trait or complex. The functional redundancy following either of these modifications to functional architecture allows either of the redundant traits to explore new morphologies (with concomitant functional sequelae) without a necessary loss of fitness. For example, Liem (1973) proposed that modifications of the pharyngeal jaw and its muscles in cichlid fishes allowed the jaw to expand its role in food processing, a behavior that was plesiomorphically specific to the oral jaws. The adoption of this behavior by the pharyngeal jaws presumably allowed the oral jaws to specialize food acquisition morphology without compromising food-processing performance (Liem 1973). The evolution of functional redundancy, then, facilitates both the acquisition of novel functions and the separate evolution of multiple functions plesiomorphically coupled to a single m-p trait or complex (Lauder 1981; Schaefer and Lauder 1996; Friel and Wainwright 1997).

The influence of functional architecture on differential rates of phenotypic evolution is easily modeled by equation (2). The rate of m-p trait evolution is a function of the magnitude of selection on the array of m-p traits, that is, the magnitude of the coefficients in \mathbf{b} (see eq. [1]). Selection on m-p trait i , in turn, is the dot product (the sums of the products) of the performance coefficients in row i of \mathbf{F} and the coefficients of selection on each performance trait $\bar{\mathbf{w}}$ (eq. [2]). A selection coefficient on an m-p trait, then, is the weighted sum of the selection coefficients on each of the performances relevant to that trait, where the weights are the performance coefficients. Because the performance coefficients are weights, the sum of the performance coefficients in row i must influence the magnitude of selection on m-p trait i and, therefore, the rate at which trait i will evolve.

As a simple, hypothetical example, imagine two m-p traits (muscle input lever length and muscle cross-sectional area) and two performance traits (ability to dig with large force and ability to rapidly rotate the limb to catch prey). The performance coefficients and the row sums are given in table 1. The selection coefficient on input lever length is then $0.5\bar{w}_1 - 0.5\bar{w}_2$, while that on muscle cross-sectional

Table 1: Simple \mathbf{F} matrix with row sums (Σ)

	Output force	Output speed	Σ
Input lever length	.5	-.5	0
Muscle area	.5	.5	1

area is $0.5\bar{w}_1 + 0.5\bar{w}_2$. If selection on the two performances (\bar{w}_1 and \bar{w}_2) is about equal in magnitude, then selection on input lever length will be near 0, and selection on muscle area will be large. Indeed, regardless of the values of \bar{w}_1 and \bar{w}_2 , selection on muscle area will always be larger than that on input lever length (note that because the w 's relate performance to fitness, these are always positive). The magnitude of selection on input lever length will only approach that of selection on muscle area if either $\bar{w}_1 \gg \bar{w}_2$ or $\bar{w}_2 \gg \bar{w}_1$. Because of functional architecture, muscle area has a high capacity to evolve, while input lever length has a limited capacity to evolve. This differential capacity is captured by differences in the row sums of the performance coefficients (table 1). Morphological and physiological traits with large row sums, in either the positive or negative direction, have the capacity to evolve more rapidly than traits with small row sums; that is, m-p traits with large row sums have a higher functional component of evolvability.

Given the conditions above (performance coefficients of equal magnitude in all rows), a large selection coefficient was available for some traits (muscle area) under many combinations of $\bar{\mathbf{w}}$, but large selection coefficients were available for other traits (input lever length) only under a restricted set of $\bar{\mathbf{w}}$. This suggests that viewing all combinations of the coefficients in $\bar{\mathbf{b}}$ as equally available is wrong. Functional architecture makes some combinations more available than others. But if the performance coefficients are not of equal magnitude (as in the simple example above), m-p traits with small row sums can have large selection coefficients and m-p traits with large row sums can have small selection coefficients, given certain combinations of coefficients in $\bar{\mathbf{w}}$. Does \mathbf{F} still constrain the pattern of coefficients in $\bar{\mathbf{b}}$, even under conditions of variable patterns of f in \mathbf{F} and w in $\bar{\mathbf{w}}$? That is, are some combinations of coefficients in $\bar{\mathbf{b}}$ still more available than others, and can the row sums predict this pattern of relative availability?

This question can be tested by measuring the Pearson correlation between the vector of row sums and $\bar{\mathbf{b}}$, given random variation in \mathbf{F} and $\bar{\mathbf{w}}$, using computer simulation. In the simulation, 100 iterations for each combination of n m-p traits and p performance variables, where $n = 24$ and $2 < p < 10$, were used to generate a distribution of correlations for each level of p . In each iteration, \mathbf{F} was filled with numbers drawn from a random normal distribution with mean 0 and variance 1, and $\bar{\mathbf{w}}$ was filled

with numbers drawn from a random uniform distribution between 0 and 1 (the results are independent of the relative scale of the variances of the two coefficients). The mean correlation between the vector of row sums and $\bar{\mathbf{b}}$, across all levels of p , was 0.88 (95% of the correlations were between 0.63 and 0.99). The correlation decreased with increasing p from a mean of 0.91 at $p = 2$ to 0.87 at $p = 10$. These simulation results clearly show the bias imposed on $\bar{\mathbf{b}}$ by the structure of \mathbf{F} and demonstrate that some m-p traits are more evolvable than others because of functional constraints on the pattern of selection available to the m-p traits.

The structure of \mathbf{F} also influences the capacity of an m-p trait to evolve variation among populations or the capacity to generate trait diversity. Again, because selection coefficients on m-p traits are weighted sums with the performance coefficients as weights, the variance of the performance coefficients in a row of \mathbf{F} (the row variances) must influence the variance of the selection coefficient on the m-p trait. That is, if we replicated a population and placed each in a new environment, each with a different $\bar{\mathbf{w}}$, then there would be among-population variation in the selection coefficient for an m-p trait because of the variation in $\bar{\mathbf{w}}$. Morphological and physiological traits with high row variances will have high among-population variance in $\bar{\beta}$ (the selection coefficient on the m-p trait) under most combinations of $\bar{\mathbf{w}}$, while m-p traits with low row variances will have low among-population variance in $\bar{\beta}$ under most combinations of $\bar{\mathbf{w}}$.

As above, this verbal argument, that the structure of \mathbf{F} influences the capacity of m-p traits to diversify, is easily demonstrated with a computer simulation to compute the correlation between the row variances in \mathbf{F} and the variance in $\bar{\beta}$ among environments. In this simulation, n and p were held constant at 1 and 6, respectively. For each of the iterations, (1) \mathbf{F} was randomly filled as above and (2) 100 random $\bar{\mathbf{w}}$ vectors were constructed (to make $\bar{\mathbf{W}}$), with each of the elements drawn from a random uniform distribution between 0 and 1. Each of these $\bar{\mathbf{w}}$ vectors (columns of $\bar{\mathbf{W}}$) effectively simulates a different environment (and a different combination of selection on each of the six performance traits). Because there is only a single m-p trait, each of the 100 environments j has a single selection-on-m-p-trait coefficient, $\beta_{i(j)} = \mathbf{f}_i \bar{\mathbf{w}}_j$. The variance of the 100 selection coefficients, $\text{Var}(\bar{\beta})$, was computed for each iteration. The row variance (the variance of the performance coefficients for the single m-p trait) is $\text{Var}(f)$. This procedure was iterated 1,000 times to obtain a distribution of $\text{Var}(f)$ and $\text{Var}(\bar{\beta})$. As expected, the structure of \mathbf{F} has a significant effect on the capacity of $\bar{\beta}$, to vary among iterations. The strength of this effect increases with p , as indicated by the r^2 of the linear regression of $\text{Var}(\bar{\beta})$ on $\text{Var}(f)$ ($p = 4$, $r^2 = 0.72$; $p =$

10, $r^2 = 0.82$). Note that since the performance coefficients act as weight, the capacity of an m-p trait to diversify among sites will not only be a function of the row variances of \mathbf{F} but also of the row sums.

Functional Constraints on the Direction of M-P Trait Evolution

Functional architecture also biases the direction of phenotypic evolution through m-p trait space by influencing correlated patterns of selection on m-p traits (correlational selection or selective covariance; Stebbins 1950; Endler 1995; Armbruster and Schwaegerle 1996). Selective covariances result from changes in trait distributions due to a “correlation of their selection pressures” (Felsenstein 1988, p. 452). Felsenstein gives as an example the evolution of darker coloration, shorter limbs, and larger body size as a correlated response to colder temperature.

Felsenstein (1988) modeled correlated evolutionary change by $\mathbf{V} = \mathbf{GCG}$, where \mathbf{C} is the selective covariance matrix and \mathbf{V} is the matrix of phenotypic variances and covariances among populations (Felsenstein 1988). The off-diagonal elements of \mathbf{C} are the measures of correlational selection between two m-p traits scaled as covariances. The first eigenvector of \mathbf{V} is the principal direction of phenotypic evolution due to the combination of genetic constraints and selective covariance.

To see how the selective covariances and, ultimately, the direction of m-p trait evolution are influenced by functional architecture, it is necessary to use equation (2) to decompose the selective covariance matrix by

$$\mathbf{C} = \mathbf{FWF}^T, \quad (3)$$

where \mathbf{W} is the matrix of selective covariances among performance traits. Equation (3) shows that selective covariances among m-p traits have two sources: (1) selective covariances among performance traits and (2) functional covariances among m-p traits. Selective covariances among performance traits occur when performances show correlated responses to common environmental factors. For example, a correlated increase in the ability to escape predators and swim in fast currents is expected in Trinidadian guppies moving into larger streams because larger streams tend to be both more rapid and have more intense predation. Functional covariances among m-p traits are the off-diagonal elements of the matrix \mathbf{FF}^T . These covariances are measures of the similarity among rows of \mathbf{F} (in fact, functional covariances are the unstandardized vector correlations among rows). Because the elements in a row of \mathbf{F} are measures of the effect of trait i on a set of functional abilities, functional covariances measure the direction and magnitude of the functional association between pairs of

m-p traits. Morphological and physiological traits that contribute to multiple functions similarly will have large functional covariances, while traits that contribute largely to different functions will have small functional covariances.

It is useful to expand equation (3), using a small example, to show how the influence of functional covariances on selective covariances among m-p traits changes with increasing levels of selective covariance among performance traits. In this example, there are $n = 2$ m-p traits and $j = 3$ performance traits. The selective covariance between the two m-p traits is the single off-diagonal element of \mathbf{C} and is numerically equal to

$$\begin{aligned} c_{12} = & \mathbf{f}_{11}(\mathbf{f}_{21} \cdot w_{11} + \mathbf{f}_{22} \cdot w_{21} + \mathbf{f}_{23} \cdot w_{31}) \\ & + \mathbf{f}_{12}(\mathbf{f}_{21} \cdot w_{12} + \mathbf{f}_{22} \cdot w_{22} + \mathbf{f}_{23} \cdot w_{32}) \\ & + \mathbf{f}_{13}(\mathbf{f}_{21} \cdot w_{13} + \mathbf{f}_{22} \cdot w_{23} + \mathbf{f}_{23} \cdot w_{33}). \end{aligned} \quad (4)$$

This expanded example of equation (3) clearly shows (with the performance coefficients in bold) that selective covariances among m-p traits are a function of functional covariances (mathematically, \mathbf{C} is a function of \mathbf{FF}^T). Thus, if there is equal selection (w) on all performance traits and no selective covariance among performance traits ($w_{ij} = 0$), equation (3) reduces to $\mathbf{C} = w\mathbf{FF}^T$. Under these conditions, the contribution of \mathbf{C} to the direction of m-p trait evolution through m-p trait space is entirely determined by patterns of functional covariances among m-p traits. If there is nearly equal selection on each performance and there is only a small selective covariance among the performance traits, then the selective covariance on the m-p trait will nearly reduce to a multiple of the functional covariance between the two m-p traits, and the contribution of \mathbf{C} to the direction of evolution through the m-p trait space will be close to the direction specified by \mathbf{FF}^T . But as the selection on performance coefficients increasingly differs, and as the selective covariances on the performance traits increase in magnitude, the pattern of selective covariances on m-p traits will resemble the pattern of functional covariances in \mathbf{FF}^T less and less.

A simulation is used to explore the effect of the magnitude of selective covariances on performance traits on the similarity between patterns of functional covariance (\mathbf{FF}^T) and patterns of selective covariance (\mathbf{C}) among m-p traits. For each iteration of the simulation, an $n \times p$ \mathbf{F} matrix with indirectly controlled vector correlations among the columns (the performance traits) and a random, $p \times p$ selective covariance matrix, \mathbf{W} , were constructed and used to compute \mathbf{C} and \mathbf{FF}^T . The number of m-p traits, n , was set to 24, and the number of performance traits, p , was set to six.

Vector correlations among the columns of \mathbf{F} were in-

directly controlled by constructing performance coefficients using $y_j + N(0, s^2)$, where y_j is a factor unique to each column and $N(0, s^2)$ is a random component. Each y_j was drawn from $N(0, 1)$, and s^2 was set to 0.1, 0.5, 1, or 10 (s^2 was always constant within an iteration). As s^2 increased from 0.1 to 10, the vector correlations among columns of \mathbf{F} decreased from a mean of 0.89 to a mean of 0.34. The latter is essentially the mean vector correlation among columns, given a completely random \mathbf{F} matrix (i.e., $y_j = 0$) when $p = 6$.

Matrix \mathbf{W} was computed as $\mathbf{W} = \mathbf{E}\mathbf{L}\mathbf{E}^T$, where \mathbf{E} is a random orthogonal matrix (Heiberger 1978; Tanner and Thisted 1982) and \mathbf{L} is a diagonal matrix in which the diagonal elements are $l_j = \text{uniform}(0, 1)/q$, with $l_1 = 1$ and q set to 1, 2, 4, or 10. The magnitude of selective covariance was indirectly controlled by q , with $q = 1$ and $q = 10$ resulting in very small and very large selective covariances, respectively. Note that the selective covariances among performance traits in this simulation are independent of the structure of the \mathbf{F} matrix. One hundred iterations at each combination of s^2 and q were performed. The influence of \mathbf{FF}^T on \mathbf{C} was measured by a matrix correlation using only the off-diagonal elements. The effect of the magnitude of the vector correlations among the columns of \mathbf{F} is significant but small, and consequently, the iterations with different s^2 but the same level of q were pooled.

The pattern of functional covariances in \mathbf{FF}^T had a strong influence on the pattern of selective covariances among m-p traits, but, as expected by equations (3) and (4), the level of this influence decreased as the magnitude of correlational selection among performance traits increased (fig. 1). Matrix correlations ranged from near unity at very low levels of correlational selection among performance traits ($r < 0.1$) to about 0.34 at high levels of correlational selection among performance traits ($r = 0.75$). Certainly some correlational selection among performance traits is expected across many functional systems. Even though at high levels of correlational selection among performance traits, where the direction is not highly correlated with the major axes of \mathbf{FF}^T , the resulting patterns of selective covariance on the m-p traits should still make functional sense. For example, the correlated evolution of big mouths, reduced armor, and inconspicuous courtship in benthic stickleback may not be predicted from \mathbf{FF}^T , but the pattern makes functional sense because feeding, antipredator, and reproductive performance are all associated with habitat in sticklebacks. Both components of selective covariance (or correlational selection), then, are functional in nature. The component due to \mathbf{FF}^T arises from internal properties of functional architecture, while the component due to \mathbf{W} arises from how functions vary among environments.

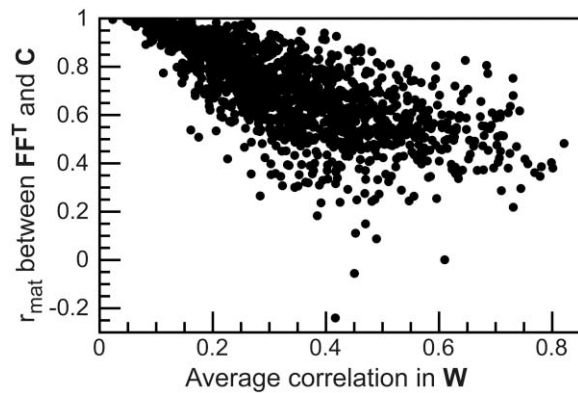


Figure 1: Effect of the average correlation within the matrix of selective covariances among performance traits (\mathbf{W}) on the relative influence of the pattern of functional covariance (\mathbf{FF}^T) on the pattern of selective covariance among m-p traits (\mathbf{C}). The relative influence is measured using a matrix correlation (r_{mat}) of off-diagonal elements between \mathbf{FF}^T and \mathbf{C} . The strong negative correlation shows that, as predicted by equation (4), the relative influence of functional covariance on patterns of selective covariance among m-p traits decreases as the strength of selective covariance among performance traits increases.

The matrix of functional covariances \mathbf{FF}^T is relevant to the many discussions of morphological and, especially, functional integration (Olson and Miller 1958; Pigliucci and Preston 2004). Functional integration, a measure of the global, functional interdependency among a set of m-p traits, is typically measured using the eigenvalue distribution of the matrix containing the statistical correlations among m-p traits (Cheverud et al. 1983; Wagner 1984). The actual functional relationships among the m-p traits are rarely tested but are inferred from simple functional models (e.g., head characters function in feeding while limb characters function in locomotion) or even from the correlation structure itself. One notable exception is the construction of an expected covariance matrix based on a detailed functional analysis of pigment patterns in butterfly wings (Kingsolver 1987; Kingsolver and Wiernasz 1987). The practice of using the intertrait phenotypic correlation matrix and simple functional models to measure functional integration suffers from two fundamental problems. First, it fails to reflect the influence of m-p traits on multiple functional abilities. Second, it is difficult to decompose the measured correlations among m-p traits into functional, developmental, and other factors. The off-diagonal elements of the matrix \mathbf{FF}^T , by contrast, precisely measure the functional association among m-p traits, and the eigenvalue distribution of \mathbf{FF}^T , normalized as vector correlations, should be used instead of the intertrait correlation matrix to estimate functional integration. The major axes of \mathbf{FF}^T can also be compared with those of \mathbf{G} to

test the hypothesis that \mathbf{G} has evolved to reflect patterns of functional integration (Van Valen 1965; Cheverud 1982, 1984, 1988) or with those of \mathbf{A} (the among-population covariance matrix) to test for the presence of a long-term bias of functional constraints on the direction of m-p trait evolution.

Functional Constraints and the G Matrix

Additional insight can be gained by addressing the questions, are functional constraints ultimately genetic in origin, and if so, can functional constraints be modeled with equation (1)? Functional constraints on the rate of evolution (the functional component to evolvability), for example, are certainly due to pleiotropy, but equation (2) shows that this pleiotropy is not modeled by the typical \mathbf{G} matrix of m-p traits but is instead modeled by the \mathbf{F} matrix. This is because functional constraints due to pleiotropy emerge above the level of the m-p traits. Nothing about the \mathbf{G} matrix of m-p traits, then, captures the functional constraints modeled in equation (2).

Nevertheless, it would be wrong to conclude that functional constraints are not ultimately genetic in origin and cannot be a function of an appropriately constructed \mathbf{G} matrix. To see this, compare figure 2A with figure 2B, both of which model the phenotypic evolution of a single m-p trait (z_1) and two performance traits (z_2 and z_3). The evolution of the m-p trait is

$$\Delta z_1 = g_{11} \cdot \beta_1 + g_{12} \cdot \beta_2 + g_{13} \cdot \beta_3$$

using equation (1) and

$$\Delta z_1 = g_{11} \cdot f_{12} \cdot w_2 + g_{11} \cdot f_{13} \cdot w_3$$

using equation (2). Given $\beta_2 = w_2$, $\beta_3 = w_3$, and $\beta_1 = 0$ (since all covariance between fitness and X_1 is due entirely to the paths through the performance traits), we have

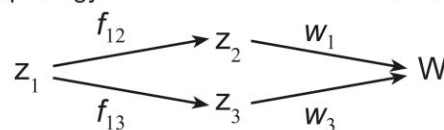
$$g_{12} + g_{13} = g_{11} \cdot f_{12} + g_{11} \cdot f_{13}. \quad (5)$$

Remembering that $\text{Cov}(X, Y) = b_{YX} \times \text{Var}(X, Y)$, we have $g_{12} = g_{11} \cdot f_{12}$ and $g_{13} = g_{11} \cdot f_{13}$. If there are >1 m-p traits, then the genetic covariance between an m-p trait and a performance trait is a function of all the genetic covariances between the m-p trait and all other m-p traits that are relevant to the function. For example, with two m-p traits (z_1 and z_2) and two performance traits (z_3 and z_4), the covariance between z_1 and z_3 is $g_{13} = g_{11} \cdot f_{11} + g_{12} \cdot f_{21}$.

Note that the right-hand side of equation (5) is \mathbf{GF} , and consequently, $\mathbf{G}^* = \mathbf{GF}$, where \mathbf{G}^* is the \mathbf{G} matrix that includes both m-p and performance traits and \mathbf{G} is the

$$\text{A. } \Delta \bar{z} = \mathbf{GF}\bar{w}$$

Morphology \longrightarrow Performance \longrightarrow Fitness



$$\text{B. } \Delta \bar{z} = \mathbf{G}\bar{\mathbf{b}}$$

Morphology \longrightarrow Fitness

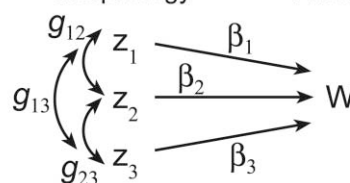


Figure 2: Path models of the phenotypic evolution of a single m-p trait (z_1) and two performance traits (z_2 and z_3) with (A) and without (B) the decomposition in equation (2). Values of f_{ij} are the performance coefficients, values of w_i are the coefficients of selection on performance, values of g_i are genetic covariances, values of β_i are the coefficients of selection on the phenotypic traits, and W is fitness.

matrix with only m-p traits. The \mathbf{G} matrix of any analysis that models performance traits as m-p traits (eq. [1]) effectively captures the effects of functional architecture (the structure of the \mathbf{F} matrix) on m-p trait evolution as long as all performance traits relevant to the set of m-p traits are included in the model. Functional constraints, then, are not something different from but are a category of genetic constraints. Functional constraints are the set of genetic constraints that arise because of how gene products (or m-p structures) interact to produce function. But, because the genetic covariances between m-p traits and performance traits in \mathbf{G}^* are a function of both genetic (co)variances in \mathbf{G} and performance coefficients in \mathbf{F} , the decomposition (eq. [2]) must be used to model the influence of functional constraints on phenotypic evolution.

Conclusion

Gould (1980, p. 101) argued long ago that “functional morphology has yielded a panoply of elegant individual examples and few principles beyond the unenlightening conclusion that animals work well.” While I sympathize with the spirit of this statement, the large body of functional morphological research has, in fact, revealed many general principles (Feder 1987; Hanken and Hall 1993; Wainwright and Reilly 1994; Weibel et al. 1998). Certainly one of the more frequently discussed general principles

within functional morphology is the concept of functional constraints on phenotypic evolution, although the meaning of this concept has been somewhat elusive, as it is used differently within and among different subdisciplines of biology. By embedding this concept into a quantitative framework, the general model of functional constraints developed here helps to disambiguate these different meanings.

The conclusions presented here should influence our view of natural selection on m-p traits and what we mean by "constraint." Gould (1989), for example, argued that constraints should be confined to mechanisms other than or that limit the "canonical" mechanism of evolution (presumably natural selection). Constraints, then, may be genetic constraints contained in the **G** matrix or developmental constraints that limit what phenotypes are available for selection. Gould's statement reflects an artificial-selection-on-individual-trait model of natural selection, which implicitly assumes that any combination of selection coefficients on m-p traits (the elements of **b**) is possible and all combinations are equally likely, given the right external environment. This view is compelling, especially given experimental work demonstrating the power of artificial selection (Weber 1990, 1992). In the wild, of course, m-p traits are not directly selected; rather, they are causally related to tasks that, in turn, are causally related to the ability to survive and reproduce. The decomposition of the breeder's equation in the general model of functional constraints clearly shows that the pattern of coefficients in **b** is itself biased, not by external environmental factors but by internal properties of complex functional systems.

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