



## SYMPOSIUM

# An Integrative Model of Evolutionary Covariance: A Symposium on Body Shape in Fishes

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From the symposium, “Contemporary Approaches to the Study of the Evolution of Fish Body Plan and Fin Shape” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2010 at Seattle, Washington.

**Synopsis** A major direction of current and future biological research is to understand how multiple, interacting functional systems coordinate in producing a body that works. This understanding is complicated by the fact that organisms need to work well in multiple environments, with both predictable and unpredictable environmental perturbations. Furthermore, organismal design reflects a history of past environments and not a plan for future environments. How complex, interacting functional systems evolve, then, is a truly grand challenge. In accepting the challenge, an integrative model of evolutionary covariance is developed. The model combines quantitative genetics, functional morphology/physiology, and functional ecology. The model is used to convene scientists ranging from geneticists, to physiologists, to ecologists, to engineers to facilitate the emergence of body shape in fishes as a model system for understanding how complex, interacting functional systems develop and evolve. Body shape of fish is a complex morphology that (1) results from many developmental paths and (2) functions in many different behaviors. Understanding the coordination and evolution of the many paths from genes to body shape, body shape to function, and function to a working fish body in a dynamic environment is now possible given new technologies from genetics to engineering and new theoretical models that integrate the different levels of biological organization (from genes to ecology).

The body shape of fishes is a complex morphology in want of an integrative symposium. The genesis of this symposium was the question, “why do fishes’ body shape vary?” A textbook answer, and many primary papers in the literature, generally focus on the fluid dynamic consequences of variation in shape and trade-offs in performance between evading predators, maneuvering in structurally complex habitat, and cruising in open water (Webb 1984; Walker 1997; Langerhans 2008 and many others).

We are using this symposium to explore a more integrative model of diversity in fishes’ body shape, one that accounts for mechanisms at multiple biological levels of organization, including genetic, developmental, organ-system, whole-animal, and ecological. We are interested in the architecture at each level of organization, including the mapping functions across levels (both lower to higher and

higher to lower), the emerging constraints on higher levels, and the feedback from higher to lower levels. We want to identify general properties that emerge at different levels such as robustness, evolvability, modularity, redundancy, and compensation. In short, we are using this symposium to explore the mechanisms that “regulate” variation in body shape.

This integrative approach follows from a simple model of the mechanisms that regulate patterns of morphological variation among species. We concentrate on morphology because the focal phenotype of the symposium is body shape, but the model equally applies to any combination of anatomical, physiological, or behavioral traits. Patterns of morphological variation are contained in the correlations between morphological traits among populations or species. What are the mechanisms that regulate the evolution of these correlations?

Our way to address this question is to begin with a simple model of the correlated evolution of a suite of traits within a population. The evolutionary response to selection across one generation in a population is  $\Delta\mathbf{z} = \mathbf{G}\beta$ , where  $\Delta\mathbf{z}$  is the change in a suite of morphological traits (more correctly the change in breeding values),  $\mathbf{G}$  is the matrix of (co)variances of traits and  $\beta$  is the vector of selection coefficients (Lande and Arnold 1983). Let the population instantly colonize different habitats each with its own adaptive peak. The  $\Delta\mathbf{z}$  vectors for each of these populations can be collected in the matrix  $\Delta\mathbf{Z} = \mathbf{G}\mathbf{B}$ , where the columns of  $\mathbf{B}$  contain the selection coefficients for each habitat. The covarying responses among the suite of traits is then

$$\mathbf{S}_A = \mathbf{G}\mathbf{B}\mathbf{B}^T\mathbf{G} \quad (1)$$

where  $\mathbf{S}_A$  is the among-population covariance matrix of the morphological traits after one generation following selection, that is, the covariances among the population means (the  $^T$  for the second  $\mathbf{G}$  in the equation has been dropped because  $\mathbf{G}$  is a symmetric matrix). The among-population or among-species covariances (or correlations) are what we are trying to explain when we ask “what are the mechanisms regulating fish body shape diversity”, so this equation is the nucleus for understanding the causal processes regulating patterns of any morphological variation (not just in fishes’ body shapes) across species.

To fully appreciate the beauty of Equation (1), we need to dissect the middle part,  $\mathbf{B}\mathbf{B}^T$ , which is equivalent to the selective covariance matrix,  $\mathbf{C}$ , described by Felsenstein (1988). The selective covariance between traits reflects a common pattern of selection on the two traits across multiple habitats. For example, deep lakes both with predators and abundant zooplankton should select for larger eyes, more streamlined bodies, and more robust armor in three-spine stickleback while shallow lakes without predators and abundant benthos should select for the opposite morphologies. Felsenstein (1988) was skeptical that we could learn much about the structure of  $\mathbf{B}\mathbf{B}^T$  but Walker (2007) showed that we can. To see this, recall that a column of  $\mathbf{B}$  is the array of selection coefficients on a suite of morphological traits within some specific habitat. Walker decomposed this array by  $\beta = \mathbf{F}\mathbf{w}$ , where  $\mathbf{F}$  is a matrix of performance coefficients and  $\mathbf{w}$  is a vector of selection coefficients for the performance traits in  $\mathbf{F}$ . A performance coefficient is a partial regression coefficient that measures the effect of a morphological

trait on a performance trait. For our instant radiation in multiple habitats described above, then, we have  $\mathbf{B} = \mathbf{F}\mathbf{W}$ , which we can substitute into Equation (1)

$$\mathbf{S}_A = \mathbf{G}\mathbf{F}\mathbf{W}\mathbf{W}^T\mathbf{F}^T\mathbf{G} \quad (2)$$

There is much that is exciting about this equation; it shows that the pattern of covariances in a suite of morphological traits after one generation of selection is a function of the genetic covariances in  $\mathbf{G}$ , which should excite geneticists, the selective covariances among the performance traits in  $\mathbf{W}\mathbf{W}^T$ , which should excite functional ecologists, and the structure of the matrix  $\mathbf{F}\mathbf{F}^T$ , which should excite physiologists and engineers.  $\mathbf{F}\mathbf{F}^T$  is an especially interesting matrix. The elements in this matrix reflect how a pair of morphological traits function synergistically or antagonistically across an array of behaviors. It is a matrix that precisely describes how morphological traits are functionally integrated (Walker 2007).

Although developed as a model of covariance patterns after a single generation of selection, Equation (2) is a good starting point for investigating the mechanisms regulating variation in body shape in fish at all phylogenetic scales. Of course, the  $\mathbf{S}_A$  measured for a group of fishes does not simply equal  $\mathbf{G}\mathbf{F}\mathbf{W}\mathbf{W}^T\mathbf{F}^T\mathbf{G}$ . It cannot, because  $\mathbf{G}$ ,  $\mathbf{F}$ , and  $\mathbf{W}$  all change as populations evolve (although at vastly different rates and for vastly different reasons) so there is no single  $\mathbf{G}$ ,  $\mathbf{F}$ , and  $\mathbf{W}$ . Nor does the model include the effects of genetic drift, historical contingency, or phenotypic plasticity on  $\mathbf{S}_A$ . Equality, however, is not the point of the model. Rather, the model suggests several research directions to investigate how these parameters regulate the evolution of patterns of phenotypic covariance. While Equation (2) is the starting point for modeling patterns of variation among populations or species, we can also use part of it to model the evolution of  $\mathbf{G}$  and the patterns of variation within populations (Arnold et al. 2008).

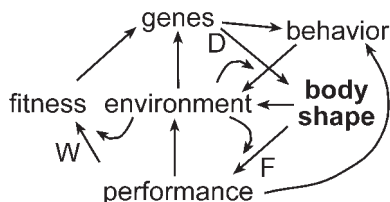
The structure of  $\mathbf{G}$ ,  $\mathbf{F}$ , and  $\mathbf{W}$  all reflect evolved architectures at different levels of biological organization. These architectures bias, or constrain, the direction of phenotypic evolution and, consequently, patterns of variation in body shape among fish in a predictable way. Knowing something about the structures of  $\mathbf{G}$ ,  $\mathbf{F}$ , and  $\mathbf{W}$ , then, facilitates the development of comprehensive models explaining why fishes’ body shapes vary the way it does, from small endemic radiations to the phylogenetically diverse convergences highlighted in textbooks. All of the contributors to this symposium were invited

because of their work on some aspect of **G**, **F**, or **W** relevant to the shapes of fishes' bodies and fins.

### A Path Model of the Regulatory Control of Fishes' Body Shapes

It is also useful to illustrate the simple path model from which Equation (2) was derived and add paths involving behavior and the environment (Fig. 1). The model highlights the fact that the form of **G** differs from that of **F** and **W**. Both **F** and **W** are mapping functions; **F** maps morphology to performance while **W** maps performance to fitness (Fig. 1). In contrast, **G** is the covariance matrix of genetic traits that map to morphology via development. This mapping is a very complex function that we label **D** (Fig. 1). The mappings **D**, **F**, and **W** are complicated by nonlinearity and epistasis, while the network as a whole is complicated by pleiotropy, multitasking, many-to-one mapping, redundancy, interactions with environment and behavior, and feedback loops (Fig. 1).

The core of the path model in Fig. 1 is the inter-generational feedback loop fitness→genes→morphology→performance→fitness. The environment both influences and is influenced by these core mappings. The influence of diet and predators on expressed body shape in fish is now classic work in phenotypic plasticity (Brönmark and Miner 1992; Wimberger 1992; Day et al. 1994). More recent work has focused on how flow affects the development of body shape (Pakkasmaa and Piironen 2000; Grünbaum et al. 2007; Fischer-Rousseau et al. 2010). Of special relevance to the major theme of this symposium, Wund et al. (2008) proposed that plasticity in body shape biased the direction of phenotypic evolution during the colonization of freshwater by the marine three-spine stickleback. The interaction effects between environment and morphology on performance are well-characterized for some phenotypes related to body shape in fish; for

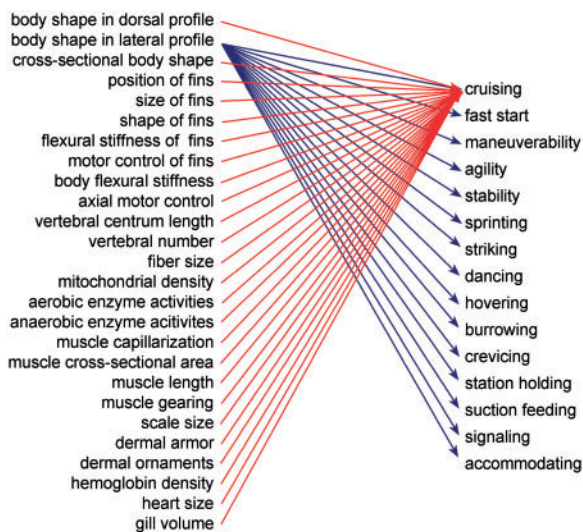


**Fig. 1** A path model of the interrelationships between genes, morphology, performance, fitness, behavior, and environment. The arrows from genes to morphology to performance to fitness are mapping functions reflecting genetic, functional, and ecological architectures. Interactions and feedback loops occur both within and between levels of biological organization.

example, performance of muscle as a function of temperature (Rome et al. 1990) or color-signaling performance as a function of water properties (Endler 1995; Lewandowski and Boughman 2008), but not for body shape itself. Certainly these interactions are important. For example, the optimal body shape for accurately striking suspended prey may vary as a function of the rate of flow carrying the prey.

The feedback loops in Fig. 1 show that the environment is not something independent of the organism but is partly determined by the organism itself. Fish may occupy the high-energy regions of a reef because they are able to do so; behavioral plasticity gives them the opportunity whereas body shape and the consequent swimming performance allow them to take advantage of the opportunity. Indeed, the organism can even create environmental features. For example, a limnetic stickleback creates a higher flow environment than that encountered by a benthic stickleback merely by swimming more frequently and at higher sustained speeds. These environments determined or created by the organism then feedback and regulate gene expression controlling body shape.

Two features of the network in Fig. 1 that profoundly affect its dynamics but that are masked by



**Fig. 2** Many-to-one mapping (red arrows converging to the right) and multitasking (blue arrows diverging to the right) are the yin and yang of functional biology. This example is at the level from morphology to performance. The left-hand column lists a subset of the many morpho-physiological traits that influence, or map to, cruising (steady swimming) performance in fish. Most of these traits could be subdivided further. Any one of these morpho-physiological traits operates within many functional systems (multitasking). The right-hand column shows many of the performance traits that are influenced by body shape.

the simplicity of the diagram are many-to-one mapping and multitasking (Fig. 2). Many-to-one mapping is the phenomenon of multiple factors at a lower level affecting a single trait at a higher level (Wainwright et al. 2005). Multitasking is the yang to many-to-one mapping's yin. It is the phenomenon of a single factor at a lower level contributing to multiple traits at a higher level.

Many-to-one mapping is well known and not controversial; many genes contribute to a single quantitative trait (Peichel, in this issue). There are multiple anatomical paths that generate the same body plan (see Ward and Mehta, in this issue; Mehta and Ward, in this issue, on the multiple paths producing elongate body shapes), and there are many functional paths that increase any performance (Ghalambor et al. 2003; Fig. 2). A major question arising from many-to-one mapping is, given selection for some trait, and multiple paths that contribute to the trait, why is the response to selection rapid along some paths but slow along others? That is, what makes some paths more evolvable? Most of the work addressing this question has focused on the structure of  $\mathbf{G}$  (McGuigan, in this issue) or the genomic factors that structure  $\mathbf{G}$  (Peichel, in this issue). Some continuous traits are more evolvable than others because they have more additive genetic variance or share less of that variance with other traits (Hansen and Houle 2008). Contingency can play a role. In a study of simulated plants colonizing the same digital habitat, for example, Marks and Lechowicz (2006) showed that the morphological path taken depended on the starting morphology of the founding population. Garland developed a beautiful experimental model that unexpectedly demonstrated the role of contingency (and stochastic processes) in the response to selection for increase in wheel-running activity (Garland et al. 2002; Houle-Leroy et al. 2003; Middleton et al. 2008). All four selected lines have the same magnitude of response but two of the four selected lines have evolved a high frequency of a “mini-muscle” phenotype that is characterized by reduced muscle mass of the hind limb and a large suite of anatomical and physiological correlates. The mini-muscle phenotype is not present in the other two selected lines but is present at low frequency in one of the control lines. This suggests that either the mini-muscle allele was not present at the founding of two selected lines or that the allele was lost in these lines due to genetic drift. The plethora of anatomical and physiological correlates in the mini-muscle phenotype could be due to pleiotropy (Garland et al. 2002) or a change in the adaptive landscape resulting from a different

“starting” morphology (reduced muscle mass of the hind limb).

Pleiotropy is the most well-known example of multitasking. Pleiotropy contributes to the shared additive genetic variance of traits, and thus could either increase (because of added variance) or decrease (because this variance is conditional) evolvability (Hansen 2003). Multitasking morphologies, however, also influence evolvability. In addressing the question of why some morphologies are more evolvable than others, Walker (2007) showed that the evolvability of a morphological trait depends on how that trait facilitates or antagonizes other traits across an array of functions.

Body shape is a supreme multitasker (Fig. 2). The geometry of the fish body affects both whole-body structural properties (Long et al., in this issue) and external fluid dynamics (Tytell et al., in this issue, Webb, in this issue) and consequently, swimming agility, stability, maneuverability, and efficiency. Through these basic functions, body shape influences the ability to perform many behaviors related to swimming, including searching, striking, and capturing prey, evading predators, migration, courtship dances, defending territories, and spawning. Body shape potentially affects nonswimming performances such as suction ability, processing of prey, burrowing, hiding, and crawling. Body shape potentially affects movements that are used as signals to a potential mate, a competitor, or a predator, or the body's geometry itself may act as a signal, or may facilitate other morphological features, such as color patterns, to act as a signal. Finally, geometry of the body has to accommodate both the musculoskeletal system required for all these behaviors and the relatively large digestive system required of all large, active animals.

Understanding why body shape varies among fishes the way it does will require good estimates of all of these performance gradients (Tytell et al., in this issue; Webb and Cotel, in this issue; Long et al. in this issue). To see this, recall Equation (2):  $\mathbf{S}_A = \mathbf{G}\mathbf{F}\mathbf{W}\mathbf{W}^T\mathbf{F}^T\mathbf{G}$ . With the exception of relatively young radiations, the covariance among morphological traits will largely be a function of the structure of two matrices, the functional integration matrix,  $\mathbf{F}\mathbf{F}^T$ , and the selective covariance matrix  $\mathbf{W}\mathbf{W}^T$  (unfortunately, contingency will also influence this by some unknown magnitude). The functional integration matrix is a measure of the magnitude of integration within a suite of traits across a range of functions (Walker 2007). Our ability to model (or explain) patterns of variation and diversity using quantitative functional morphology will be a function of both

how many and which performance gradients are measured. The more the better, and the more relevant (that is, performances that are strongly correlated with fitness) the better. Most functional morphologists/ecologists modeling variation in body shape among populations or species have focused on two performances, endurance in swimming and the ability to make fast starts. Certainly these are easy to measure, and likely relevant to fitness (Walker et al. 2005; Langerhans 2009), but what are the effects of body shape on different feeding-related performances (Mehta and Wainwright 2007; Wainwright et al. 2007) or on ability to climb waterfalls (Blob et al., in this issue), or achieve success in mating? (Rosa-Molinari, in this issue; Langerhans, in this issue).

## The Grand Challenge

Understanding genetic architecture, both its own evolution and its influence on phenotypic evolution, has motivated much of genetics research (Lynch 2007). Given the large volume of research on body shape in fishes, frustratingly little of this research has focused on its genetic and developmental architecture (with the exception of the head region) (Albert et al. 2008). In contrast, there is a long history on the diversity of body shape and this diversity's performance and ecological sequelae. With a few notable exceptions (Schluter 1996; McGuigan et al. 2005), models of variation in body shape of fishes have failed to account for the  $\mathbf{G}$  in Equation (2). The beauty of Equation (2) is that it provides a quantitative framework to fully integrate genetics/developmental genetics and body-shape functional morphology/ecology, two research programs that have matured largely independently of each other.

While there is a long history of research on functional architecture (although very little of this has focused on body shape), its evolution, and its influence on phenotypic evolution, this field has lacked any general model to organize concepts and focus future research. For example, the hypothesis that functional redundancy (Liem 1973; Lauder 1981) or complexity (Alfaro et al. 2004) facilitates diversification can be modeled using Equation (2). Hypotheses of functional integration have generally been inferred either from the phenotypic covariance matrix or from simple qualitative models of function. Kingsolver and Wiernasz (1991) developed a quantitative model of functional integration based on a single measure of performance. The functional integration matrix,  $\mathbf{FF}^T$ , is effectively a generalization of Kingsolver and Wiernasz's specific example. A quick

scan of the literature on performance suggests that we are focusing on too few morphological factors to adequately model trade-offs. The net trade-offs and facilitations matrix,  $\mathbf{F}^T\mathbf{F}$  (Ghalambor et al. 2003), highlights the importance of accounting for all performance-related morphologies when modeling trade-offs. Finally, Equation (2) highlights the need for a research program to systematically measure functional architecture in order to investigate questions similar to those pursued in the study of genetic architecture, such as: What is the shape of performance surfaces? (if nonlinear, then  $\mathbf{F}$  will change as morphology evolves); How pervasive are interaction effects? (an interaction effect reflects a change in the relationship between morphology and performance, given a change in the background morphology. This is analogous to epistasis in the genetic architecture literature) (Koehl 1996); What is the distribution of effect sizes of morphology on performance? How functionally integrated are morphological traits? How modular is functional architecture? Do functional trade-offs and facilitations predict performance trade-offs and facilitations? Developing such a research program should be a high priority, and truly grand, challenge (Schwenk et al. 2009).

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