

**Introduction: The Evolution of Morphology, Performance, and Fitness<sup>1</sup>**

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INTRODUCTION

*Just as the alchemist yearned for a formula that would turn lead into gold, so the modern biologist longs for a conceptual framework that will make any data set coruscate with revelations. The framework described here falls considerably short of such expectations, but then, modern chemistry has not fulfilled the alchemists' most ardent dreams.*

S. J. Arnold (1983, p. 357).

The concept of performance is fundamental to organismal and integrative biology. An organism must perform key tasks or functions—regulate water, ions and temperature; photosynthesize, feed, digest, move, and grow—that are crucial for its survival and reproduction. Understanding how lower-level physiological, morphological, and behavioral traits determine the performance of organisms in various environmental conditions is a central aim of the fields of physiology, functional morphology, and biomechanics (Bartholomew, 1958; Levins, 1968; Bock, 1977, 1980; Huey and Stevenson, 1979).

Similarly, the concept of natural selection is fundamental to evolutionary biology. Selection—the relationship between variation in phenotypic traits and variation in fitness among individuals in a population—is the key driving force of adaptive evolution. Understanding the patterns and intensities of selection on phenotypic traits, and how such selection causes adaptive evolution, are central aims of the fields of evolution and ecology (Endler, 1986; Kingsolver *et al.*, 2001).

In an ASZ symposium 21 years ago, Steve Arnold outlined a novel framework (“morphology, performance, and fitness”) that addressed linkages connecting lower-level phenotypic traits, organismal performance, and fitness. Arnold proposed combining laboratory measurements of individual variation in morphology (or physiology) and in performance with field studies of selection and evolution (Arnold, 1983). He also proposed a specific statistical model for quantifying the magnitude of connections among phenotype, performance, and fitness. Arnold illustrated these connections with a simple path diagram (Fig. 1) showing how different morphological traits influenced (directly

and indirectly) various performance traits, which in turn influenced (directly and indirectly) fitness. By decomposing complex relationships into component parts and linkages, Arnold elegantly illustrated how individual variation in phenotype and performance could be directly related to the mechanisms and patterns of selection and evolution of quantitative traits (Arnold, 1983; Lande and Arnold, 1983).

Despite Arnold's skepticism that his proposed framework would turn lead to gold (see quote above), his paper instantly became a gold mine for diverse biologists. For functional biologists, Arnold's framework provided a way for them to see and study the direct and indirect effects of traits on performance, as well as appreciate the fitness consequences of variation in those traits. Indeed, this framework was a key innovation that contributed to the origin of the field of evolutionary physiology (Feder *et al.*, 1987, 2000; Garland and Carter, 1994).

For evolutionary biologists, who were traditionally focused on evolutionary processes rather than on functional biology, Arnold's paper provided the impetus to look into the black box of functional morphology and physiology. In particular, Arnold's emphasis on the centrality of performance opened a window to exploring mechanistic and functional issues that underlie phenotypic traits.

Perhaps most importantly, Arnold's paper provided a unifying conceptual model that enabled functional biologists and evolutionary biologists to begin to interact productively. Not surprisingly, this paper (and a related one by Lande and Arnold, 1983) continues to be widely cited (Fig. 2) by both functional and evolutionary biologists.

It is worth recalling that the period just prior to Steve's paper was the heyday of Gould and Lewontin (1979), whose blistering critiques of the “adaptationist programme” were both puzzling and deeply unsettling to functional and evolutionary biologists who were accused (with some justification!) of promulgating a Panglossian view of biology. Steve's response (Arnold, 1983, p. 359) was timely, clear cut, and constructive: “It is not enough to complain that adaptation is often invoked without critical evidence (Williams, 1966; Lewontin, 1978, 1979; Gould and Lewontin, 1979). We also need an analytical approach that emphasizes *what can be accomplished* (emphasis ours). The strategy outlined here is a step in the right direction.”

THE ONTOGENY OF MORPHOLOGY—  
PERFORMANCE—FITNESS

The basic concept behind morphology, performance, and fitness is old. The key elements of the

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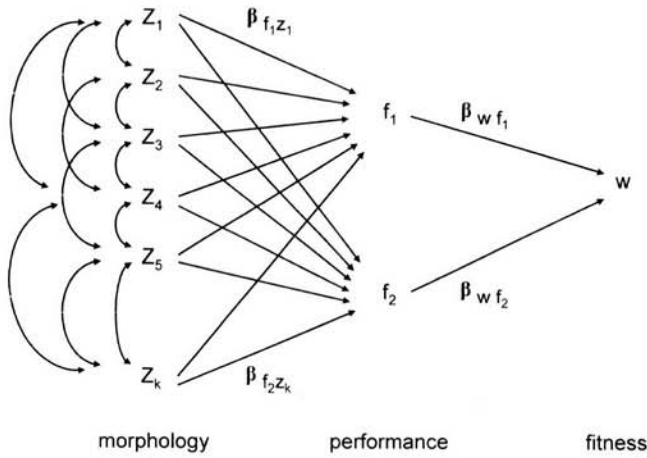


FIG. 1. Path diagram representing the relationships of phenotypic traits ( $z$ ), performance measures ( $f$ ), and fitness ( $w$ ). Redrawn from Figure 3 of Arnold (1983).

concept can be seen in the distinction between proximate *versus* ultimate explanations in biology (Tinbergen, 1951; Mayr, 1961). Functional biologists clearly understood the links between morphology (physiology) and performance: indeed, any textbook of comparative physiology or morphology emphasizes “form-function” relationships. Such a perspective is found in many papers of leaders in this field such as Carl Gans, Knut Schmidt-Nielsen, Walter Bock, and David Wake. Arnold himself acknowledged that his paper was a statistical implementation of a laboratory and field phased program advocated by Bock (1977, 1980).

Perhaps the most famous explication of the concept is found in the writing of George Bartholomew (1964): “. . . there are a number of levels of biological integration and. . . each level finds its explanations of mechanism in the levels below, and its significance in the levels above.” Bart’s statement recognizes that the different “parts” of an organism are inextricably interlinked to other traits and also to the environment, and especially that there was a logical hierarchy of levels of form and function (Bartholomew, 1964).

That was the state of our understanding of form, function, and fitness when Arnold presented his ideas at a symposium at the December 1981 meetings of the American Society of Zoologists. The topic of the symposium, organized by F. Harvey Pough, was “Feeding mechanisms, body size, and the ecology and evolution of snakes.” The bulk of that symposium was classical functional biology and ecology on snakes—to learn what snakes can tell us about adaptation.

Arnold’s paper led off the symposium (or at least the published volume), and it was a striking outlier. The first sentence gave ample warning that something new was “afoot” (admittedly an inappropriate choice of words for a symposium on snakes): “My thesis. . . is that it is possible to measure adaptive significance directly.” What followed must have been shocking to an audience of functional biologists, most

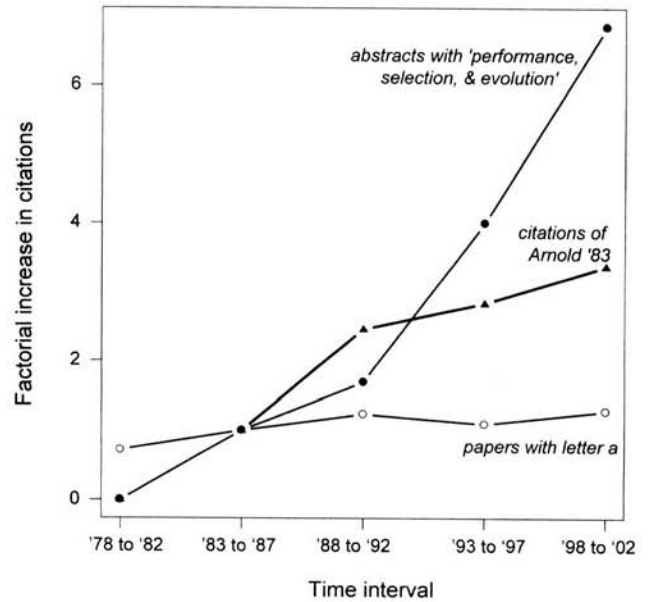


FIG. 2. Factorial increase in the number of citations in BIOSIS of Arnold (1983) (solid triangles), and abstracts that contain the words “performance” and “selection” and “evolution” (solid circles). As a control for changes in BIOSIS with time, the number of citations to papers containing the letter “a” is also included (open circles). Each line is standardized to a value of 1 for the time period 1983 to 1987.

of whom had never previously been exposed to G matrices, selection gradients, path diagrams, and their ilk. Nevertheless, their attraction to this complex new world was smoothed and encouraged by Arnold’s graphical depiction of his concept (Fig. 1).

To implement his approach Arnold advocated a phased research program that started with laboratory measurements of morphology and of performance, and was followed by a field component studying how variation in performance influenced fitness, and how variation in fitness interacted with the underlying genetic architecture to determine the short-term response to selection.

This was a radical and synthetic fusion. Arnold (1983) built upon the models of Lande (Lande, 1979; Lande and Arnold, 1983), which laid out a conceptual and statistical framework for the multivariate generalization of selection theory based on quantitative genetics. Moreover, Arnold emphasized the importance of individual variation within populations, a notion largely unappreciated by functional biologists at the time (see Bennett, 1987). He brought in field approaches, such as those that had successfully measured selection on traits in nature (Fox, 1975; Boag and Grant, 1981). He drew heavily from functional biologists such as Al Bennett, with whom he soon developed a pioneering set of studies on the morphological bases of individual variation in snake locomotor performance (*e.g.*, Arnold and Bennett, 1988). Finally, he adopted Sewall Wright’s method of path analysis, which provided an elegant way of visualizing and quantifying complex relationships (Wright, 1921). Per-

haps the most impressive aspect of the paper is that it showed the connections among approaches that were rarely linked, and that it saw that the solution to a complex problem is to break it down into individual parts that were each amenable to quantification.

#### COMMON THEMES AND VARIATIONS IN THE SYMPOSIUM

The ideas outlined in Arnold (1983) have become an integral part of integrative and evolutionary biology. The relationships of morphological and physiological variation to variation in performance have now been explored in many systems (Garland and Carter, 1994; Feder *et al.*, 2000). Similarly, estimates of the strength of phenotypic selection on quantitative traits in the wild are abundant (Kingsolver *et al.*, 2001). A growing number of case studies have documented microevolution in phenotypic traits in nature (Reznick and Ghalambor, 2001). Nevertheless, implementing Arnold's approach remains a challenging task that requires intensive, long-term studies in carefully chosen study systems. As a result, we are only now able to address Arnold's motivating question—What are the mechanisms and patterns of selection and microevolution of organismal performance in nature?

The papers in this symposium represent progress reports in addressing this question. Collectively they explore a diversity of kinds of organisms, habitats, traits, and environments. The performance traits encompass a diversity of functions and levels of organization, and the environmental features causing selection on those traits are also wide ranging.

Given this biological smorgasbord of taxa, traits, habitats and environments, do any general patterns emerge? We see several recurrent themes: some represent extensions and elaborations of Arnold's original path model, but others explore new directions.

#### ENVIRONMENT, PERFORMANCE, AND FITNESS

Arnold's (1983) approach of correlating performance in the lab with fitness in the field assumes implicitly that performance in the lab is strongly associated with performance in the field. In complex natural environments, this may not be the case. For example, Irschick (this volume) shows how locomotor speed of lizards varies with task, microhabitat, age, and ecological context, and that lab and field measures of speed can sometimes differ dramatically. More generally, behavior can modulate the levels of organismal performance in response to the internal state of the organism or to external environmental conditions, in ways that can obscure or enhance the relationship of morphology to performance (Huey *et al.*, 2003). Moreover, organisms do not always try to be Olympic athletes (Hertz *et al.*, 1988): less performance is sometimes more.

Environmental conditions may also directly affect the expression of the morphological, physiological, or performance traits of an individual or genotype—thus traits are not fixed but are phenotypically plastic. Arnold (1983) notes that behavior, ontogeny, and envi-

ronmental variation may complicate the relationship of performance to fitness; and he proposes modifications to his approach to deal with these issues. Not surprisingly, these issues have become a major focus of the studies represented here; and they emphasize the complex interconnections among environment, performance and fitness.

The relationship between the phenotype value of an individual or genotype and environmental conditions is called a "reaction norm." The environment may alter morphological traits that influence performance, or may impact performance directly. Many of the studies in this volume explore selection and evolution of performance in the context of reaction norms. For example, Schmitt *et al.* (this volume) demonstrate how the ratio of red:far-red light impacts growth and stem elongation in plants, thereby affecting the competitive performance of different genotypes in different light environments. Wikelski and Romero (this volume) show how the thermal environment of marine iguanas affects body size, which in turn impacts many aspects of performance and fitness. Kingsolver and Gomulkiewicz (this volume) and Podolsky (this volume) illustrate how growth, development and reproductive performance in terrestrial insects and intertidal gastropods varies with environmental temperatures, over time scales ranging from hours to days. Lee *et al.* (this volume) document high levels of genetic variation in reaction norms for salinity in populations of copepods.

Environmental conditions can also impact the relationship between performance and fitness. For example, Kingsolver and Gomulkiewicz (this volume) and Schmitt *et al.* (this volume) use models and empirical studies to explore how the frequency distribution of environmental conditions determines the strength of selection on reaction norms, including performance.

These studies illustrate that behavior and environment are integral parts of the impact of performance on fitness of organisms in nature. Many important aspects of performance represent continuous reaction norms that serve as excellent systems for studying selection and evolution of developmental and physiological plasticity. Our mechanistic understanding of light responses in plants and of thermal responses of ectotherms is aiding development of new theoretical models connecting environmental variation, performance and selection.

#### EXPERIMENTAL APPROACHES: UNTANGLING COMPLEX PATHWAYS

In keeping with its emphasis on the consequences of natural variation, Arnold's (1983) path model relies on the statistical (descriptive) correlations among natural morphology, performance and fitness within populations. However, we often take advantage of natural 'experiments' that can generate independent evolutionary events in different populations. For example, the differing environmental conditions on different Galapagos islands have led to enormous differences in mean body size of marine iguanas among islands, al-

lowing biologists to explore the performance and fitness consequences of size (Wikelski and Romero, this volume). Similarly, the replicated invasion of marine copepods into different freshwater river drainages provides compelling evidence for the evolution of salinity tolerance and its consequences for other aspects of performance (Lee *et al.*, this volume). However, it is clear that a mechanistic understanding of the complex pathways from phenotype to fitness must require direct experimental manipulations—we can not rely only on natural variation or natural experiments (Mitchell-Olds and Shaw, 1987; Sinervo *et al.*, 1992). The papers in this symposium illustrate different kinds of such experimental manipulations. Several papers rely on “phenotypic engineering” approaches. Sinervo and Calsbeek (this volume) and Schmitt *et al.* (this volume) use hormone implants or light alterations to manipulate morphological and behavioral traits, to demonstrate the phenotypic targets of selection. Common-garden and reciprocal-transplant experiments are used in many systems to dissect genetic variation and selection on reaction norms. Huey *et al.* (this volume) use experimentally generated mutation accumulation lines in *Drosophila* to magnify variation in performance, and then to demonstrate that the correlations between performance and fitness are weaker than those between life history traits and fitness.

Environmental manipulations are also represented here. The capacity to simulate and manipulate field environmental conditions in the lab or greenhouse is now an important tool for exploring the fitness consequences of performance (Podolsky, this volume; Lee *et al.*, this volume; Schmitt *et al.*, this volume).

In some systems, the selective environment in nature can be manipulated. For example, predator exclusion and addition experiments have elucidated the evolution of predator escape and its life history consequences in guppies (Ghalambor *et al.*, this volume). Similarly, manipulations of the relative frequencies of color morphs reveals the frequency-dependent evolutionary dynamics underlying mating strategies in male side-blotched lizards (Sinervo and Calsbeek, this volume).

These types of experimental manipulations have proven essential for dissecting the complex linkages among morphology, performance, and fitness. The range of experimental tools includes phenotypic, genetic and environmental manipulations, and has been particularly successful in identifying mechanisms of selection in the field. The availability of new genomic and transgenic tools will no doubt expand the use of genetic manipulations in studying performance in the field (Feder, 1999). The contributions by Schmitt *et al.* (this volume) and Sinervo and Carlsbeek (this volume) illustrate elegantly how applying a combination of experimental methods in a single well-chosen system can provide a comprehensive and quantitative level of understanding.

#### TRADEOFFS, CONFLICTS AND CONSTRAINTS

Sustained, directional selection on a set of phenotypic traits should, given appropriate genetic variation, lead to increased mean fitness and greater adaptedness (Lande, 1979). However, the tradeoffs and conflicts that constrain or prevent adaptation are also of interest, and are a major focus of the studies here. Such constraints come in a variety of forms. Ghalambor *et al.* (this volume) expand Arnold's original model to incorporate the tradeoffs among different aspects of performance; they illustrate this model with empirical evidence on tradeoffs between predator escape and reproductive effort in guppies, as mediated by the biomechanics of body shape. Brodie and Ridenhour (this volume) describe how resistance to newt toxin is inversely related to crawling speed in garter snakes. For reaction norms, tradeoffs in performance under different environmental conditions may be widespread. For example, Lee *et al.* (this volume) demonstrate a genetic tradeoff in tolerance to low- vs. high-salinity conditions in copepods.

The divergent evolutionary “interests” of different life stages or different sexes may also generate conflicts that constrain adaptation. For example, Podolsky (this volume) uses a combination of lab, modeling and field studies to show that both embryo survival and timing of adult reproduction are associated with predictable variation in maximum temperatures in the field in an intertidal gastropod. However, embryo survival does not appear to benefit from the non-random pattern of adult reproduction in the field. In side-blotched lizards, clutch size and egg mass are negatively correlated genetically and selectively, leading to conflicting patterns of selection on females and their offspring (Sinervo and Calsbeek, this volume). Similarly, selection on male color morphs may negatively impact the fitness of female progeny, because of the underlying correlations involving hormonal determinants of male mating strategy (including color) and female survival and reproduction (Sinervo and Calsbeek, this volume).

Tradeoffs and conflicts have long been central concepts in evolutionary ecology, essential for understanding the evolution of ecological specialization and diversity (Levins, 1968). Empirical evidence of tradeoffs for individuals within populations has often been elusive, however (Futuyma and Moreno, 1988; Via, 1990). Collectively, the papers in this volume suggest that the study of performance provides particularly fertile ground for documenting tradeoffs and conflicts, perhaps because performance may be closely linked to major fitness components such as age-specific survival and reproduction.

#### BEYOND LINEAR SELECTION

Arnold's (1983) model addresses directional selection on morphological traits mediated by their effects on performance, as represented by linear relationships between traits, performance and fitness. At the time,

evidence for the strength of direction selection on quantitative traits in natural populations was still limited (Endler, 1986); and very little was known about the fitness consequences of individual variation in performance (see ONTOGENY OF THE CONCEPT). Recent studies of selection have emphasized more complex patterns of selection, and this is strongly reflected in this symposium.

Arnold (this volume) extends his original linear model to the quadratic case. This extension is advantageous because it allows one to consider how interactions among traits and among different aspects of performance can generate peaks, ridges, and troughs in the surfaces that relate morphology, performance and fitness. By incorporating this analysis into models of multivariate evolution, Arnold also explores the evolution of performance on adaptive landscapes.

Simple path analyses of selection require that the strength of relationships between morphology, performance and fitness is independent of the density or relative frequency of different genotypes or phenotypes. Several papers explore the consequences of violating these assumptions. For example, selection favoring stem elongation in low-light environments in plants is driven by local population density: rapid stem elongation enables a plant to out-compete neighbors for light under low light conditions (Schmitt *et al.*, this volume). However, manipulation experiments show that stem elongation is actually deleterious at low plant densities, even in low light. Similarly, the success of different male mating strategies in side-blotched lizards depends on the relative frequencies of male mating types in the population; the resulting frequency-dependent pattern of selection on male color generates evolutionary cycles in the frequencies of male and female phenotypes (Sinervo and Calsbeek, this volume).

Brodie and Ridenhour (this volume) describe a new theoretical analysis, based on Lande and Arnold's (1983) model for multivariate evolution, that explores the "reciprocal selection" generated by coevolutionary interactions among species. Their model demonstrates how between-species interactions readily generate correlational selection on suites of behavioral, physiological and other traits. Their analyses of the interactions between snakes and toxic newts illustrate the complex fitness surfaces that can result from reciprocal selection.

The existence of complex fitness surfaces for performance traits is not surprising, because combinations of traits must interact functionally to contribute to whole-organism performance. The papers in this volume illustrate how mechanistic understanding of how trait values impact performance and fitness can inform our analyses of the topography of such fitness surfaces. It remains an open empirical question whether natural fitness surfaces are filled with bumps, ridges and saddles, or have the "normal peaks on a flat plane" topography considered by most theoretical models.

#### CONCLUDING REMARKS—ON THE FUTURE PATH OF MPF

There is a natural ontogeny to many compelling concepts and problems in science. They begin as simple constructs, attract much attention and study, but inevitably become so complex and baroque that they eventually bog down by their own inertial mass. At that point, biologists often abandon ship for new concepts and problems that are still at an early (=easy) developmental stage.

Morphology–performance–fitness clearly addressed a compelling problem in biology: understanding the mechanisms of selection on whole-organism performance in nature. But what sold the idea was its graphical linking of disciplines (Fig. 1) that were traditionally evolving along independent trajectories. After two decades, however, the inevitable complexity once unseen behind that original, simple path diagram is now strikingly apparent, as illustrated by some of the path diagrams presented in papers in this volume (*e.g.*, see Fig. 1 in Irschick; Figs. 1 and 2 in Brodie and Ridenhour; Fig. 1 in Ghalambor *et al.*; Fig. 1 in Sinervo and Calsbeek).

Will morphology–performance–fitness suffer the fate of implosion from complexity, such that biologists will abandon it for newer and easier paradigms? To some extent this must happen. By any standards, it takes a special type of person not to be daunted by figures such as those of Sinervo and Calsbeek (their Fig. 1)! But we think it more likely that Arnold's basic concept will continue to "coruscate with revelations." It will no doubt continue to grow in complexity, to mutate, to recombine with other ideas and approaches, and to spawn interesting empirical studies and theoretical developments that take integrative and evolutionary biology in new directions. That will be the true measure of the long-term fitness of Arnold (1983).

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