

## Multi-trait Selection, Adaptation, and Constraints on the Evolution of Burst Swimming Performance<sup>1</sup>

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**SYNOPSIS.** Whole organism performance represents the integration of numerous physiological, morphological, and behavioral traits. How adaptive changes in performance evolve therefore requires an understanding of how selection acts on multiple integrated traits. Two approaches that lend themselves to studying the evolution of performance in natural populations are the use of quantitative genetics models for estimating the strength of selection acting on multiple quantitative traits and ecological genetic comparisons of populations exhibiting phenotypic differences correlated with environmental variation. In both cases, the ultimate goal is to understand how suites of traits and trade-offs between competing functions respond to natural selection. Here we consider how these two complimentary approaches can be applied to study the adaptive evolution of escape performance in fish. We first present an extension of Arnold's (1983) quantitative genetic approach that explicitly considers how trade-offs between different components of performance interact with the underlying genetics. We propose that such a model can reveal the conditions under which multiple selection pressures will cause adaptive change in traits that influence more than one component of fitness. We then review work on the Atlantic silversides and Trinidadian guppies as two case studies where an ecological genetics approach has been successfully applied to evaluate how the evolution of escape performance trades-off with other components of fitness. We conclude with the general lesson that whole organism performance is embedded in a complex phenotype, and that the net outcome of selection acting on different aspects of the organism will often result in a compromise among competing influences.

### INTRODUCTION

Whole organism performance (*e.g.*, locomotion or foraging) represents the integration or co-adaptation of numerous morphological, physiological, and behavioral traits. How does selection act on such integrated phenotypes to produce adaptive changes in whole organism performance? In theory, performance should evolve in response to the direct and indirect effects of selection acting on the suite of traits that augment performance (Arnold, 1983). However, documenting the relationship between the suite of traits that determines performance and the factors that selected for the evolution of these traits remains a challenging and controversial task (Dawson *et al.*, 1977; Gould and Lewontin, 1979; Gould and Vrba, 1982; Reeve and Sherman, 1993; Rose and Lauder, 1996; Irshick and Garland 2001). This difficulty arises because in most cases ancestral phenotypes and the agents of selection can only be inferred rather than directly measured. One approach to this problem is to directly measure the strength and form of selection acting on performance in natural populations using quantitative genetic models for the evolution of multiple, correlated traits (*e.g.*, Lande, 1979; Lande and Arnold, 1983; Arnold, 1983). Such an approach describes how variation in functionally important morphological traits directly and indi-

rectly influences some measure of performance, which in turn can be related to fitness differences among individuals within a population (*e.g.*, Jayne and Bennett, 1990; Garland and Losos, 1994; Irshick and Garland, 2001). Thus, laboratory studies of functional morphology and physiology can be integrated with field studies of selection to provide insight into the adaptive significance of phenotypic variation within a natural population.

While the quantitative genetics approach focuses on how selection acts on variation among individuals within populations, an ecological genetics approach focuses on the environmental context responsible for phenotypic differences among populations. Ecological genetics thus complements quantitative genetics by focusing on the products of natural selection and their potential causes (Reznick and Travis, 1996). One application of this latter approach to studying the relationship between morphology, performance, and fitness could entail 1) finding populations known to be subjected to different selection pressures; 2) testing for functional morphological and performance variation among populations; 3) evaluating the genetic basis for any morphological and performance differences by rearing organisms in a common environment, and; 4) evaluating the impact of this variation on fitness (see also Reznick and Travis, 1996). The ecological genetics approach to the study of adaptation has provided some of the classic examples of evolution by natural selection in the wild, such as industrial melanism in moths (*e.g.*, Kettlewell, 1955), heavy metal tolerance in plants (*e.g.*, McNeilly, 1968), and shell banding patterns in *Cepaea* snails (Cain and Sheppard, 1954).

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Some common themes revealed from these studies of adaptation have been that the selective environment is often complex, with multiple selection pressures acting on multiple aspects of the phenotype and that adaptation often involves trade-offs or compromises among competing functions (Reznick and Travis, 1996; Reznick and Ghalambor, 2001). These lessons apply particularly well to the evolution of whole organism performance. Multiple selection pressures are known to act on the suite of traits that influence performance. For example, foraging behavior, predation risk, and stream velocity have all been suggested as important selection pressures acting on the relationship between body shape and swimming performance (*e.g.*, Webb, 1978, 1984; Lowe-McConnell, 1987; Schluter and McPhail, 1992; Skúlason and Smith, 1995; Walker, 1997). Likewise, the concept of trade-offs plays a central role in constraining the evolution of whole organism performance, such as the trade-off between speed *versus* endurance (*e.g.*, Bennett *et al.*, 1984; Reidy *et al.*, 2000; van Damme *et al.*, 2002), or stability *versus* maneuverability (Maynard Smith, 1952; Weihs, 2002). Yet, despite the success of an ecological genetics approach in documenting adaptation in natural populations, its application to the evolution of performance has been limited.

Here, we show how both the quantitative and ecological genetics approach can be applied to study how selection acts on multiple, interacting traits to influence the evolution of the fast-start escape response of fish. We focus on how selection acts on trade-offs with escape performance at multiple levels. First, we present a framework for quantifying the strength of trade-offs between different components of performance in a conceptual extension of Arnold's (1983) quantitative genetics approach. Second, we present two ecological genetics case studies demonstrating how selection acts on escape performance via trade-offs and interactions with other components of fitness. We conclude with a discussion of how these two approaches can be merged to evaluate the evolution of performance within the context of the integrated phenotype.

#### THE FAST START ESCAPE RESPONSE

We begin with a short discussion of the fast start escape response in fishes, which will be used as both a heuristic device to develop our theoretical model, and in our empirical examples of how trade-offs influence performance. The fast start escape response is a burst of movement used to rapidly move a fish out of the path of a striking predator (Weihs, 1973). In stage I, a rapid wave of muscle contraction along one side of the vertebral axis bends the fish into a C-shape. In stage II, a large amplitude wave of contralateral muscle contraction rapidly passes caudally. Stage III is variable, but can include braking, gliding to a stop, small to moderate axial undulations that maintain swimming speed, or moderate to large amplitude axial undulations that continue to accelerate the fish. Fast starts are rapid and fast: peak acceleration can occur

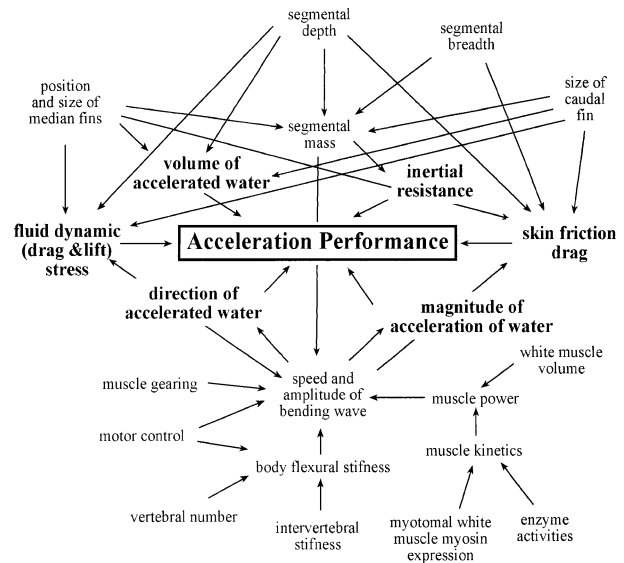


FIG. 1. A path diagram illustrating a few of the many, interrelated factors that potentially influence acceleration performance in the fast start escape response. This diagram highlights the multiple pathways for increasing fast start performance. Adaptive evolution of fast start performance will not only depend on the sign and magnitude of the relationship between each of the characters and acceleration, but also between each of the characters and all other performances that are affected by each character.

within 0.02 sec and has been measured as high as 40 body lengths per second (Domenici and Blake, 1997). Because the fast start is a fundamental locomotor behavior directly related to survival, it is an excellent model to study within Arnold's (1983) morphology-performance-fitness paradigm.

#### A MODEL FOR INVESTIGATING THE EVOLUTION OF PERFORMANCE

Many features, from the molecular to whole organismal level, potentially affect fast start performance (Fig. 1). Figure 1 illustrates a major methodological problem in studies of morphological evolution of characters related to functional performance: quantifying the *causal* effect of any one of the characters on performance variation (Walker, 2002). Our purpose in this paper is not so much to understand morphological evolution but the evolution of performance. It might seem obvious that one could study the evolution of fast start performance by simply focusing on the characters that cause acceleration to vary. But the evolution of acceleration and, ultimately, fast start performance will depend on how changes in these features affect other fitness-related performances. For example, we can envision a scenario where increasing caudal fin area increases the speed of fast starts, decreases swimming endurance, decreases the amount of energy available for the development and maintenance of other tissues, and enhances a male's attractiveness to females who choose mates based on caudal fin area. Changes in any one character will thus have some positive, some negative and many neutral consequences on the perfor-

mance of other functional systems. One consequence of having multiple characters affect performance variation is that there are many pathways to increase performance. Selection will favor change in those characters that simultaneously have the most positive and fewest negative effects on fitness. If each character also affects different types of performance, then adaptation to one function may in turn constrain the evolution of other functions. A consequence of having one character affect multiple performances is the potential for functional trade-offs and its opposite, functional facilitations.

We can quantitatively model the idea of trade-offs and facilitations by expanding Arnold's (1983) model of the relationship between morphology, performance and fitness. Arnold started with the familiar equation modeling the evolution of morphology,  $\Delta z$ , from one generation to the next, in response to selection (Lande, 1979; Lande and Arnold, 1983)

$$\Delta z = G\beta \tag{1}$$

where  $G$  is the genetic covariance matrix of the characters, and  $\beta$  is the vector of selection gradients (the standard partial regression coefficients of fitness on character  $z_i$ ). In his brilliant synthesis of laboratory-based physiological studies of functional performance, natural history based studies of fitness, and quantitative genetic theory, Arnold (1983) decomposed  $\beta$  into  $F$ , the matrix of functional performance gradients (the standard partial regression coefficients of performance  $f_j$  on character  $z_i$ ) and  $w$ , the vector of fitness gradients (the standard partial regression coefficients of fitness on functional performance  $f_j$ )

$$Fw = \beta \tag{2}$$

(Arnold's original presentation used a path model but we are using matrix notation to maintain consistency with what follows). The effect of multiple performances on  $\beta$  is important; to correctly model the evolution of morphology one must know not only all the characters affecting performance but also all of the performances affected by each character.

The evolution of performance ( $\Delta f$ ) from one generation to the next is

$$\Delta f = F^T \Delta z \tag{3}$$

where  $T$  indicates a matrix transpose. Using equations 1 and 2, we can rewrite equation 3 as

$$\Delta f = F^T G F w \tag{4}$$

which shows that the dynamics of performance evolution is not only constrained by the genetic covariances among the morphological traits in  $G$  and the relationships between performance and fitness in  $w$ , but also by the structure of  $F$ . The rows of  $F$  represent how variation in a single character affects multiple performance traits and the patterns in these rows reflect two types of constraints on the evolution of performance. The first of these is the functional trade-off, which occurs when the performance gradients for two

different performance traits on the same character are of opposite sign. The second of these is the functional facilitation, which occurs when the performance gradients for two different performance traits on the same character are of equal sign. Take the case of the effect of caudal fin area as an example. The performance gradients for maximum escape speed, swimming endurance, and attractiveness to females on caudal fin area respectively might look like

$$F_{\text{caudal fin area}} = [2 \ -1 \ 1]$$

(these values represent only the relative magnitude and not the actual standard partial regression coefficients). Increasing caudal fin area will increase escape speed and attractiveness (positive signs) but decrease swimming endurance (negative sign). There is a functional trade-off or constraint between endurance on the one hand and escape speed and attractiveness on the other. By contrast, there is a functional facilitation between escape speed and attractiveness.

The trade-offs and facilitations between any two performance traits is a function of many different characters; the net trade-offs and facilitations are summarized in the matrix

$$F^T F \tag{5}$$

Negative off-diagonal elements represent a net functional trade-off between the associated performance traits while positive off-diagonal elements represent a net functional facilitation between associated performance traits. For our one character x three performance trait example from above, the net trade-off and facilitation matrix is:

$$\begin{bmatrix} 4 & -2 & 2 \\ -2 & 1 & -1 \\ 2 & -1 & 1 \end{bmatrix}$$

Here we see that increases in maximum escape speed will be negatively correlated with endurance and positively correlated with attractiveness. The more negative the off-diagonal element of  $F^T F$ , the larger the trade-off; the more positive the off-diagonal element, the larger the facilitation.

Just as the  $G$  matrix represents the genetic constraints on character evolution, the  $F^T F$  matrix represents the functional constraints on performance evolution. By constraints, we simply mean a positive (facilitating) or negative (limiting) bias (e.g., Maynard Smith *et al.*, 1985) on the rate and direction of evolution. The rate of performance evolution is a function of the structure of  $F^T F$  and the magnitude of the fitness gradient (equation 4). Trade-offs resist while facilitations augment the evolution of performance. The relative ranking of the functional constraints on performance evolution is:

$$c = F^T F \cdot \mathbf{1} \tag{6}$$

where  $\mathbf{1}$  is a vector of ones. A more positive element indicates a stronger functional bias in the direction of

the performance optimum while a more negative element indicates a stronger resistance to evolution in the direction the optimum. The actual rate and direction of evolution will depend on  $\mathbf{G}$  and  $\mathbf{w}$ . Using our hypothetical example, the functional constraints on the evolution of escape speed, swimming endurance, and female attractiveness are

$$\begin{bmatrix} 4 \\ -3 \\ 2 \end{bmatrix}$$

Escape speed evolution is the least resisted because it has a large performance gradient, is facilitated by one performance trait (attractiveness), and forms a trade-off with a trait (swimming endurance) that has a small performance gradient. In contrast, swimming endurance evolution is the most resisted because it has a small performance gradient, is not facilitated, and has trade-offs with two performance traits, one of which has a large performance gradient.

Of course how evolution proceeds will ultimately be determined by the interaction between  $\mathbf{G}$  and  $\mathbf{F}^T\mathbf{F}$ . Yet, how such genetic and functional constraints interact with each other to shape the rate and trajectory of phenotypic evolution will remain an open question until attempts are made to explicitly examine how they jointly or independently respond to selection. Our objective here is simply to present a case for why functional constraints are important and how they can be incorporated into quantitative genetic studies of performance.

#### A TRADE-OFF BETWEEN ESCAPE PERFORMANCE AND LIFE HISTORY TRAITS

The multivariate selection model of performance evolution highlights one consequence of having many traits interacting to influence performance: traits not typically measured under the morphology  $\rightarrow$  performance  $\rightarrow$  fitness paradigm may play major roles in the evolution of performance as well as other important phenotypic traits. For example, functional morphologists and evolutionary physiologists interested in the evolution of swimming performance have largely focussed on morphological (*e.g.*, Webb, 1982, 1984), physiological (*e.g.*, Jayne and Lauder, 1993; Wakeling and Johnston, 1999), and biochemical (*e.g.*, Garenc *et al.*, 1998; Gibb and Dickson, 2002) traits as potential targets of selection. Yet, relatively few studies have considered how swimming performance is influenced by and integrated with life history traits such as growth and reproduction (Kolok and Oris, 1995; James and Johnston, 1998; Plaut, 2002). Likewise, evolutionary ecologists interested in life history evolution have focussed their research efforts on how selection acts on traits such as growth rate, fecundity, and survival (Stearns, 1992; Roff, 1992), without fully integrating measures of performance into their studies. An exception to this separation in focus and an inspiration to our own studies has been the research to understand

the evolutionary and ecological integration of reproductive investment, foraging behavior, ecology, and locomotion in terrestrial animals (*e.g.*, Shine, 1980; Bauwens and Thoen, 1981; Huey and Pianka, 1981; Seigel *et al.*, 1987; Sinervo *et al.*, 1991). Below, we focus on two case studies that have merged these mostly independent fields by documenting the joint evolution of escape performance and life history traits in fish. First, we focus on work by David Conover and colleagues on adaptive variation in growth rate in populations of Atlantic silversides (*Menidia menidia*). We then discuss our own work on the consequences of adaptive variation in reproductive allocation for escape performance in Trinidadian guppies (*Poecilia reticulata*).

#### Case study 1: Atlantic silversides

Populations of Atlantic silversides occur along a latitudinal gradient where northern populations are exposed to lower temperatures and a shorter growing season compared to southern populations (Conover and Present, 1990; Conover, 1992). As a result, northern populations are under strong selection to grow fast and achieve a critical size in order to avoid size-dependent winter mortality (Conover, 1990). Results from natural populations and common garden experiments have revealed that northern silverside populations exhibit rates of food consumption and growth rates that can be two to threefold higher than their southern counterparts (Conover and Present, 1990; Present and Conover, 1992), thus providing evidence for adaptive differences among populations in feeding and growth rates. While it is clear why northern populations should exhibit rapid growth and increased energy acquisition rates, it is less obvious why sub-maximal growth and acquisition rates should be maintained in southern populations (Billerbeck *et al.*, 2001; Lankford *et al.*, 2001). The presence of sub-maximal growth suggests that rapid growth comes at a cost to other components of fitness due to trade-offs with other performance traits such as sustained and escape swimming ability (*e.g.*, Kolok and Oris, 1995; Arendt, 1997, 2003; Gregory and Wood, 1999). While no underlying mechanism has been identified to date, rapid growth could reduce fast start performance by its negative affects on body and fin shape (for example, by allocating excess energy to growth, there may be less energy for growing and maintaining median and caudal fin tissue), muscle enzyme activities, muscle kinetics, and muscle fiber diameter (Fig. 1).

Billerbeck *et al.* (2001) tested the trade-off hypothesis by comparing the swimming performance of northern *versus* southern populations of silversides and between growth manipulated phenotypes reared in a common garden setting. Northern silversides were found to have significantly lower escape and sustained swimming performance compared to southern silversides over a range of temperatures (Billerbeck *et al.*, 2001). Similarly, the "fast" growth-manipulated phenotypes had significantly lower escape and sustained

performance than “slow” growth-manipulated phenotypes. Both results are consistent with a trade-off between growth rate and swimming performance and suggest an important fitness cost to rapid growth (Billerbeck *et al.*, 2001). Complimenting these results, Lankford *et al.*, (2001) compared the vulnerability of mixed schools of northern and southern silversides and mixed schools of growth-manipulated silversides in the presence of natural piscine predators. As expected based on the intrinsic difference in burst swimming performance, northern silversides and the fast-growth phenotypes suffered significantly higher mortality than the southern silversides and slow growth phenotypes respectively (Lankford *et al.*, 2001). Collectively these results suggest that the evolution of escape performance is determined by its trade-off with growth rate and the local selection pressures. In northern populations, escape swimming performance is sacrificed at the expense of rapid growth, whereas in southern populations the opposite is true.

#### Case study 2: Trinidadian guppies

Natural populations of Trinidadian guppies show significant differences in color patterns, behaviors and life histories, all of which are strongly associated with the piscivorous predators they coexist with (Endler, 1994). In larger streams, guppies co-occur with a suite of piscivorous fish that result in high levels of predator driven mortality (*e.g.*, Endler, 1978; Reznick *et al.*, 1996). These predators are excluded from upstream tributaries by rapids and barrier waterfalls. Upstream communities have progressively fewer species, often resulting in small streams with just guppies and the killifish, (*Rivulus hartii*), which preys only on juvenile guppies. This pattern of predator exclusion is repeated among drainages, resulting in a repeated pattern of streams with high and low predation communities. Guppies from high predation communities evolve earlier maturity, increased fecundity, and larger reproductive allocations (% body weight consisting of developing embryos) than their low predation counterparts, providing empirical support for theoretical models of how life histories should evolve under high extrinsic mortality (*e.g.*, Reznick, 1982; Reznick and Bryga, 1996; Reznick *et al.*, 1990, 1996).

Has adaptive life history evolution in guppies constrained the evolution of other traits? Because guppies are live-bearing fish, an unavoidable consequence of pregnancy is an increasing mass and volume as developing embryos cause the female’s abdomen to swell (*e.g.*, Plaut, 2002). Adaptive differences in reproductive allocation between guppy populations may therefore result in reduced escape performance for a number of biomechanical reasons. First, mass is the property of matter that resists acceleration. Consequently, increased clutch mass increases the inertial resistance to acceleration during the fast start. Second, the increased volume necessary to accommodate the larger clutch may increase flexural stiffness and limit axial bending during burst swimming (Beamish, 1978;

James and Johnston, 1998). Third, the increased surface and cross-sectional area that result from the increased volume may increase drag (Beamish, 1978). Finally, excess allocation of energy to eggs and developing embryos may negatively influence the contractile properties of muscle and decrease power output (James and Johnston, 1998). Reduced swimming performance in pregnant females could pose a significant fitness cost, particularly in high predation localities where reproductive allocation and the risk of predation are both higher than for females in low predation environments (Reznick *et al.*, 1996). Indeed, reproduction is known to impair locomotor performance and increase the risk of predation in a wide range of vertebrate and invertebrate species (*e.g.*, Shine, 1980; Bauwens and Thoen, 1981; Seigel *et al.*, 1987; Sinerovo *et al.*, 1991). However, burst swimming performance may also be a target of selection independent of the life histories, because predators are known to select for traits that increase the probability of evading predation (*e.g.*, Seghers, 1974; Feder, 1983; Taylor and McPhail, 1985; Magurran *et al.*, 1992; Watkins, 1996; O’Steen *et al.*, 2002). Predator-mediated selection on swimming performance leads to the alternative prediction that guppies from high predation environments have been selected for faster burst swimming performance. How have guppies responded to these conflicting selection pressures imposed by their predators? We conducted burst swimming trials on second-generation lab born guppies reared in a common environment and found high predation female guppies achieve faster maximum acceleration, maximum velocity, and travel a greater distance compared to females from low predation populations (Ghalambor *et al.*, *in review*). These results suggest that predators have selected for increased escape performance. However, we also found that high predation females pay a higher locomotor cost of reproduction; maximum velocity and the distance traveled decline more rapidly in high predation females as they approach parturition, presumably because of their larger reproductive allocation (Ghalambor *et al.*, *in review*). Thus, the same selection pressure (predator-induced mortality) appears to have selected for increased performance, while simultaneously selecting for reduced performance via adaptive increases in reproductive allocation. These results demonstrate that the evolution of increased reproductive allocation has come at some cost to components of escape performance, such that high predation females have been unable to simultaneously evolve increased reproductive investment while maintaining high levels of escape performance throughout pregnancy.

#### GENERAL PRINCIPLES AND INTEGRATION OF APPROACHES

Adaptations are often described as: “x” is an adaptation to “y.” For example, the change in bill size in Galapagos finches in response to rainfall can be described as an adaptation to the change in the size spec-

trum of available seeds caused by either high rainfall or drought (Boag and Grant, 1981; Price *et al.*, 1984; Gibbs and Grant, 1987). Bill size is thus an adaptation that maximizes the intake of food. However, bill size is correlated with body size, which is an independent target of selection that does not necessarily have a correlated impact on fitness (Price and Grant, 1984). Bill size also affects vocal performance and hence mating success via female mate-choice (Podos, 1997, 2001). How bill size ultimately evolves will thus be a composite of all of the factors that are correlated with bill size and are also components of fitness.

One of the consistent lessons revealed by all extended studies of adaptation is that any given feature of an organism is embedded in a complex phenotype. Because selection acts on phenotypes, the effect of selection on any given facet of the organism is necessarily a composite of direct and indirect effects. Said differently, the net outcome of selection on different aspects of the organism is generally a compromise among competing influences. These influences can be different types of selection that act on the same trait, such as the effects of stream velocity, foraging mode, and predation on the evolution of swimming performance and body shape in fish (Webb, 1984; Lowe-McConnell, 1987; Schluter and McPhail, 1992; Skúlason and Smith, 1995; Walker, 1997). The outcome can also be shaped by interactions or trade-offs among the different components of the phenotype that contribute to fitness, such as the role of growth and reproduction on escape performance in silversides and guppies (see above). If we view the evolution of performance in the context of multiple selection pressures acting on multiple interacting traits, it becomes apparent that diverse perspectives and a multi-disciplinary approach are needed to better understand the conditions under which performance will evolve. The net must be cast more widely if we are to understand the web of traits that are targets of selection and interactions among them that influence the evolution of performance. Likewise, greater progress can be made in understanding how performance evolves if both quantitative and ecological genetic approaches are merged. If we begin with our modification of Arnold's (1983) approach to studying the evolution of performance, we can first characterize the composite effect of selection by incorporating the costs and benefits associated with the multiple components of fitness that are affected by a given aspect of performance. If we apply this logic to the *Menidia* example, then we predict that, in northern latitudes, growth rate has a *large* performance gradient and trades off with escape performance and sustained swimming, which apparently have smaller performance gradients (Billerbeck *et al.*, 2001). The balance shifts at lower latitudes, so that growth rate has a smaller selection gradient than swimming ability and predator avoidance (Lankford *et al.*, 2001). If we applied this logic to guppies, then there clearly is a large selection gradient in favor of both increased predator escape ability and increased investment in reproduc-

tion in high predation environments (Ghalambor *et al.*, in review). The higher rate of decline in swimming performance in later stages of pregnancy in high *versus* low predation guppies suggests that the selection gradient for increased reproduction in females may be larger than that for predator escape ability. High predation guppies are thus potentially slower or no different than low predation guppies when they are in an advanced stage of pregnancy.

The virtue of this perspective is that it views individual adaptations as being embedded in a complex phenotype that incorporates trade-offs, plus yields testable predictions about the relative magnitude of selection gradients for each component of fitness. Alternatively, one could begin with an evaluation of selection gradients then predict trade-offs among competing adaptations. A critical aspect of our approach is that it is associated with comparisons among populations, rather than focusing on just variation within populations, as has been the case in virtually all applications of Arnold's (1983) paradigm. The comparative perspective is essential because the adaptive value of any aspect of performance is context dependent. For example, we assume that a juvenile silverside will always have higher fitness if it is both faster and is larger at the end of its first season (Conover, 1990, 1992). The comparison among populations yields information on the relative value of each component of fitness in different contexts and highlights the way different components of fitness interact with one another. Large size predominates in the high latitude populations while speed and predator escape predominate in the low latitude populations. Similarly in guppies, high predator induced mortality selects for both increased burst swimming speed and increased reproductive allocation, but the interaction revealed in the inter-population comparison shows that the degree to which each aspect of fitness evolves is constrained by its trade-off with the other component of fitness. If we are to evaluate the evolution of adaptive changes in performance in such an integrative fashion, then it is necessary to incorporate such comparisons among populations for which there is a change in the balance of selective factors in order to see the context-dependent nature of the adaptation.

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