

Functional Morphology as a Tool in Ecological Research

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INTRODUCTION

It is axiomatic in biology that phenotypic differences among individuals and species are related to differences in their ecology. Indeed, this notion is a cornerstone of our understanding of the nature of organismal diversity. In general biology texts it is common to see pictures of birds with bills of different sizes and shapes and to read that this variation is related to differences among species in feeding behavior and diet. Thus, the inference is that the morphological differences determine ecological attributes. To the extent that morphology does, in fact, determine ecological patterns, understanding the mechanisms of this relationship can be a powerful explanatory tool in ecological research. But, what exactly is the role of functional morphology in shaping ecological patterns? What major questions in ecology can be addressed through research in functional morphology? And how can the impact of morphology on ecology be assessed rigorously? This chapter will address these questions in an evaluation of the utility of functional morphological approaches in ecology.

Performance: The Link Between Morphology and Ecology

One of the central paradigms in ecomorphology focuses on the role of organismal performance as a crucial link between the organism's phenotype and its ecology (fig. 3.1; Arnold, 1983; Emerson and Arnold, 1989; Huey and Stevenson, 1979; Wainwright, 1991). Here, and throughout this chapter, I use "performance" to refer to an organism's ability to carry out specific behaviors and tasks (e.g., capture prey, escape predation, obtain mates). An individual's phenotype (the way it is constructed) will determine the limits of its performance, because the ability to perform many behaviors is rooted in the design of underlying functional systems. For example, many aspects of flight performance in bats are determined by the aerodynamic consequences of wing shape (Norberg and Rayner, 1987; Norberg, chap. 9, this volume). Thus, design of the locomotor system

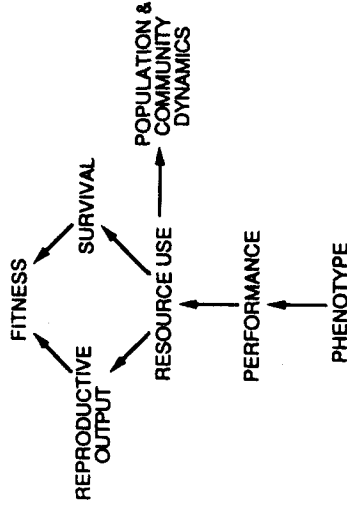


FIGURE 3.1 Flow diagram showing the paths through which phenotypic variation influences individual fitness and population and community ecology. Organismal design (the phenotype) affects ecology because it determines the limits of an individual's ability to perform day-to-day behaviors. Performance capacity interacts with the environment to constrain and shape patterns of resource use. Resource use is the key internal factor determining the two components of fitness, reproductive output and survival. In addition, patterns of resource use play a central role in determining patterns of ecology at the individual level. Individual ecology is compounded to produce population dynamics and community structure. Functional morphology (and other functional sciences) provide an understanding of the causal relationship between phenotype and performance and thus, can play an important role in providing mechanistic explanations for classical ecological questions. Note that the levels of this hierarchy can also exert forces in a downward direction and that direct connections between most levels are possible. For example, locomotor performance can directly influence survival by determining escape-success in predator encounters.

places limits on sprint speed, design of the visual system places limits on visual acuity, and design of the jaw places limits on biting force. Understanding the relationship between the phenotype and organismal performance is the realm of functional morphology and other fields concerned with how organisms function (note that physiology, biomechanics, biochemistry, and molecular biology fit into the scheme discussed in this chapter in much the same way that functional morphology does). The crucial role played by the functional sciences in ecological morphological research is that of elucidating the *causal* relationships between organismal design and behavioral performance.

Once the relationship between morphology and performance has been determined the latter may be related to aspects of ecology. Performance capacity affects ecology in two major ways. First, limitations on performance will constrain the range of environmental resources that individuals can exploit (fig. 3.1). For example, bats with relatively short wings and high wing loading exhibit relatively poor hovering performance and are therefore ineffective hovering nec-

tarivores (Norberg and Rayner, 1987). Morphology shapes ecological patterns by determining the behavioral capacity to exploit resources. Patterns of resource use by individuals combine to produce patterns at the levels of population dynamics and community structure.

A second impact of performance on ecology is its influence on the individual's fitness (fig. 3.1; Arnold, 1983; Emerson and Arnold, 1989; Lande, 1979). Organismal performance affects fitness with varying degrees of directness. Of the two major components of fitness, reproductive output and survival, the latter may be affected directly by predator-escape performance, but, the major path by which performance capacity influences fitness is through its role in shaping patterns of resource use by individuals. Reproductive output is determined by a complex assortment of factors such as the energy available to devote to gamete production and the ability to obtain mates. Performance capacity may play a major role in determining energy intake or success in sexual competition for mates and provides a link between the phenotype and fitness through such channels.

Performance testing is a crucial step toward understanding the ecological and fitness consequences of morphological variation (fig. 3.1) and is a central component of research in ecological morphology. The importance of the functional basis of organismal performance has long been appreciated in comparative physiology (Bartholomew, 1987), but the recognition of its role as a link to ecological and evolutionary issues is more recent (Arnold, 1983; Bock, 1981; Huey and Stevenson, 1979; Lande, 1979). In the following sections I examine the link between morphology and ecology by means of behavioral performance testing and emphasize the power of this approach in resolving ecological questions.

The Role of Functional Morphology

The importance of functional morphology (or any of the functional sciences) in the scheme of linking the phenotype to ecology lies in its use in establishing a causal connection between morphology and performance (Lauder, 1990; Wainwright, 1991; Zweers, 1979). A common approach is to measure the correlation between morphology and performance. Univariate and multivariate correlative analyses are used to explore the relationship between morphology and performance, among species or among individuals within species (Arnold and Bennett, 1988; Ehlinger and Wilson, 1988; Losos, 1990a, b), but a difficulty arises in the interpretation of observed correlations between morphology and performance. Significant correlations do not demonstrate causation, and because so many morphological features tend to covary, both ontogenetically and phylogenetically, the danger of finding spurious correlations is usually high (Lauder, 1990; Wainwright, 1987). For example, larger mammals run faster than smaller mammals

(Garland, 1983), but which of the many functional features that change with body size is the basis of this phenomenon?

To determine the effect of morphology on performance and to separate causal features from spurious correlation it is necessary to understand how a particular functional system operates. Through a functional/biomechanical or physiological analysis of the relevant system, one can generate specific predictions about how variation in particular morphological features will influence performance capacity. When such predictions are supported by the results of laboratory or field performance experiments, the interpretation of the causal nature of the interaction between morphology and performance is greatly enhanced by the biomechanical or physiological principles that underlie the functional analysis. Thus, our belief that the long, slender wings of some bat species cause their relatively poor hovering performance is rooted in our confidence in the aerodynamic theory that underlies the interpretation of wing design.

FROM PHENOTYPE TO PERFORMANCE

The functional basis of behavioral performance is a poorly investigated area of ecomorphology, yet it is an area crucial to developing a more general understanding of the role of morphological variation in shaping ecological patterns. Identifying the performance consequences of morphological variation involves two major steps: (1) a functional analysis, which is used to predict the consequences of variation in morphology for performance, and (2) tests of these predictions with performance experiments, contrived laboratory or field situations usually designed to test the limits of an individual's ability to perform a specific act.

In successful analyses, quantitative predictions of performance can be made on the basis of functional analyses, but only if the functional basis of performance in the behavior under study is clearly understood. However, instances where precise predictions of behavioral performance have been made from only a few morphological variables are rare, usually only occurring in biomechanically simple systems (Kiltie, 1982; Lawrence, 1957; Wainwright, 1987, 1988; Werner, 1974). An example is the pharyngeal jaw apparatus of labrid fishes (Wainwright, 1987, 1988), which is used to crack mollusc shells and other hard prey. The pharyngeal jaw apparatus consists primarily of a single pair of muscles originating from either side of the skull and inserting on either side of a robust lower jaw bone that is suspended below the skull. Mollusc prey are crushed between the pharyngeal jaws as the muscles contract and lift the lower jaw bone up against stationary upper jaw bones. This simple prey-crushing system involves no lever arms, and mollusc-crushing performance is a direct function of the

force-producing capacity of the paired crushing muscles (Wainwright, 1987), a feature that can be independently measured and has a clear morphological basis in the size and the architecture of the muscles. In this case, variation among species and among size classes within species in the morphology of the crushing muscle accurately predicted differences in mollusc crushing performance (Wainwright, 1987, 1988).

Performance studies can be used to dissect systems with complex functional bases. In most cases the exact contribution of any one morphological feature to overall performance in some behavior is not clearly known. Further, performance at most behaviors (e.g., sprint speed, locomotor endurance, auditory acuity) has a complex functional basis, and performance may depend not on a single variable, such as leg length or locomotor muscle mass, but rather some combination of features. In these situations it is possible to address the relative importance of several variables to performance through multivariate analyses such as multiple regression and path analysis. In multiple regression, several independent variables (e.g., body length, hind limb length) can be measured and simultaneously regressed on the performance measure (Garland, 1984; Lauder et al., 1986; Losos, 1990a). To the extent that the independent variables under consideration do not entirely covary, multiple regression can be used to identify those variables most tightly correlated with performance. In cases where suites of performance and morphological variables have been measured, canonical correlation analysis can be used to examine more complex relationships among multiple independent and dependent variables. However, because multiple regression and canonical correlation analyses have no mechanism for distinguishing direct from indirect effects, spurious correlations may plague them just as in univariate cases. The strength of causal interpretations in multiple regression or any statistical analysis depends on a sound understanding of the biomechanical or physiological mechanisms that underlie the inferred causal relationship between phenotype and performance.

An example of such an analysis comes from work on locomotor endurance in the lizard *Crotosaurus similus* (Garland, 1984). In an ontogenetic series of seven lizards, 90% of the variation in endurance capacity (body size-corrected variation) was explained by the combined effects of two morphological variables (thigh and heart mass), citrate synthase activity, and maximum oxygen consumption. This analysis simultaneously ruled out the predictive power of several additional variables, and the results are consistent with the prevalent view that endurance capacity is limited primarily by the maximal capacity of organisms for aerobic metabolism (Bennett, 1984, 1989; Davies et al., 1982; Garland, 1984). Because the capacity for aerobic metabolism cannot be assessed by measurement of a single morphological or physiological variable, but rather is a complex attri-

bute with many components, it was logical to use an approach where the combined effects of several potentially important factors were examined simultaneously.

An interesting twist on the multivariate regression approach has recently been illustrated with work by Emerson and her coworkers on the functional basis of "flying" in frogs (Emerson and Koehl, 1990; Emerson et al., 1990). "Flying" frogs have specialized morphology, enlarged webbed feet and body fringes, that have been thought to be the key components of "flying" ability in these animals, but the consequences of this morphology for performance depend on the postural orientation of the limbs such that some orientations actually decrease performance relative to the unmodified morphology. Further, the suite of morphological modifications do not affect "flying" performance in a simple additive manner; rather, specific combinations produce positively nonadditive effects on performance (Emerson et al., 1990). This case study illustrates the crucial role of behavior in mediating morphological determinants of performance and the potentially complex relationship between morphology and performance.

Performance studies can also be used to test competing functional hypotheses where the functional basis of performance is poorly understood (see also Emerson et al., chap. 6, this volume). An example is provided by Emerson and Diehl (1980), who examined the basis of sticking ability in tree frogs. Several mechanisms of sticking by tree frogs had previously been proposed, including suction, capillarity, and adhesion. These mechanisms suggest very different outcomes of sticking performance of individuals under various conditions. No change in sticking performance was observed when animals were placed in pressure-controlled chambers and exposed to reduced air pressure, thus suggesting that suction is not a major mechanism of sticking. Animals immersed in water immediately slipped from their perch, ruling out capillarity as a sticking mechanism. In these cases the performance tests were used to provide critical tests for hypothesized sticking mechanisms and permitted the researchers to rule out several mechanisms of sticking by tree frogs.

Measuring Performance

The choice of laboratory performance measures is a crucial step in ecological analyses and depends on the goal of the study. In general, when ecological consequences of morphological variation are being studied, performance tests should be designed to mimic the ecologically relevant behavior. However, realistic behaviors are usually complex and may not isolate the function of a single system. Consider the functional basis of sprint speed and its role in determining the ability of individuals to escape predation. Sprint speed can be measured on a race track, but a more ecologically relevant performance measure might entail a staged encounter between predator and prey. Escaping predation

involves more than just sprint speed, however. Prey can choose when to begin their escape movement, and they may differ in their ability to detect and respond to an oncoming predator. In some systems prey rely on a lack of motion to escape detection (e.g., McPeck, 1990). The functional basis of sprint speed may be easier to determine than the functional basis of escape performance, but if staged encounters show that rapid locomotion plays a significant role in avoiding capture, it may be possible to integrate the two tests. A more complex approach, where more than one performance measure is used and in which the performance measures form a natural hierarchy, could help forge a stronger link between morphology and ecology. For example, by measuring both sprint speed and performance in the predator encounter, one can look for patterns of correlation between these two measures that will strengthen the ultimate argument for a causal link between phenotype and ecological patterns.

Performance tests may emphasize an individual's maximal capabilities within a single tightly controlled set of conditions, or the aim may be to determine the effect of some experimentally controlled variable. For example, one of the most heavily studied environmental variables is temperature. Body temperature has pervasive effects on biological rate processes, including behavioral performance (Bennett, 1980, 1990; Prosser, 1973; Wardle, 1975) and their functional basis (Bennett, 1984; Jayne et al., 1990; Josephson, 1981). Similarly, the effects of prey size or type on a predator's capture success and handling time are frequently explored themes in feeding studies (Osenberg and Mittelbach, 1989; Reilly and Lauder, 1988; Stephens and Krebs, 1986, and references therein; Wankowski, 1979; Werner, 1974, 1977).

In most performance tests, experimental individuals are assumed to make a maximal effort, and this assumption is critical in efforts to relate performance to functional design, but it is unlikely that individuals are maximally, or even similarly, motivated to perform during tests. Variation among individuals or among species in motivation level may obscure the relationship between functional determinants and performance. Standardized research protocols may reduce variation in motivation, but problems of motivation are likely to continue to be a key concern in performance studies.

Variation is Fundamental

A key feature of the ecomorphological paradigm illustrated in figure 3.1 is that morphological variation among individuals or among species can be causally linked to variation in performance and ultimately to variation in resource use and fitness. This observation is especially important for two reasons. First, variation is the attribute that gives the paradigm great potential as an explanatory tool in ecology. We seek the consequences of individual variation in morphology for

variation in ecology. Variation in performance that has its roots in morphological differences may account for a tremendous portion of the variation in ecological patterns. Thus, the interaction between the individual's functional capacity and its environment can play a prominent role in shaping ecological patterns at the level of the individual (Schoener, 1986).

Second, naturally occurring morphological variation is convenient for experimental purposes. Several sources of natural variation can be exploited: variation among species, intraspecific body size-related variation, and variation among individuals that is independent of body size. The choice of the source of morphological variation is usually determined by the ecological questions that are of interest. In species comparisons and comparisons among size classes of a single species, body size becomes a complicating factor because nearly all anatomical features covary strongly with body size. Removing the confounding effects of body size by calculating residuals from regressions of the morphological variable on some proxy for body size (usually body length or body mass) has become routine and can be used in both inter- and intraspecific studies (e.g., Garland, 1984; Jayne and Bennett, 1990a, b). In comparisons among size classes of a single species in which the effect of body size is not removed, it may be necessary to rely on the quantitatively different predictions of the relationship between body size and performance produced by the biomechanical models of different components of the functional system (e.g., Wainwright, 1987).

In some situations it may not be possible to isolate completely the effects of a single morphological factor, even by removing the effects of body size, because of the feature's tight correlation with other anatomical structures. In these instances experimental manipulations of morphology can provide tests of the causal connection between morphology and performance (Emerson and Koehl, 1990; Lauder and Reilly, 1988; Nishikawa and Roth, 1991; Reilly and Lauder, 1991; Webb, 1977). If one or a few aspects of morphology are isolated and manipulated, hypotheses about the functional significance of that particular feature can be tested directly. One ingenious approach has been applied by Sinervo and Huey, who manipulated egg yolk of snake embryos to isolate the effects of body size on locomotor performance of newborns (Sinervo, 1990; Sinervo and Huey, 1990). Other manipulative approaches have provided unexpected results and emphasize the need for critical tests of conventional wisdom. For example, Jayne and Bennett (1989) explored the effect of tail length on locomotor performance in the garter snake *Thamnophis sirtalis fitchi*. They found that naturally occurring intermediate tail length was significantly correlated with burst speed in a wild population of snakes. They then tested the implied influence of tail length on burst speed by artificially removing one third of the tail in sixteen snakes and two thirds of the tail in sixteen additional snakes. Loss of one third of the tail had no

influence on burst speed, whereas loss of two thirds of the tail decreased performance by only 5%. These results show that the original correlation between tail length and locomotor performance probably arose from their correlated responses to some other, unmeasured variable.

THE ECOLOGICAL QUESTIONS

Determining the ecological consequences of variation in performance is the second step in an ecomorphological analysis (fig. 3.1). Behavioral performance may underlie patterns of resource use, survival, and reproductive success of individuals. For all of these, the use of performance to explain patterns is a potentially powerful and generally unexploited approach. In this section, I consider the ecological issues that can be addressed within this framework, discuss how those studies can be accomplished, and present some examples.

My aim here is to emphasize the use of functional morphology in answering questions about patterns of resource use. In so doing I will mostly bypass an important third part of the paradigm illustrated in figure 3.1, relating functional design to individual fitness. Interest in studies of natural selection within functional morphology and physiology has recently expanded (Jayne and Bennett, 1990b; Schluter, 1989). These works illustrate the connection between morphology and fitness emphasized by Arnold (1983) and Lande (1979) and have emerged as a powerful way of studying the evolution of functional characters at the population level, but although fitness has become a major focus of ecomorphological research, the use of physiology and functional morphology to explain resource, population, and community dynamics has been almost completely neglected. This not only represents a fertile source of explanations for classical ecological questions but should become an integral part of selection studies in the future. Except in cases where selection acts directly on performance variation, the influence of performance on fitness is mediated by the influence of performance on resource use. In most cases, understanding how performance affects fitness requires understanding how it affects resource use (see, e.g., Boag and Grant, 1981; Grant and Grant, 1989).

Resource Use

The ecological identity of an individual is determined by the suite of environmental resources it uses. It is not surprising, then, that identifying the mechanistic basis of resource use patterns is one of the fundamental problems in ecology (Began et al., 1986; Schoener, 1986). The major environmental resources used by individuals are generally considered to be space, time, food, and reproductive mates. In the discussion that follows, I mostly consider the food resource for convenience, but the comments apply broadly to other resource types as well.

Many factors interact to determine patterns of prey use by predators, but two are fundamental. First, only prey that are physically available can be eaten. The density and relative abundance of different prey ultimately determine their relative desirability, but here I focus on presence or absence in the environment. Hence, the availability of particular prey is the first factor that determines which are consumed by a predator. The second factor is the predator's effectiveness. Only prey that the predator is able to locate, capture, handle, and digest can be included in the diet. Relative proficiency in feeding on different prey is also significant, but here I simply distinguish those prey that can be eaten from those that cannot. Thus, two factors interact to determine what a predator eats, one an environmental factor and the other an intrinsic property of the predator that is a consequence of the design of the feeding system. This principle will apply generally to the use of other environmental resources; patterns of resource use develop as a function of the *interaction* between availability of the resource and the individual's ability to exploit the resource. Because the individual's ability to exploit the resource may have a strong basis in the design of relevant morphological systems, functional morphology holds promise as a source of mechanistic explanations for resource-use patterns.

Other factors may further shape the pattern of prey use, but these factors must exert their effects within the limits determined by prey presence and the predator's capability. Among the most common and important additional factors are the relative energy return involved in foraging on various prey, competitive interactions with other individuals and other species, and the threat of predation associated with foraging in specific habitats. With each of these three forces—energetics, competition, and predation—the behavioral capabilities of the individual play a significant role. Thus, individual performance affects resource use directly by setting absolute limits and more subtly through its role in determining prey choice. For example, a central consideration in optimal foraging models is the relative energy return involved in locating and consuming various prey types (Stephens and Krebs, 1986). For a given prey type, this cost-benefit curve can differ among species or among individuals within species because the capabilities of predators differ (Emerson et al., chap. 6, this volume).

Linking Performance to Resource Use

The ability of an organism to perform some ecologically relevant task can be used to predict the limits of potential resource use. For example, the size of potential prey can be predicted from laboratory feeding experiments (e.g., Werner, 1977). These predictions are then compared with documented patterns of resource use with three possible outcomes. First, actual resource use may fall well below the maximal capabilities of the organism, indicating that some factor other

than the constraint of functional capacity is limiting resource use. Second, the realized resource use may approach the potential resource use indicated by the maximal capabilities of the organism. In this instance performance and its functional basis provide a mechanistic explanation for the pattern of resource use. The third possible outcome is that real resource use may exceed that predicted on the basis of the performance experiments. In this seemingly impossible case, the explanation is that either the performance measures were inaccurate or the individuals are able to invoke some behavioral shift or other strategy that permits them to operate beyond the expected range. An example is the use of protected microhabitats within rocky intertidal shores to avoid the waveforce rigors of immediately adjacent environs (Denny, 1988). Sessile invertebrates and algae exposing themselves to the full force of incoming waves may face certain dislodgement, but by using specific microhabitats, they can avoid the high wave forces and face a more benign environment.

Remarkably, the role of maximal performance in shaping resource use has been tested in few cases (Grant, 1986; Hertz et al., 1988; Kiltie, 1982; Wainwright, 1987). How often do individuals use their maximal capabilities when capturing prey, escaping predators, or obtaining mates? Are maximal capabilities important on a day-to-day basis, or do they only take on prominence during ecological bottlenecks? Little is known of these critical ecomorphological issues.

A much more common approach, and one that has met with considerable success, has been to explain differences in resource-use patterns among species or among size classes within species by identifying key performance differences that allow one species or size class to exploit a resource that another cannot (Osberg and Mittelbach, 1989; Wainwright, 1988). This approach has been a mainstay in physiological ecology since the 1950s (Bennett, 1987; Feder, 1987). Physiologists have directed considerable attention toward the functional capacities of organisms that live in extreme environments. In this context, behavioral capacity is viewed as a permissive feature for one group and a constraint for the other. One well-studied example within functional morphology involves two species of North American sunfishes (Centrarchidae) that commonly co-occur in midwestern lakes, the bluegill (*Lepomis macrochirus*) and the pumpkinseed (*L. gibbosus*). Adult pumpkinseed diets are dominated by snails, whereas bluegill virtually never eat snails, feeding more broadly on zooplankton and benthic invertebrates (Mittelbach, 1984). Pumpkinseeds are able to crush snails with their pharyngeal jaws, but bluegill cannot crush snails (Lauder, 1983; Mittelbach, 1984). The capacity for predation on snails by pumpkinseeds has a clear functional basis in the hypertrophied muscles and bones in the pharyngeal-jaw crushing apparatus and the presence of a phylogenetically derived neuromuscular pattern (Lauder, 1983). This novel muscle activity pattern permits pumpkinseeds

to use their pharyngeal jaws to exert a lethal crushing force against snail shells. Even when bluegill eat snails they do not crush them. Thus, adult pumpkinseeds gain a competitive refuge from bluegill by feeding on a prey resource that bluegill are incapable of eating. In this case the difference between the co-occurring fish species in prey-use patterns can be explained by a difference in snail-crushing ability, which has a functional basis in the design of the feeding system.

Beyond Individual Resource Use to Populations and Communities

Schoener (1986) argued for a hierarchy within ecology where patterns and processes observed at each level have a mechanistic basis in lower levels. He emphasized a three-tiered hierarchy of individual ecology, population ecology, and community ecology. Thus, understanding patterns at the community level ultimately requires the identification of mechanisms determining patterns at the individual-ecological level. I have argued above that individual patterns of resource use are shaped by the interaction between resource availability and behavioral capabilities. The utility of functional morphology in establishing mechanisms that forge community level patterns will depend on the future success of work with individuals.

Case studies of the impact of organismal design on population and community dynamics have been presented by the Grants and their coworkers (summarized by Grant, 1986; Grant and Grant, 1989), and Kingsolver (1989). Theoretical work has also begun to incorporate concepts of organismal function into models of population dynamics (Nisbet et al., 1989; Tilman, 1982). One particularly well-studied example of the link between functional morphology and population and community ecology comes, again, from work with the North American sunfishes (Lauder, 1983; Mittelbach, 1981, 1984, 1986, 1988; Osenberg and Mittelbach, 1989; Osenberg et al., 1988; Werner, 1977; Werner and Hall, 1976, 1977, 1979; Werner et al., 1983). This body of work has shown that the limits of feeding capability of the bluegill and pumpkinseed sunfishes and their primary predator, the largemouth bass (*Micropterus salmoides*) interact with environmental variables to shape patterns of habitat use and the relative abundance of these species.

As discussed above, pumpkinseed sunfish possess phylogenetically derived morphological and neuromuscular specializations that permit adult individuals to feed on snails, a prey resource that bluegill are ineffective at utilizing (Lauder, 1983; Mittelbach, 1984). Correlated with the difference in diet between these species is a difference in habitat use by the adults (Mittelbach, 1984). Pumpkinseeds forage in vegetated areas where snails are found, whereas bluegill feed on open-water zooplankton.

Diet and habitat use by small individuals (<75 mm) of both species contrast with the adult patterns. Small fish of both species feed on soft invertebrate prey

associated with vegetation, even though they might more profitably forage on open-water zooplankton (Mittelbach, 1981). Two explanations for this pattern of resource use by the smaller size classes have been advanced and both have clear bases in functional morphology of the feeding mechanism. First, small pumpkinseeds are unable to use gastropod prey effectively because their crushing muscles are not sufficiently developed (Lauder, 1983; Wainwright et al., 1991). Second, predation pressure from largemouth bass constrains the ability of small fish to exploit open-water habitats. Piscivory by bass is limited by mouth diameter. Prey-handling time increases exponentially as prey diameter approaches that of the bass's mouth (Werner, 1977). Thus, the vulnerability of bluegill and pumpkinseeds drops sharply between 50 and 100 mm body size (Hall and Werner, 1977). At about this body size bluegill leave the vegetated habitat and begin feeding in open water (Hall and Werner, 1977; Werner and Hall, 1977). In a controlled field experiment, Werner et al. (1983) showed that bluegill of all sizes will forage in open-water habitats if they are more profitable but that, in the presence of largemouth bass, smaller fish use the vegetated habitat more heavily. Thus, several lines of evidence indicate that the threat of predation by largemouth bass has a differential impact on patterns of habitat use by fish of different size. In this example, the functional constraint of bass mouth size plays a central role in shaping patterns of habitat use by bluegill and pumpkinseed sunfish.

The differences in diet between bluegill and pumpkinseed are related to variation among lakes in population sizes. Mittelbach (1984) found that the abundance of bluegill relative to pumpkinseeds varied considerably among three lakes, from about 25:1 to 1:1. Relative abundance of the species was directly correlated with the relative abundance of the vegetated and open-water habitats. Habitat abundance is further correlated with abundance of the dominant prey of each species, vegetated habitat with snail abundance and open-water habitat with zooplankton abundance. The population sizes of bluegill and pumpkinseeds, thus, seem to be determined by the availability of the adult trophic resource of each species. Here, the interaction between adult fish feeding mechanics and prey availability shapes not only adult diet but also adult population sizes.

The sunfish example illustrates how the availability of resources (snail and zooplankton prey and their associated habitats) and the threat of predation (by largemouth bass) interact with the feeding capabilities of the bluegill, pumpkinseed, and largemouth bass to provide a mechanistic explanation for at least three prominent features of the bluegill-pumpkinseed communities: (1) patterns of prey use by small and large bluegill and pumpkinseeds, (2) patterns of habitat use by the two major size classes of each species, and (3) the relative abundance of the two species. Functional morphological analyses have identified the basis of snail-eating performance in pumpkinseeds and the basis of size-limited predation

in largemouth bass. In future work, these insights may provide the basis for making predictions about the community level consequences of such things as a change in the morphology of the primary predator species or a change in growth rates of the snail-crushing musculature in pumpkinseeds.

CONCLUSIONS

Functional morphology provides the crucial link between individual variation in morphology and fundamental ecological parameters, patterns of resource use, and survival. I have argued that functional morphology may provide mechanistic explanations for ecological patterns by describing individual variation in performance. The limits of performance capacity interact with environmental resources to shape actual patterns of resource use and fitness of individuals. Individual patterns interact and sum to produce population- and, ultimately, community-level characteristics. Functional morphology thus shows promise as a tool in ecological research, a potential explanation for ecological patterns at many levels. Understanding the functional basis of performance is a task for functional morphologists and physiologists, but relating performance to ecological questions will require integrative efforts by both functional biologists and ecologists. As research in this area accumulates, several questions will be crucial to a general understanding of the role of functional morphology in ecological systems. Some of these are listed below.

First, how important are the maximal capabilities of individuals in shaping ecological patterns? What is the relationship between the limits of performance and actual patterns of resource use? Are individuals frequently limited by their performance capacities, or do other factors (i.e., competition, threat of predation) constrain them first, causing them to operate away from these limits? Thus, how precise is the predictive power of functional morphology in ecology?

Second, how frequently do organisms mitigate the effects of functional constraints by means of behavioral adjustments? It is clear that behavioral responses are a fundamental component of the individual's repertoire, but under what conditions is the effectiveness of behavioral adjustment maximized and minimized?

Third, do functional systems that differ in their importance for resource use and fitness in a population show corresponding differences in their expression? Are the phenotypic components of less significant systems expressed more variably and with looser organization than systems experiencing strong directional or stabilizing selection?

Finally, how do functional systems respond to selection on individual performance? Do changes occur at all levels of design of the system, or are certain components more conservative while others change readily (Lauder, 1990)? Future studies integrating ecology and functional morphology promise to an-

swer these questions and to make unexpected contributions to both fields. Biologists have disputed the predictive power of morphology in ecology for years (Alexander, 1988; Bock, 1981; Bock and von Wahlert, 1965; Dullemeijer, 1972; Frazzetta, 1975; James, 1983; Lewontin, 1978; Morse, 1980), but no consensus has yet emerged. Integrative efforts that capitalize on the experimental and theoretical heritage of both functional morphology and ecology offer the greatest hope for a more holistic understanding of organismal design.

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