ECOLOGICAL EXPLANATION THROUGH FUNCTIONAL MORPHOLOGY: THE FEEDING BIOLOGY OF SUNFISHES[1]

Peter C. Wainwright

Department of Biological Science, Florida State University, Tallahassee, Florida 32306-3050 USA

Abstract. Researchers have been using simple morphological measures as indicators of ecological features for some time. The utility of morphological variables as ecological indicators depends upon our understanding of how the variable affects the ability of the organism to perform a particular task. Functional morphological analyses identify those features that can be directly related to behavioral performance and help to distinguish causal functional relationships from spurious correlations. The behavioral abilities of the individual, in turn, shape patterns of resource use and fitness by placing limits on the range of resources that can be utilized and by shaping the cost/benefit curve for resource choices. Examples from research on the feeding biology of North American sunfishes are discussed to illustrate how functional morphology can be used to provide explanations for differences between species in patterns of prey use, patterns of habitat use, ontogenetic diet switches, and population size. Trends from analyses of the evolution of fish feeding mechanisms suggest specific functional features that are most likely to vary among taxa and underlie differences in feeding performance and diet. Included in this group of predictive variables are the organization of lever arms in the jaw opening and closing systems, the size of the mouth, and the size of muscles used in prey-crushing behaviors. The link between morphology and ecology will be made most firmly when variables are chosen that clearly reflect the ability of the organism to perform relevant behaviors.

Key words: Centrarchidae; ecomorphology; evolutionary morphology; feeding; functional morphology; organismal design; performance.

INTRODUCTION

Biologists have recognized a general relationship between organismal form and ecology for years (MacArthur and Levins 1964, Bock and von Wahlert 1965, Dullemeijer 1972, Frazzetta 1975, Lewontin 1978, Levinton 1982, James 1983, Alexander 1988). For example, Hutchinson (1959) suggested that a size ratio between ecologically similar species of 1.3 was evidence of character displacement indicating that the species occupied different enough trophic regimes that competition was avoided. Hutchinson's suggestion that linear measurements of trophic structures could be used as indications of the degree of ecological overlap reflected the belief that different morphologies would be better suited to using different prey. The abundance of character displacement studies that followed Hutchinson's initial discussion (see review by Schoener 1984) and the more recent refinement of this approach (Simberloff and Boecklen 1981, Dayan et al. 1990) reflect the persistent attraction of the notion that one can infer aspects of an organism's ecology from its morphology.

[1] For reprints of this Special Feature, see footnote 1, page 1319.

But, what exactly is the relationship between an animal's anatomy and the habitat it uses, the prey it feeds on, and the success it experiences in obtaining mates? My aim in this paper is to briefly discuss this conceptual link between morphology and ecology, and indicate how this relationship may be exploited as a basis for prediction. For illustration I draw mostly from research on the functional morphology and ecology of North American sunfishes (family Centrarchidae) that has been conducted over the past two decades, but it is expected that the comments will apply broadly to the consequences of design in other functional systems.

HOW MORPHOLOGY AFFECTS ECOLOGY

Much of our understanding of the nature of organismal diversity reflects a feeling that one can explain differences among taxa in life style by differences in the design of various functional complexes in the body. The idea is that morphology shapes the relative ability of taxa to perform important tasks, and that performance in turn shapes the way in which the animal makes its living. For example, wing shape varies among species of bats in ways that suggest differences in flight performance (Norberg and Rayner 1987). Our intuition may correctly suggest that a short, broad wing
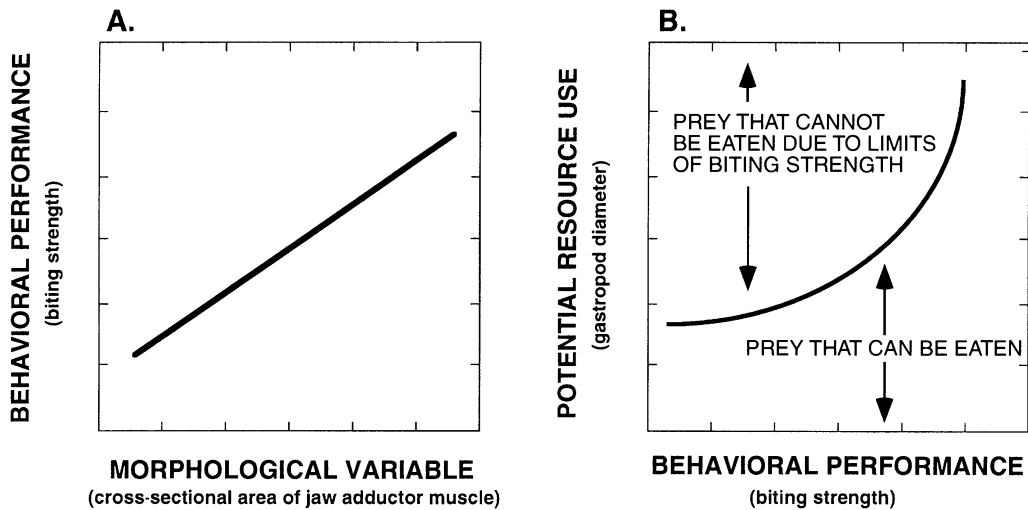
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FIG. 1. Illustration of the conceptual steps involved in measuring morphological variables as indicators of ecological variables, using the example of biting strength and its influence on the ability to crack snail shells.. Behavioral performance is determined by the design of underlying functional systems. The ability to select morphological variables that provide insightful indications of ecological patterns depends upon the quality of the understanding of how functional systems operate. (A) The best morphological indicators of ecology will be those for which the function can be drawn between the variable and some measure of behavioral performance of the individual. This is because (B) behavioral performance influences both the range of potential resources and individual can obtain, as well as the effectiveness of utilizing resources that fall within the limits of what can be used.

confers superior hovering ability relative to a long, thin wing. However, a complete functional analysis of wing design and flight performance would not only indentify the specific performance consequences of various wing shapes, it would also provide knowledge of why certain features affect flight ability, allowing us to generalize our understanding of wing morphology to other taxa. In other words, it is important to understand exactly why the short, broad wing is better at hovering so that our attempts to infer hovering ability from wing shape in other bats (and birds) meets with the greatest accuracy.

Recognizing the intermediate position of performance between morphology and ecological patterns raises a point about the selection of morphological variables as indicators of ecology. The most useful morphological variable will be one for which the function can be constructed of the effect of the variable on behavioral performance (Fig. 1A). Understanding why particular morphological patterns are associated with sets of ecological features depends upon our understanding of how the morphology influences the behavioral abilities of individual animals. In any system, there may be many morphological variables that show an association with an ecological gradient. Separating those that actually influence the association from those that correlate spuriously will depend on the quality of the functional interpretation of the variables in question.

*Behavioral capabilities shape
resource use*

A key notion here is that it is useful to recognize that morphology shapes ecological attributes through its affect on performance. This leads to the recognition that it is valuable to both relate morphology to performance and the latter to ecological variables (Fig. 1). Differences in performance between taxa shape ecological attributes of the species in at least two major ways: by determining the limits of potential resource use and the relative efficiency within those limits. Morphological constraints can set the maximum capacity of the individual to make use of specific resources. For example (Fig. 1), the maximum biting strength of a snail-crushing predator is set by the physiological cross-sectional area of the biting muscles. Biting strength will limit the range of snails that can be eaten. Similarly, there are numerous examples from both the bird and fish literature of mouth size limiting the size of prey that can be handled and consumed, and thus constraining the range of prey that can be eaten (Werner 1974, 1977, Kislaliaglu and Gibson 1976, Wheelwright 1985). Patterns of resource use directly or indirectly influence fitness, and herein lies the conceptual link between organismal design and natural selection that has been elegantly articulated by Arnold (1983) and others (Huey and Stevenson 1979, Emerson and Arnold 1989). Here I focus on the role of morphology in shap-

ing resource use patterns as a link to the more proximate ecological patterns that shape what we normally think of as features of population and community structure.

In addition to establishing the limits of an individual's ability to perform a specific task, design of functional systems also determine how well, or efficiently, behaviors can be performed. The limits of performance set ultimate boundaries within which an individual must operate (e.g., the gape-limited predator cannot eat prey too large to fit in the mouth), but the size distribution of consumed prey may not even fall near those limits. Prey susceptibility is not generally an all or none quantity for any given predator, and the design of the feeding mechanism will contribute to the relative ease of finding and handling prey within the range of prey that can be taken. The role of behavioral efficiency, or effectiveness in prey capture is recognized and incorporated into foraging models (e.g., Stephens and Krebs 1986). Both the maximum-sized prey a predator can eat and the optimum-sized prey are determined by predatory abilities that have their basis in the design of underlying functional systems.

Case Study: Functional Morphology and Feeding Ecology in Sunfishes

Some of the greatest success in relating organismal design to ecology has come in studies that seek to understand 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 (Mittelbach 1984, Norberg and Rayner 1987, Osenberg and Mittelbach 1989, Westneat 1994). One well-studied example involves two lake-dwelling species of North American sunfishes (family Centrarchidae); the bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*). Patterns of adult prey use differ markedly between the species. Pumpkinseed primarily eat snails, whereas bluegill only rarely eat snails, feeding instead on zooplankton and benthic invertebrates (Mittelbach, 1984). A key performance difference between the two species is that pumpkinseeds can crush snails with their pharyngeal jaw apparatus, but bluegill cannot crush snails and instead swallow them whole in the rare instances when they do prey upon them (Lauder 1983, Mittelbach 1984). Snail crushing by pumpkinseeds has a clear functional basis in (1) the enlarged muscles and bones of the pharyngeal jaw apparatus that permit a stronger biting action than seen in bluegill, and (2) the presence of a derived pattern of muscle contraction that drives the snail-crushing behavior (Lauder 1983). In lakes in the midwestern United States where the two species commonly co-occur, adult pumpkinseeds gain a competitive refuge from

bluegill by feeding on a prey resource that bluegill are incapable of eating (Mittelbach 1984). Thus, the difference between the species in patterns of food use can be understood through the difference in snail-crushing ability, which has a functional basis in the design of the feeding system and permits the pumpkinseed to exploit gastropods as a prey resource, free of competition from bluegill.

Associated with the difference between bluegill and pumpkinseed in feeding habits is a difference in adult habitat use. Pumpkinseeds forage in the vegetated regions of the littoral zone where snails are found, whereas bluegills feed in the open water on zooplankton (Mittelbach 1984). The adult patterns of prey and habitat use contrast markedly with patterns observed in juvenile individuals less than ≈75 mm, who feed in the vegetated regions of the lakes on soft-bodied invertebrates (Mittelbach 1981). Juvenile pumpkinseed do not eat snails because their snail-crushing apparatus is not sufficiently developed (Lauder 1983, Wainwright et al. 1991). Furthermore, juvenile pumpkinseed are restricted from feeding on zooplankton in open water by the activities of their primary predator, the largemouth bass, *Micropterus salmoides*. The threat of predation from bass causes juvenile fish to seek a refuge in the littoral zone. The feeding ability of largemouth bass is limited by the diameter of their feeding apparatus (the mouth and throat region, Lawrence 1957, Werner 1977). The effect of this constraint on feeding performance in bass, in conjunction with the size distribution of adult bass in the population, is that bluegills and pumpkinseeds reach a size refuge from predation by bass between 50 and 100 mm body size (Hall and Werner 1977). Significantly, it is at about this body size that bluegill leave the vegetated littoral habitat and enter the pelagic habitat to feed on zooplankton (Hall and Werner 1977, Werner and Hall 1977). The conclusion that this switching of habitats is related to the size refuge from predation is supported by a controlled field experiment (Werner et al. 1983) showing 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. In summary, the available evidence indicates that the threat of predation by largemouth bass plays a central role in determining juvenile bluegill and pumpkinseed habitat use, feeding habits, and the ontogenetic diet switch that characterizes bluegill in these populations.

Differences between bluegill and pumpkinseeds in population sizes, within and between lakes is largely a function of the abundance of habitat in which specific prey are found. The abundance of bluegills relative to pumpkinseeds varies considerably among lakes (from ≈25:1 to 1:1, Mittelbach 1984). In this study relative

fish abundance was correlated with the relative abundance of the vegetated and open-water habitats and hence the dominant prey of each species. Thus, the population sizes of bluegill and pumpkinseed appear to be limited by the availability of adult prey for both species.

These studies illustrate how the feeding capabilities of the bluegill, pumpkinseed, and largemouth bass interact with the availability of resources (prey and the habitats they are found in) and the threat of predation by largemouth bass, to provide a causal explanation for several features of these communities. First, ontogenetic changes in food use have a basis in snail-cracking performance for pumpkinseeds. Second, patterns of habitat use by the two major size classes of both bluegill and pumpkinseed are linked either to their own feeding abilities or to the size-limited predation of largemouth bass. Third, the population size of both sunfish species appears to be limited by the availability of the adult prey. Functional morphological studies have elucidated the basis of snail-eating ability in pumpkinseeds and the basis of size-limited predation in largemouth bass.

The above discussion serves to illustrate that some understanding of the functional morphology of the feeding system can provide the necessary insight to explain major patterns of resource use in these fishes. However, these examples offer only after-the-fact explanation. Can we use functional morphology to develop predictions of feeding habits and population dynamics in other taxa? If so, is there anything that can be gained from the functional morphology that might be overlooked with a more traditional approach?

Consider the case of the redear sunfish, *Lepomis microlophus*, sister species to the pumpkinseed (Mabee 1993) and the only other centrarchid sunfish that feeds mainly by crushing molluscs and displays the same suite of morphological and physiological specializations for this behavior (Lauder 1983). Interestingly, the redear and pumpkinseed have almost nonoverlapping geographic distributions, as the redear replaces the pumpkinseed in the southern half of eastern North America (Trautman 1981). Morphological measures of the physiological cross-sectional area of the levator posterior muscle of the pharyngeal crushing apparatus provide accurate estimates of the mollusc-crushing strength of sunfishes (Osenberg and Mittelbach 1989, Osenberg et al. 1992) and other mollusc-crushing taxa (Wainwright 1987, 1988). Interestingly, this crushing muscle has been estimated to be 50% stronger in redear than in pumpkinseed (Lauder 1983). The difference between species in body-size-specific crushing strength suggests several predictions, both about the feeding biology of the redear, and of the interaction between the two species in communities where one species is introduced into a native habitat of the other species. The redear sunfish is a standard fixture of Fish and Wildlife farm pond introduction programs and is frequently planted in lakes throughout the native range of the pumpkinseed (e.g., Trautman 1981). Hence, this case has implications for understanding the consequences of a standard wildlife management practice for native species.

Differences between pumpkinseed and redear in the body size at which a switch to eating snails is possible may lead to differences in growth rate, reproductive rate, and population size. Size-specific growth rate increases markedly in pumpkinseed when they switch to a diet of snails (Osenberg et al. 1992), and redear are known to undergo a similar ontogenetic switch from insects to snails (McLane 1955) that is associated with increased growth rates (Huckins 1996). The observation that the snail-biting strength of redear is about 50% higher than pumpkinseed leads to the predictions that redear could (1) switch to eating snails at a smaller size than pumpkinseeds and thus, (2) achieve higher growth rates at a smaller size. The higher rates of growth in redear may also be predicted to lead to larger population sizes, relative to pumpkinseeds, in lakes where the species occur together.

EVOLUTION OF FISH FEEDING SYSTEMS

Thus far I have argued that functional design and behavioral performance are key parameters in the equation that determines individual patterns of resource use, and that these resource use patterns are in turn central to shaping population and community level processes. Given this basic role of organismal design in ecological processes, what can be gained from knowledge of how functional systems change during evolution? Do the tendencies of historical transformation in functional morphology offer any insight into how the ecological processes may evolve, and can we use such patterns as a basis for predictions? Continuing with the case study of feeding in sunfishes, I consider the evolution of feeding mechanisms in these fishes and ask how this information can be used in ecological analyses.

Many functional analyses of fish feeding systems have assessed two major components of the mechanism, the morphology of the system and the patterns of muscle contraction and skeletal motion observed during feeding behaviors. One of the more striking general results of these studies is that the patterns of muscle contraction that underlie feeding behavior tend to be conserved during evolution, even in the face of considerable morphological change. This trend is illustrated by a study of North American sunfishes in which four species representing the morphological diversity found within the family were studied (Wainwright and Lauder 1986). Included in the analysis were the large-
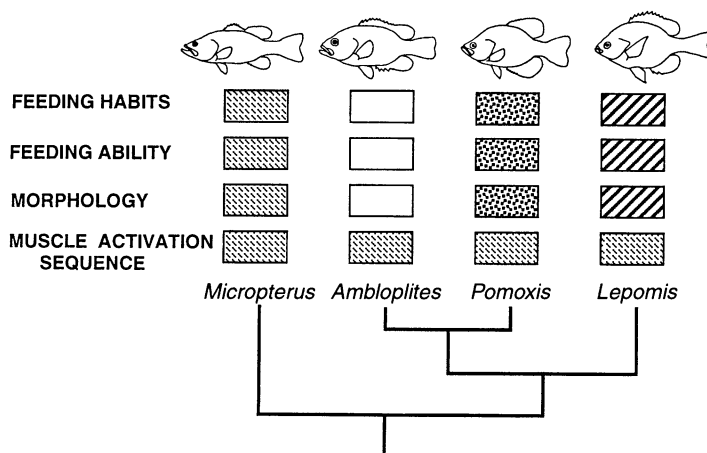
FIG. 2. Aspects of the feeding biology of four sunfishes (Centrarchidae) distributed on a phylogeny of the group (phylogeny from Mabee 1993). Feeding habits, feeding ability, and trophic morphology all vary among species (as indicated by different patterns in the figure), while the pattern of muscle activation used to drive prey-capture behavior differs little among species (Wainwright and Lauder 1986). This indicates the central role of morphological evolution during the trophic diversification of this group of North American fishes (redrawn after Wainwright and Lauder 1992).

mouth bass, bluegill sunfish, and two additional species (Fig. 2). As indicated previously, largemouth bass and bluegill have very different feeding abilities and feeding ecologies. Interestingly, when feeding on a common prey type (e.g., small fish) very few differences among species were found in the pattern of muscle contraction that drives prey capture (only 1 of 11 variables differed among species; Fig. 2). The salient point is that the drastic differences among sunfishes in prey capture performance (Werner 1977) cannot be explained by the presence of different neuromuscular patterns that drive the motions of the strike. Instead, differences in prey capture abilities within this group appear to have their basis in the size and shape of the jaws, as well as the design of other functional systems (Wainwright and Lauder 1992). Quantitative comparisons of fairly closely related taxa (i.e., confamilials) have repeated this basic observation in other fish groups (Sanderson 1988, Wainwright 1989, Wainwright and Westneat 1989).

This is not to say that muscle activity patterns cannot change during evolution. There are cases where the evolution of major changes in feeding abilities is intimately related to transformations in muscle activity patterns (Liem 1980, Lauder 1983). The best documented of these cases involves the evolution of snail-crushing behavior in sunfishes (Lauder 1983).

The key factor that seems to characterize cases in which motor patterns change during evolution is that a radically different feeding behavior is introduced with the novel motor pattern. Sunfishes use suction feeding when capturing prey and we see little evidence that differences in suction-feeding performance are related to changes in muscle activity patterns. Snail crushing, in contrast, involves a novel behavior of prolonged crushing action by the pharyngeal jaw apparatus. Crushing behavior is not present in species that cannot crush gastropods. The novel behavior requires a novel

muscle activation pattern. This association between the evolution of novel feeding behaviors and novel muscle activity patterns applies to the other well-documented case of motor pattern evolution, involving the evolution of algae scraping in cichlid fishes (Liem 1980).

Biomechanical analyses of the consequences of morphological differences among fish taxa have met with considerable success. Two important conclusions from this body of research are best illustrated by examples outside of sunfishes. The first point is that mechanical lever systems of the jaw mechanisms are a major site of evolutionary modification in trophic radiation, and the second point is that scale, or body size, has drastic consequences for the performance of the feeding system.

The mechanisms whereby fishes open and close their mouth and expand the oral cavity involve lever systems that translate the force and speed of muscle contraction to those actions. Transformations in the mechanical lever systems that open and close the jaws have been shown to have predictable consequences for movement patterns of the head during feeding and feeding performance (Muller and Osse 1984, Westneat 1994), and lever system changes appear to play a major role in explaining the diversity of trophic habits in several groups of fishes (Westneat 1994, Turingan et al. 1995, Wainwright and Richard 1995). Further variation among species is often found in the size of trophic structures such as bones and muscles, that can be related directly to the strength and speed of motion during feeding (Wainwright 1988, Norton 1991, Turingan 1994, Turingan et al. 1995).

A final point to be distilled from comparative functional analyses of fish feeding systems is that body size has profound effects on feeding performance. One of the more interesting consequences of this trend is that interspecific differences in diet are often mirrored by transformations that occur during the ontogeny of a

single species. The example of Caribbean species of the Serranidae, or groupers, serves to illustrate what appears to be a general phenomenon. More than most fish taxa, groupers have tended to conserve body shape and design of the feeding system during their radiation. Most members of the family are large-mouthed fish shaped much like a largemouth bass. The principal difference among many species is in average adult body size, which varies from ≈20 mm to >1000 mm in the Caribbean (Randall 1967). Given that body shape is relatively conserved, this group offers an excellent opportunity to examine the consequences of changing the scale of the feeding mechanism. What emerges is a striking correlation between body size and the major dietary components. As species increase in size, the dietary transformation proceeds as follows: copepods, amphipods, decapod shrimp, crabs, and fish. Sufficient data exist for two grouper species to show that the ontogeny of diet mirrors this interspecific transformation series (Wainwright and Richard 1995). In phylogenetic groups that vary in shape, including North American sunfishes, similar trends have been observed when diet is related not to body size, but rather to the relevant features of morphology such as mouth size (Wainwright and Richard 1995) or the size of the crushing musculature (Wainwright 1988) which may vary between species independent of body size.

These trends in the evolution of fish feeding systems have a number of implications for the study of trophic ecology. The analyses have suggested that an important first question that should be answered when comparing the functional basis of interspecific differences in trophic ecology is to establish what technique is being used by the fish to capture and handle their prey. If there is a common technique being used (e.g., suction feeding, crushing hard prey) it is unlikely that differences among taxa in motor patterns underlie differences in feeding performance. Thus, in such cases we would not expect to see differences at that level of design. Instead, previous research would suggest that one look first at the size of structures relevant to the specific feeding technique. If the prey capture technique is suction feeding, mouth size is implicated first, followed by aspects of lever design in the jaw opening and closing systems. If the prey are crushed, the size of the muscles generating the biting force or the organization of lever systems would explain differences in crushing performance. Size of specific structures can be altered either as a correlated response to changes in overall size, as has apparently happened in the evolution of groupers (Wainwright and Richard 1995), or through selection on the structure, independent of body size, as seems to have happened frequently in sunfishes (Wainwright and Lauder 1992).

Understanding the functional basis of feeding per-

formance also permits us to make specific predictions about the broader ecological consequences of evolution in the size of structures or changes in lever arms of the jaws. Thus, if the average adult body size of largemouth bass in midwestern lakes was 400 mm instead of the current 200 mm this would result in a doubling in the size of the average bass mouth and a similar increase in the range of prey sizes that could be taken. This could have a dramatic effect on the populations of bluegill. Bluegill would no longer be able to escape predation through a size refuge until they reached a very large body size, and this might have drastic consequences for the ability of bluegill to forage in the open water habitat, influencing feeding habits and ultimately the size of the population. This point has important implications for conservation and fisheries concerns of the ubiquitous sunfish communities in North America. Largemouth bass are a major target species of sport fishermen and one of the characteristic effects of human fishing pressure is to alter the size structure of the target population (i.e., to reduce the mean body size of adult fish). Understanding the effect of size limited predation by bass on bluegill populations and the morphological basis of bass feeding ability may permit predictions of the influence of changing the size distribution of bass, and some of the effects of introducing other piscivorous species into communities.

Knowledge of the details of the feeding mechanism may also provide more subtle pieces of information that influence our expectations for how selection might be expected to act on the system. For example, the precise factor that limits snail crushing performance in young pumpkinseeds and effectively prevents them from becoming molluscivores until ≈80 mm body size is not known. Clearly the small size of the snail-crushing musculature indicates that smaller forces can be brought to bear on snail shells, but an alternative factor that can play an important role in limiting mollusc predation by fish is the limitations on prey size imposed by the gape of the pharyngeal jaw apparatus (Wait-wright 1991). Whether it is the limitations on the size of snails that can be wedged between the pharyngeal jaws for crushing, or the strength of the crushing muscles that actually constrain mollusc predation in young pumpkinseeds is not actually known. Unless we know exactly what limits snail-crushing performance we are limited in our ability to predict how selection might act on the feeding system.

CONCLUSIONS

In many situations morphology can be used successfully as an indicator of the biomechanical or physiological properties of a functional system. Thus, morphology can often be used to identify specific differences between taxa in the ability to perform certain

tasks and behaviors. Whether such differences result in meaningful differences in patterns of resource use or other ecological patterns is a separate question. Only when the variation among individuals or taxa in behavioral performance accounts for ecological patterns can the utility of morphological features as indicators of ecology be confirmed. It follows that using morphological variables in ecomorphological studies without an understanding of the functional implications of the morphology will result in the discovery of patterns of association between form and ecology that cannot be interpreted in a causal vein, and will therefore be difficult to generalize. Thus, morphology is a major determinant of ecological patterns, but to understand the role of morphology in ecology one needs to know both the role of morphology in determining performance and the role of performance in shaping resource use. Observed trends in the evolution of fish feeding mechanisms indicate features that are most likely to underlie transformations in prey use patterns and underscore the need to know how prey are captured and processed before meaningful predictor variables can be selected. An understanding of the functional basis of feeding performance may allow one to predict the consequences of changes in the feeding mechanism for community and population structure.

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