Using Functional Morphology to Examine the Ecology and Evolution of Specialization[1]

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SYNOPSIS. Researchers strive to understand what makes species different, and what allows them to survive in the time and space that they do. Many models have been advanced which encompass an array of ecological, evolutionary, mathematical, and logical principles. The goal has been to develop ecological theories that can, among other things, make specific and robust predictions about how and where organisms should live and what organisms should utilize. The role of functional morphology is often an under-appreciated parameter of these models. A more complete understanding of how anatomical features work to allow the organism to accomplish certain tasks has allowed us to revisit some of these ideas with a new perspective. We illustrate our view of this role for functional morphology in ecology by considering the issue of specialization: we attempt to align several definitions of specialization based upon shared ecological and evolutionary principles, and we summarize theoretical predictions regarding why an organism might specialize. Kinematic studies of prey capture in several types of fishes are explored with regard to the potential ecological and evolutionary consequences of specialization, most notably in the area of trade-offs. We suggest that a functional morphological perspective can increase our understanding of the ecological concepts of specialization and it consequences. The kinds of data that functional morphologists collect can help us to quantify organismal performance associated with specialization and the union of functional morphology with ecology can help us to better understand not just how but why organisms interact in the manner that they do.

INTRODUCTION

Communities are shaped by the interactions among species and among individuals, as well as interactions between the organisms and the environment. It is the nature of these interactions that ultimately leads to differences among species and separates them in both space and time, thus allowing them to coexist (for example Hutchinson, 1957, 1959). Ecological models attempt to describe how these interactions typically work, and to predict what will happen in new and unique systems.

Energy acquisition is paramount to organism and species survival and fitness, and so diet has been a prevalent focus of modeling efforts. The prey capture abilities of an organism will affect diet, and may be determined by heritable traits, such as morphology or physiology, and also shaped by environmental influence on those traits (Fig. 1). The capacity for organisms to choose which behaviors to perform will also affect what items are taken from the environment and included in the diet (although behavior, or the capacity for certain behaviors, may be shaped by evolution as any morphological or physiological trait might). Interactions among community members will also influence prey availability and what can be successfully captured by the organism. Similarly, environmental conditions will constrain which prey are available to the predator and its competitors (Fig. 1).

A series of "filters" exists that eliminates many potential prey and ultimately determines what an organism can and will eat (Fig. 2). Organisms must first encounter a potential prey item, which involves primarily being in the right place at the right time. Second, the organism must be able to detect the prey, using visual, auditory, or other sensory abilities. The predator must then recognize the prey as something good to eat, which may depend upon acquired knowledge or learning. This must be followed by a decision to attack the prey, which may be based upon an assessment of the prey's energy value, and handling costs. The decision to attack may also be mediated by factors external to the prey item such as risk to the predator of being attacked by a larger predator. Ultimately, the predator must then possess the ability to successfully capture the prey.

The filters described in Figure 2 are not simply passive sieves; they act and interact with one another creating a probability distribution at each juncture. The probability that a predator routinely encounters a certain prey item can affect the probability that the same predator will then recognize that prey item as something good to eat, for example. And, working in the opposite direction on the figure; the probability of a successful capture given the morphology of the predator may influence the probability that the predator decides to capture the prey item. Thus, Figure 2 represents a simplified series of steps that lie between a predator and its prey.

Nonetheless, the filters and the traits that shape them are the features that distinguish species and separate their Hutchinsonian-type niches. Potential prey may be the same for all species. The prey that species encounter, however, will differ if species' search behaviors are different. Prey detection may then depend upon the differing neurological abilities of species, for
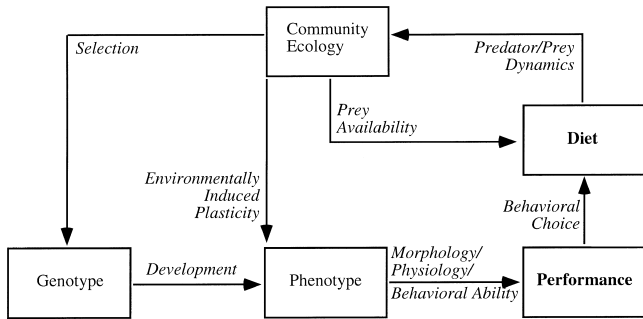
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Fig. 1. Possible scenario for how diet is determined. Implied in the Community Ecology Box are abiotic effects that impact interactions among species.

example, as might prey recognition. The decision to attack will depend at least in part upon the predator's ability to assess features of the prey and to evaluate those features, effectively weighing them against some scale established previously. The decisions that are made and the ability to follow through on those decisions can further separate species and their diets.

In many systems the mechanism that will determine which prey are taken from the environment is behavioral (*i.e.,* the ability to perform effective prey capture behaviors), or morphological (*i.e.,* possession of the right "tools" to capture the prey). These are mechanisms that impart their effect primarily at the last filter in the above example, and translate into the variables most typically quantified by functional morphological researchers. Although, other mechanisms such as neurological traits (*i.e.,* prey detection abilities), or locomotor abilities (*i.e.,* an aspect of prey search ability determined by morphology) could be included.

While we think that there are several fruitful areas of research related to functional morphological mechanisms and how they relate to foraging ecology, our focus will be on the ecological and morphological concept of specialization. We chose this area because we think specialization is a process of fundamental im-

portance to functional morphologists and ecologists alike. Thompson (1994) notes that studies of specialization in the first half of the 20th century focused primarily on evolutionary patterns and morphological change. Since the 1960s there has been a shift in focus to the study of ecological interactions (see also Berenbaum, 1996). Part of the fascination for ecologists includes the fact that the degree of specialization can, in large part, determine the distributions of organisms in time and space (McPeek, 1996). It is time to bring these seemingly separate fields of research together into one to address questions related to specialization more completely.

In this paper we consider several definitions of dietary specialization and categorize these based upon shared ecological, morphological and evolutionary principles. We briefly summarize ecological theory regarding why an organism might specialize. We use functional morphological examples to highlight some hypotheses regarding the potential ecological and evolutionary consequences of specialization, and will provide kinematic data to explore how such hypotheses can begin to be addressed. Finally, we attempt to identify and define the characteristics of functional morphological systems that make them useful for examining ecological models and testing predictions.

What Is Specialization?

Specialization, as a term, is always a subjective designation assigned relative to other community members or species in a clade (Futuyma and Moreno, 1988). Most biologists are willing to accept that the term specialist is not necessarily based upon quantifiable attributes of the species (Futuyma and Moreno, 1988). A species that eats a few prey items from a broad range of available prey, for example, is frequently termed a specialist without regard for underlying mechanisms that determine how the species manages to identify, select, and capture the prey item. A specialized predator may not necessarily be equated with
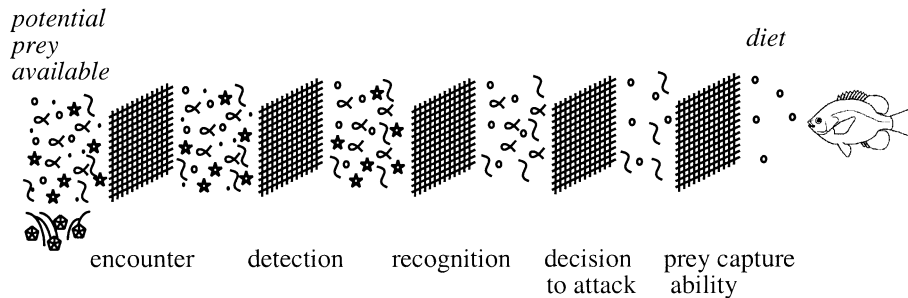

Fig. 2. Schematic representing the set of factors that ultimately determines what an organism can eat and where they act in the process of foraging: *encounter* with prey, *detection* of the prey of the predator, *recognition* of the prey as something to eat, the *decision* to attack the prey, and ultimately, the *ability* to then successfully capture the prey. Note that after each filter fewer types of prey remain available to the predator due to the exclusion of certain prey types. Prey types might be excluded because they are not *encountered* due to the part of the habitat used by the predator or due to the ecological interactions that restrict where the predator forages. Prey may not be *detected* or *recognized* due to sensory ability. Prey also may not be recognized due to behavioral learning (or a lack of it). The predator may *decide* not to attack the prey due to ecological interactions external to the prey item, such as predation risk, or because of behavioral cues that cause the predator to choose not to attack, such as they prey is too far away to be captured successfully. The *ability* to capture the prey successfully depends upon morphological, physiological, or behavioral capabilities. Functional morphologists frequently work with the last filter.

TABLE 1. *Concepts of specialization.*

Type of specialization	Definition
Ecological specialist	A species that utilizes a narrow range of resources.
Realized specialist	A species that is excluded to a narrow range of the available resources due to any number of ecological interactions including competition or predation.
'Mechanistic' specialist	A species that is excluded to a narrow range of the available resources because it is 'mechanically' constrained to that subset. This definition provides a mechanism to explain ecological specialization.
Functional specialist	A species whose morphology (or physiology) constrains it to a subset of available resources.
Behavioral specialist	A species whose behavior constrains it to a subset of available resources, either because it lacks the necessary behaviors to utilize other prey (*ability based*), or because it chooses to eat a subset of the available prey (*choice based*).
Novelty specialist	A species whose behavior or morphology allow it to utilize a totally novel subset of available sources.
Evolutionary specialist	A species that is excluded to a narrow range of the available resources due to the actions of evolutionary processes on the above interactions and mechanisms. This definition provides a process to explain why said interactions and mechanisms arose.
Adaptive specialist	A species that is mechanistically constrained to a narrow subset of available resources and that mechanism is considered an adaptation.

a derived or apomorphic morphology, the predator may merely possess a narrow niche (Futuyma and Moreno, 1988).

We recognize the utility of creating a somewhat flexible definition. It allows for the easy designation of specialists and generalists in any given system. However, with too flexible a definition the terms are redefined each time that they are applied. This leads to the situation where "specialists" cannot be compared across research programs and study systems, as there is no unifying metric to serve as the basis for quantifying similarity or difference. Further, different disciplines have their own notions of what specialized is; be this in an ecological, physiological or morphological, or evolutionary sense. We find it necessary to attempt to align these various perspectives based on shared principles so that we can better understand what specialization is before we can begin to address why species are specialists or specialized.

The existing definitions lend themselves to three basic categories (Table 1): ecological specialization, mechanical specialization (encompassing both physiological and morphological specializations), and evolutionary specialization. While these follow the discipline-based boundaries identified above, the categories are not mutually exclusive, and in many ways build upon one another. A single species may fall into several categories simultaneously. However, the progression of these categories necessarily leads from the more subjective to the more objective use of the term specialist, as the designation is based upon an increasingly deeper understanding of the cause(s) of a narrow diet breadth. Note that a species may be considered a specialist based upon its utilization of any of the resources in a habitat; space, shelter, mates, or food, to name a few. We focus on food resources or prey, although any of the definitions or scenarios that we include in this manuscript can be used to describe patterns of utilization of other resources.

In their review of ecological specialization Futuyma and Moreno (1988) made two distinctions that we consider a first level of discrimination. They were careful to separate the fundamental niche of a species from the species' realized niche. The fundamental niche is the manifestation of the species genotype within the environment. The realized niche reflects how extrinsic factors (*i.e.,* predation and competition) affect a species diet, and is frequently narrower than the fundamental niche. Thus, the general term ecological specialist reflects the observation that species X utilizes a narrower range of prey than species Y which lives in the same community or region, without regard to why or how they utilize those prey. It may be the case that an ecologically specialized species utilizes a small subset of the available prey because it is excluded to those items by competitors, thus it is a realized specialist (Table 1; Fig. 3A).

Applying these designations is not as simple as it may seem. Species or even individuals may appear locally specialized due to any number of ecological factors, but are generalized over their entire range (Fox and Morrow, 1981; Werner and Sherry, 1987). Polymorphic and phenotypically plastic species consisting of specialist genotypes for various seasonally occurring prey are sometimes referred to as generalist species (McPeek, 1996 and references cited therein). Taxonomy may also play a role. Species regarded as broadly distributed dietary generalists have turned out to be species complexes of specialists upon taxonomic reexamination (Berenbaum, 1996).

Equally problematic is determining what constitutes a diet that is sufficiently narrow to be called specialized; the utilization of a single prey resource everywhere, a single family of prey resources, or simply a single kind of prey resource (Fox and Morrow, 1981)? How this usage relates to the prey available can also be important. A species may locally utilize only one prey item, yet only one item exists in that region (Fig. 3B). It would seem that more information is needed to determine if this species should truly be called a specialist, such as whether the utilization of a particular local prey requires a certain physiology or morphology.

To remedy this, at least in part, specialization can be secondarily broken into additional categories based
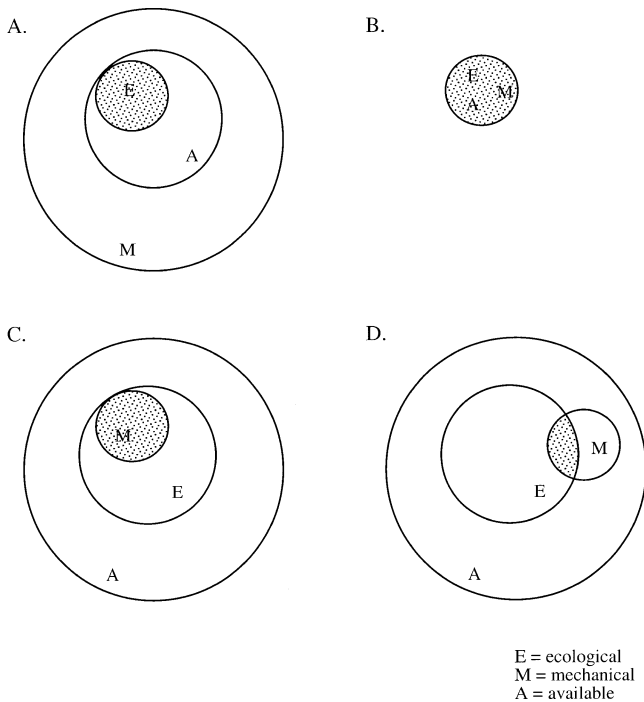
E = ecological
M = mechanical
A = available

Fig. 3.   Alternatives for how different types of specialization might contribute proximally to diet composition. Not all possible permutations are shown here. The symbol A refers to the set of all prey resources, M the set of resources utilizable based upon mechanical (*i.e.,* functional or behavioral) ability or constraint, and R the realized set of resources determined by competitive and other ecological interactions. In each case, the shaded portion is the resource set that composes the diet. A) a realized specialist; B) a relative specialist; C) a mechanical specialist; D) an illustration of the possible interactions between types of specialization and ultimate diet composition.

upon the tools of specialization, or mechanical specialization (Table 1). The term mechanical, in this sense, is used broadly to cover a wide range of possible tools or traits, be they morphological, physiological or even behavioral. Understanding the physical or physiological mechanism at work requires an additional level of investigation, beyond the designation of ecological specialist, as it necessarily includes information pertaining to why or how the species in question has a narrow diet. Using this definition, a specialization is the underlying mechanism that determines how the species manages to identify, or select, or capture a particular narrow set of prey items (*sensu* Holmes, 1977; Fig. 3C). A narrow diet breadth is the result of such specialization. In this sense, the diet is not said to be specialized; rather, the predator is specialized and a specialization, now used as a noun, is a trait or feature that facilitates a narrower diet.

Mechanical definitions of specialization can be broken into additional categories based upon the specific morphological or physiological mechanism at work. A functional specialist might be a species whose morphology constrains it to a few available prey (Ferry-Graham *et al.*, 2001*a*). Similarly, a behavioral specialist would be a species that possesses a generalized

morphology but lacks the behavioral repertoire to successfully capture more than one or a few items from the prey available (Ralston and Wainwright, 1997; Ferry-Graham, 1998*b*). A selective predator that is capable of eating many items but simply chooses to eat only one might also fall into this category, as behavior still serves as the mechanism of dietary specialization (Table 1). A behavioral specialist may possess a subset of the behaviors found in the generalist, leading to ability-based behavioral specialization (see Foster, 1999). Or, a specialist might have evolved wholly new behaviors not found in generalists, such as in the case of some sunfishes who are able to utilize snails as a diet item and have developed a unique crushing motor pattern for utilizing hard prey (for example Lauder, 1983). In the case of novel behaviors, ability-based or choice-based specialization can arise (Table 1). If new behaviors are traded for an old or unused set of behaviors, the result will be ability-based prey selection. If the novel behavior is added to an existing suite of behaviors, choice-based specialization may arise. Or, a third category of specialization may be present; the ability to perform a novel behavior or the possession of a novel morphology. This morphology or behavior is often referred to as a specialization (see novelty specialization, Table 1), despite the fact the potential diet becomes broader overall. This is frequently because such abilities enable the predator to utilize a resource that is not utilized by other species in the habitat. Actual diet is frequently narrow as utilizing only the novel item offers a competitive refuge. Such abilities are often thought of as key mutations or key innovations (Stiassny and Jensen, 1987; Schluter, 1996).

The idea of being specialized in many ways has its roots in the notion that the animal in question has been honed by evolution. Thus, the term specialization can be extended to include evolutionary specialization (Table 1). Evolution acts at the genotypic level (Fig. 1). A specialization, therefore, may be a trait that has been shaped by evolutionary processes to be different from other closely related species. Further, specialization as a term may also be used in this sense as a verb to describe the evolutionary process of becoming specialized. Evolutionary and ecological definitions of specialization may overlap here as the fundamental niche of an ecologically specialized species may be the result of the expression of specific unique traits shaped by evolution that exclude the predator to a small subset of the total resources available (Fig. 3A, B). Mechanistic definitions of specialization will also overlap with both of these categories, as the traits that preclude the predator to a small subset of resources may be any one of those listed previously (Fig. 3C, D). The primary difference, however, is that this level of designation requires a third level of understanding, it implies a process by which mechanisms arise that lead to specialization. This level addresses the ultimate, not the proximate, cause of specialization.

Within evolutionary specialization we can define a subset of all possible evolutionary mechanisms. One

such subset should include traits that are considered adaptations or that lead to adaptive specialization (Table 1). This distinction excludes specializations that arise through evolutionary processes such as genetic drift, and specialization that are pre-adaptations or exaptations (*sensu* Gould and Vrba, 1982), all of which would be included in the more general category of evolutionary specializations. Adaptive specializations are derived traits and can only be revealed within a phylogenetic framework. Testing for such traits is subject to all of the other criteria established for determining adaptation (*i.e.,* Gould and Lewontin, 1979), and most notably should confer a quantifiable performance advantage to the species in question for some action or activity. Traits should be heritable (note that Futuyma and Moreno, 1988 also propose this latter criterion), and therefore should not change in space and time (*i.e.,* be plastic, unless plasticity itself is the trait in question Robinson and Wilson, 1994, 1998). Thus, this last category of specialization, while the least subjective, may be the most difficult to apply practically.

While identifying types or categories of specialization has helped to create definitions so that we each might understand better what is meant when the term specialized is used, it has not created a single or unified definition that necessarily makes specialization comparable across studies or study systems. This is perhaps a next step for researchers in this area. For the next section, we will focus on the particular area of specialization that we have named evolutionary specialization. We will work towards an understanding of why evolutionary specialization arises and identifying the consequences of such specialization.

WHY SPECIALIZE?

Species commonly do not utilize the same array of prey as their close relatives; but rather a distinct subset, or entirely different set of prey. The challenge for biologists is to understand what facilitates the change to fewer or newer prey types. Do organisms simply possess the tools to utilize a diverse array of food item, thus they exercise their ability to make choices when they switch from one prey to another? Or, does utilizing a specific prey item require altering the existing phenotype in favor of the development of new tools, presumably through the actions of natural selection? If organisms are making choices, will they continue to choose the singular prey item, or will they exhibit prey switching? Does phenotypic alteration mean that the organism is committed exclusively to utilizing a new prey item, and can the behaviors used in procuring one prey over another become fixed in the same manner?

To understand specialization due to behavioral choice (which is typically not thought of as being determined by evolution), optimal diet theory (ODT) is most typically applied (for a review of the faults and merits of ODT see Sih and Christensen, 2001). The theory originally stated that an increase in sheer number of a single prey item should lead to an increase in dietary specialization by an individual. This is due to the fact that the search time needed to find the prey is reduced when the prey is abundant (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971). Similarly, as prey abundance increases there should be an increase in the total number of specialists. This can be refined to state that foragers should prefer the prey that yield the most energy per unit time (Schoener, 1971; Sih and Christensen, 2001). Energy return can be individually or simultaneously maximized in terms of time spent searching, handling time, or net value per prey item, to name a few. As that prey becomes more abundant, less profitable prey should be dropped from the diet. Even from a sheer biomass perspective, it would not be profitable, given the ease with which a single prey type is detected and procured, to add other prey to the diet that require decision making and possible errors in choice of capture behaviors. There is no risk in specializing as food is not limiting. When resources decrease in abundance species may demonstrate their generalist abilities and utilize other resources, as seen in many Darwin's Finches (Grant, 1999).

There are additional behavioral models that predict a narrowing of dietary breadth and do not depend on the abundance of the prey resource. These fall under the general heading of behavioral selectivity. Behavioral selectivity is said to occur when prey items are taken from the environment in proportions that appear to have no relation to their abundance (Strauss, 1979). In these instances, the predators select prey based upon cues other than the amount of energy available, and may be selecting prey due to preference for a certain nutrient, for example (see reviews in Abrams, 1987*b*; Naganuma and Roughgarden, 1990). While the cues leading to specialization in this scenario might not be simple resource abundance, the models based upon resource abundance can be used by changing the independent variable to the selected factor (*i.e.,* sodium, see Belovsky, 1978) to make predictions regarding when the predator should be selective or specialize (for a consideration of various spatial scales and the factors that might regulate selectivity see Morris, 1987).

The above theories are typically used to describe how foraging individuals should behave within their respective lifetimes. In other words, what should an individual choose to eat, with or without respect to the current environmental conditions and associated prey availability. The above theories do not necessarily describe why specialized species should evolve over many generations or evolutionary time. They do not address phenotypic or behavioral alteration through natural selection per se. Consider the two examples of specialized diets stated at the onset of this section: a species uses a distinct subset of prey relative to other species, or a species utilizes an entirely different set of prey relative to other species. In the evolutionary sense, specialization is defined by comparing a putative specialist with an ancestor; or more practically, other members of its clade (Fig. 4).
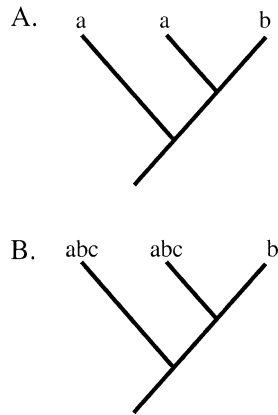
Broadly speaking, specialized species should evolve

FIG. 4. The alternatives for why an organism should have evolved to eat something new (A) or something specific (B). Phylogenies indicate the diet found in the ancestral species and specialized species.

because the traits thought of as specializations confer a fitness advantage to the individual members of the species and the traits are selected for. The easiest cases to imagine are density-independent. For example, a species might evolve to utilize a particular prey resource because the prey item offers a higher energy return. This higher energy return confers increased fitness for same basic reasons as the ODT examples above, assuming a reliable, long-term supply of the high-energy prey item. Note that if changes in environment are stochastic, no one trait is favored, and the evolution of specialists is less likely (Wilson and Yoshimura, 1994).

As in the above example, genetic trade-offs may not be necessary for evolving specializations (see also examples in Fry, 1996; McPeek, 1996). However, if there are trade-offs, for example in the handling of different kinds of prey, species might evolve the ability to use only one kind of prey. Retaining the ability to use many kinds of prey might come at the cost of procuring any one kind of prey efficiently. Specializing on one prey should then increase prey handling efficiency and lead to increases in fitness, due ultimately to the ability to obtain more energy per unit effort. For example, sympatric populations of stickleback fish (*Gasterosteus*) feed in different environments (benthic and limnetic); the mechanism responsible for facilitating this dietary difference is different head and gill arch morphologies. It is argued that the morphological traits that lead to more efficient exploitation of resources in each of these environments cannot be simultaneously maximized, thus the populations have diverged and specialized on the respective resources (Schluter, 1996; note that this basic argument has been promoted as a general reason for the diversity of genotypes present in nature *in toto,* see Whitlock, 1996).

A number of density-dependent reasons for why a reduction in the number of items in the diet should lead to an increase in fitness also exist. If resources are generally limiting, species that share a habitat could partition the resource so that each utilized different components to avoid competition, potentially leading to the phenomenon known as character displacement. Resources may be limiting in this fashion in the case of Caribbean *Anolis* populations, as indicated by food supplementation experiments and experimental introductions of similar species morphs (reviewed in Losos, 1994). Larger lizards appear to consume larger species of insects on islands where resource partitioning occurs (Pacala and Roughgarden, 1985; Naganuma and Roughgarden, 1990). Like the previous stickleback example, Adams and Rohlf (2000) found that two species of *Plethodon* (salamanders) in sympatry exhibit differences in morphology that correlate with differences in diet. These two morphologies facilitated performing the behaviors needed to capture their respective prey successfully. It is suggested that performing the alternative behavior for each prey would not be as effective for capturing each prey, and that morphological differentiation was associated with a competitive release (no morphological or diet differentiation was noted for the two species when they existed in allopatry).

Along the same lines, density-dependent regulation within different habitats, for example, may cause the evolution of preference for generally underutilized habitats (see review in Jaenike and Holt, 1991). Competition for a limited, shared resource is generally thought to fuel evolutionary divergence as the phenotypes that can exploit novel resources will do so (Schluter, 2000*a*, *b*, but see also Abrams, 1987*a*). The new prey may be even more costly to obtain. However, competition for the 'better' resource may be so great that the release from competition causes the "poorer" prey to yield more net energy. A compelling example with *Drosophila* suggests that cadmium-intolerant flies experiencing high competition for cadmium-free food will evolve to utilize cadmium-laced food despite the detrimental effects of cadmium (cadmium is relatively toxic and detrimental to fly growth). Flies in high competition treatments evolved cadmium tolerance much faster than flies in low competition treatments (Bolnick, 2001). It is important to note with this example that a density-independent perspective would cause cadmium specialization to appear costly in terms of fitness, however, a more complete accounting of the fitness function in these flies revealed a net benefit to using cadmium-laced food.

There is, however, at least one additional scenario that should be considered here where a trait might arise over an evolutionary time scale that leads to a narrower diet breadth in the absence of natural selection. Imagine that the ability to use three different prey resources, A, B and C, are genetically independent traits A′, B′ and C′. That is, procuring prey A requires ability A′, which is independent of B′, and so on. A species may initially possess all three abilities, be they behavioral, morphological, or physiological abilities. However, long term exposure to only one resource, prey A, perhaps due to environmental conditions, re-
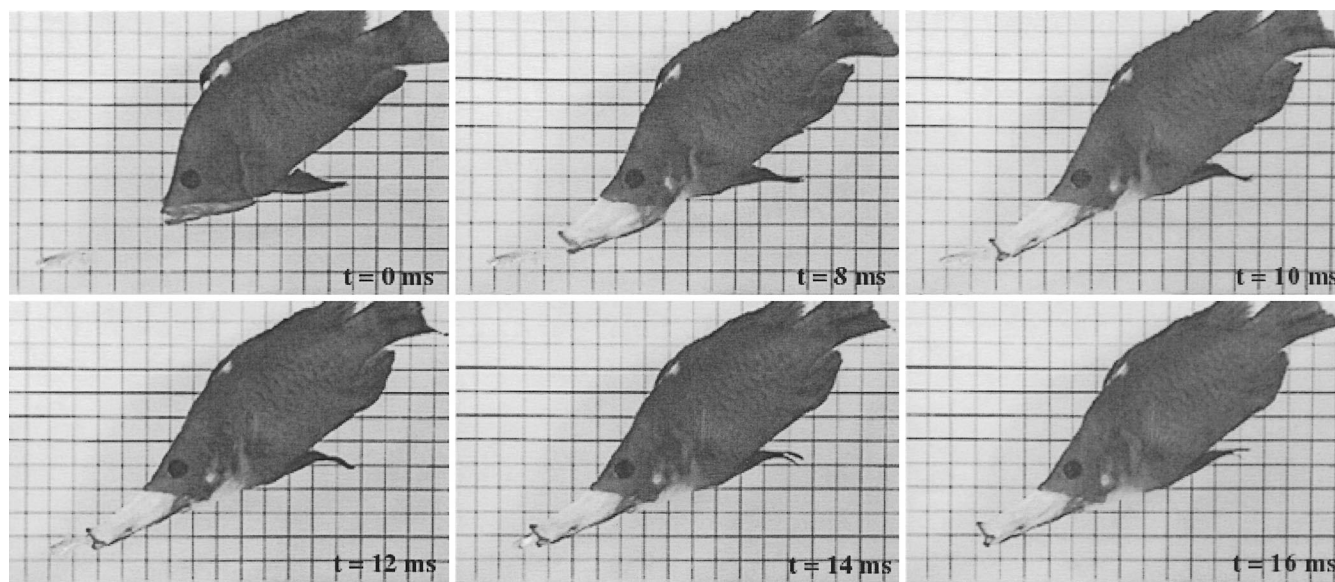
FIG. 5. Composite image showing the prey capture event in *Epibulus insidiator*. The prey item is a live, unrestrained guppy (*Poecilia*). The times of each image are shown in the lower right corner of each frame. Images were obtained with a NAC ci digital high-speed video camera filming at 500 frames sec^{-1}. The tank was illuminated with three 650 W lights. The grid in the background is 1×1 cm squares.

laxes selection for B′ and C′. Mutation accumulation leads to a loss of B′ and C′, and the species is subsequently specialized. Similar scenarios could certainly occur due to other evolutionary processes such as genetic drift, which should not be discounted.

SPECIALIZATION TO WHAT END?

Despite the fact that the process of specialization appears to frequently result from net fitness advantages, the outcome is also thought to result in both advantages and disadvantages in the form of trade-offs for the possessor (see reviews in Fry, 1996; McPeek, 1996; Whitlock, 1996). In general, theories predict that specialists should be better at obtaining the particular prey items for which they are suited. Thus, when competing for a shared prey resource, a specialist should win over a generalist (Schoener, 1974, see also 1976). However, generalists presumably retain the ability to utilize many different resources, a distinct advantage if a single prey resource becomes unavailable. What do such predictions mean for actual organism performance? We can measure wins and losses in competitive trials between generalists and specialists. Life history consequences (*i.e.,* growth rates, body size, reproductive output, population size) are now understood in several systems (for example Pacala and Roughgarden, 1985; Chase, 1996). But, such information fails to elucidate the actual mechanism facilitating any kind of performance advantage. In a head to head contest, how or why is the specialist better, if it is, in fact, better? In this area, the tools of functional morphology may provide particularly informative insights.

We will explore the existence of several trade-offs in this section with empirical data. One potential advantage of specialization that we observed is greater precision in prey capture by a functional specialist. We will also provide data to suggest that at least two trade-offs of increased specialization exist: the reduced ability to perform alternative behaviors, and the reduced capture success with alternative prey types. Our observations suggest that these two examples represent negative consequences of ability-based behavioral specialization. Trade-offs are difficult to fully demonstrate empirically (Futuyma and Moreno, 1988), and our three are preliminary explorations. However, they also suggest that trade-offs exist and that the tools of the functional morphologist are useful for continued and more rigorous hypothesis testing in this context.

Increased precision

As mentioned above, specialization is supposed to provide for improved performance. How might this manifest itself in a functional morphological sense? What do we measure about prey capture that provides us with an indication of "better" or "worse"? We suggest that specialization might lead to greater precision in performing behaviors associated with that morphology. We define precision, in this sense, as a reduction in the variance associated with the expression said behaviors (see also Sanderson, 1988). *Epibulus insidiator*, the sling-jaw wrasse, is a highly derived, morphologically modified predator that utilizes extreme lower jaw protrusion to capture highly elusive, mobile prey (Fig. 5). The morphological modifications present in *E. insidiator* presumably have lead to the ability to eat prey items that closely related species cannot; this trophic specialist eats primarily highly elusive fish and crustacean prey. Most other closely related wrasses utilize a combination of suction and biting to take less elusive invertebrate prey (Westneat, 1995). We compared kinematic data from *E. in-*

sidiator and *Cheilinus oxycephalus*, which coexist on central Indo-Pacific coral reefs like the Great Barrier Reef (Randall *et al.*, 1990). The genus *Cheilinus* forms the sister group to the lineage containing *Epibulus* (Westneat, 1995).

Using high-speed video, we recorded multiple strikes (20–35) from single individuals to quantify within individual variation in strikes (see Ferry-Graham *et al.*, 2001*c* for methodological details regarding high-speed video data). We chose to examine single individuals at this stage of our analysis because the combined data from several individuals may falsely give the impression of being generalized. This is because even though each individual may be specialized, their respective behaviors may not overlap and combined data gives the illusion of a singularly broad repertoire for all the individuals of the species. *Cheilinus* was fed live mysid shrimp (*Acetes* sp.), a prey item representative of natural diet items. We used live guppies (*Poecilia* sp.) in the *Epibulus* experiments since this species eats live fish (Westneat, 1995). We measured the time to peak gape in each species as an element of prey capture performance. Peak gape includes a large degree of jaw protrusion in *Epibulus* (Fig. 5); thus, the mean time to peak gape is longer in *Epibulus*. However, the point here is not the difference in the average values, but the variance in performing that motion (Fig. 6). Time to peak gape in *Epibulus* shows a tighter distribution around the mean, with a standard deviation of 3.1 msec. The standard deviation for the *Cheilinus* data is 7.1 msec, which is significantly greater (F-test, $P = 0.0001$).

It is difficult to draw robust conclusions from these data, and additional experiments will be necessary with multiple individuals and a high degree of replication per individual. We offer these observations as a foundation for the hypothesis that species possessing a high degree of morphological modification for prey capture should also show increased precision in prey capture performance. We add the tantalizing information that in at least one system, specialists are faster and more efficient decision-makers than generalists (Bernays and Funk, 1999); a hypothesis that has yet to be tested for any fish species as far as we know.

Reduced ability to perform alternative behaviors

If a species normally eats only one or a few prey types, it is reasonable that the behaviors associated with procuring that prey should be refined in much the same way that morphology might be. Thus, specialists may have a smaller repertoire of behaviors to choose from. One might view this as a benefit, as there is less chance of making an error by choosing the 'wrong' behavior to use on a certain prey item. However, this reduction in behavioral ability may also be costly. A narrow distribution of behaviors may lead to a reduced ability to respond to different prey with alternative prey capture behaviors.

Such a trade-off may be found in the comparison of the feeding behaviors exhibited by two species of car-
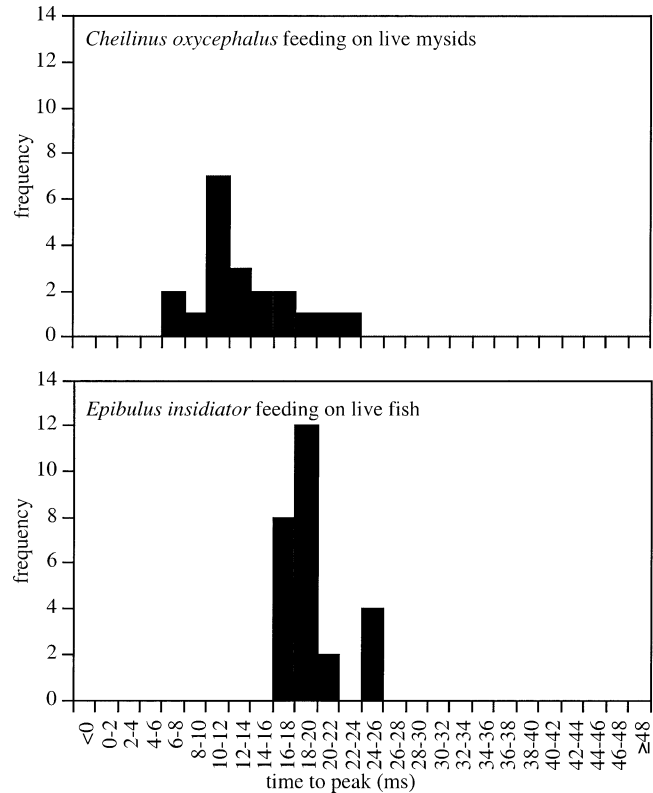

FIG. 6. Frequency histograms for *Cheilinus oxycephalus* and *Epibulus insidiator* of time to peak gape (or gape/protrusion in the case of *Epibulus*). Time to peak gape was determined by viewing the high-speed video sequences and noting the time at which jaw movement began (t_0) and the time at which maximum displacement occurred. The *Cheilinus* and *Epibulus* plots are for one individual each, thus indicating the within individual variation inherent in performance.

chariniform sharks from southern California (USA): the leopard shark, *Triakis semifasciata*, and the swellshark, *Cephaloscyllium ventriosum* (Fig. 7). The diet of the leopard shark is quite broad, and includes items such as small fishes, crabs and other benthic invertebrates, and clams and infaunal invertebrates (Talent, 1976). The leopard shark forages in the kelp forest, in the surf zone, and in shallow embayments and estuaries (Russo, 1975). The swellshark, in contrast, eats fishes in the water column (Compagno, 1984), and appears to rely almost exclusively on a single kelp forest species, the blacksmith *Chromis punctipinnis* (Tricas, 1982). This shark species will scavenge dead prey occasionally, as evidenced by their occasional capture in commercial lobster traps baited with dead fish. It has been demonstrated that the swellshark appears to exhibit only one prey capture behavior (Ferry-Graham, 1997), while the leopard shark is able to modulate its prey capture behavior in response to the prey at hand (Ferry-Graham, 1998*a*). Here we compare the prey capture kinematics performed by the two shark species feeding on large and small prey (fish pieces). We measured multiple kinematic variables and used principle component analysis to subsequently reduce the dimen-
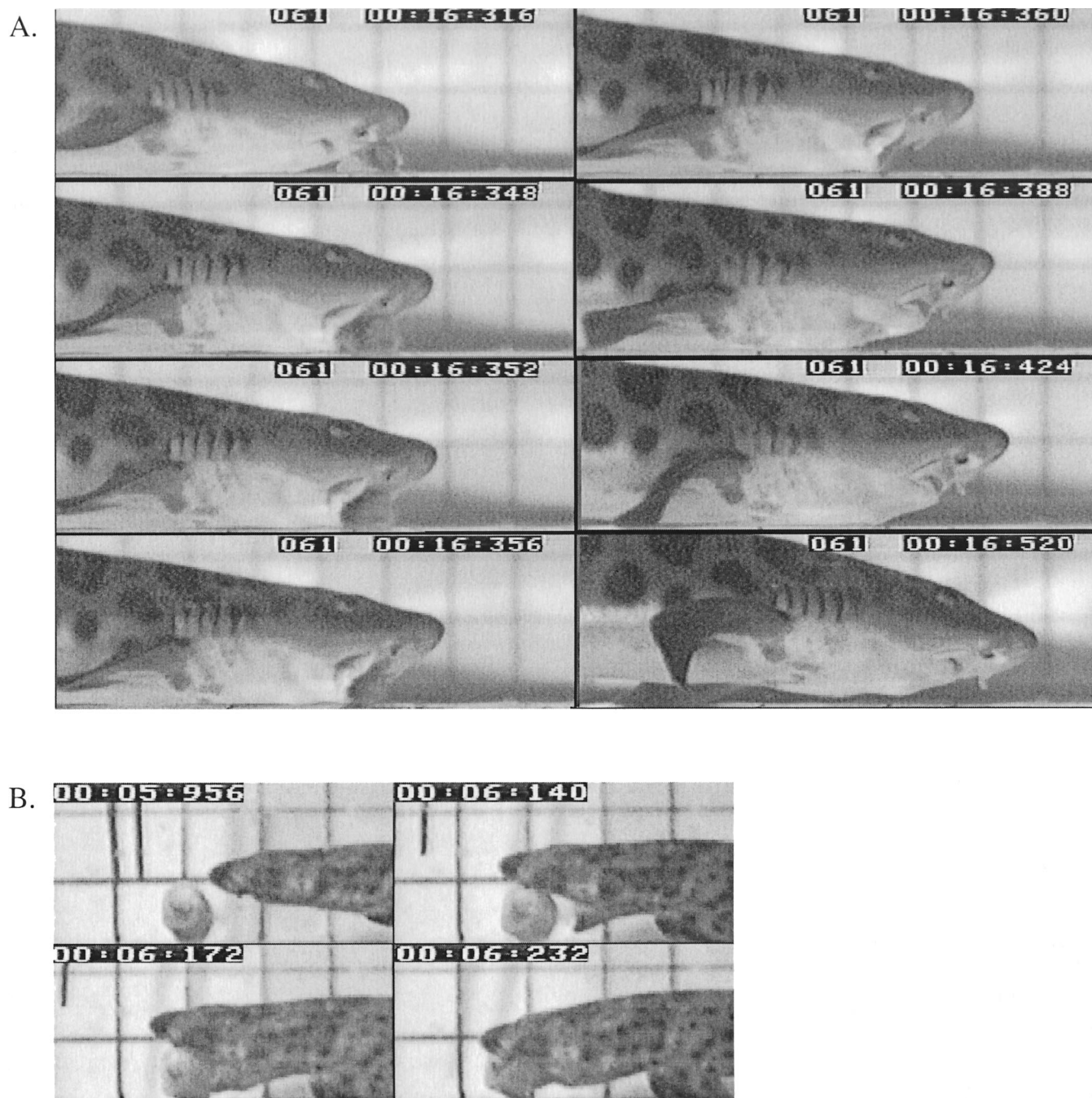
FIG. 7. Composite image showing the prey capture event on small prey in the swellshark *Cephaloscyllium ventriosum* (A) and the leopard shark *Triakis semifasciata* (B). The swellshark uses a maximally expanded mouth cavity to capture all sizes of prey, as shown in this capture of a small prey item. Times indicated on the frames are min:sec:msec. Images were obtained with a NAC analog high-speed video camera filming at 250 frames sec^{-1}. Tanks were illuminated with 500 W lights. The grid in the background is 2×2 cm squares.

sionality of the dataset. Graphically the swellshark occupies more behavioral space, but appears to have only one cluster or one type of prey capture behavior (Figs. 7B, 8, no significant differences detected among prey types). In contrast, the leopard shark shows two tight clusters that have significantly different means for PC2 (Fig. 8, F = 8.71, $P < 0.0001$), which contains behaviors associated with head expansion, although not for PC1 which contains variables that describe the timing of the strike (F = 2.26, $P = 0.09$).

The inability of the swellshark to modulate or change any prey capture behaviors in a consistent manner in response to different stimuli suggests that it might be a behavioral specialist, a feature that facilitates an extremely specific diet. It has been shown that this stereotyped behavioral pattern is present in hatch-
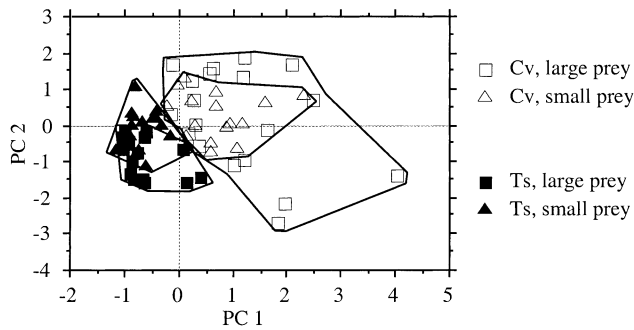
FIG. 8. A plot of a principle components scores from an analysis of several kinematic variables: maximum gape distance, maximum gape angle, maximum hyoid depression, maximum upper jaw protrusion, time to maximum gape distance, time to maximum gape angle, time to maximum hyoid depression, and time to maximum upper jaw protrusion. PC1 describes the timing variables, with time increasing as you move towards the right on the X-axis. PC2 describes the head expansion variables, with expansion increasing as you move up the Y-axis. The symbols correspond to large prey (triangles) and small pieces (squares). Data for the swellshark, *Cephaloscyllium ventriosum*, is in open symbols and the leopard shark, *Triakis semifasicata*, in solid symbols. Note the larger variation in the data for swellsharks, with the data from strikes on small prey being well within the data for strikes on large prey. The leopard sharks show less variation in behavior and show some separation of the clusters on PC2.

ling sharks at their first feeding event (Ferry-Graham, 1998*b*). There is a small amount of evidence at this time for evolution of similar behavioral specializations when comparing these data with observations of the Pacific angel shark *Squatina californica* (Fouts and Nelson, 1999), and the horn shark *Heterodontus franciscani* (Edmonds, 1999). In addition, in at least one group of bony fishes (pufferfishes, *Chilomycterus*) there is evidence for a correlation between the ability to perform a broader range of prey manipulation behaviors and diet breadth (Ralston and Wainwright, 1997).

Reduced success with alternative prey types

Perhaps an even stronger case can be made for the existence of costs associated with specialization in a species where an evolutionary reduction in prey capture success on common prey has gone hand in hand with extreme morphological modification for prey capture (Fig. 9A). In species of butterflyfish (Chaetodontidae), there exist long and short-jawed forms. The extremely long-jawed form, *Forcipiger longirostris*, feeds exclusively on highly elusive decapod shrimp, and is morphologically modified for capturing such prey. It possesses novelties in the suspensorium not unlike *Epibulus insidiator* that facilitate anteriorly directed jaw protrusion (Ferry-Graham *et al.*, 2001*b*). However, we studied its ability to capture less elusive prey and compared that ability with the less modified *F. flavissimus* and *Chelmon rostratus*, and unmodified *Heniochus acuminatus* and *Chaetodon xanthurus*, closely related species (Fig. 9B).

We offered the five species of butterflyfish brine shrimp prey and filmed the strikes with high-speed

video as described in previous sections (see Ferry-Graham *et al.*, 2001*a, b* for details). Among the variables quantified was capture success. The long-jawed species missed the prey item in approximately 17% of attempted capture events. This was more often than moderately modified species feeding on the same prey item in carefully replicated feeding experiments (Fig. 9B). The unmodified species never missed the brine shrimp prey. In the modified species studied the likelihood of missing was correlated with the distance from which the strike was initiated. The failed capture attempts were kinematically similar in all regards to successful attempts except that they were attempted from significantly farther away (Ferry-Graham *et al.*, 2001*a*). Brine shrimp should be easier to catch than the elusive shrimp found in the diet of *Forcipiger longirostris*, yet capture success still was not 100%. It is possible that a prey item that is not normally found in the diet is more difficult for highly specialized species to capture.

It is worth noting that a more general phenomenon may be at work here. When feeding on elusive prey normally found in the diet, *Epibulus insidiator* still missed the prey about 25% of the time. It may be that, regardless of prey item, precision and accuracy do not increase synchronously.

FUTURE DIRECTIONS FOR FUNCTIONAL MORPHOLOGISTS

Futuyma and Moreno (1988) criticize interspecific studies of functional trade-offs because negative correlations between traits may arise after specialization evolves, or speciation occurs. Consequently, it is not possible to distinguish between true trade-offs and subsequent negative correlations. They advocate the study of comparisons within species, or other interbreeding units, where genetic recombination should break down negative correlations between traits if actual fitness trade-offs do not exist (for example Robinson *et al.*, 1996). We agree that intraspecific studies of specialization are valuable. Inter-individual differences in a functional trait can be often be correlated with a known environmental condition since the trait's evolutionary history is short and more likely to reflect current conditions (intraspecific examples include Werner and Hall, 1979; Lasker and MacCall, 1983; Wainwright *et al.*, 1991*b*; Baumgartner, 1992, 1995; Mittlebach, *et al.*, 1992; Day *et al.*, 1994). Different species have presumably experienced a long history of independent evolution in historical environments that cannot easily be determined. However, intraspecific comparisons are still sensitive to incidental negative correlations. Even within-population comparisons may be misleading if the researcher does not understand the functional link between traits that are thought to be traded off. We maintain that careful studies are necessary to understand how the populations arose (see Labin and McPhail, 1985; Thompson *et al.*, 1997), and whether the traits of interest have any relation to an actual performance or fitness advantage (also see Day and McPhail, 1996). Categorically excluding interspe-
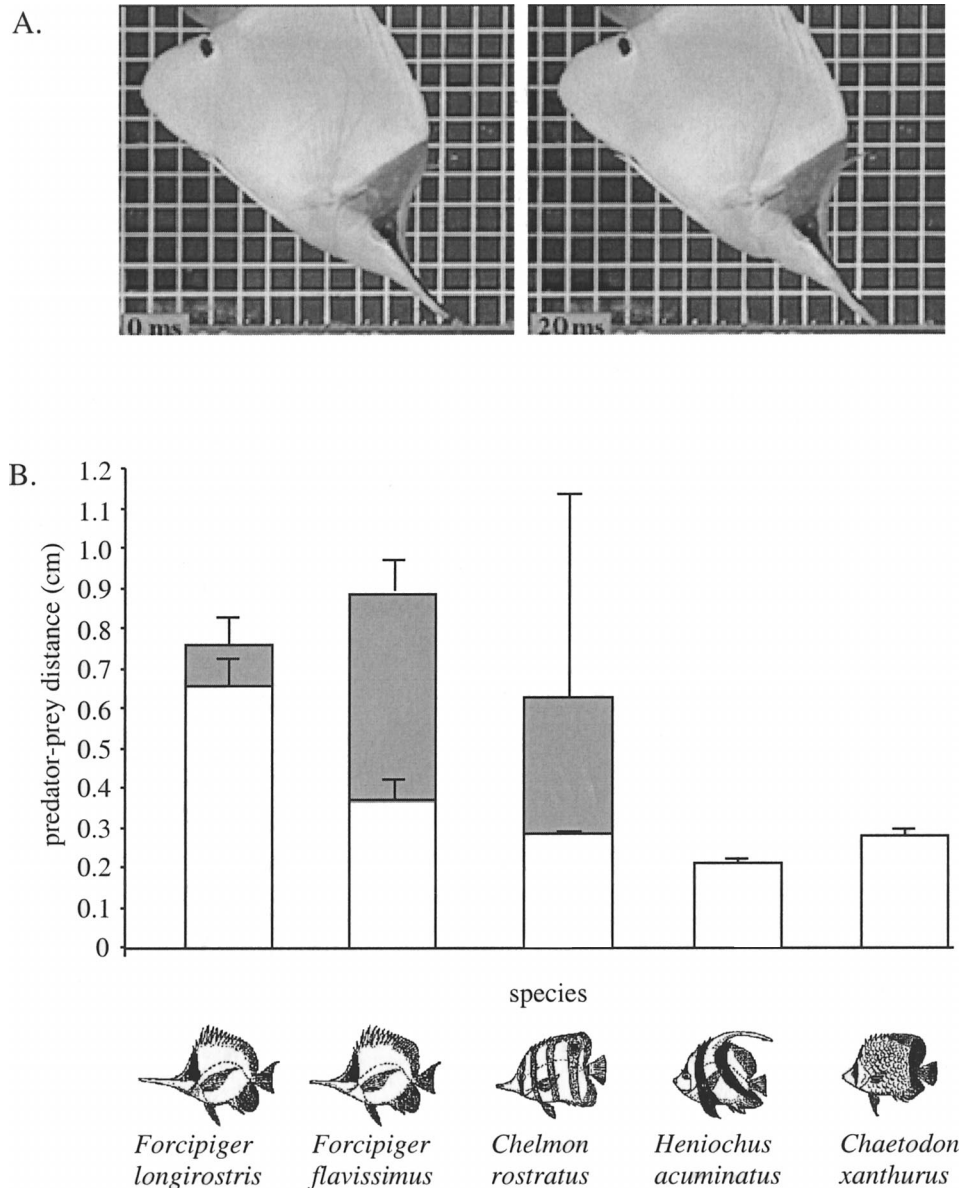
FIG. 9. A) Composite image showing the prey capture event on brine shrimp in the moderately modified *Forcipiger flavissimus*. Times are indicated on the frames. Images were obtained with a NAC ci digital high-speed video camera filming at 250 frames sec^{-1}. Tanks were illuminated with 650 W lights. The grid in the background is 1×1 cm squares. B) Butterflyfish capture success data from five species: The highly modified *F. longirostris*; the intermediately modified *F. flavissimus* and *Chelmon rostratus*; and the unmodified *Heniochus acuminatus* and *Chaetodon xanthurus* (after Ferry-Graham *et al.*, 2001 and 2002*a*). The bars for missed strikes begin at zero and are behind the successful strikes for the species in which they occurred for visual comparison. Plots are means of three individual means $\pm$ SE for each species (n = 3 for each species). *F. longirostris* missed approximately 17% of the time, while the species with intermediate morphologies, *F. flavissimus* and *C. rostratus*, missed 7% and 5% of the strikes respectively. Missed strikes were always followed by successful re-attempts at capture.

cific comparisons from the study of specialization is unwarranted, and all studies of specialization must consider the phylogenetic history and functional biology of the species or populations of interest.

The butterflyfish system and the *Epibulus* system are ideal because in each case a species with a novel morphology exists that differs from its closest relatives mostly in that morphology. These systems also lend themselves to the collection of functional morphological data. Thus, we can determine the actual mechanism of specialization at work. These lines of evidence together allow us to be reasonably sure that changes in performance can be attributed specifically to that novel morphology. When looking at ecological consequence, we are in a position to understand exactly how the ecology of the organism has changed. We do not know, however, if the morphological change came about in response to selective pressures towards specialization, or if the morphological change occurred for some other reason and then facilitated an ecological shift, a pre-adaptation of sorts (*sensu* Gould and Vrba, 1982). To answer this question we must rely on

plausibility arguments and indirect evidence from modern patterns of selection and of convergent evolution.

We encourage functional morphologists to search for such systems and work with their ecological counterparts so that the field can move beyond questions of ''how does it work'' and into ''why did it come to be this way'' and ''at what consequence?'' In the same vein we encourage ecologists to consider not only ''how do these species interact,'' but also include questions of ''what facilitates such interactions'' and ''what evolutionary events led to this interaction?'' The strength of functional morphology is that it really provides us with the power to understand the mechanisms underlying specialization. Consider a study of two co-existing species that can utilize prey item X. Species A eats exclusively X, while species B sometimes eats X but also eats a wide range of other prey items. Ecological studies may reveal that in head-to-head competition trials species B is competitively excluded from X; species A is better at obtaining X. However, a comparative study of the functional morphology of prey capture in species A and its close relatives reveals that A is only doing what all other members of that clade do to capture prey. There is nothing special about the ability to capture prey item X, it is ancestral baggage that it brought along to the current ecological interaction. Without the comparative study of the mechanisms at work, we might have concluded that the diet of species A or B was shaped exclusively by the competitive interactions that it faced. The complementary nature of ecological, phylogenetic, and functional studies allows a more complete understanding of the interactions that occur between organisms and how they are formed. And, studies of function are all the more powerful if they can be linked to specific performance consequences. We hope that we have provided some background into the interesting phenomenon of specialization, and the functional morphological techniques and systems that are useful for elucidating the mechanisms at work.

REFERENCES

Abrams, P. A. 1987a. Alternative models of character displacement and niche shift 2. Displacement when there is competition for a single resource. Am. Nat. 130:271–282.

Abrams, P. A. 1987b. Alternative models of character displacement and niche shift: I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. Evol. 41:650–661.

Adams, D. C. and F. J. Rohlf. 2000. Ecological character displacement in Plethodon: Biomechanical differences found from a geometric morphometric study. Proc. Natl. Acad. Sci. USA. 97:4106–4111.

Baumgartner, J. V. 1992. Spatial variation of morphology in a freshwater population threespine stickleback, Gasterosteus aculeatus. Can. J. Zool. 70:1140–1148.

Baumgartner, J. V. 1995. Phenotypic, genetic, and environmental integration of morphology in a stream population threespine stickleback, Gasterosteus aculeatus. Can. J. Fish. Aq. Sci. 52:1307–1317.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore—moose. Theor. Pop. Biol. 14:105–134.

Berenbaum, M. R. 1996. Introduction to the symposium: On the evolution of specialization. Am. Nat. 148:S78–S83.

Bernays, E. A. and D. J. Funk. 1999. Specialists make faster decisions than generalists: Experiments with aphids. Proc. Royal Soc. London, B 266:151–156.

Bolnick, D. I. 2001. Intraspecific competition favours niche width expansion in Drosophila melanogaster. Nature. 410:463–466.

Chase, J. M. 1996. Differential competitive interactions and the included niche: An experimental analysis with grasshoppers. Oikos 76:103–112.

Compagno, L. J. V. 1984. Sharks world. FAO Species Catalogue, Vol. 4.

Day, T. and J. D. McPhail. 1996. The effect of behavioral and morphological plasticity on foraging efficiency in the threespine stickleback (Gasterosteus sp.). Oecologia 108:380–388.

Day, T., J. Pritchard, and D. Schluter. 1994. A comparison of two sticklebacks. Evol. 48:1723–1734.

Edmonds, M. 1999. Prey capture kinematics horn shark, Heterodontus francisci. Department of Biology. University of South Florida, Tampa.

Emlen, J. M. 1966. The role of time and energy in food preference. Am. Nat. 100:611–617.

Ferry-Graham, L. A. 1997. Feeding kinematics of juvenile swellsharks, Cephaloscyllium ventriousm. J. Exp. Biol. 200:1255–1269.

Ferry-Graham, L. A. 1998a. Effects of prey size and mobility on prey capture kinematics in leopard sharks Triakis semifasciata. J. Exp. Biol. 201:2433–2444.

Ferry-Graham, L. A. 1998b. Feeding kinematics of hatchling swellsharks Cephaloscyllium ventriosum (Scyliorhinidae): The importance of predator size vs. predatory experience. Mar. Biol. 131:703–718.

Ferry-Graham, L. A., P. C. Wainwright, and D. R. Bellwood. 2001a. Prey capture in long-jawed butterflyfishes (Chaetodontidae): the functional basis of novel feeding habits. J. Exp. Mar. Biol. Ecol. 256:167–184.

Ferry-Graham, L. A., P. C. Wainwright, C. D. Hulsey, and D. R. Bellwood. 2001b. Evolution and mechanics of long jaws in butterflyfishes (Family Chaetodontidae). J. Morph. 248:120–143.

Ferry-Graham, L. A., P. C. Wainwright, M. W. Westneat, and D. R. Bellwood. 2001c. Modulation of prey capture kinematics in the cheeklined wrasse Oxycheilinus digrammus (Teleostei: Labridae). J. Exp. Zool. 290:88–100.

Foster, S. A. 1999. The geography of behavior: An Evolutionary perspective. Trends Ecol. Evol. 14:190–195.

Fouts, W. R. and D. R. Nelson. 1999. Prey capture by the Pacific angel shark, Squatina californica: Visually mediated strikes and ambush-site characteristics. Copeia 1999:304–312.

Fox, L. R. and P. A. Morrow. 1981. Specialization: Species property or local phenomenon? Science 211:887–893.

Futuyma, D. J. and G. Moreno. 1988. The evolution of ecological specialization. An. Rev. Ecol. Sys. 19:207–233.

Fry, J. D. 1996. The Evol. of host specialization: Are trade-offs overrated? Am. Nat. 148:S84–S107.

Gould, S. J., and R. C. Lewonton. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique adaptationist programme. Proc. Roy. Soc. London B:581–598.

Gould, S. J. and E. S. Vrba. 1982. Exaptation—a missing term in the science of form. Paleobiology 8:4–15.

Grant, P. R. 1999. *The ecology and evolution of Darwin's finches*. Princeton University Press, Princeton, New Jersey.

Holmes, E. B. 1977. Is specialization a dead end? Am. Nat. 111:1021–1026.

Hutchinson, G. E. 1957. Concluding remarks: Cold Spring Harbor Symposium. Quant. Biol. 22:415–427.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93:145–159.

Jaenike, J. and R. D. Holt. 1991. Genetic variation for habitat preference: Evidence and explanations. Am. Nat. 137:S67–S90.

Labin, P. A. and J. D. McPhail. 1985. The evolution of freshwater diversity in the threespine stickleback (*Gasterosteus aculeatus*): Site-specific differentiation of trophic morphology. Can. J. Zool. 63:2632–2638.

Lasker, R. and A. MacCall. 1983. New ideas on the fluctuations clupeoid stocks off California. CNC/SCOR Proc. Joint Oceanographic Assembly 1982–General Symposia, pp. 110–120. Ottawa, Canada.

Lauder, G. V. 1983. Functional and morphological bases of trophic specialization in sunfishes (Teleostei, Centrarchidae). J. Morph. 178:1–21.

Losos, J. B. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. An. Rev. Ecol. Sys. 25:467–493.

Mac Arthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. 100:603–609.

McPeek, M. A. 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. Am. Nat. 148S:S124–S138.

Mittelbach, G. G., C. W. Osenberg, and P. C. Wainwright. 1992. Variation in resource abundance affects diet and feeding morphology in the pumkinseed sunfish (*Lepomis gibbosus*). Oecologia 90:8–13.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evol. Ecol. 1:379–388.

Naganuma, K. H. and J. D. Roughgarden. 1990. Optimal body size in Lesser Antillean *Anolis* lizards: A mechanistic approach. Ecol. Mon. 60:239–256.

Pacala, S. W. and J. Roughgarden. 1985. Population experiments with the *Anolis* lizards of St Maarten and St. Eustatius [Netherlands Antilles]. Ecol. 66:129–141.

Ralston, K. R. and P. C. Wainwright. 1997. Functional consequences of trophic specialization in pufferfishes. Funct. Ecol. 11:43–52.

Randall, J. E., G. R. Allen, and P. C. Steene. 1990. *Fishes Great Barrier Reef and Coral Sea*. University of Hawaii Press, Honolulu.

Robinson, B. W. and D. S. Wilson. 1994. Character release and displacement in fishes: A neglected literature. Am. Nat. 144:596–627.

Robinson, B. W. and D. S. Wilson. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. Am. Nat. 151:223–235.

Robinson, B. W., D. S. Wilson, and G. O. Shea. 1996. Trade-offs of ecological specialization: An intraspecific comparison of pumkinseed sunfish phenotypes. Ecol. 77:170–178.

Roughgarden, J. 1972. Evolution of niche width. Am. Nat. 106:683–718.

Russo, R. A. 1975. Observations on the food habits of leopard sharks (*Triakis semifasciata*) and brown smoothhounds (*Mustelus henlei*). Cal. Fish and Game 61:95–103.

Sanderson, S. L. 1988. Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). Brain Behav. Evol. 32:257–268.

Schluter, D. 1996. Ecological causes of adaptive radiation. Am. Nat. 148:S40–S64.

Schluter, D. 2000a. Ecological character displacement in adaptive radiation. Am. Nat. 156:S4–S16.

Schluter, D. 2000b. Introduction to the symposium: Species interactions and adaptive radiation. Am. Nat. 156:S1–S3.

Schoener, T. W. 1971. Theory of feeding strategies. An. Rev. Ecol. Sys. 2:369–403.

Schoener, T. W. 1974. Competition and the form of habitat shift. Theor. Pop. Biol. 6:265–307.

Schoener, T. W. 1976. Alternatives to Lotka-Volterra competition: Models of intermediate complexity. Theor. Pop. Biol. 10:309–333.

Sih, A. and B. Christensen. 2001. Optimal diet theory: When does it work, and when and why does it fail? Anim. Behav. 61:379–390.

Stiassny, M. L. J. and J. S. Jensen. 1987. Labroid intrarelationships revisited: Morphological complexity, key innovations, and the study of comparative diversity. Bull. Mus. Comp. Zool. 151:269–319.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Trans. Amer. Fish. Soc. 108:344–352.

Talent, L. G. 1976. Food habits leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. Cal. Fish and Game 62:286–298.

Taper, M. L. and T. J. Case. 1985. Quantitative genetic models for the co-evolution of character displacement. Ecol. 66:355–371.

Thompson, C. E., E. B. Taylor, and J. D. McPhail. 1997. Parallel evolution of lake-stream pairs of threespine sticklebacks (*Gasterosteus*) inferred from mitochondrial DNA variation. Evol. 51:1997.

Thompson, J. N. 1994. *The coevolutionary process.* University of Chicago Press, Chicago.

Tricas, T. C. 1982. Bioelectric-mediated predation by swell sharks, *Cephaloscyllium ventriosum.* Copeia:948–952.

Wainwright, P. C., G. V. Lauder, C. W. Osenberg, and G. G. Mittelbach. 1991a. The functional basis of intraspecific trophic diversification in sunfishes. *In* M. Wake (ed.), *The unity of evolutionary biology,* pp. 515–529. Dioscorides Press,

Wainwright, P. C., C. W. Osenberg, and G. G. Mittelbach. 1991b. Trophic polymorphism in the pumkinseed sunfish (*Lepomis gibbosus* Linneaus): Effects of environment on ontogeny. Funct. Ecol. 5:40–55.

Werner, E. E. and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecol. 60:256–264.

Werner, T. K. and T. W. Sherry. 1987. Behavioral feeding specialization in Pinaroloxias inornata, the "Darwin's Finch" of Cocos Island, Costa Rica. Proc. Natl. Acad. Sci. U.S.A. 84:5506–5510.

Westneat, M. W. 1990. Feeding mechanics of teleost fishes (Labridae; Perciformes): A test of four-bar linkage models. J. Morph. 205:269–295.

Westneat, M. W. 1995. Feeding, function, and phylogeny: Analysis of historical biomechanics in labrid fishes using comparative methods. Syst. Biol. 44:361–383.

Whitlock, M. C. 1996. The red queen beats the jack-of-all-trades: The limitations on the evolution of phenotypic plasticity and niche breadth. Am. Nat. 148:S65–S77.

Williams, G. C. 1956. *Adaptation and natural selection.*

Wilson, D. S. and J. Yoshimura. 1994. On the coexistence of specialists and generalists. Am. Nat. 144:692–707.