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Integrative approaches to the study of predation: general thoughts and a case study on sunfish and salamander larvae

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An integrative study of predation uses a blend of several approaches in evolutionary biology (conflicting selection pressures, phylogenetic constraints, genetics, development) to explain the proximate mechanisms that control "limiting" traits that influence predator-prey dynamics. Predation often has strong, but variable effects on prey. Variation in predator impacts on prey can often be explained by variation in prey behavior. Many systems have prey that show ineffective antipredator behavior; these prey thus do poorly with predators. Ineffective antipredator behavior can be explained by conflicting demands within or across situations. Alternatively, ineffective behavior might be explained by phylogenetic, genetic or developmental constraints. The study of constraints can yield useful insights; however, there are also important limitations on the value of these approaches for adaptation-oriented evolutionary ecologists. I used an integrative approach to study the responses of streamside salamanders, *Ambystoma barbouri*, to predatory sunfish. *A. barbouri* suffers heavy sunfish predation due to relatively high prey activity in fish pools in the day-time. A phylogenetic perspective suggests that this species has actually evolved in the wrong direction with regard to this key "bad" behavior. The apparent explanation for the evolution of ineffective antipredator behavior in this system is conflicting selection pressures generated by behavioral tendencies (high activity levels) that carry over across situations.

1. Introduction

The theme of this volume is predation. Predation clearly has important effects on prey behavior (Sih 1987, Lima & Dill 1990), life histories (Reznick et al. 1990, Crowl & Covich 1990), population dynamics (Taylor 1990, Sih et al. 1992) and community structure (Sih et al. 1985). These effects are seen on both an ecological and an evolutionary time scale. However, as important as predation is, it is still clearly only one of several factors having major effects at each of these levels. In many systems, prey are also faced with food limitation, competition, physical stress

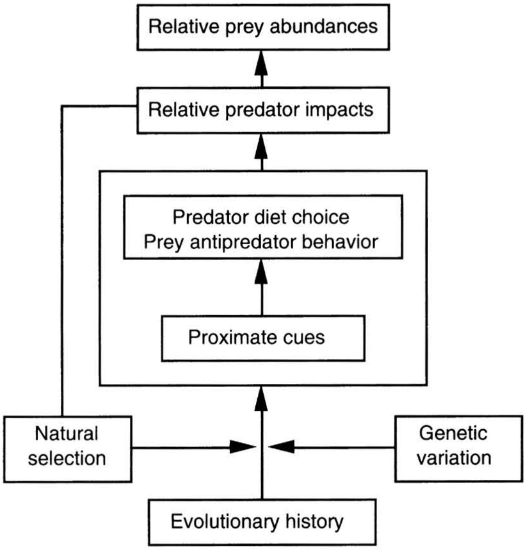

Fig. 1. A conceptual overview of an integrative approach to addressing predator-prey interactions. See the text for details.

and disturbance in a spatially and temporally variable, unpredictable habitat.

This suggests the need for two sorts of integrative approaches to the study of predation:

1) within any given level of study (e.g., behavior, population dynamics or community structure), investigators should integrate information on the influence of predation with effects of other demands; and
2) studies should integrate across levels of study.

To understand mechanisms determining population and community dynamics, look at species interactions. To understand species interactions, examine the traits (in particular, the behavior) of individuals, and to understand individual behavior, use a combination of proximate and evolutionary approaches (Fig. 1). This holistic, integrative view is the theme of this paper.

Of course, others have espoused the value of an integrative approach to evolutionary ecology (e.g., MacArthur & Wilson 1967, Werner 1977, Schoener 1986). Here, I offer my own insights on this approach. My focus will be on behavior: the evolution of behavior and consequences for population/community dynamics. My goals will be to:

1) address ways of connecting behavior to population/community patterns; and
2) discuss multiple approaches to understanding ecologically-important behaviors.

For the latter, I will examine:

3) conflicting demands in behavioral ecology that deserve more attention; and
4) benefits and limitations of integrating alternative approaches in evolutionary biology.
5) Finally, I will present a progress report on my use of an integrative approach to study interactions between sunfish and salamander larvae.

2. Studying ecologically-important behaviors

If possible, an integrative study focusing on ecologically-important traits should include field work to identify forces that influence population/community dynamics; i.e., if possible, investigators should do field surveys followed by field experiments to test the importance of focal selective agents in their system. The field work identifies the patterns in nature that we seek to explain. Are predators important in a given system? Do predators have a greater impact on some prey than others? Or, are predators rare or ineffective such that they have little effect on prey? Is food limitation important? Or, do predators or disturbances keep consumer densities so low that food is usually superabundant? How do prey respond to predators or food limitation in nature?

Many behavioral ecology studies do not include information on the importance of the assumed selective agent in nature. For example, optimal foraging studies often lack clear evidence that food limitation or feeding rate has important effects on fitness in field conditions (see Wiens 1977 for an earlier comment). Of course, a behavioral study need not be tied to ecology; many behaviorists are motivated by questions that do not rely much on ecological bases. If, however, the rationale for studying a behavior is its ecological importance, then my suggestion is that the overall research program should include population studies under field conditions. Such studies will help to not only ascertain the importance of a particular agent, but might also identify interactions between that agent and others that should guide further behavioral study.

3. "Limiting" traits

Having documented the major selective agents in a system, the next step in an integrative study should be to pinpoint the key organismal traits that influence performance relative to those major selective agents. For example, if prey (individuals, populations, species) vary in their ability to coexist with predators, a valuable next step should be to identify the key traits (behavior, morphology, chemistry or life history) that explain the variation in antipredator performance. Three techniques can be used in tandem. Multivariate statistical analyses can quantify relationships between variation in prey traits (e.g., prey activity, escape ability, morphology) and predation rates (Sih & Moore 1990). To gain stronger inferences on cause-and-effect, when possible, one should experimentally manipulate prey traits to quantify their effects on prey performance relative to predators; e.g., compare predation rates on prey with versus without induced defenses (Harvell 1990). Finally, one can devise a model that uses information on prey behavior (or other traits) to predict predation rates; if the model's predictions fit observed predation rates, then the model can be used to provide quantitative tests of the importance of a behavior in determining predation rates (Sih et al. 1988).

One common view for relating traits to population/community dynamics focuses on adaptive behavior (Werner et al. 1983, Abrams 1984, Sih 1984, 1987, Belovsky 1986, Persson 1990). If, for example, predation is important, investigators examine adaptive predator-prey behaviors to explain predator-prey dynamics. Alternatively, one can focus on "limiting traits"- traits that explain poor performance relative to a particular selective agent. For example, imagine a prey species that shows a suite of adaptive responses to a predator, but also shows one inappropriate response. If this one inappropriate response results in high predation rates, then this response is the limiting trait. Limiting traits can likely answer some fundamental questions in population/community ecology. At the population level, limiting traits might explain a species' inability or poor ability to coexist with a particular predator. At the community level, limiting traits can explain the relative impacts of predators on different prey. It is no mystery why many prey persist with predators; these prey have evolved appropriate antipredator traits. What is more interesting is the common occurrence of prey that suffer heavy predation rates and thus fare poorly with a particular predator. What are the limiting traits of these prey and what constrains the evolution of these traits?

4. Multiple conflicting demands

The adaptationist program can provide a good starting point for the study of the evolution of most ecologically-important traits. A major benefit of using the adaptationist program is its logically clear, well developed, theoretical and experimental framework (Maynard Smith 1978, Mitchell & Valone 1990). It also has a history of success (Stephens & Krebs 1986), though mixed with some failure. In addition, it is not trivial that for many of us, our original interest in biology was fueled by the apparent adaptive nature of organisms and behavior.

The value of the adaptationist program is obviously most clear when studying traits that look adaptive. In contrast, in the previous section, I emphasized the value of studying limiting traits, traits that, at first glance, appear non-adaptive. In some cases, to understand these traits it might be necessary to use approaches that emphasize constraints on natural selection (e.g., phylogenetic, genetic or developmental constraints; see below). Limiting traits, however, might also be explained by natural selection, albeit, complex, conflicting selection pressures.

Evolutionary ecology has progressed considerably in its treatment of conflicting selection pressures. Some early adaptation-based studies suffered from "naive adaptationist" thinking, often due to a combination of "atomism" (the tendency to study a trait in isolation from its suite of correlated traits) and a lack of accounting for conflicting selection pressures (Gould & Lewontin 1979). In the last decade, the study of effects of conflicting demands on behavior has become one of the central themes in behavioral ecology. In particular, numerous studies have focused on tradeoffs between foraging and antipredator needs (Sih 1987, Lima & Dill 1990).

In contrast, relatively few studies have examined other conflicting demands. Even if we consider only six categories of ecologically-important behaviors (foraging, antipredator, mating, parental care, aggression, cooperation), there are 15 possible "two-factor conflicting demands" and 20 possible three-factor combinations. Of these, only a handful have been addressed by modern theory and experiments. Fundamental issues such as effects of antipredator or feeding needs on mating dynamics are well known to be important, but have rarely been addressed by explicit optimality theory or by experiments (Magnhagen 1991). Real organisms, particularly during the mating season, might often be faced with balancing feeding, antipredator, mating, territorial and parental care needs. Theory and experiments accounting for a greater degree of the complexity of selection pressures faced by real organisms will no doubt yield important insights (see Sargent 1990).

To make things even more complicated, real organisms must attempt to balance conflicting demands in a world of uncertainty. A great deal of literature addresses the potential responses of foragers to uncertainty. Foragers can avoid uncertainty (Real & Caraco 1988) or sample their environment to reduce uncertainty (Stephens & Krebs 1986). In contrast, few experiments and little theory exists on the effects of uncertainty on other behaviors. Sih (1992) argues that uncertainty about predation risk can have a major impact on prey behavior. The process of gathering information about predation risk might often require prey to expose themselves to predation risk; sampling the predation regime might then be prohibitively dangerous. Uncertainty about risk might thus force prey to stay in hiding as a way of life, even if predators are only rarely present; uncertainty would then represent a major constraint on adaptive prey responses to predators. Uncertainty might have similar fundamental effects on other behaviors; further work on the effects of uncertainty on adaptive behavior, using the literature on foraging uncertainty as a guide, should prove rewarding.

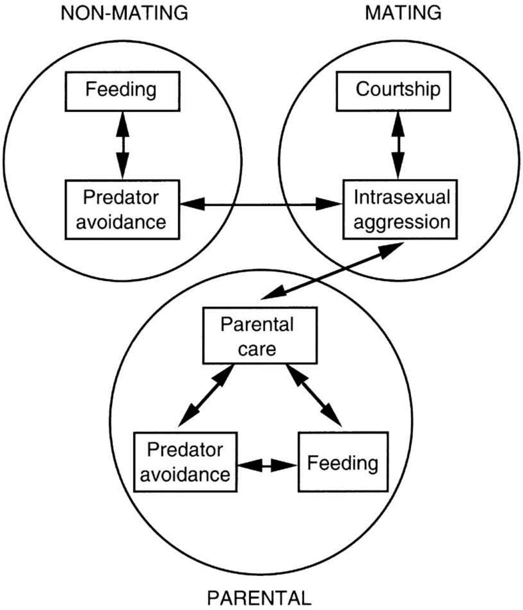

Fig. 2. Within- versus across-situation conflicting selection pressures. The three situations are: a non-mating period, a mating period, and a parental care phase. Arrows link some potential conflicting selection pressures. Each circle encloses some common within-situation conflicts; e.g., between feeding and predator avoidance. Arrows linking boxes in different situations indicate possible across-situation conflicts; e.g., between intrasexual aggression during the mating season and parental care in the parental phase.

5. Conflicts across situations

A distinction can be drawn between conflicts "within versus across situations" (Fig. 2). Conflicting selection pressures exist when correlated traits influence fitness in antagonistic ways. The standard type of conflict is a time budget conflict. For example, time spent in refuge increases fitness by decreasing exposure to predators, while time spent feeding increases fitness by increasing energy intake rates. The two are conflicting demands if time spent hiding is time taken away from feeding and vice versa; i.e., if the two traits are negatively correlated. Time budget conflicts also exist between parental care, mate guarding and searching for new mates (Westneat &

Sherman 1992); between predator avoidance and searching for mates or mate guarding (Sih et al. 1990, Crowley et al. 1991); and between feeding, interacting with conspecifics and scanning for predators (Pulliam & Caraco 1984); see Fig. 2 for other within-situation conflicts.

Conflicts, however, can also occur "across situations" if individuals show behavioral correlations across situations. Such behavioral correlations are expected if animals show behavioral tendencies that carry over across situations. For example, individuals might vary in inherent aggressiveness; some individuals are more aggressive, while others are relatively submissive. All individuals might increase or decrease their aggressiveness depending on the situation; however, some individuals are consistently more aggressive than others (Huntingford 1982). The variation in aggressiveness might have physiological or hormonal correlates (Wingfield 1990, Crews 1992).

Conflicts occur across situations if more aggressive individuals are favored by selection in some situations, but are selected against in other situations. For example, aggressive males might dominate in male-male conflicts and thus gain access to more females; however, if these same males are overly aggressive towards females they might not enjoy high mating success, and their aggressiveness might make them poor parents or might predispose them to take greater predation risks (perhaps this should be termed the "Rambo effect"). If such behavioral tendencies exist, then selection works on the overall behavioral tendency as manifested in many contexts, not on its observed level in any one context. Selection favoring reduced aggressiveness in other contexts can then have important effects on the evolution of aggressiveness in intrasexual conflicts, and selection favoring aggressiveness during conflicts can explain apparently mal-adaptive behaviors such as poor parental care, and inappropriate attacks on females or predators.

This idea is not new. Ethologists seem to see it as obvious. Nonetheless, we do not, at this time, have much data on behavioral tendencies across situations. That is because most of us are conceptual specialists. We study mating, or we study predator-prey interactions, or perhaps parental care. We do not usually study lifetime behavior. In practical terms, most of us do not follow our organisms across situations to see what they might be doing in other contexts. Indeed, for predator-prey behavioral ecologists, a common procedure is to purposely discard animals after one trial to preserve statistical independence of replicates. The study of behavioral correlations across situations is explicitly the study of non-independence of behavioral phenomena across situations. My suggestion is that more integrative study of behavioral tendencies across situations might reveal new, complex views on the nature of conflicting selection pressures.

Returning to limiting behaviors, the notion is that they might be explained by conflicting selection pressures within situations (time budget conflicts) or perhaps by unsuspected conflicts across situations.

6. Alternative evolutionary approaches

Given that limiting behaviors often appear maladaptive, it is reasonable to embrace non-adaptationist approaches to understand their evolution. As many others have noted, natural selection is not the only force explaining evolutionary pathways or the current state of traits (Gould & Lewontin 1979, Brooks & Wiley 1986, Rose et al. 1987). Traits are not generated *de novo*; they evolve from some previous state. The evolutionary history of a trait can constrain the set of possible pathways for further evolution; such constraints are referred to as ancestral, historical or phylogenetic constraints. Evolution from a previous state involves a series of steps:

1) development- which converts an existing genotype into a phenotype;
2) natural selection- which "chooses" among phenotypes; and
3) genetics- which converts phenotypes into the next generation's genotypes and directs development.

Thus selection need not be alone in directing the path of evolution; genetics and development can also play a role. If the genetic or developmental systems constrain the path of evolution; i.e., if they prevent selection from driving the system to an optimal state, then we see genetic or developmental constraints (Lande & Arnold 1983, Maynard Smith et al. 1985). The issues here are: what are the benefits of integrating these approaches into a study of ecologically-important behaviors? What are some limitations to these approaches?

6.1. Phylogenetic constraints

I begin by looking at phylogenetic inferences typically generated by using an independently derived evolutionary tree to look at the path of evolution of a trait (Sillen-Tullberg 1988, Donoghue 1989, Bjorklund 1991). This procedure can yield information on the direction of evolution (did A evolve from B or vice versa or both from C?), on the number of statistically independent evolutionary events (do 10 occurrences of an association represent 10 independent events or one evolutionary event followed by speciation?; Felsenstein 1985), and in some cases, on the circumstances accompanying an evolutionary change (did the trait evolve recently or in the distant past? what other traits did the ancestor likely possess? what were likely ecological conditions associated with the change?).

The above issues are obviously crucial for understanding the evolution of traits. In particular, they can be relevant for the study of limiting traits. When evolutionary ecologists see an apparently adaptive association between a trait and an environmental condition, they usually assume that this reflects adaptive evolution driven by natural selection in the observed habitat; i.e., that "current utility" is the result of evolution by natural selection. Frequent observations of current utility might then imply that organisms generally show adaptive evolution in response to changing environments. An alternative explanation, however, is that the organism's traits limit the possible environments used by the organism; i.e., that the organism is "stuck" with a set of traits and can thus only persist in habitats that are suitable for those traits. In the latter scenario there is little adaptive evolution. When habitats change, organisms migrate or do poorly in the new habitat, and perhaps go locally extinct. In this view, limiting traits that explain species distributions are explained largely by phylogenetic constraints.

The above considerations suggest that phylogenetic information might often yield major insights for behavioral ecologists. In particular, a phylogenetic perspective is crucial when using a comparative approach to understand evolution (i.e., comparing traits and associations of traits for many taxa; Harvey & Pagel 1991). Many, if not most, behavioral ecologists, however, do not rely on the comparative approach. Indeed, many confess to having little interest in evolutionary pathways, but are interested primarily in current utility. These investigators examine current utility by comparing the behavior of one or at most a few taxa, to the predictions of an optimality model.

Behavioral ecologists that study only one or a few taxa will often draw little benefit from phylogenetic perspectives. If the observed behaviors fit an optimality model, an investigator interested in current utility will see little reason to seek explanations involving phylogenetic constraint. Even if observed behaviors do not fit an optimality model, in most circumstances, phylogenetic data are unlikely to provide powerful explanations for the discrepancy. The problem is one of low sample size. Evolutionary trees are statements of the most likely (e.g., most parsimonious — requiring the fewest evolutionary changes) evolutionary scenario based on many taxa and many independent traits; i.e., statements based on large sample sizes. For example, a cladistic analysis might say, with some confidence, that for 40 species, trait A appears to have generally evolved from trait B and not vice versa. Little confidence, however, can be attributed to any statement about the evolution of one trait for one species pair. Imagine a situation where species X has trait A, species Y has trait B, and an outgroup has trait B. The hypothesis that species X evolved trait A from an ancestor with trait B requires one evolutionary change, while the opposite hypothesis that trait A is ancestral requires two evolutionary changes. The difference is obviously too small to use parsimony as a reliable judge.

Thus for evolutionary ecologists that focus on detailed studies of one or a few specific taxa (as opposed to those that compare many taxa), there are limitations to the use of phylogenetic methods alone to infer evolutionary pathways or to study phylogenetic constraint. This is not to say that it is impossible to derive strong inferences on the path of evolution for a specific taxon. If across many taxa, the path of evolution for a given trait is overwhelmingly in one direction and not the other, most people will accept this pathway for a specific taxon. Inferences are also strengthened if they are reinforced by independent evidence. For example, if a species with a derived trait is exposed to a new selection regime that potentially explains the evolution of that trait, and if a closely related species with the ancestral trait has genetic variation in that trait that should allow it to evolve, inferences on the path of evolution can be quite strong.

6.2. Genetic constraints

Quantitative study of genetic variation can potentially provide useful information on the role of genetic constraints in determining evolutionary pathways (Lande & Arnold 1983, Rose et al. 1987). In theory, the evolution of a trait depends on direct selection and heritability of that trait, and indirect selection and genetic correlations between that trait and others (Lande & Arnold 1983). A research program combining path analysis to measure selection gradients and controlled crosses to measure genetic parameters should thus yield useful predictions on the path of future evolution. Of particular interest to adaptation-oriented evolutionary ecologists is the notion that quantitative genetic study provides predictions on how genetic constraints might prevent the evolution of optimal strategies.

Unfortunately, it is probably impractical in many systems (e.g., for behaviors of mobile organisms in natural conditions) to actually measure quantitative genetic parameters. Even more importantly, the quantitative and perhaps qualitative predictions of quantitative genetic theory are robust only under highly restrictive conditions that are probably rarely seen in nature (Mitchell-Olds & Rutledge 1986). For example, the theory only applies if:

1) selection gradients and genetic variance/covariance matrices are constant in space and time, which requires weak selection (which is unlikely to hold for ecologically-important behaviors),
2) there is no inbreeding,
3) there is no gene × environment interaction (but see Via & Lande 1985), and
4) no gene × environment correlation; i.e., no local adaptation.

Given this set of restrictions, what useful role can quantitative genetic studies play in an integrative program in evolutionary ecology? My view is that until new theory arises, detailed data on genetic variances and covariances are of limited value. While it should be useful to know whether a trait is heritable at all, and whether a genetic correlation exists, the extra effort required to get "accurate" estimates of these environment-dependent parameters might not prove insightful. The problem is not simply that genetic parameters are likely to be environment-dependent. Many other phenomena (e.g., selection pressures) are also environment-dependent but still important to behavioral ecologists; indeed, behavioral responses to changing selection pressures in variable environments are at the heart of behavioral ecology. The problem instead is that if genetic parameters are environment-dependent (or if a host of other assumptions are violated, see above), then quantitative genetic studies might not provide reliable information on genetic constraints that can explain suboptimal behaviors; i.e., quantitative genetic information might not be useful to behavioral ecologists.

In contrast, I am impressed by the potential value of using path analysis or other multivariate statistics to provide a quantitative understanding of natural selection. In particular, I like Arnold's (1983) integrative approach of quantifying relationships between both: 1) a trait (e.g., morphology, behavior) and a performance variable (e.g., running speed), and 2) between performance and fitness. For example, a study of foraging might quantify individual variation in foraging behavior, feeding rates, growth rates and fecundity and survival to see if adaptive patch use or diet choice actually results in higher feeding rates and whether higher feeding rates actually translate into higher fitness.

This approach has several benefits for behavioral ecologists. First, it quantifies the actual effects of apparently ecologically-important behaviors on fitness. Behavioral ecologists routinely infer that if a behavior fits the predictions of an optimality model, that it demonstrates that the behavior maximizes fitness. In fact, behavioral ecologists, particularly those that study predator-prey behaviors, rarely measure relationships between a behavior and any component of fitness (but see Sih 1982; Ritchie 1990). Arnold's (1983) approach not only quantifies relationships between behavior and fitness, but also provides some insights on mechanisms underlying effects of behavior on fitness. Because the approach focuses on individual variation, to implement the approach an investigator must follow individuals; ideally, this should yield information on behavioral tendencies and on conflicts across situations (see above). In concert with data on the existence of genetic correlations, path analyses can thus provide some insight on the effects of indirect selection on a focal trait.

6.3. Developmental constraints

The developmental program clearly provides constraints on the evolution of morphology; i.e., given a particular developmental system, not all morphologies are equally likely to evolve (Maynard Smith et al. 1985, Gould 1989). Developmental constraint might play a similar role in shaping the evolution of behavior (Jamieson 1986, 1989). In addition, understanding the developmental system might provide mechanistic explanations for genetic correlations (Cheverud 1984, Kingsolver & Wiernasz 1991). Evolutionary biologists are only beginning to develop a practical, quantitative framework for studying developmental constraints. This field thus offers compelling arguments for its importance, with little consensus on how an evolutionary ecologist might actually incorporate developmental study into an integrative program.

Some participants at the Nordic conference suggested that study of developmental constraints should be avoided because of a lack of theoretical and empirical framework. My suggestion is that evolutionary biologists that are only beginning their careers, or that have the energy to re-train, should consider getting training in both developmental biology and evolutionary ecology. There is a strong feeling that the integration of these two fields will yield major insights; we need more people with the appropriate training to take on the challenge.

7. Proximate control of behavior

By the "proximate" control of behavior I mean either the:

1) cues and rules of thumb that guide behavior; or
2) neural, hormonal or physiological correlates of behavior.

This information is obviously worthwhile in its own right. For the adaptation-oriented behavioral ecologist, studies on proximate mechanisms can be valuable in that they can potentially explain both adaptive behavior and conditions when organisms show non-adaptive behavior.

For example, some prey seem to avoid predators by avoiding all large, fast objects. This results in adaptive avoidance of predators that are large and fast, but can explain unnecessary avoidance of non-predatory stimuli. The result can be wasted effort and an "imprecise" behavioral response to predators (Sih 1986).

Of course, the study of proximate cues should be coupled with an evolutionary view; selection, phylogeny and genetics all influence the evolution of proximate mechanisms. A recent symposium volume of the American Naturalist provides some nice examples of studies on the evolution of proximate mechanisms that control behavior (American Naturalist, volume 139, supplement).

8. Summary — suggestions for integrative studies

1) Conduct field surveys and experiments to quantify key selective agents.
2) Identify the key traits that influence performance relative to key selective agents.
3) Focus on limiting traits — traits that explain poor performance of some individuals, populations or species relative to a particular agent.
4) Examine the effects of conflicting selection pressures (both within and across situations) and organismal uncertainty on key traits.
5) Study behavior in a phylogenetic context; use systems where phylogeny and other sources of evidence provide strong inferences on the path of evolution.

6) Use path analysis to quantify effects of key traits on performance and fitness. Gather some information on heritability and genetic correlations.
7) Study proximate mechanisms. They can provide insights on both adaptive, and more importantly, non-adaptive behavior.

9. A case study: sunfish and salamander larvae

The central issue that forms the backdrop for this case study is the variable impact that predators have on prey. In most communities, some prey are relatively unaffected by predators, while other prey are wiped out by predators (Sih et al. 1985). What explains this variation in predator impact? Two obvious candidates are predator diet choice (i.e., more profitable prey are more likely to be attacked and thus suffer greater predator impacts), and variation in prey antipredator traits (i.e., prey that have less effective antipredator traits are the ones that get wiped out by predators). Literature surveys suggest that in freshwater predator-prey systems, particularly those where prey have potentially effective antipredator responses (e.g., fish-fish, insect-insect or insect-zooplankton interactions), the main determinant of variation in predator impacts is prey behavior, rather than predator diet choice (Woodward 1983, Sih & Moore 1990). In particular, prey that are less active in the presence of predators, or that hide effectively from predators, tend to suffer less predation than prey that are more active. Prey activity results in more time spent exposed to predators, and attracts the attention of predators. If prey activity results in high predation rates, why do many communities have prey that show high activity in the presence of predators?

To study this issue, I focused on a system that is particularly amenable to ecological, behavioral and evolutionary study: the responses of streamside salamander larvae (*Ambystoma barbouri*) to predatory green sunfish (*Lepomis cyanellus*) in small stream pools. Below, I summarize my laboratory's ongoing published and unpublished work on this system. The overall project integrates information on population/community ecology, behavioral ecology, limiting behaviors, proximate cues, phylogenetic inertia, complex conflicting selection pressures within and across situations, and a bit of quantitative genetics. The result is a scenario on the evolution of key behaviors that explain a species interaction that determines field patterns of abundance.

9.1. Population ecology of *Ambystoma barbouri*

Ambystoma barbouri are extremely abundant in small, headwater streams in central Kentucky, USA. These streams consist of a series of pools (with relatively low current velocity) connected by fast-flowing riffles; *A. barbouri* live primarily in pools. *A. barbouri* feed on macroinvertebrates and have major effects on macroinvertebrate densities (Huang & Sih 1991a). Some pools contain green sunfish, most do not. In pools without sunfish, major agents of larval mortality are:

1) severe floods in some years in early spring;
2) food limitation and intraspecific competition in years without floods; and
3) early stream drying in most years (Petranka & Sih 1986).

Adult female streamside salamanders avoid laying eggs in fish pools (Kats & Sih 1992); however, larvae drift among pools so that about 30–40% of all larvae experience fish pools (Sih et al. 1992).

Field surveys of over 100 streams show that *A. barbouri* are virtually always very rare in pools with fish, and are absent from streams with fish in most pools (Petranka 1983; Sih et al. 1992). A controlled, field experiment manipulating sunfish presence showed that green sunfish severely reduce densities of streamside salamander larvae (Sih et al. 1992). More than 90% of the larvae that drift into fish pools do not survive for even 3 days; those that survive do so by drifting out the downstream end of fish pools. Larval survival with fish is influenced by the presence of alternative macroinvertebrate prey; thus the system includes complex interactions among sunfish, salamanders and macroinvertebrates (Huang & Sih 1990, 1991b). However, in all circumstances, larvae show poor survival with fish.

9.2 Identifying the limiting larval behavior

Field observations of larval behavior showed that larvae respond to fish by hiding under rocks and avoiding the central, deeper regions where fish forage; very few larvae were seen out in the open in fish pools (Sih et al. 1992). Thus the field experiment yielded a paradox; while larvae appear to be showing appropriate antipredator responses, they also suffer heavy mortality. More detailed observations in semi-natural pools showed, however, that while larvae hide under rocks, they do not stay there well enough; i.e., larvae emerge from refuge at a measurable rate and shortly after emerging, are attacked and either consumed or driven back into refuge. In addition, exposed larvae tend to be active, thus drawing the attention of fish. A quantitative model relating behavior to predation rates suggested that the observed larval activity was high enough to explain heavy predation rates (Sih et al. 1988). The key larval limiting behaviors are thus a relatively high emergence rate from refuge and high activity while outside of refuge. Why do larvae do these behaviors when the result is heavy mortality?

In contrast to *A. barbouri*, the two-lined salamander, *Eurycea bislineata* coexists relatively well with sunfish. Sunfish show similar attack rates on active, exposed larvae of the two species; however, two-lined salamanders are rarely killed because they are much less active than streamside salamanders in the presence of sunfish. Thus, in keeping with studies in many other freshwater systems, the key trait that appears to explain variation among prey in predator impacts is prey activity.

A. barbouri larvae also respond to sunfish by attempting to disperse out of fish pools at night. This pattern seems adaptive. Larval mortality in fish pools is so high that larvae have essentially no chance of completing their larval period (i.e., of undergoing metamorphosis) in fish pools. Their only chance for long-term survival is to drift out of a fish pool. Sunfish are less active at night; thus it makes sense to attempt to drift out of fish pools at night. The overall notion is that an adaptive response to being in a fish pool might be to hide under rocks all day, and then attempt to drift out at night. *A. barbouri* larvae follow this basic pattern; however, they do not do it well enough to enjoy high survival with fish.

The remainder of this paper discusses several approaches for explaining the key larval limiting behavior: relatively high larval activity in fish pools in the daytime.

9.3. Proximate cues

A. barbouri larvae respond to waterborne chemical cues emanating from sunfish (Kats et al. 1988, Sih et al. 1992). The smell of fish causes larvae to reduce their activity, hide under refuges, get easily alarmed if they are outside of refuge, and tend to drift out of pools. Larvae also respond to visual cues from fish. Chemical cues that can penetrate under rocks are, however, presumably the main cues that reach larvae that are hiding under rocks; i.e., chemical cues might play the major role in mediating a key limiting behavior, larval emergence rate from refuge.

Larval responses to chemical cues could explain the relatively high larval daytime activity in fish pools if larvae habituate to fish chemicals within a brief period. Habituation to predator cues, if it occurs, seems maladaptive, but might represent a neural constraint on adaptive behavior. Larvae begin emerging from refuge within four hours after entering fish pools. To explain this by habituation, larvae must habituate in this initial period. In fact, experiments show that larvae do not habituate to fish smell within three days (we did not test them beyond three days). Thus even if habituation occurs eventually (e.g., after a few weeks), this does not explain the initial high activity that results in high fish predation rates.

Larval response to fish chemicals can explain one interesting, probably non-adaptive behavior. Larvae tend to disperse unnecessarily from fishless pools that are downstream from fish pools; this can result in enhanced larval movement from "safe" pools into dangerous fish pools further downstream (Sih et al. 1992). Larvae presumably do this because they receive chemical cues from the fish pool upstream.

9.4. Phylogenetic constraint

Perhaps *A. barbouri* larvae respond poorly to fish because they lack a long evolutionary history with predatory fish. This sort of hypothesis is the usual explanation for poor responses of island fauna to introduced predators. To test this hypothesis, we need a phylogenetic perspective; i.e., we need to infer the traits and habitat (with or without fish) of *A. barbouri*'s recent ancestors. In most systems, this sort of historical information is not available. In *A. barbouri*, however, we have a relatively clear picture of its evolutionary history. *A. barbouri* is one of only two species in its genus that lives in streams; all other species live in ephemeral ponds, generally without fish. For this and other reasons, it is generally accepted that *A. barbouri* is derived from a pond-dwelling ancestor.

A. barbouri has a sister species, the small-mouthed salamander, *A. texanum*, that lives in fishless, ephemeral ponds. Until recently (Krause & Petranka 1989), *A. barbouri* and *A. texanum* were considered two races of the same species. *A. barbouri* is found only in the Bluegrass region of Kentucky and surrounding areas, whereas *A. texanum* is found in much of the rest of the Eastern United States. A likely historical scenario is that ancestors that closely resembled contemporary *A. texanum* colonized into streams from ephemeral ponds when these ponds in the Bluegrass dried up during a warm, dry era about 8000 years ago. In the rest of *A. texanum*'s range, it stayed in ephemeral ponds. If we accept this overall scenario, then the traits of contemporary *A. texanum* provide a reasonable indication of the traits of *A. barbouri*'s ancestor. Comparisons of the two species can then be used to examine the path of evolution of anti-fish behavior.

Fig. 3 illustrates the "phylogenetic inertia hypothesis" for *A. barbouri*. Salamanders like *E. bislineata* have low activity with sunfish and thus persist well with sunfish. In contrast, *A. barbouri* are too active and thus suffer heavy sunfish predation (i.e., they show a lifestyle that is too "fast" (cf. Sih 1987) to cope with sunfish predation). *A. barbouri* is derived from an ancestor that lived in an ephemeral, fishless habitat. Because of the need to be active and feed, grow and develop rapidly in ephemeral ponds, and because of the low cost of high activity in fishless ponds, the ancestor might have evolved a very fast lifestyle, and thus a very poor ability to cope with fish. Perhaps *A. barbouri* has evolved to be better than its ancestor at coping with fish, but due to its evolutionary history, it is still poor at persisting with fish.

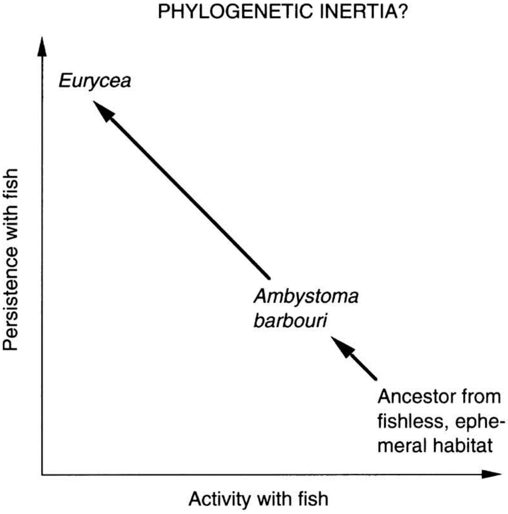

Fig. 3. A phylogenetic inertia hypothesis to explain the high activity and poor persistence of *A. barbouri* with sunfish. High activity is associated with poor persistence with sunfish. *Eurycea bislineata* show low activity that allows them to persist with sunfish. Perhaps *A. barbouri* show high activity and poor persistence with sunfish because *A. barbouri* is recently derived from an ancestor that lives in fishless, ephemeral habitats.

To test this idea we compared the anti-fish behavior, in particular, the emergence rate and activity, of larvae of the two sister species. The hypothesis is supported if *A. texanum* shows higher activity than *A. barbouri*, particularly if the two species show similar high activity. We ran our experiments in semi-natural pools (see Sih et al. 1988 for methods) and found a fascinating result. In all circumstances, with or without fish present, for three larval size classes, *A. barbouri* were more active and showed higher emergence rates (Fig. 4) than did *A. texanum*. That is, evolution of activity went in the wrong direction as far as fish predation was concerned.

The evolutionary increase in activity, which ought to increase predation rates, was offset by the evolution of increased escape success. The suggested mechanistic explanation for this is as follows. *A. barbouri* have evolved an increase in their response to fish chemical cues. The increase in response to fish smell is accompanied

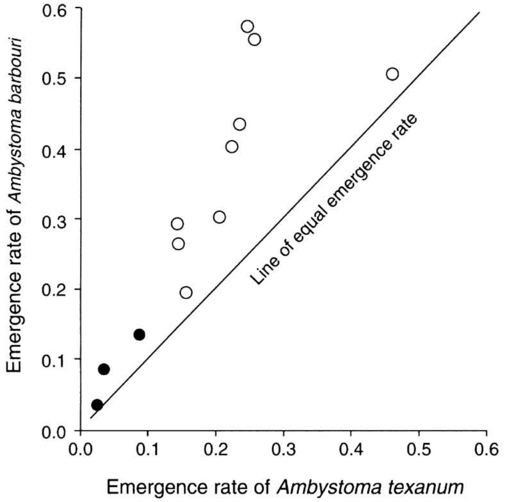

Fig. 4. Emergence rates from refuge for *Ambystoma barbouri* and *A. texanum*. Open circles = fish absent, closed circles = fish present. Each point represents mean emergence rates (4–6 replicates per species per point) recorded in a series of experiments comparing the species under a range of identical conditions. Notice that emergence rates are lower in the presence than absence of fish, and that all points fall above the line of equal emergence rate for the two species.

by an increased tendency to show alarm responses to the approach of a fish. Increased alarm makes larvae harder to catch; alarmed larvae initiate an escape response when fish are relatively far away. The evolution of increased escape success offsets the increased exposure to fish; thus for three larval size classes, *A. texanum* and *A. barbouri* larvae do not differ significantly in their survival with fish. Both species do poorly with fish. For *A. texanum* this is expected, they live in fishless ponds. For *A. barbouri* we have compounded the mystery: not only are they too active to cope with fish, but, in addition, they have apparently increased their activity over evolutionary time.

Our work also included full sib comparisons that yield some inferences on genetic variation in antipredator behavior. Interestingly, 3/12 sibships of *A. texanum* showed significant responses to fish smell, despite the fact that these larvae live in fishless ponds. In contrast, for *A. barbouri*, 19/20 sibships responded significantly to fish smell. The evolution of increased response to fish smell provides evidence that fish have exerted significant selection pressures on these salamander larvae. These data should be interpreted, however, with caution because they do not account for possible maternal effects nor for non-additive genetic variation. The potential for doing more detailed quantitative genetic studies on ancestral traits that have since evolved is, I suggest, an additional benefit of doing studies on a system with a known, extant ancestral representative.

9.5. Conflicting selection pressures

The most obvious conflicting selection demand that might explain larval emergence from refuge is hunger. Larvae might come out to feed. This is the standard, within-situation, time budget conflict between feeding and hiding. In fact, in this system this is probably not a viable adaptive scenario. At field temperatures, larvae can withstand weeks without food without starving to death (Maurer & Sih, in review); thus if larvae come out to feed they are taking a tremendous predation risk to offset very little risk of starvation. More importantly, larval behavior does not fit this hypothesis. If they emerge because they are hungry, then they should emerge at a higher rate when they are hungrier. Experimental manipulations of larval hunger level showed no significant effect of hunger on larval emergence rate in the daytime, in the presence of fish (Sih et al. 1988).

Perhaps a better within-situation adaptive hypothesis involves the possible effect of low feeding rates on developmental rates. Recall that larvae face a high risk of mortality due to desiccation if they do not develop rapidly enough to undergo metamorphosis before pools dry up (Petranka & Sih 1986, 1987). Indeed, larval mortality rates from habitat drying are higher for *A. barbouri* than for *A. texanum* (Petranka & Sih 1987). Perhaps even a day or two of hiding under rocks throws larvae significantly behind schedule on a developmental trajectory that they must stay on to transform successfully before pools dry. If this explains high larval activity in fish pools, then at any given time, larger larvae (that are ahead of others on the developmental trajectory) should show lower emergence rates. In fact, larger larvae showed higher emergence rates than smaller larvae. Thus the observed larval behavior does not support this hypothesis either.

What about across-situation conflicts? For these to exist, we need to see both benefits of being highly active in other situations and a positive correlation between activity across different situations (i.e., activity must be a general behavioral tendency that carries over across situations). Our experiments showed that these conditions indeed hold. High activity in fishless conditions is favored; larvae that are more active, feed at a higher rate and thus grow and develop more rapidly (Maurer & Sih, in review). For this to explain high activity in the presence of fish there must be a carryover of high activity from fishless to fish conditions. Comparisons of individual activity in the two conditions showed significant correlations between activity in fish and fishless conditions (*A. barbouri*: $r = 0.67$, $P < 0.001$; *A. texanum*: $r = 0.65$, $P < 0.001$); i.e., some individuals (indeed, some sibships) were more active in both conditions, while other individuals (and sibships) were less active in both conditions. Only the least active larvae spent virtually all of their time under refuge in the presence of fish; all other larvae showed activity levels that were likely to result in death by fish predation.

High activity is also favored in fish pools at night. Comparisons of drift and activity in *A. barbouri* consistently show positive correlations between the two. This can explain high activity in fish pools in the day, if there are positive day/night activity correlations. Over a four day period, these correlations are consistently significantly positive; i.e., the same individuals are more active than others day and night for 4 consecutive days.

Why do larvae show these activity carryovers when they appear to result in very heavy mortality? Why has natural selection been unable to break this behavioral correlation? My guess is that the correlation has some physiological basis; perhaps highly active larvae simply cannot immediately "gear down" their metabolic needs sufficiently to stay under rocks all day. My auxiliary hypothesis is that the activity correlations only last a few days; after a while, larvae can fully "gear down". Unfortunately for the larvae, even a 2–3 day behavioral time lag results in very heavy fish predation.

9.6. The evolution of limiting traits in streamside salamanders

My proposed scenario for the evolution of limiting traits that explain the distribution of *A. barbouri* is presented in Fig. 5. *A. barbouri* larvae face two important changes in selection pressures since colonizing streams: increased fish predation and increased mortality due to habitat drying. In response to fish predation, larvae have evolved:

1) an increased response to fish chemicals that increases their mean level of alarm that, in turn, makes larvae harder to catch; and
2) an increased tendency to be active at night and to drift out of fish pools at night.

In response to early stream drying, larvae have evolved higher activity in the day that is associated with higher feeding, growth and developmental rates and thus an enhanced probability of undergoing metamorphosis before pools dry up (Maurer & Sih, in review).

Unfortunately for these larvae, they have a suite of correlated activities. Selection favoring higher activity in fishless pools and in fish pools at night appears to have overridden selection against high activity in the day in fish pools. Although we do not have detailed estimates of the magnitude of these conflicting selection pressures, the population's natural history fits the suggested selection scenario. In most years, all larvae face potential mortality from early stream drying, whereas only about 30–40% of all larvae experience fish. Of those that experience fish, very few survive to breed (fish pools appear to be a "sink" habitat for *A. barbouri*); the survivors are primarily individuals that drifted out at night. As a result, larvae have evolved an increase in their activity in fish pools in the day, despite the concomitant increase in daytime predation rates. This increase in predation rate offsets the evolution of decreased predation rates due to increased escape success. The overall result is no improvement in larval survival with fish, despite strong selection pressure from fish. The behavioral correlations might also explain the high larval mortality relative to stream drying; the evolution of even higher activity in fishless pools might be constrained by selection against high activity in fish pools in the day.

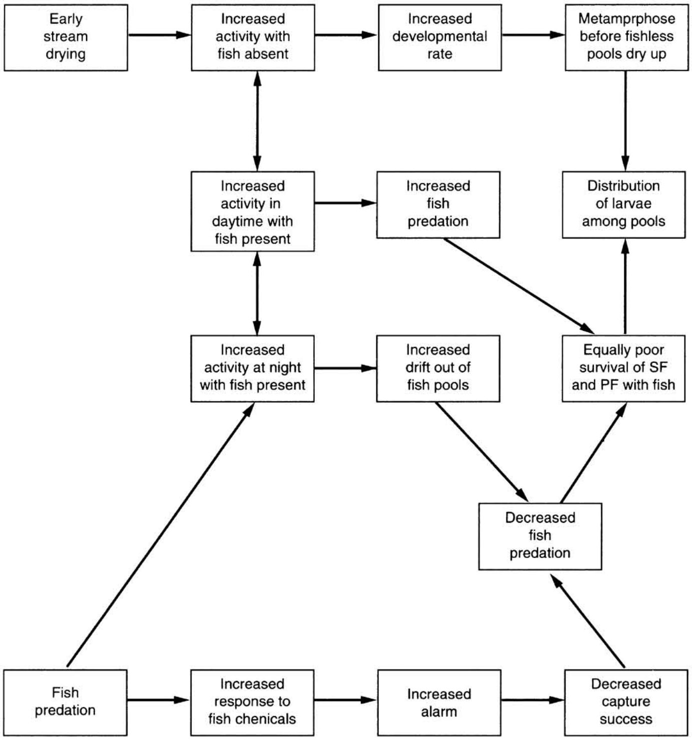

Fig. 5. An integrated evolutionary scenario outlining the effects of new selection pressures in streams (far left) on the evolution of behaviors that explain survival with fish and patterns of metamorphosis that, in turn, explain the distribution of *Ambystoma barbouri* among stream pools (far right).

Overall, I suggest that an integrative approach to studying this predator-prey interaction has generated numerous insights that could not be gained without a holistic view. I am now using a similar integrative approach to study the evolution of life histories in the same system.

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