

# THE FOSSIL RECORD OF PREDATOR-PREY ARMS RACES: COEVOLUTION AND ESCALATION HYPOTHESES

GREGORY P. DIETL<sup>1</sup> AND PATRICIA H. KELLEY<sup>2</sup>

<sup>1</sup>Department of Zoology, North Carolina State University, Raleigh, NC 27695-7617 USA

<sup>2</sup>Department of Earth Sciences, University of North Carolina, Wilmington, NC 28403-3297 USA

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**ABSTRACT**—Arms races between predators and prey may be driven by two related processes—escalation and coevolution. Escalation is enemy-driven evolution. In this top-down view of an arms race, the role of prey (with the exception of dangerous prey) is downplayed. In coevolution, two or more species change reciprocally in response to one another; prey are thought to drive the evolution of their predator, and vice versa. In the fossil record, the two processes are most reliably distinguished when the predator-prey system is viewed within the context of the other species that may influence the interaction, thus allowing for a relative ranking of the importance of selective agents. Detailed documentation of the natural history of living predator-prey systems is recommended in order to distinguish the processes in some fossil systems. A geographic view of species interactions and the processes driving their evolution may lead to a more diverse array of testable hypotheses on how predator-prey systems evolve and what constraints interactions impose on the evolution of organisms. Scale is important in evaluating the role of escalation and coevolution in the evolution of species interactions. If short-term reciprocal adaptation (via phenotypic plasticity or selection mosaics among populations) between predator and prey is a common process, then prey are likely to exert some selective pressure over their predators over the short term (on ecological time scales), but in the long run predators may still exert primary “top-down” control in directing evolution. On the scale of evolutionary time, predators of large effect likely control the overall directionality of evolution due to the inequalities of predator and prey in control of resources.

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“Every animal has its enemies, and Nature seems to have taxed her skill and ingenuity to the utmost to furnish these enemies with contrivances for the destruction of their prey...For every defensive device with which she has armed an animal, she has invented a still more effective apparatus of destruction and bestowed it upon some foe, thus striving with unending pertinacity to outwit herself.” —Forbes, 1887

## INTRODUCTION

THE ARMS RACE CONCEPT is all too familiar to those of us who have grown up during the latter half of the twentieth century. More controversial, however, is the idea that evolutionary arms races between interacting species (such as predator and prey) have characterized the history of life on Earth. Predation is a nearly universal pressure affecting individual animals as well as the

organization of ecosystems. Darwin’s metaphor of the “struggle for existence” indicates that he viewed biotic struggle (or interactions within and between species) as a major evolutionary force in the history of life: “The relation of organism to organism is the most important of all relations” (Darwin, 1859, p. 477). Arms races between species over evolutionary time are likely wherever individual organisms have enemies with a capacity for evolutionary response (Dawkins, 1986). Such interaction (from an economic standpoint) is argued to drive or shape the evolution of life (Dawkins, 1986; 1995; Vermeij, 1987; 1999).

Dawkins (1986) credited H. B. Cott with having been the first author to apply the arms-race analogy to the biology of predator-prey systems:

“...In the primeval struggle of the jungle, as in the refinements of civilized warfare, we see in progress a great evolutionary armament race—whose results, for defense, are manifested in such

devices as speed, alertness, armor, spinescence, burrowing habits, nocturnal habits, poisonous secretions, nauseous taste; and for offense, in such counter-attributes as speed, ... ambush, allurement, visual acuity, claws, teeth, stings, ...[and] poison fangs. Just as greater speed in the pursued has developed in relation to increased speed in the pursuer; or defensive armor in relation to aggressive weapons; so the perfection of concealing devices has evolved in response to increased powers of perception" (Cott, 1940).

Arms races are usually envisioned as attack-defense "games" that are slowly played out over long periods of evolutionary time, gradually molding species interactions, especially in predator-prey systems (Futuyma and Slatkin, 1983a; see also the recent popular account by Levy, 1999). Thus it is generally thought that, as the quote by Cott suggests, offensive adaptation on one side is countered by defensive adaptation on the other side and vice versa. To paraphrase Dawkins and Krebs (1979), claws get stronger, so shells get thicker, so claws get stronger still. But is this reciprocity the only, or even the most likely, way that the elaborate feeding structures of predators and the defenses of their prey evolve?

The arms race concept has emerged in several related forms in the modern literature of evolutionary ecology and paleoecology, including through the hypotheses of coevolution and escalation. Both of these processes assume that biological factors are major agents of natural selection and that organisms are able to respond evolutionarily to selective factors imposed by other organisms in the environment.

Coevolution is defined traditionally as the evolution of two or more species in response to one another (Futuyma and Slatkin, 1983b). The term "coevolution" was first used to describe the evolution of species interactions by Ehrlich and Raven (1964). Various definitions have been ascribed to coevolution; in the strict sense the term has been applied to reciprocal adaptation of species, in which each species evolves in response to the other (Fig. 1). The interacting species may be predator and prey, competitors, parasite and host, or mutualists. The term "diffuse coevolution" has

been applied to interactions involving more than two species (for instance, a predator with multiple prey species).

"Arms races" may also occur without involving coevolution, as argued by Vermeij (1983, 1987, 1994). Vermeij's hypothesis of escalation claims that biological hazards have become more severe with time, and adaptations to those hazards have increased in expression. The hypothesis of escalation considers the most significant selective agent to be an organism's enemies. However, adaptation need not be reciprocal (Fig. 1). Vermeij (1987) has argued that prey respond to their predators, but that predators are more likely to respond to their own enemies (for instance, *their* predators) than they are to their prey. Thus adaptation is unilateral. However, coevolution may occur if both escalating parties are enemies (such as in the case of a predator and dangerous prey, or parasite and host). Escalation has two components: the "gap" between an organism and its biological environment (or hazard) and the level of the hazard. Escalation occurs when the level of the hazard increases and the gap narrows. In other words, escalation occurs when adaptations to the hazard become better expressed.

Thus, in coevolution, the claws of the predator get stronger and the prey's shell becomes thicker in reciprocal response. In escalation, increased defense in the prey is a response to the stronger claws of its predator, but the increased claw strength of the predator is a response to agents other than the prey. Coevolution and escalation clearly are related but they differ in what agents are responsible for selection when it occurs (Fig. 1) (Vermeij, 1994). The distinction between coevolution and escalation is not always clear in the literature, in part because the term coevolution has sometimes been defined to encompass the concept of escalation. For instance, prior to Vermeij's introduction of the term escalation for enemy-driven evolution, this phenomenon was described as "unilateral coevolution" (Futuyma and Slatkin, 1983b).

The fossil record of invertebrate predator-prey systems has excellent potential for testing arms race hypotheses, but it is not always straightforward to

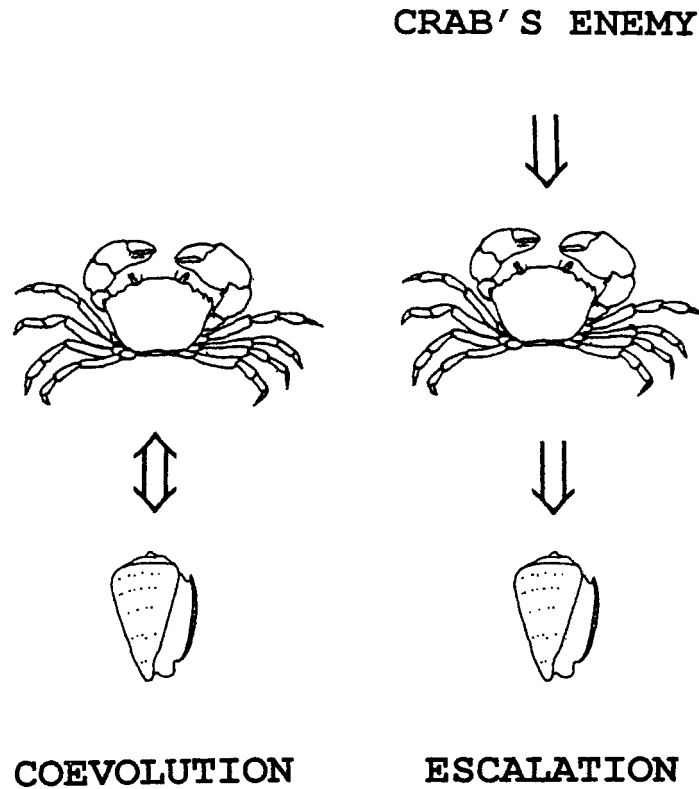


FIGURE 1—Direction of selective pressures in coevolution and escalation of predator-prey interactions.

determine what process was responsible for the pattern we observe. Such tests require a) demonstration that two species interacted as predator and prey, and b) evidence of evolution of one or both members of the system in response to one another. Chapters in the first two sections of this volume describe various lines of evidence and methods used to analyze predation in the fossil record. In this chapter, we discuss the dynamics of the evolutionary processes responsible for the history of predator-prey systems. We assess the likelihood of the occurrence of coevolution and/or escalation for several fossil invertebrate predator-prey systems, in order to address the fundamental question: Are there any general “rules,” or overriding principles, that govern the ecological and evolutionary trajectories and outcomes of predator-prey interactions (see also Herre, 1999)? We also explore the effect of scale in our perception of processes and patterns of predator-prey evolution.

## MODELS OF COEVOLUTION AND ESCALATION

*Red Queen Hypothesis.*—The extreme view of an arms race is represented in Van Valen’s “Red Queen Hypothesis.” Van Valen (1973, 1976) argued that adaptation by one species has a deleterious effect on all other species within its effective environment; this idea is an extension of Fisher’s (1930) view that any well-adapted species will experience a “constantly deteriorating” environment, owing to “the evolutionary changes...in associated organisms.” As Van Valen (1976, p. 181) suggested: “A change in the realized absolute fitness of one species is balanced by an equal and opposite change in the realized absolute fitness of all interacting species considered together.” Thus a species must be running in place (continually adapting) simply to survive in the context of a changing biological environment, even if no change occurs within the

abiotic environment. If species do not adapt they will eventually go extinct. A world run on Red Queen conditions would involve continuous coevolution, in the form of a series of progressive “linear” improvements or endless cycles of defenses and counterdefenses (Parker, 1983; Dieckmann et al., 1995) among the interacting species (Thompson, 1986; Stenseth and Maynard Smith, 1984).

Slatkin and Maynard Smith (1979; see also Kitchell, 1982) questioned why predators do not evolve the ability to overexploit their prey and why prey defenses do not outpace predator capabilities. If either side gains the advantage in adaptation the interaction will terminate. Early attempts at modeling the process of continuous coevolution predicted by the Red Queen Hypothesis assumed that adaptation was not constrained, that coevolving systems had to be stable, and that rates of change in prey and predator were balanced—this leads to an endless arms race in which neither species is expected to “win the race” (Rosenzweig, 1973; Schaffer and Rosenzweig, 1978; Slatkin and Maynard Smith, 1979; Roughgarden, 1983). This type of approach was not motivated by abstract considerations of predator-prey systems, but by observations that many morphological traits are related to feeding or defense and that predator-prey systems do not seem to undergo frequent severe population fluctuations and extinctions in nature (Slatkin and Maynard Smith, 1979; Murdoch and Oaten, 1975).

Although the arms-race view of continuous evolution is a valuable heuristic tool (Thompson, 1986), it has its limitations. Rosenzweig et al. (1987) pointed out that the conditions required for the continuous evolution predicted by the Red Queen Hypothesis may seldom occur in nature. The Red Queen requires the existence of phenotypic traits that are independent and boundless (Rosenzweig et al., 1987). In other words, phenotypes take more and more extreme values as a result of directional selection (or cycle endlessly through maintenance of multiple defenses and counterdefenses by frequency-dependent selection). For example, the Red Queen would predict that the relatively weak claw of the crab *Calappa* should

evolve to infinitely more efficient prey-crushing shapes that would increase its strength (or mechanical advantage). However, claw shape of *Calappa* is under other selective pressures for digging ability and maintaining respiratory pathways for water currents while the crab is buried (Hughes and Elnor, 1989). The additional function of the claws in digging compromises limitless or infinite evolution of claw shape (and strength) in this predator. Calappid crabs also have a highly specialized, hooked tooth (an adventitious structure) on their right claw that is used to peel the lip of gastropod shells (Shoup, 1968; Vermeij, 1982a), and to break the shell of some mussel prey (Hughes and Elnor, 1989). The adventitious structure of the claw, which has a high mechanical advantage, may serve to compensate for the otherwise weak claw (in terms of what type of prey can be crushed successfully).

An evolutionary race may stop if selection for greater prey defenses or predator offenses should be counteracted by their greater costs or tradeoffs with other competing functions (Futuyma, 1986; see also Vermeij, 1987, 1994; Brodie and Brodie, 1999). A potential reason for such costs is that defensive characters that increase survivorship against one predator may make the species more vulnerable to others (or to abiotic change). For example, the degree of expression of induced defense (see below), such as shell thickness, in the mussel *Mytilus edulis* is predator specific. Mussels produce thicker shells in response to the shell-drilling and shell-crushing predators, *Nucella lapillus* and *Carcinus maenas*, respectively; the increased-thickness response of *Mytilus* is greater to *Nucella* (Smith and Jennings, 2000). In contrast, mussels exposed to the crab *Carcinus* grow larger shells than those exposed to *Nucella*. Thus, there may be a tradeoff between shell thickness and shell growth that may increase the time it takes *Mytilus* to achieve a size refuge from predation. The specificity in response may create conflicting defenses (Smith and Jennings, 2000). Similarly, the capabilities of the predator for handling one prey species may come at the expense of handling others (Futuyma, 1986). Although adaptation by natural

selection is a powerful force in shaping the phenotypic traits of organisms, constraints (the “spandrels” of Gould and Lewontin, 1979), which are common and sometimes inescapable features of living systems, may also be important in limiting evolutionary response in an arms race.

As a result of these costs, tradeoffs, and constraints, an adaptive “stalemate” may be a more likely outcome of an arms race than the continuous evolution predicted by the Red Queen (Rosenzweig et al., 1987; Vermeij, 1994). These limits to infinite adaptation suggest that most of the history of selection in an interaction may be more appropriately modeled with a stabilizing function, rather than the directional (i.e., the stronger the claw the better) function usually applied to arms races (Brodie and Brodie, 1999). However, these limits to adaptation can be broken, leading to directional change that can be tracked in the fossil record—if changes in the rules governing adaptive compromise are introduced (see Vermeij, 1973; 1987; 1994). In this way, selection is viewed as an episodic rather than continuous process (Vermeij, 1994) acting on interactions among species.

*The nature of evolutionary trends predicted by the Red Queen.*—The Red Queen’s prediction of linear (or “lock-step”; Bakker, 1983) evolutionary trends in predator and prey has led some authors to conclude that interactions among species are not driving evolutionary change if the expected pattern is not evident in the fossil record (Stanley et al., 1983; Bakker, 1983). For example, Boucot (1990, p. 562) stated that, “after the geologically rapid, initial relation has been established [between interacting species] the fossil record suggests that there is no subsequent, coevolutionary change, i.e., stabilizing selection sets in.” To address this type of skepticism, DeAngelis et al. (1984) developed a coevolutionary model of the energetics of the predator-prey interaction between drilling naticid gastropods and their bivalve prey. In contrast to earlier models of coevolution, their model was developed with its empirical utility in mind. (The fossil record of naticid predation is extensive and has been key to tests of the importance of biotic interactions in evolution—see Vermeij, 1987; Kelley

and Hansen, 1993, 1996.) Their model incorporated an explicit potential for coevolutionary feedback through size effects (Kitchell, 1986), based on size-dependent variation in the outcome of successful predation (Kitchell et al., 1981). The predator was assumed to maximize its energy intake per unit time of foraging and the prey its allocation of energy to reproduction and defense. The models assume that there is a tight link between predator and prey. (The underlying assumption of optimality theory is that natural selection favors those individuals that are most efficient in their behavior.)

In the first version of the model, only the influence of increasing naticid predation on the allocation of bivalve energy among reproduction, overall growth in size, and shell thickness was analyzed (DeAngelis et al., 1985). Simulation results showed that, as predation intensity increased, an initial single bivalve defense (represented as a peak in an adaptive fitness landscape) changed to three different strategies (or peaks) that varied in the amount of energy diverted to shell growth and thickness. The three alternative means of dealing with predation are: 1) postponed reproduction (effectively running the predation gauntlet as the prey tries to grow quickly into a size refuge from predation); 2) early reproduction coupled with some allocation of energy to thickness increase; and 3) significant allocation of energy into thickness as a defense to minimize selection by the predator (DeAngelis et al., 1985).

In a later version of the model (summarized in Kitchell, 1990) predator size was allowed to evolve simultaneously with the prey traits (thus maximizing both predator and prey fitnesses as interdependent dynamic responses). A two-way feedback was thereby introduced. As traits in the prey varied to increase prey fitness, the prey in turn affected the adaptive landscape of the predator and caused it to change its own traits in order to maximize its own fitness. These changes in the predator’s traits (size), in turn, affected the prey’s adaptive landscape, causing it to adjust its own evolutionary trajectory.

Simulation results suggested that the potential exists for both stasis and change within the dynamics

of a positive-feedback system of coevolving biotic interactions, and the changes may be sudden and discontinuous as well as gradual and continuous (Kitchell 1990). This view contrasted markedly with Futuyma and Slatkin's (1983b) conclusion that the "ideal paleontological evidence [for coevolving lineages] would be a continuous deposit of strata in which each of two species shows gradual change in characters that reflect their interaction." In this restricted view of Futuyma and Slatkin, if prey shell thickness is a deterrent to predation, increased predation pressure should favor the evolution of thicker shells in the prey. Similarly, if the predator increases in size (invading the size refuge of the prey), general models predict an increase in prey size as the likely evolutionary response. The model results summarized in Kitchell (1990) suggest that these examples are not that straightforward, and general theory can predict prey responses other than increased size or shell thickness, even without any change in the direction of selection. Thus the lack of the intuitively expected "linear" response in arms races between predator and prey cannot be used as evidence that biotic interactions were unimportant in evolution.

*When is it coevolution and not escalation?*—Although the analogy of an arms race in coevolution between predators and prey has been widely used (and assumed) to characterize predator-prey interactions, such studies often lack empirical evidence that the predator responds evolutionarily to its prey (see Brodie and Brodie, 1999). Despite the assumption of a tight reciprocal link between naticid gastropods and their bivalve prey in the models of DeAngelis et al. (1984, 1985), there is no empirical evidence of reciprocal adaptation. Kelley (1989) interpreted the changes in thickness of the Miocene bivalves she studied as a response to naticid predation; species preyed upon most heavily displayed the greatest increase in thickness. However, evolutionary changes in the predator are more interpretable as defenses against the gastropod predator's own enemies. Kelley (1992) did not find any significant trends in most characters thought to affect predator efficiency. One character of the predator that could be interpreted

as a reciprocal response to evolution in the prey was a size increase in the predatory genus *Neverita* (size was an important morphological character in the models of coevolution discussed previously). Kelley (1992) pointed out, however, that the size increase in *Neverita* also could be interpreted as an evolutionary response to its own enemies. This interpretation is supported by the fact that the predator's shell thickness also increased, most likely as a response to the naticid's own predators.

The study of the interaction between crabs and gastropods in Lake Tanganyika, Africa, also highlights the lack of empirical evidence for predator response to prey. In general, Tanganyikan gastropods have thicker, more ornate shells (unusual for freshwater species; Vermeij and Covich, 1978) than other closely related lacustrine taxa from outside the lake. They also display a considerably higher incidence of shell repair (a measure of the effectiveness of the shell as a defense) in response to unsuccessful predatory attacks by crabs (West et al., 1991). The endemic Tanganyikan crabs possess larger, more robust crushing claws than other African crabs. A reciprocal coevolutionary arms race was invoked to explain the observed pattern (West et al., 1991, p. 605): "To protect themselves from durophagous predators, Tanganyikan gastropods have increased their shell size, strength, and sculpture. Tanganyikan crabs have concordantly increased their shell-crushing capacity with large robust chelae lined with broad molariform dentition"—it is the argument that claws get stronger, so shells get thicker, so claws get stronger still. While it is clear that prey shell characters evolved in response to selection from predators, a correlation between the morphological features of the predator and prey does not unequivocally establish reciprocal selection and evolution between predator and prey. It is equally probable that the prey responded evolutionarily to the crabs, but the crabs, instead of responding to their prey, evolved in response to competition with other crabs for prey, space, and/or mates (an escalation interpretation; Vermeij, 1978).

McNamara and Long (1998) implicated a coevolutionary arms race in the evolutionary trends

seen in cassid gastropods and spatangoid sea urchins. Cassids, such as *Cassis tuberosa*, capture and immobilize their prey by arching and extending their foot over the top of the urchin's test (Hughes and Hughes, 1981). McNamara and Long (1998) assumed that evolutionary increase in size of the urchin *Lovenia* was driven by selection pressure to reach a size refuge from cassid predation, and that reciprocal selection for increased capture efficiency of larger urchin prey led to an evolutionary increase in predator size. However, it seems equally likely that the cassids evolved larger sizes in response to their own predators or competitors.

Another example includes the highly specialized appendages of gonodactylid stomatopods that function effectively as hammers (Caldwell and Dingle, 1976). These mantis shrimp attack hard-shelled prey such as gastropods, bivalves, and crabs. Prey are caught and then hammered by repeated strikes of the raptorial appendages. As with the Tanganyikan gastropod-crab interaction, a coevolutionary arms race is easily envisioned in this system. However, these appendages are also used in agonistic encounters with conspecifics. The appendages are often employed during territorial contests for shelter cavities, which often result in serious injury to conspecifics (Berzins and Caldwell, 1983). The consequences of injury to the raptorial appendages include a reduction in fighting ability, which affects the outcome of territorial contests (Berzins and Caldwell, 1983); injury also increases the likelihood of falling victim to cannibalism and predation, as well as lost mating opportunities. Which interpretation is correct? The fact that these appendages are much less developed among stomatopods that occupy soft substrates (and do not compete for cavities; Dingle and Caldwell, 1978) suggests that response to prey is less important than response to enemies.

Whether or not escalation (in which most evolutionary change in predators is driven by their own enemies and not by their prey) explains the evolution of the predator-prey systems discussed above, the hypothesis does highlight the uncertainty with which the coevolutionary arms

race analogy applies to some predator-prey systems. The theory of why predators should be expected to respond to the selective pressures of their enemies rather than their prey is discussed in the next section. Unfortunately, there have been few detailed studies of the evolution of species interactions that extend their scope beyond the supposed tight interaction of predator and prey to consider also the role of the predator's enemies.

*Visualization of selection pressure on predator and prey.*—Brodie and Brodie (1999) developed an approach in which selection is formalized as the covariance between traits and fitness. Such an approach is designed to test whether predators should respond reciprocally to their prey (that is, to test whether prey are actually enemies of the predator). Selection is stronger when the covariance between phenotype and fitness is highest, and selection is weaker when the covariance is low. In potential coevolutionary interactions, the covariance of interest is between the fitness of individuals of one species (e.g., predators) and the values of traits at the phenotypic interface in the other species (e.g., prey) (Brodie and Brodie, 1999).

Selection that results from an interaction between predator and prey is viewed by regressing predator fitness (or some function of the predator's traits) on the phenotype of the prey species with which it interacts (Fig. 2) (Brodie and Brodie, 1999). In biological terms, the slope of the regression line reflects the rate of increase or decrease in the expected fitness of the predator as prey morphology changes. A steep slope (Fig. 2A, 2B) indicates that the effects of the interaction are strong (i.e., change in prey morphology drastically affects predator fitness). The amount of scatter around the regression line reflects the predictability of predator fitness for a particular prey phenotype (Brodie and Brodie, 1999). Selection is strong (and hence coevolution is likely) when the covariance is high between predator fitness and prey morphology.

Without experimental evidence from living animals to indicate whether fitness costs associated with feeding are likely, an analysis based solely on fossils can only assume that predators are tightly linked to their prey. The interaction between

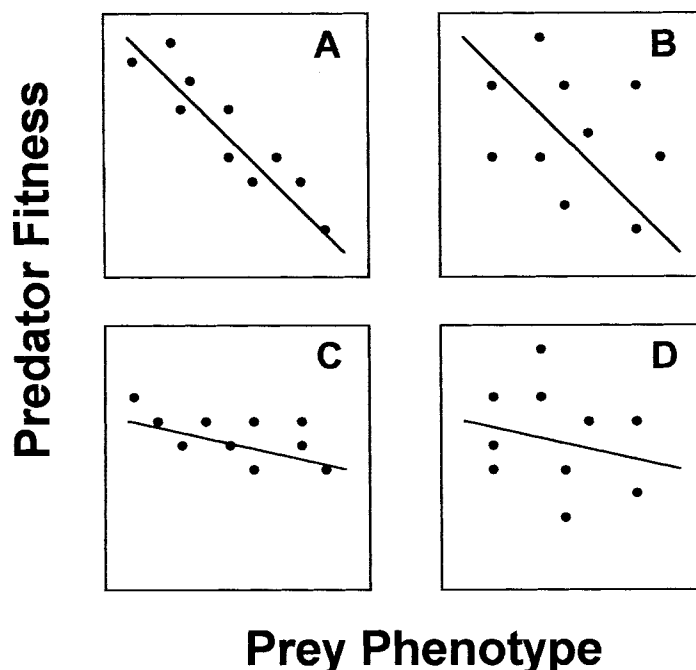


FIGURE 2—Covariance between predator fitness and prey phenotype. Redrawn from Brodie and Brodie (1999, Figure 1, p. 560). A and B, see text. C, low but predictable fitness consequences (low slope but narrow spread of points). D, low and unpredictable fitness consequences (low slope, wide spread).

predatory whelks of the genus *Busycon* and their tightly closing bivalve prey, *Mercenaria*, can be used to highlight the utility of the covariance approach to selection. Where they occur sympatrically, more than 70% of adult *Mercenaria* mortality often can be attributed to whelk predation (Chestnut, 1952; see also Kraeuter, 2001). Whelks actively use their shell lip to chip open their prey, a mode of attack that often inflicts shell damage on both predator and prey. Breakage must be repaired and this represents a diversion of energy away from somatic growth or reproduction. Whelks that often break their shells while attempting to feed are faced with a potential tradeoff between subsequent reproduction and shell repair (Geller, 1990). If feeding rate is reduced significantly during repair of the injury, breakage also may lead to a net energy loss (or negative energy budget) for the whelk resulting in a reduced growth rate. Breakage of the whelk's shell may thus have severe fitness consequences because it increases the time the individual spends at a smaller size, leaving it

more vulnerable to its own predators like the stone crab *Menippe mercenaria* (Magalhaes, 1948; Kent, 1983). The selective consequences for predatory whelks interacting with *Mercenaria* of varying sizes are predictable (Fig. 2A) (Dietl, in review). Predators that select large bivalve prey increase the likelihood that their shell lip will be broken in the process of attempting to open their prey. Adaptive response of the predator to the prey is *possible* in this system of interacting predators and prey, with predators expected to evolve increased effectiveness in opening prey (perhaps represented as a temporal decrease in the frequency of repaired feeding-inflicted shell breakage). Traces of the predation event are retrievable from the fossil record (Dietl, unpublished data); ongoing work is examining the origin(s) of the chipping mode of predation and the evolutionary history of the predator-prey interaction.

Vermeij (1994) argued that the central issue in the debate about escalation and coevolution is the nature of selection; most current models of



coevolution do not consider the process of selection. “In order to make headway in the study of coevolution and escalation, we need to study the sources, frequencies, and cost-benefit effects of selection. This entails careful observation of encounters between species, together with an evaluation of the effects of such encounters on survival and reproduction” (Vermeij, 1994, p. 232; see also Herre, 1999, and below). It is important to distinguish when selection occurs and what agents are responsible (Vermeij, 1994). For an interpretation of reciprocal adaptation to be appropriate, selection by the prey on its predator has to be stronger—with predictable consequences (Brodie and Brodie 1999)—than that caused by other enemies of the predator.

*Inequalities in interaction.*—Slobodkin’s (1974) expectation that prey in an evolutionary race can “keep ahead” led Dawkins and Krebs (1979) to point out that coevolution (reciprocal adaptation) between predator and prey gives the prey an inherent evolutionary advantage. Thus predator and prey are not equal partners from an economic point of view in an arms race. They termed this asymmetry in the evolutionary outcome between predator and prey the “life-dinner principle.” It is a widely cited explanation for why predators may not respond evolutionarily to prey adaptation (Vermeij, 1982b; Kelley, 1992; Brodie and Brodie, 1999). If a predator fails, it only loses a meal (and some energy and time), whereas failure for the prey means death (or at least injury). The consequences of the interaction clearly are more severe for the individual prey, suggesting that selection by the predator on the prey for improved defenses is stronger than selection by the prey on the predator for improved offensive capabilities. Asymmetry in selection is assumed to result in faster evolution of prey than predators, leaving predators unable to keep pace (in the evolutionary race) with their prey.

Vermeij (1982b) reasoned that the prey’s contribution to selection for improved predator capability is further reduced if a predator preys on more than one species; the short-term response of the predator might be to avoid the increasingly well-defended prey. Vermeij (1982b) took this to imply

that selection for predatory improvement is likely to be far stronger from the predator’s own enemies than from its prey; thus interactions among multiple species decouple the coevolutionary responses of a given pair of species. This was the major impetus for the formulation of the escalation hypothesis and its view that prey play a minor role in directing the evolution of their predators.

Dawkins (1982) proposed the “rare enemy effect” as a means of balancing the asymmetry inherent in the life-dinner principle and allowing coevolution to occur. Because rare predators represent a minor selection pressure on the prey, the predators are thought to “win” or “keep ahead” in the arms race (Dawkins, 1982). However, if a predator is rare, the risk of predation for any individual prey is low, and the prey would not be expected to evolve costly morphological or avoidance defenses. If selection pressures on the prey are weak, coevolution of predator and prey is difficult to envision (see also Abrams, 1986). In such a case, an opposite asymmetry may arise in which the prey do not respond to evolution of the rare predator.

Abrams (1986) has argued, on theoretical grounds, that the life-dinner principle does not take into account the fact that if a predator loses enough races, it will also lose its life. Predators that rarely catch prey will suffer the same fate (death) as an unsuccessful prey individual. Furthermore, the frequency or probability of attacks, as well as their outcome, has to be taken into account in determining the net lifetime effect on survival, reproductive output, and fitness. The cost per unsuccessful attack is typically low for predators, but predators typically have a low success rate and must make many unsuccessful attacks for every successful one. In contrast, the cost to a prey is much higher, but the number of attacks experienced per individual may be much lower over a lifetime. Thus, even though the consequences of one individual attack are highly asymmetrical between predator and prey, the net outcome is not readily obvious (J. A. Rice, pers. comm., 2002).

In addition, Brodie and Brodie (1999) pointed out that the life-dinner principle, as formulated,

oversimplifies the process of phenotypic evolution, which is a combination of selection and inheritance. Evolutionary change in a trait is equal to the product of the strength of selection on the trait and its heritability (the percentage of variation in a trait that is controlled by additive effects of genes; see Futuyma, 1986). Thus if shell thickness of the prey and claw strength of the predator were to experience exactly the same strength of selection, the species with the greater heritability for the trait in question would evolve faster. If selection is unequal, as the life-dinner principle predicts, the rate of evolutionary change may still be equal if heritabilities differ. If selection is stronger on prey than on predators, prey should have less genetic variation in their defenses, based on Fisher's fundamental theorem of natural selection, which states that the rate of increase in fitness is limited by the amount of additive genetic variation (Brodie and Brodie, 1999). If this is the case, heritability differences might balance the asymmetry in strength of selection predicted by the life-dinner principle, resulting in comparable rates of evolution.

Brodie and Brodie (1999) noted that a major difference between predator-prey interactions and other victim-exploiter systems is the intimacy of the interaction (i.e., the extent to which each species experiences the consequences of the interaction). In predator-prey interactions, prey that do not successfully escape face the direct consequence of interaction with the predator; that is, death (or zero fitness). By contrast, predators, in their interaction with prey, are able to avoid many of the selective consequences that would occur in a more intimate interaction; this inequality in interaction may help explain why selection on prey is thought to be stronger than on predators (Brodie and Brodie, 1999). The consequences for the individual predator of losing a prey may be strong enough to start an arms race. But the predictability of this consequence for any individual predator is low (Fig. 2B); a predator might capture the very next prey it interacts with, negating the consequences of the prior interaction, or may switch to an alternative prey (Brodie and Brodie, 1999).

Brodie and Brodie (1999) argued that the only predator-prey systems likely to result in a coevolutionary arms race (in which selection pressures between predator and prey are symmetrical) are systems in which predators interact with dangerous prey, a conclusion Vermeij (1982b) also advocated. If a prey is dangerous to a predator, the predictability of consequences for the predator is expected to be high (small residuals) (Fig. 2A) and therefore selection is strong. Coevolution is likely to occur in this system of interacting predators and dangerous prey. In this sense predators are "forced" into experiencing selection from dangerous prey (Brodie and Brodie, 1999). This situation leads inevitably to an evolutionary response in the predator as long as variation in the predator's offensive trait (either morphological or behavioral) is present.

The dangerous prey concept was used to explain evolutionary shifts in stereotypic placement of holes drilled by naticids on confamilial prey (Dietl and Alexander, 2000). Because an escaped aggressive prey may become the predator and drill its former attacker (a case of the hunter becoming the hunted), naticid prey may be considered dangerous to their confamilial predators. Naticids may have shifted the position of drill holes on confamilial prey in order to neutralize the potentially larger prey foot or more aggressive retaliatory behaviors of such dangerous prey (Dietl and Alexander, 2000). This concept remains relatively unexplored in the fossil record of predator-prey interactions.

The interaction between predatory crabs and their hard-shelled prey also may have a coevolutionary component. If we were to play Devil's advocate, West et al.'s (1991) example of the interaction between Tanganyikan gastropods and crabs discussed earlier could involve coevolution between predator and prey if the evolution of more powerful claws of the predator were a counter-adaptation to increased defensive strength of the prey's shell. This could result from the increased likelihood of breakage or damage to their claws (as a consequence of fatigue failure), which occurs commonly in living crab species (Juanes and Hartwick, 1990); in this case, the

Tanganyikan gastropods would be dangerous prey. The consequences of claw breakage for the predatory crab *Cancer magister*, feeding on the hard-shelled bivalve *Protothaca staminea*, include longer prey-handling times (decreasing feeding rates) and reduced growth, molting ability, and mating success (Juanes and Hartwick, 1990). Careful observations are required to determine when claw breakage frequency, and hence selection pressure, increases, in order to clarify the processes shaping these interactions.

### TIME SCALE AND ECOLOGICAL AND EVOLUTIONARY ARMS RACES

*Geographic mosaic theory of coevolution.*—Scale is important in ecology and evolution. For instance, Futuyma and Slatkin (1983c) were confounded by an apparent lack of directional trends in the fossil record of predator-prey interactions, despite the documentation of adaptation between species at ecological scales. Rapid, fluctuating, short-term (tens to hundreds of years) selection (frequency- or density-dependent) that does not result in the production of long-term trends is thought of as evolutionary “noise” (Thompson, 1998). However, these short-term fluctuations may be viewed as the first steps towards long-term directional selection (the microevolutionary processes that operate on ecological time scales may have macroevolutionary consequences). Such a link between scales can be achieved if short-term fluctuating selection leads to adaptive innovations (or changes in the developmental sequence that break genetic covariances—or constraints on evolution—allowing traits to vary independently), or if this selection establishes new mutually beneficial partnerships among species (see also Vermeij, 1994).

At the interface between ecology and evolution, Thompson (1988, 1994) has addressed the role that variation in the outcome of interspecific interactions on an ecological time scale plays in the coevolution of species interactions. The existence of geographic variation both in the expression of defenses and in

the selection pressures caused by different groups of enemy species is thought to produce a selection mosaic for evolutionary arms races between antagonists, such as predator and prey (Thompson, 1994). Thompson termed his hypothesis the geographic mosaic theory of coevolution. In general, it is hypothesized that coevolutionary dynamics are driven by components of geographic structure: there is a selection mosaic among populations that favors different evolutionary trajectories to interactions in different populations, and there are coevolutionary “hot spots,” which are subsets of communities in which reciprocal adaptation actually occurs (Fig. 3). Selection mosaics occur when natural selection on interactions and gene flow between populations vary (Gomulkiewicz et al., 2000); the apparent selective asymmetry due to the life-dinner principle in predator-prey arms races discussed earlier can be either increased or decreased by consideration of selection mosaics.

Hot spots are communities in which interacting species have reciprocal effects on each other's fitness; they are usually embedded within communities in which selection affects only one or neither of the interacting species (cold spots) (Gomulkiewicz et al., 2000). Because there are differences in outcome among populations, an interaction between two species may coevolve, affect the evolution of only one of the species in the interaction, or have no effect on the evolution of either of the interacting species (Thompson, 1994).

The geographic mosaic theory incorporates two observations that have often been used as evidence against coevolution: lack of apparent coevolution in the interaction between a local pair of species, and lack of biogeographic congruence in the interacting species distributions (Thompson, 1994). Thompson summarized the basic idea of his theory when he wrote that the geographic mosaic theory “suggests that the coevolutionary process is much more dynamic than is apparent from the study of individual populations or the distribution of characters found in phylogenetic trees (e.g., see p.285 in Brooks and McLennan, 1991). Adaptations appear and are lost. Some populations become highly specialized for the interaction as others

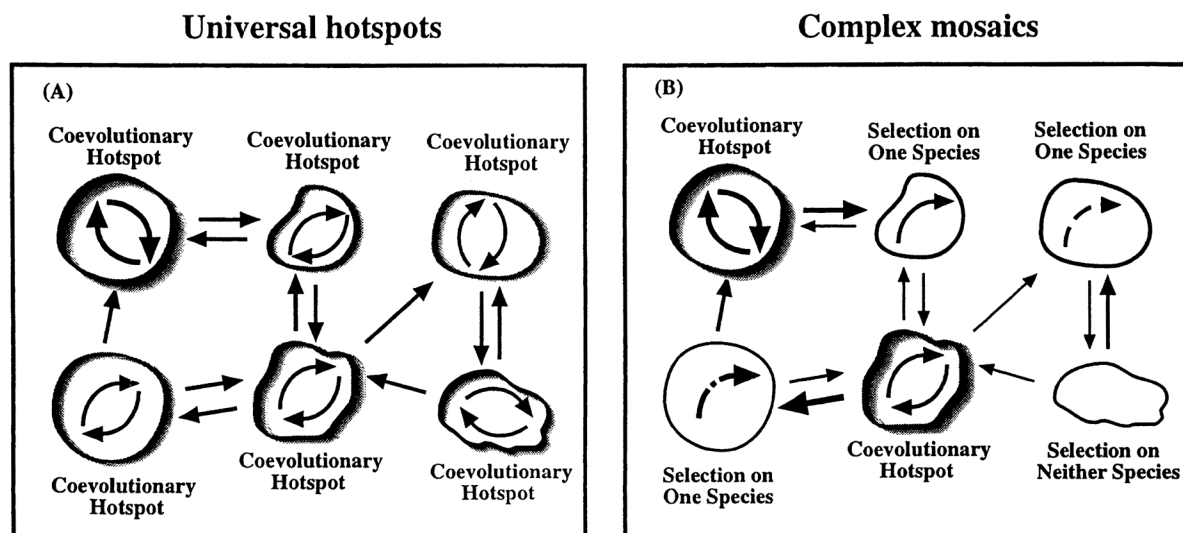


FIGURE 3—A geographic mosaic of coevolution between two interacting species. Circles represent biological communities. Arrows within circles indicate selection on one or both species in the interaction; arrow directions (within circles) represent different (co)evolutionary trajectories. Arrows between circles indicate gene flow. A, Coevolution occurs in all populations in which the interaction takes place; B, coevolutionary hotspots (in which reciprocal selection occurs) are intermixed with populations in which reciprocal selection is not occurring (cold spots). From Thompson (1999a, Figure 1, p. S4) with permission of the University of Chicago Press.

remain or become less specialized. Some populations may fall outside the geographic range of the other species, lose some of their adaptations for the interaction, and then later be drawn back into the interaction. A few populations may temporarily become evolutionary 'hot spots' for the overall trajectory of coevolution between the species, whereas other populations act as evolutionary sinks. The overall course of coevolution between any two or more species is driven by this ever shifting geographic mosaic of the interaction" (p. 223).

This geographic view of an arms race generates three general *ecological* predictions: populations of a species will differ in the traits shaped by coevolution; traits will be well matched in some communities and mismatched in others; and there will be few species-level coevolved traits that are distributed across all populations of a set of interacting species (Thompson, 1999a).

Thompson's mosaic view of coevolution may be limited to highly specialized species interactions.

In predator-prey interactions most morphological prey defenses are general adaptations that work against a number of different predators, and are not specific to a single predator species (G. J. Vermeij, pers. comm., 2002). The same is true for the offensive capabilities of the predator. For instance, size and thickness of the shell are two general defenses in molluscs that are effective against shell-crushing crabs or fish, as well as shell-drilling snails, not to mention boring parasites (Vermeij, 1987). How does this generality in adaptation affect the ecological predictions of the mosaic hypothesis of coevolution, which assumes a specialized or tightly linked interaction between predator and prey? For instance, although the range of a predator may not overlap the entire range of its prey, another predator species that selects for the same prey defense might be present. In this case, the selection pressure for increased thickness is always present. This selective reinforcement calls into question Thompson's prediction that few traits will be

distributed across all populations of a set of interacting species. It is easy to imagine how the same defense can be adaptive locally even if the source of the predation pressure changes among populations. The other ecological predictions may hold in specific cases, but this level of variation is likely lost (or masked or misinterpreted as a high degree of phenotypic lability) in the fossil record.

Thompson's (1994, 1998) mosaic view of the evolution of species interactions suggests how reciprocal evolutionary change can shape species interactions that are asymmetric at the species level (one species interacting with multiple species—i.e., a diffuse interaction) (Fig. 1) but are specific at the local level. Thus, although a predator may prey on a number of species, a single prey species may be most important in driving the evolution of the predator. There is some theoretical backing for Thompson's argument. Abrams (1991) has shown from models that interactions between a predator, a prey species, and a third species (either the predator's own predator, or a second prey species) often increase the magnitude of coevolutionary response in the predator or prey (or both) to evolutionary changes in the additional species. Thus multiple prey species may intensify the response of a predator to its main prey. If empirical data are found to support Abrams' models, one of the tenets of the hypothesis of escalation may be brought into question (i.e., that predators are unlikely to respond specifically to any one prey species because of the catholic diet of most predators; Vermeij, 1987, 1994).

*What are the implications of the mosaic hypothesis for the fossil record of species interactions?*—In general, the mosaic view of the evolution of species interactions incorporates variation that occurs over a larger spatial scale (the range of the species) than we usually consider (i.e., within a local population) when evaluating arms race hypotheses. As paleontologists, we are usually only able to trace traits that have spread among all the populations of a species, but this does not mean that the coevolutionary meanderings or continual reshaping of interspecific interactions are unimportant. Interactions may come and go within

the ecological context of a local population through time. A prey population with a geographic range that extends beyond that of its predator may escape attack for many generations, lose (or more likely decrease) its level of defense, and then fall victim again as the range of the predator expands. Just as a lack of evidence for local adaptation is not conclusive evidence that coevolution (or for that matter escalation) has not occurred, the lack of directional trends through successive stratigraphic intervals in traits important to an interaction is not evidence that biotic factors were unimportant. Gould (1990, p. 22) commented that “positive feedback [should drive the evolution of an interaction] to its furthest point in a geological instant, while most actual events [trends] span tens of millions of years”; positive feedback is thought to require “locking of biotic interactions” over the duration of the trend. In other words, how can long-term biotically driven trends be accounted for if reciprocal adaptation is expected to occur only early in the history of the interaction (see also Futuyma, 1985)? The mosaic view of selection suggests that the degree of adaptation to local conditions may increase or decrease depending on the amount of contact with other populations. The spatial distribution of genetic variation “determines the degree and scale over which populations have been (or are) evolutionarily independent, and consequently free to evolve in response to local variation in selection” (Grosberg and Cunningham, 2001, p. 61). In general, species with restricted gene flow are expected to exhibit local adaptation to spatially varying selection; as the level of gene flow among populations with different selective regimes increases, the selective costs of local adaptation increase (Grosberg and Cunningham, 2001). Thus, the geographic structure of a species may favor long-term trends in the evolution of species interactions. Kelley and Hansen (2001) further added that the condition of “locking” or maintenance of specific predator-prey interactions is not necessary if escalation (which does not require a strong coevolutionary component) is the most important process in the evolution of species interactions.

Few interacting species have identical

geographic ranges. In addition, the outcome of an interaction often varies among environments with the varying context of the other species present. In modern habitats predation varies at different scales, from local to regional. Not surprisingly, then, many studies have shown that predation pressure is also highly variable on both large and small spatial scales within time-averaged assemblages in the fossil record (Vermeij, 1980; Geller, 1983; Schmidt, 1989; Hansen and Kelley, 1995; Hoffmeister and Kowalewski, 2001; Nebelsick and Kowalewski, 1999; Alexander and Dietl, in press). This sets up the conditions for a possible selection mosaic of hot and cold spots that have fluctuated in both space and time.

The question that studies on spatial variability in predation have neglected to ask is how variability in the frequency of hot and cold spots affects the rate of evolution of species interactions (or traits involved in the interaction). While it is important that we evaluate temporal trends in coevolution- or escalation-related traits among ecologically similar habitats (i.e., because local adaptation is context dependent; Vermeij, 1994), in doing so we ignore the variation across other populations in the selection mosaic. The degree of connection between populations may change as the frequency of hot and cold spots (the mosaic of spatially varying selection pressures) changes temporally. If the frequency of hot spots is low relative to cold spots, and the scale of gene flow exceeds the scale over which selection varies, beneficial adaptive changes (such as an increase in shell thickness) are unlikely to spread quickly to all populations of the species. Further work is needed to determine the general applicability of the conclusion of Bush et al. (2002) that degree of variation in time-averaged fossil assemblages mirrors within-generation variability of living populations; if these results hold, then geographic and temporal mosaics of change should be observable in the time-averaged fossil record.

The outcomes of interactions also can vary among environments as changes occur in the effectiveness of traits involved in an interaction (Thompson, 1988). Thompson has called the range

in effectiveness of a particular trait an interaction norm—by analogy with reaction norm, which is the range of phenotypes a given genotype expresses among environments. In order to understand selection and constraints on the evolution of species interactions, patterns of geographic variation in the outcomes of such interactions might have to be considered (see also Thompson, 1988). Vermeij (1982b) has shown convincingly that predatory attacks are not always successful. It is this failure that he argues is driving the evolution of adaptations to enemies (Vermeij, 1982b, 1987, 2002). Geographic variation in sublethal predation thus provides an opportunity to understand how combinations of different traits affect the outcomes of interactions over evolutionary time (Vermeij, 1982b), or favor the evolution of new associations or innovations important to an interaction between species. How do different environments affect selection on interactions (or the interaction norm)? Thompson has argued that differences in outcome among environments could potentially be great enough to shift the mean outcome along a continuum of antagonism, commensalism, and mutualism.

*Adaptive phenotypic plasticity.*—Heterogeneity in predation pressures among habitats in ecological time also favors the evolution of adaptive phenotypic plasticity. Inducible defenses are phenotypic changes induced directly by chemical cues associated with biotic agents. Induced morphological defenses include the production of antipredatory structures (bryozoans, cladocerans, rotifers) and protective variation in shell thickness (barnacles, gastropods, mussels) in the presence of the predator (Harvell, 1984; Lively, 1986; Trussell, 1996, 2000; Leonard et al., 1999). For instance, thicker shells are induced in the gastropod *Littorina obtusata* by the presence of the predatory crab *Carcinus maenus* (Trussell, 1996).

Induced defenses are likely favored over constitutive defenses because they account for the unpredictability inherent in most habitats. Inducible defenses in the prey are thought to evolve via two routes: “cost-benefit” (=“inducible” in Fig. 4) and “moving target.” The cost-benefit model (Fig. 4) applies when four conditions are met: 1) Selective

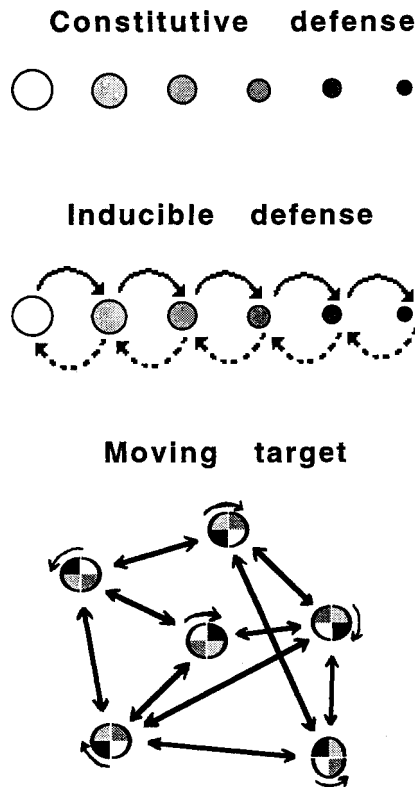


FIGURE 4—Constitutive, inducible (cost-benefit), and moving-target strategies. Circles represent different phenotypes; circle size represents growth rate in absence of predation and shading represents degree of defense. Arrows indicate switching in presence of predation and dashed arrows indicate switching in absence of predation. See text for comparison of cost-benefit (inducible) and moving-target models. From Adler and Karbon (1994) with permission of the University of Chicago Press.

pressure of the inducing agent (the predator) must be variable and unpredictable, but sometimes strong. If the antagonist is constantly present, constitutive defenses should evolve. 2) Availability of nonfatal predictive cues is necessary to indicate the proximity of the threat of future attack and activate the defense. 3) The defense must be effective. And 4) most defenses should incur direct allocation costs or other tradeoffs. The prey trade the risk of predation against the cost of defense.

In the moving target model, changes in defense (against herbivory or predation) are induced as a

form of nondirectional phenotypic escape from adverse conditions rather than a ratcheting up of defenses (Fig. 4). Under this approach, prey phenotypes cannot be arrayed along a single axis from undefended to well-defended because the prey's defenses are affected by a variety of extrinsic environmental factors other than the presence of their predator, each of which has an independent component of effect on the predator (Adler and Karban, 1994). Consequently, there is a tradeoff in the effectiveness of different defensive phenotypes. It is predicted that prey will not fix their defense to one predator if that state leaves them vulnerable to another predator. The tradeoff in the moving target case does not therefore depend on the cost of defense, but on the array of predator types that respond differently to different prey phenotypes (Adler and Karban, 1994). A moving target defense is favored if environments are unpredictable and uninformative (Adler and Karban, 1994). Thus environments that change frequently in ecological time might not allow for a specific inducible defense to be targeted by selection over evolutionary time.

Predator responses to inducibly defended prey can be morphological, physiological, or behavioral, such as foraging movement strategies and life history changes (Levin et al., 1990). Reciprocal phenotypic change has been observed in predator-prey systems. Smith and Palmer (1994) showed that morphology and claw strength of the predatory crab *Cancer productus* was plastic. When crabs were fed mussel prey (*Mytilus*) with shells, they developed larger and stronger claws than when fed mussels that had had their shells removed. Smith and Palmer (1994) suggested that these short-term adaptive responses to a changing environment (prey phenotype), if heritable, could produce evolutionary changes in claw size. Conversely, mussels respond to the presence of predators (e.g., crabs) by inducing thicker shells (Leonard et al., 1999; Smith and Jennings, 2000). Agrawal (2001) argued that, because species interactions are intrinsically variable in space and time, and if reciprocal phenotypic change is the result of adaptive plasticity for both predator and prey, then

it is reasonably predicted that coevolution may result in inducible defenses as opposed to constitutive adaptations.

If trends in predation-related traits involve inducible, rather than constitutive, defenses, our interpretation of such trends is complicated. Although evolutionary trends in both constitutive and inducible defenses result from predation, the mechanism differs. In cases of consistently high predation pressure, natural selection will act directly to favor constitutive defenses (Tollrian and Harvell, 1999). However, if predation has a variable or unpredictable impact, inducible defenses will be favored; in that case, selection acts indirectly by affecting the norm of reaction (Travis, 1994). As the degree and variability of predation changes, defenses may alternate between constitutive and inducible or perhaps be lost entirely, depending on constraints. This may affect what direction and what rate an evolutionary trend might take.

Most studies have focused on plasticity from the prey's point of view, as a defense against its predators. However, adaptive plasticity not only provides a mechanism through which prey may avoid predation, but, in turn, may give predators the opportunity to respond reciprocally to overcome the prey defense. Thus, inducible defenses may have the potential to alter both the short-term dynamics and long-term evolution of predator-prey systems (Adler and Grunbaum, 1999; Harvell, 1990). However, it is unclear if in the long run predators would still exact primary "top-down" control in directing the prey's evolution as predicted by the escalation hypothesis (see also Vermeij, 2002). Communities that are dominated by generalized predators that are capable of switching among diverse prey, such as the crab *Callinectes sapidus* in marine soft-bottom habitats, often control the distribution and abundance of a number of co-occurring species (Virstein, 1977; Peterson, 1979; Hines et al., 1990).

It is important here to distinguish reciprocal selection or within-generation change in phenotype distribution from evolutionary reciprocal adaptation, which is a change in phenotype distribution across generations (Fisher, 1930). The conditions under

which selection for induced prey defenses and predator offenses operates in nature remain unclear. Is an inducible "dialogue" between predator and prey played out in ecological as well as evolutionary time? If selection targets the norm of reaction of both predator and prey, coevolution may occur over the long run (Smith and Palmer, 1994). There is experimental evidence that partners in an interaction continually respond in a reciprocal fashion over ecological time (Agrawal, 2001). Reciprocal change in ecological time may thus have resulted from long-term evolution in which the environment (the species interaction) has been variable.

## FINAL REMARKS

There are two major underlying themes of this paper. Our first goal was to clarify the conceptual differences between coevolution and escalation. The major difference between the two processes is in the nature of selection (Vermeij, 1994). Escalation is enemy-driven evolution. In this view, the role of prey (with the exception of dangerous prey) is downplayed in arms races between predator and prey. In coevolution, prey are linked tightly to their predator and are thought to drive the predator's evolution. Janzen (1980) posed the question: "When is it coevolution?" to draw attention to the ways in which the process was misunderstood. Similarly, we ask: "When is it coevolution and not escalation?" The answer to this question depends on the predator-prey system of interest. The naticid gastropod predator-prey system was initially envisioned as a coevolutionary system (Kitchell et al., 1981), but fossil evidence supports an interpretation of escalation (Kelley, 1992). In systems in which prey are dangerous to the predator, coevolution is the appropriate model (e.g., confamilial naticid predation; Dietl and Alexander, 2000; *Busycon* whelk predation on bivalve prey such as *Mercenaria*; Dietl, in review). However, even in these coevolving systems, the role other enemies play in reinforcing the selection pressure exacted by prey should not be overlooked—evolution does not take place in an "ecological vacuum" (*sensu* Boucot, 1983) even when considering a coupled



predator-prey interaction. These systems do, however, provide more definitive results because traces of predation are preservable in the fossil record. Crab-gastropod predator-prey systems typically have been characterized as exhibiting coevolution (Trussell, 2000; West et al., 1991), but alternative interpretations can be offered (see above); the same can be said for the cassid gastropod-sea urchin predator-prey interaction. In such cases, the question remains open as to what process was important.

Our discussion of coevolution models has repeatedly highlighted that approach's main point of contention with the escalation hypothesis; that is, predators are not expected to respond to changes in their prey (the "decoupling" argument). Coevolution models (Abrams, 1986, 1991; Kitchell, 1986, 1990) have assumed that positive feedback between interacting populations, in terms of changes in population size or density, or energy intake, is the same as reciprocal adaptation (Vermeij, 1994). But are changes in population dynamics or energy intake of interacting species an appropriate representative of selection-based processes (see also Vermeij, 1994)? If progress is going to be made in the debate about coevolution and escalation we must search for empirical evidence of evolutionary responses in nature. This requires not only a description of the products of selection in terms of births and deaths, or energy intake, but also an evaluation of how interactions among organisms affect the opportunity for adaptation (Vermeij, 1994). Interactions have consequences in the form of success and failure; traces of predation allow the ranking of importance of various selective agents (Vermeij, 1987). "Those agencies that affect a large number of individuals ... should ... play a larger role in adaptive evolution than do agencies that affect a minority of individuals" (Vermeij, 1987, p. 23). Distinction between the two processes in the fossil record will require documentation of sources, frequencies, and cost-benefit effects of selection (which for many systems requires evidence from living animals; Vermeij, 1994).

Our second theme is that rates of evolutionary change of traits important in species interactions

may vary from very short, rapid changes taking place on the ecological time scale (tens to hundreds of years; Thompson, 1998) to longer spans of evolutionary time (millions of years; Vermeij, 1987, 1992). Trends over evolutionary time are also not necessarily directional—although directional trends in antipredatory characters do occur, including increases in shell thickness (Kelley and Hansen, 2001) or ornamentation (Dietl et al., 2000)—but may be highly dynamic in nature (Kitchell, 1990). These findings suggest that a lack of the predicted ideal unbounded, progressive trend is not sufficient evidence to argue against the importance of interactions among species as a driving force in evolution (Kitchell, 1990). Despite the apparent antiquity of many predator-prey associations in the fossil record (Boucot, 1990), there are still few detailed studies testing arms race hypotheses. This does not imply that the inherent directionality (at the level of "megatrajectories"; see Knoll and Bambach, 2001) in evolution is unimportant. Given that economic inequalities abound in nature between enemies (Vermeij, 1999), such direction is inevitable. Such directionality does not assume that within evolving lineages adaptation is boundless as predicted by the Red Queen Hypothesis. There are likely to be periods of directionality in an arms race (increasing mean values of traits) but also occasional reversals or even periods of stasis (Dawkins, 1986; Kitchell, 1990). Vermeij (1994) also espoused this view of the episodic nature of selection.

The fossil record is the only place where the long-term effects of interactions among species can be traced; thus it remains a valuable resource for testing predictions based on these processes. If the geographic mosaic process envisioned by Thompson is a common feature of the evolution of predator-prey interactions, then escalation and coevolution studies may have to incorporate an understanding of the population structure of the species being studied. A geographic perspective in our approach to species interactions and the processes driving their evolution may allow for a more diverse array of testable hypotheses on how predator-prey systems evolve (see also Thompson,

1994). How do connections among multiple populations affect the processes shaping the evolution of interactions among species? By identifying general patterns, we can better understand the constraints that interactions impose on the evolution of organisms. In addition, if short-term reciprocal adaptation (via inducibility) between predator and prey is a common process, then prey are likely to exert some selective pressure on their predators over the short term (and perhaps in specific cases over the long term; see above).

At ecological time scales, reciprocal adaptation is likely to occur (Thompson, 1999b); coevolution may also characterize the long-term evolution of specific predator-prey systems. However, at the largest scale of paleontological study, the escalation hypothesis may be the most important description of the evolutionary process (see also Thompson, 1999b). Over the long run, then, we believe, it is likely that predators control the overall directionality in evolution (i.e., evolutionary megatrajectories) because of the inequality of predator and prey in control of resources (Vermeij, 1999, 2002). Predators of large effect influence community structure by way of their high rates of consumption and their generalized diets (Vornstein, 1977; Peterson, 1979; Paine, 1980; Hines et al., 1990; Birkeland, 1996), and likely are “chiefly responsible for organizing the economy, for defining the roles and attributes of the entities with which they interact, and for setting the course of economic change” within the community (Vermeij, 1999, p. 247).

The fundamental question raised in the introduction was whether there are any general “rules” that govern the ecological and evolutionary trajectories and outcomes of interactions (see also Herre, 1999). In order to address this question, we must recognize that predator-prey interactions are complex systems and that multiple factors may influence the outcome of encounters between predator and prey. Thus “it is important to understand the interactions among several different types of species in order to provide the context to properly pose and test evolutionary hypotheses about any of them” (Herre, 1999, p. 235). Once other agents of selection are considered, the

intuitive expectation of the type of arms race driving the evolution of a species interaction is often called into question. Thus it is important to view any predator-prey system within the context of the other species that may influence the interaction, and to clearly understand the functional interrelationships among them. We have not come to any firm conclusions on the “rules” governing the processes of coevolution and escalation in any specific predator-prey interaction because in many systems the question is still open. This does not imply that the governing “rules” that yield explanatory power concerning the outcomes of species interactions and their long-term effects in evolution are not important. Instead, as Herre (1999, p. 236) pointed out, “understanding why the rules work in the cases that they do is crucial, as is the appreciation that context and scale determine the applicability of those rules we presently recognize.” Distinction between escalation and coevolution can most reliably be achieved with careful documentation of the details of the natural history of different systems (Vermeij, 1994). As Kohn (1989, p. 1095) eloquently stated: “Natural history, in focusing on the individual whole organism in its environment, occupies a central position in the spectra of spatial and temporal scales appropriate to biological science.” Solutions to the conceptual conflicts between the coevolution and escalation processes fundamentally depend on growing collaboration among ecologists and paleontologists. This collaboration remains an attractive but seemingly elusive goal; but with it will come a much deeper understanding of the processes that have shaped and continue to shape the evolution of predator-prey systems.

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