

THE EVOLUTIONARY INTERACTION AMONG SPECIES: Selection, Escalation, and Coevolution

Geerat J. Vermeij

Department of Geology and Center for Population Biology, University of California
at Davis, Davis, California 95616

KEY WORDS: macroevolution, evolutionary trends, adaptation, Red Queen hypothesis,
optimality theory

Abstract

The hypothesis of escalation states that enemies—competitors, predators, and dangerous prey—are the most important agents of natural selection among individual organisms, and that enemy-related adaptation and responses brought about long-term evolutionary trends in the morphology, behavior, and distribution of organisms over the course of the Phanerozoic. In contrast to this top-down view of the role of organisms in determining the directions of evolution, the hypothesis of coevolution holds that two interacting species or groups of species change in response to each other. I review and evaluate these hypotheses in the light of criticisms about the existence of evolutionary trends and the role of interactions of species in evolution.

Models describing the evolutionary effects organisms have on each other have been based largely on population dynamics and on cost-benefit analyses of the net outcome of interactions between species. Yet, the hypotheses of escalation and coevolution are statements about the nature, frequency, causes, and role of selection. Although these models have provided valuable insights and have forced some modifications in the hypotheses of escalation, studies seeking to distinguish between escalation and coevolution will require empirical observations and cost-benefit evaluations of the discrete events of interaction that collectively constitute organism-caused selection.

INTRODUCTION

In 1987, I published a book supporting and elaborating a hypothesis first clearly set forth by Darwin (19), which I called the hypothesis of escalation (79). This hypothesis states that enemies—predators, competitors, and dangerous prey—are the most important agents of selection among individual organisms, and that enemy-related adaptation brought about long-term evolutionary trends in the morphology, ecology, and behavior of organisms over the course of the Phanerozoic. With its emphasis on the evolutionary role of enemies, escalation embodies a “top-down” interpretation of the way evolution is affected by organisms themselves. I supported the hypothesis of escalation with paleontological data on the modes of life, environments, and functional designs of fossil organisms. Indeed, without such evidence from the fossil record, the hypothesis would not be testable and might never have been proposed in the first place.

A different conception of the role of organisms in evolution is that two interacting parties change in response to each other. This idea of coevolution, whose modern version was introduced by Ehrlich & Raven (24) in a landmark paper on the evolution of butterflies and plants, provided the impetus for Van Valen’s (71) influential Red Queen hypothesis. According to this hypothesis, the probability of extinction of a population is approximately constant regardless of a taxon’s age (see also 52, 56). Van Valen explained this constancy by noting that evolutionary changes in other species cause the environment for any given species to deteriorate unless the latter species compensates by evolving continuously. Organisms are therefore seen as major agents of extinction as well as of evolution.

Escalation, coevolution, and the Red Queen hypothesis have been criticized on several grounds. Gould (33) maintains that natural selection acting at the level of the individual organism has been of only incidental and fleeting significance in shaping the overall pattern of evolution, and that competition is not necessarily an important mechanism of natural selection. In Gould’s view, the factors that determine speciation and extinction of lineages not only act independently of (or antagonistically to) natural selection, but in the long run they outweigh its evolutionary effect. A related claim is that evolutionary trends are at most short-term phenomena more often interpretable as changes in the variance of a trait than as changes in the mean or median value (34, 65). A true reading of the history of life might reveal few if any trends. Margulis (47) argues that innovation in evolution is mainly the result of symbioses arising from an integration of genomes with separate prior histories, and that natural selection among randomly generated mutants is at best a minor agency of evolutionary change. Still another viewpoint is that evolution is controlled largely by extrinsic change related to climate and tectonics rather than by organisms (11–13, 22, 37, 44).

Some of these differences in interpretation arise from ambiguities in the definition and recognition of trends. Others spring from doubts about the nature and importance of adaptation by natural selection. Still other criticisms flow from theoretical models of coevolution and escalation.

Scientific debates often end not in resolution but in confusion and indifference. Perhaps because of the appeal of the hypothetico-deductive method in science, possible explanations for patterns in nature are often portrayed as strict alternatives when they would be better regarded as complementary (see also 69). Critical assumptions remain hidden and unevaluated, and empirical observations are frequently neither sought nor considered. My purpose here is to evaluate models of coevolution, escalation, and related phenomena, and to redirect attention toward the study of the discrete events in the lives of individuals when selection due to other organisms takes place.

THE HYPOTHESIS OF ESCALATION

I begin with a summary of the hypothesis of escalation as presented in my 1987 book (79). The main features of the hypothesis are as follows.

1. Most resources needed by living things are either other organisms (prey and mates, for example) or are under the control of organisms (shelters, food, mates, information, nutrients, and energy). Therefore, acquisition and retention of resources by an individual organism requires that individual to prevent others from obtaining or monopolizing those resources (see also 71–73).

2. The survival and reproductive success of individuals depend on the ability of individuals to acquire and defend resources by competing with or eating other individuals. Insofar as traits related to this competition in the broad sense are heritable, competition for resources is an important means by which natural selection occurs.

3. Competition-related selection favors the evolution of several kinds of traits. (a) The rapid location and incorporation of resources and information enables individuals to deplete resources available to competitors and reduces exposure to enemies (see also 67). Enhanced sensory systems, high growth rates, and especially high metabolic rates make this possible. (b) Retention or appropriation of resources from other individuals is accomplished by resisting, interfering with, escaping from, or remaining undetected or unrecognized by would-be enemies. Armor, offensive weaponry, high locomotor performance, toxicity, crypsis, and intimate association with well-defended species are among the ways in which resources can be better retained, appropriated, and regulated.

4. Individuals often fail to acquire or retain resources during encounters with other individuals. Insofar as failure reduces the probability of survival or opportunities for reproduction, there is room for adaptive improvement. The

potential for improvement can be roughly gauged by the frequency and cost of failure.

5. The extent to which adaptation in any one direction can occur is limited by conflicting functional demands, that is, by trade-offs among incompatible requirements. These incompatibilities are most evident when populations are stable or in decline and when energy availability is low.

6. Circumstances that reduce functional trade-offs enable adaptive innovations to become established and escalation between species and their enemies to take place. These favorable circumstances include increased per-capita energy, that is, a higher metabolic rate, and expansion of populations in the presence of enemies. Such expansion is possible when habitable areas increase, when primary productivity rises, and when surviving populations recover after a major extinction event. Architectural innovations as well as symbioses may also eliminate functional trade-offs (see also 47, 60).

7. Extinctions accompany, and may often be caused by, reductions in primary productivity. They will tend preferentially to eliminate organisms with high metabolic demands as well as those with few energy reserves. Consequently, those species that are most functionally specialized, most highly escalated, and most energy-demanding are especially prone to extinction.

8. If natural selection due to enemies is an important cause of evolutionary change, there should be a long-term (but by no means a constant) trend for competition-related characteristics, which improves means of acquiring and controlling resources and information, to increase in expression and in frequency through time among functionally similar species inhabiting similar environments. Extinctions have temporarily interfered with escalation but have not eliminated the trend. This is because the diversity of life has generally increased through time (18, 39, 80).

9. Species unable to adapt to the increasing risks and hazards posed by enemies do not suffer extinction; instead they are restricted to environments where energy availability is low and where enemies are few in number and of small effect. These safe environments initially included the pelagic realm (see also 63), fresh water, the dry land, caves, the deep sea, and habitats within rocks, beneath the surface of sediments, or on or in the bodies of other organisms.

10. Escalation in the safe environments stimulates the recycling of nutrients and other resources and therefore increases the opportunity for further escalation in the biosphere as a whole. There is thus a strong positive feedback in the process of escalation (see also 25, 68).

11. Although the directions of evolution are determined largely by organisms, the timing of evolutionary events is dictated by extrinsic causes related to climate, sea level, tectonic movements, and mass extinctions.

THE RECOGNITION AND INTERPRETATION OF TRENDS

Almost all inferences about coevolution and escalation derive from the existence of trends in the expression of traits that function during interactions between species. Some criticisms of coevolution and escalation pertain to the reality of trends, which are defined as consistent statistical changes in the traits along a time axis (54).

With the general acceptance of cladistic methods by systematists, it has become commonplace to insist that evolutionary patterns, including trends, be looked for and verified only by analyzing ancestor-descendant relationships within monophyletic groups, or clades (see for example 34, 35, 54, 84, 85). Although many trends are indeed best sought in this way, others cannot in principle be detected within single clades and instead arise when ecologically and functionally comparable clades replace each other through time (53, 79).

All adaptive transformations occur within clades, but not all cases of branching or within-lineage evolution are expected to conform to the predictions of coevolution or escalation. Many, if not most, evolutionary changes involve an ecological or geographical shift rather than functional improvement relative to other species in the ancestral setting. This is nicely exemplified by lizards of the genus *Anolis* in the West Indies (46) and by intertidal gastropods of the genera *Littorina* and *Nucella* in the North Pacific and North Atlantic Oceans (16, 57). Consequently, it is generally inappropriate to test for trends with respect to traits involved in escalation or coevolution by tracking the mean value of such traits only within monophyletic groups. Only when descendant taxa are functionally and ecologically similar to ancestral ones would such within-clade tracking be suitable.

The most reliable method for detecting trends in escalation-related traits is to plot the expression of these traits among ecologically and functionally similar species through time. For example, one could test whether locomotor performance of large herbivorous tetrapods increased through time not by considering all such tetrapods, but by restricting the analysis to tetrapods of a given habitat such as open woodland. Failure to restrict the analysis could yield misleading results. Locomotor demands are quite different in open woodland as compared to deep forest or grassland environments, so that animals from these various settings are not functionally or ecologically comparable. For open woodland tetrapods, the analysis of the Mesozoic fossil record would concentrate mainly on dinosaurs, whereas the Cenozoic record is chiefly one of mammals and a few flightless birds. The important point is that, because adaptation is inextricably context-dependent, one cannot seek patterns in adaptation through time without taking the context into account.

Failure to incorporate the ecological context has led some critics to reject

or downplay the role of interactions in selection, and to accord a minor role to natural selection in evolution. It is interesting that such points of view have been especially widely held by scholars living in cities. If one does not observe organisms functioning in nature, one is quite naturally inclined to discount the potential role that competition and selection play in daily life as well as in the longer-term dynamics of species, ecosystems, and the biosphere as a whole.

If biological interactions are important causes of selection, and if such selection is an important cause of evolutionary change (79), patterns in the expression of traits related to such interactions should be widespread. Whether these patterns arise from coevolution or escalation continues to be the subject of controversy. The remainder of this essay is devoted to a comparison and evaluation of models of coevolution and escalation, and to a discussion of how the two processes can be distinguished empirically.

MODELS OF COEVOLUTION AND ESCALATION

During its lifetime, any individual in nature interacts with members of many species, including its own. All these species are potentially important agents of selection. If two parties respond evolutionarily to changes in each other, the result is coevolution. This process thus implies reciprocal responses. If the responses involve only two species, there is said to be strict coevolution; if one or both interacting parties consist of more than one species, coevolution is said to be diffuse (30). Participants may be competitors, mutual beneficiaries, predator and prey, or host and guest. In coevolution, the two interacting parties may be each other's most important selective agents; that is, survival and reproduction of members of the interacting groups depend to a greater extent on interactions between the parties than on other potential sources of selection. In escalation, most evolution is caused by selection due to enemies—predators, competitors, parasites, and dangerous prey—that have the capacity to injure, kill, or depress the reproductive output of individuals. Escalation would be equivalent to coevolution if interacting parties are mutual enemies.

Most models that have been constructed to probe the effects species have on each other are variations on a coevolutionary framework. Although coevolution and escalation are ideas based on the roles and sources of natural selection, models of these processes have been built largely by ecologists more concerned with the population-level outcomes of selection than with the mechanics of the processes themselves.

The Red Queen Hypothesis and Models Derived From It

In 1973, Van Valen (71) published a compilation of paleontological data implying that the probability of extinction of a taxon is independent of the taxon's age, measured from the taxon's time of origin. From this point of

departure, Van Valen developed the Red Queen hypothesis, which states that the environment of any given species deteriorates at a more or less constant rate. This deterioration, much of which is due to the evolution of co-occurring species, will eventually lead to extinction, unless the species in question adapts to counteract the environmental deterioration. Species must, in other words, be "running in place" (constantly evolving) just to keep up with the changes induced by evolution in their biological surroundings.

The Red Queen hypothesis is in many ways similar to the hypothesis of escalation, and it arises from a similar view of the importance of biological interactions during the course of evolution; but its two central predictions differ from those embodied in the hypothesis of escalation. These predictions are: (i) that there is continuous coevolution among interacting species, and (ii) that except during times of mass extinction, environmental deterioration due to organisms is the major cause of extinction. It is important to note that these predictions flow from theory, not from the data on extinction rates that prompted Van Valen to develop the theory. Indeed, the data are also compatible with interpretations for escalation. In my view of escalation, adaptation typically occurs only when populations of many species are able to expand simultaneously. At other times, there is a kind of evolutionary gridlock, or mutual stasis, because adaptive improvements in any one direction are prevented as organisms and the physical environment impose conflicting functional demands. The idea that organisms are important agents of extinction (50, 58, 61, 71, 89) is supported for island biotas exposed to continental invaders and perhaps for some instances among ants and large vertebrates, but not for most marine invertebrates, small vertebrates, or plants (79, 82).

Following pioneering work by Maynard Smith (49) and Stenseth & Maynard Smith (66), Rosenzweig and colleagues (59) modeled the evolution of interacting species by using assumptions collectively embodied in the so-called evolutionarily stable strategy (ESS). Traits are assumed to evolve toward a local optimum. In their model, Rosenzweig and colleagues (59) assumed that this optimal phenotype lies somewhere within the limits of the set of all possible phenotypes rather than at the extremes of the phenotypic range, because most phenotypes reflect adaptive compromises.

Although continuous evolution of the kind predicted by the Red Queen hypothesis is theoretically possible, a more likely outcome of the model by Rosenzweig and colleagues (59) is a mutual adaptational stalemate (60, 66). The only way to stimulate evolution among the interacting species is to introduce changes in the rules governing adaptive compromise. Such design changes are most likely when trade-offs among incompatible functions are reduced or eliminated (59, 60).

This can be achieved in several ways. One is by adaptive breakthroughs or "key innovations," changes in the developmental sequence (or rules of con-

struction) that enable previously linked or covarying traits to vary independently (see also 10, 45, 62, 76). Another way is to enter into a mutually beneficial partnership with another organism (see also 47). Such partnerships enable animals to photosynthesize, vertebrates to digest fresh plant material, vascular plants to take up nutrients from the soil, hermit crabs to gain protection from sea anemones living on and increasing the size of their shell homes, and so on. Partnerships make for formidable competitors. Increases in metabolic rate provide still another means. With more energy available, fewer and less stringent compromises in energy allocation are necessary (79). Population expansion provides a fourth way to reduce the constraint of compromise. In expanding populations, costs associated with novel traits or novel combinations of traits are relatively low, because more individuals are able to survive than in populations that are stable or in decline.

The common element of these mechanisms is that the range of permissible phenotypes is increased. Moreover, all these mechanisms are subject to strong selection at the level of individual organisms. Margulis (47) has expressed the view that partnerships involving the genetic integration of two or more independently evolved organisms represent a departure from evolution by natural selection, but Maynard Smith (51) persuasively argues that such partnerships are subject to selection in the same way that other phenotypes are, provided that genetically intimate partnerships behave as units of evolution (that is, as entities characterized by multiplication, variation, and heredity).

The appearance of changes in design may be critical in propelling major episodes of escalation. For example, the evolution of predators may have led to the evolution of mineralized skeletons and of burrowers near the beginning of the Cambrian (81, 70). Partnerships between mycorrhizal fungi and vascular land plants may have set the stage for greater exploitation of the dry land by organisms beginning in the Devonian (64). Elsewhere I propose that these changes in design, which typically require high rates of supply of energy and nutrients, are most likely when extrinsic factors (especially the warming and nutrient enrichment associated with submarine volcanism and tectonically related phenomena) cause productivity to rise. The stimulating effects of extrinsic triggers are therefore greatly amplified through positive feedback by intrinsic improvement on per-capita performance.

An interesting case in which continuous evolution of the type predicted by the Red Queen hypothesis could occur is that of tightly coupled reciprocal coevolution involving chemical deterrents. Any new chemical variant may confer a survival advantage to a plant that is being exploited by a trophically specialized herbivore. If the new chemical is in some way harmful to the herbivore, any trait of the herbivore that reduces this harmful effect or puts the chemical to use as its own defense will be favored. Once reciprocal evolution has occurred, further alteration or abandonment of the chemical in

the plant may begin the coevolutionary process anew. This kind of coevolution could occur continuously and, because there is no long-term genetic memory for previously abandoned defenses, need not result in a long-term directionality of adaptation. Rosenzweig and colleagues (59) point out, however, that the conditions required for this kind of aimless yet continuous evolution may be very seldom satisfied in nature.

The Life-Dinner Principle and Cost-Benefit Models

Dawkins & Krebs (20) took a cost-benefit approach to adaptation when they formulated the life-dinner principle to describe coevolution. They suggested that there is an inherent asymmetry in the evolutionary outcome for predator and prey in encounters between the two. Success for the prey means life (survival), whereas failure means death or, perhaps more commonly, injury. For the predator, success means another meal, whereas failure translates into postponing a meal. The stakes for the prey are thus usually higher than for the predator, although obvious exceptions come to mind. Failure for the predator might entail injury or, if the predator had not eaten for some time and expended much effort to acquire its prey, even death.

I took Dawkins & Krebs's (20) argument to imply that coevolution between predator and prey would be highly asymmetrical, with the prey responding more rapidly and more effectively to the predator than the predator does to the prey (77–79; see also 41 for an excellent example involving bivalved prey eaten by drilling naticid gastropods). For this reason, I accorded a minor role to coevolution between predator and prey, and I argued instead that both parties respond more effectively to their respective enemies than they do reciprocally (79).

Abrams (1–5) has taken issue with Dawkins & Krebs's (20) and my analyses. He modeled predator-prey coevolution by employing principles of cost-benefit analysis and population dynamics. For the prey, the per-capita rate of population growth was expressed in terms of the prey's food resources and in terms of the effect of the predator on the prey population density. The predator's per-capita population growth was expressed only in terms of the available prey resource. Out of 24 possible cases Abrams (1) examined, 20 show adaptive responses by the prey to improvements in prey capture by the predator; whereas 16 show responses by the predator to antipredatory adaptation in the prey. In 14 cases there is the potential for predator-prey coevolution. The outcomes depend on how improvements affect birth and death rates. These results showed that, although prey were more likely to respond to predators than predators were to prey, coevolution (a predator-prey arms race) is by no means inevitable when predators and prey interact. Abrams (1) also showed that the life-dinner principle would not apply when predators are rare and when their selective impact on the prey is small.

If selection by organisms depends on encounters between them, then one measure of the effectiveness of individuals and of their attributes during such encounters is the probability of success (77–79). From the prey's point of view, adaptive improvement means that the number of encounters during which the prey succeeds in not being eaten by the predator will increase relative to the total number of encounters with the predator. For the predator, improvement by the prey translates into a reduced proportion of successful attacks. I suggested further that improvement by the predator could be measured as an increase in the number of successful attacks on the prey relative to the total number of encounters (77–79).

Abrams (2), however, has convincingly argued that this increase does not necessarily imply improvement in the predator, and further points out that improvement by the predator often accompanies a decrease in the proportion of successful encounters. His argument may be summarized as follows. If failed encounters from the point of view of the predator are of low cost in energy or time and involve little risk to the predator, evolutionary changes that result in a higher absolute number of prey killed may be accompanied by a reduced success rate. As long as enough prey are killed, it may matter little to the predator's economic budget how many times the predator fails. Improvement, Abrams (2) and Kitchell (43) argue, should be measured in terms of absolute food intake. If predators do increase food intake while at the same time decreasing the proportion of successful attacks, both predator and prey will improve with respect to the predator-prey interaction. The result would therefore be what many observers would interpret as predator-prey coevolution in which both parties benefit.

Such positive feedback between interacting parties may be very common. For example, frequent failures by predatory crabs to break prey snail shells may be energetically cheap and take relatively little time. By increasing the rate of encounters without sacrificing efficiency, predators will increase their food intake and subject a greater proportion of the shell-bearing prey population to attacks. The larger the number of unsuccessful encounters from the point of view of the predator, the better adapted the prey is to the predator.

Interactions between drilling gastropod predators and bivalved prey provide the basis for coevolutionary models (21, 42, 43) whose results have been claimed to conflict with expectations derived from the hypothesis of escalation (43). These models assume a close and specialized link between predator and prey, as well as the existence of functional trade-offs among growth rate, reproductive output, and shell thickness (a measure of prey defense). Another central assumption is that each species maximizes energy intake. Evolutionary change is generated by the circumstance that energy maximization by interacting species is attempted but never fully realized.

The models indicate that patterns of energy allocation to growth and repro-

duction vary according to the intensity of predation. A low intensity of predation favors early reproduction by the prey and little allocation toward growth and shell thickening; whereas more intense predation favors an emphasis on rapid growth, shell thickening, and delayed reproduction (43). These predicted changes in energy allocation in the prey occur even if the predator's pattern of prey selection remains the same. Unidirectional response should therefore not be expected in predator-prey coevolution (43). The important point is that responses of interacting parties depend on the population densities and therefore on the frequency of interaction of the species involved (see also 5).

A good example of a complex response is offered by the evolution of cephalopods (15, 79, 86, 87). From the Late Cambrian (when cephalopods first appeared) to the Late Cretaceous, most cephalopods had an external shell, which functioned for protection as well as for buoyancy control. During this long interval, cephalopods exhibited many trends toward increased passive protection (greater sculpture, elaboration of the aperture, elaboration of septa separating internal shell chambers), as well as trends toward greater maneuverability and higher absolute speed. However, fundamental incompatibilities exist among buoyancy control, passive protection, and locomotor performance. In the Late Cretaceous, cephalopods had reached the limits of adaptational compromise in the functional design of the external shell as predators and competitors continued to become faster, more powerful, and more numerous. With further intensification of predation and competition, especially by fishes, only those cephalopod lineages that had abandoned the shell persisted and rediversified after the mass extinction of the end-Cretaceous. Without the shell, cephalopods were able to exploit high-energy modes of life, including rapid jet-propulsion and effective buoyancy control. Thus, although the rules of engagement may have remained broadly constant throughout the history of cephalopods, the increasing intensity of predation and competition eventually made previously workable adaptive solutions obsolete and disallowed the resurgence of long-established trends. The latter were replaced by trends emphasizing speed and maneuverability.

Because most predator-prey interactions take place in communities composed of many species, their coevolutionary nature is potentially influenced by interactions with these species. I argued (79) that predators are unlikely to respond uniquely to any one prey species because most predators have a catholic diet and tend not to be specialized to a single prey species (see also 26, 27, 40). Moreover, the composition of communities often changes dramatically through time even if individual species do not change significantly (8). Abrams (4), however, argues from models that alternative prey often magnify the response of a predator to its main prey. The predator's own predators have a similarly enhancing effect on the predator's evolutionary response to its principal prey (4).

Theory Versus Observation

Despite claims that the conclusions derived from the models of DeAngelis et al (21) and Kitchell (42, 43) conflict with the predictions of the hypothesis of escalation, these and other coevolutionary hypotheses as well as the escalation hypothesis incorporate ideas about functional trade-offs and positive feedback. Not surprisingly, therefore, observed patterns of evolution of interacting species are consistent with most if not all of the proposed models. The various models emphasize different aspects of interaction, but they are in most respects logically equivalent.

Conformity with reality does not, however, imply that the coevolutionary models are adequate or relevant. Their utility is compromised by unwarranted assumptions and by the even more fundamental problem that they do not consider the process of selection, which is after all supposed to be responsible for the evolutionary dynamics of interacting species. Abrams's (1–5) models, for example, incorporate the effects of predators on prey populations, but they do not take into account the effects of the predator's own enemies. The models by DeAngelis and his colleagues (21, 42, 43) assume a tight reciprocal linkage between predator and prey; yet, both predator and prey interact with a host of other species (17, 40), and in the system of drilling predators and bivalved prey for which these models were specifically designed, there is no evidence of reciprocal interaction. Instead, Kelley (41) finds in her exceptionally careful analysis of fossil evidence from the Miocene of Maryland that, although evolutionary changes in clams are interpretable as responses to drilling predators, the main changes in the predators are interpretable as defenses against the snails' own enemies. All the models treat selection very indirectly by incorporating its effects on population dynamics of interacting species.

An important question arising from the models, especially those of Abrams (1–5) and Kitchell (42, 43), is whether positive feedback between interacting populations is equivalent to coevolution (that is, reciprocal adaptive response). Is selection in favor of higher food intake by predators caused by the prey, or is it due to the predator's own enemies? The answer is likely to be complex. The evolutionary role of interactions among species depends on the costs and benefits involved. Minimal costs and minimal benefits will have little effect; high costs and large benefits make a big difference. For a very hungry predator, the cost of failure to secure a given prey may be very high; for a sated predator, the cost is apt to be low. Kitchell (43) is therefore correct in pointing out that, even if the pattern of selection (the traits of the winners as compared to the traits of the losers) remains unaltered, the effect of this selection depends on how costs and benefits change with such ecological variables as population density of predators relative to that of the prey.

For predatory mammals, fossil evidence points to a large role of competitors in the evolution of equipment such as claws, saber-like canines, and other weaponry for securing and gorging prey rapidly (7, 74, 75). West and her colleagues (88) argued that in the case of crabs and prey molluscs in Lake Tanganyika, the prey may be the more important agents of selection in view of the fact that crabs do not fight much among themselves. Whether this interpretation is correct, however, remains to be seen. Marine crabs with similarly enlarged claws frequently do fight and use their claws in defense against competitors and predators, as well as in overcoming the armor of prey molluscs.

Important as the insights offered by coevolutionary models are, I believe the models miss the essential distinction between coevolution and escalation. Populations of species may have positive effects on one another, but such effects do not imply reciprocal evolution. Population dynamics are not the same thing as selection. Given that coevolution and escalation are fundamentally about the nature, source, and intensity of selection, no models describing the population dynamics of interacting species can adequately describe selection-based processes such as coevolution and escalation.

COEVOLUTION OR ESCALATION: A DEBATE ABOUT SELECTION

A central issue in the debate about escalation and coevolution is the nature of selection. Most studies of adaptation and natural selection emphasize the net genetic or phenotypic outcome of the process rather than the way in which selection occurs. Yet, if we are to distinguish empirically between coevolution and escalation, it is essential to ascertain when selection occurs, how frequently selection takes place, and especially which agents or agencies are responsible.

My view is that selection is episodic. It occurs as events during which an individual organism has an encounter with an agency capable of influencing the individual's survival or reproduction. These events can be observed and counted, and their outcomes can be evaluated in terms of success or failure. A more difficult problem is to assess the cost of failure and the benefit of success. Some encounters may be inconsequential, whereas others mean the difference between death and survival or between reproductive failure or success. A coevolutionary interpretation implies that the selection that occurs during encounters between the two species (or groups of species) in question is more intense or more effective than is selection due to other agents. An interpretation of escalation, on the other hand, requires that selection due to enemies takes precedence over that effected by a food species, unless that food species is also a potential enemy.

As an example, consider the evolution of high speed in running. Speed in principle provides the obvious advantage of escape from predators; it also enables individuals to maintain larger territories and to arrive at food sources or mates before potential competitors do. If both predator and prey show increases in speed, a coevolutionary interpretation is tempting (see for example 7). A similar pattern could be obtained if both the prey and its predator were responding evolutionarily to their own enemies. The debate cannot be settled through modeling of predator-prey dynamics; a resolution depends entirely on empirical observations of both the prey and the predator. When do these animals use their high speed, and what are the outcomes of individual episodes of running? At least for lizards, the tentative answer to this question is that high speed is used mainly in escapes from predators (38).

Similar questions apply to the evolution of host-guest relationships. Small, poorly defended organisms may find substantial shelter from enemies by entering evolutionarily into intimate partnerships with larger, well-defended hosts. Although many of these partnerships are parasitic in nature, others have evolved into mutualisms, in which the guest provides competitive or defensive benefits to its host. These mutualisms imply an element of coevolution or mutual accommodation between host and guest, but the extent to which this partnership has evolved or become specialized may be determined strongly by selection imposed by enemies of both the host and the guest (for more or less similar views see 9, 14, 29). A better empirical understanding of the origin of intimate partnerships requires careful observations of encounters that the host and guest have with each other and with other species.

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.

Models should be constructed not only by expressing the net outcome of selection in terms of births and deaths or energy intake, but by evaluating systematically how encounters of various kinds affect opportunities for functional improvements among interacting species. It is important to express the encounter rate not merely in terms of population densities of the interacting species, but to scale these densities according to metabolic rates and, in the case of predators, according to handling time. High-energy species (those with high metabolic rates) are apt to encounter members of other species more frequently than do low-energy species (79). Predators that take a long time to find, pursue, and subdue prey will have a low effective encounter rate with prey even if their population density is high (3). Encounter rates, and therefore the opportunities for coevolutionary response or escalation, depend on population densities as well as on the metabolic properties of the species involved.

Because survival and reproduction require only that a given individual's genes make it more fit than its neighbors, models based on optimality theory should in my view be abandoned. Optimality in its many forms assumes that there exists a single "best" phenotype toward which selection "strives." It may be that individuals in some circumstances are extraordinarily well adapted, and that they therefore approach some engineering standard of perfection; but under other circumstances, individuals are sloppily constructed and would, on engineering grounds at least, seem to fall far short of the "best" or even a good design. Imperfection and errors abound in nature (28, 77). Optimality implicitly assumes that there are absolute standards of design, and that the further organisms are from meeting the specifications the faster evolution will proceed toward the optimum (49). The fact that degrees of specialization among ecologically similar species vary widely in the world today strongly implies to me that design standards in nature are relative, not absolute (83). Given that the correspondence between structure and function is often far from precise (6, 23, 32, 36), we should expect organisms to embody ad hoc and often rather clumsy solutions to functional demands, solutions that bear a deep stamp of history and ancestry. As long as they work, they will not be disadvantageous, and they will not be purged until a better solution comes along, usually in the bodies of individuals belonging to an entirely different evolutionary line. Even then, the tendency for incumbents to prevail may prevent superior solutions from gaining a foothold (60). Some unusual opportunity, such as an extinction or a circumstance favorable to population increase in many species simultaneously, may be necessary to permit more effective designs to become established.

CONCLUDING REMARKS

Debates about the role of selection in evolution and about the role of competition in selection are important. They should not be allowed to end in a tangle of unstated, unwarranted, or untested assumptions and partisan rhetoric. The modeling efforts by Abrams (1–5) and others (21, 42, 43, 49, 60) have yielded some important insights, but the roles of coevolution and escalation and the essential distinction between these two processes remain matters of empirical observation of living species, and detailed studies of interactions among fossil species over long intervals of time will go a long way toward understanding how interactions among species have affected the course of evolution.

**Any *Annual Review* chapter, as well as any article cited in an *Annual Review* chapter, may be purchased from the Annual Reviews Preprints and Reprints service.
1-800-347-8007; 415-259-5017; email: arpr@class.org**

Literature Cited

1. Abrams PA. 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms-race analogy. *Evolution* 40:1229-47
2. Abrams PA. 1989. The evolution of rates of successful and unsuccessful predation. *Evol. Ecol.* 3:157-71
3. Abrams PA. 1991. The evolution of anti-predator traits in prey in response to evolutionary change in the predators. *Oikos* 59:147-56
4. Abrams PA. 1991. The effects of interacting species on predator-prey coevolution. *Theor. Pop. Biol.* 39:241-62
5. Abrams PA. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *Am. Nat.* 140:573-600
6. Alexander RM. 1991. Apparent adaptation and actual performance. *Evol. Biol.* 25:357-73
7. Bakker RT. 1983. The deer flees, the wolf pursues: incongruencies in predator-prey coevolution. See Ref. 31, pp. 350-82
8. Bennett KD. 1990. Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* 16:11-21
9. Bernays E, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69:886-92
10. Bock WJ. 1959. Preadaptation and multiple evolutionary pathways. *Evolution* 13:194-211
11. Boucot AJ. 1975. *Evolution and Extinction Rate Controls*. Amsterdam: Elsevier
12. Boucot AJ. 1983. Does evolution take place in an ecological vacuum? *J. Paleont.* 57:1-30
13. Boucot AJ. 1985. Silurian-Early Devonian biogeography, provincialism, evolution and extinction. *Philos. Trans. R. Soc. Lond. (B)* 309:323-39
14. Brower LP. 1958. Bird predation and foodplant specificity in closely related procrystic insects. *Am. Nat.* 92:183-87
15. Chamberlain JA Jr. 1991. Cephalopod locomotor design and evolution: the constraints of jet propulsion. In *Biomechanics in Evolution*, ed. JMV Rayner, PJ Wootton, pp. 57-98. Cambridge: Cambridge Univ. Press
16. Collins T, Fraser K, Palmer AR, Vermeij GJ, Brown W. 1994. Evolutionary history of Northern Hemisphere *Nucella* (Gastropoda, Muricidae): Molecules, morphology, ecology and fossils. In review
17. Commiato JA. 1987. *Polinices* predation patterns and Mercenaria morphology models. *Am. Nat.* 129:449-51
18. Cracraft J. 1985. Biological diversification and its causes. *Ann. Missouri Bot. Garden* 72:794-822
19. Darwin C. 1859. *The Origin of Species by Natural Selection or The Preservation of Favored Races in the Struggle for Life*. New York: Colliers
20. Dawkins R, Krebs JR. 1979. Arms races between and within species. *Proc. R. Soc. Lond. (B)* 205:489-511
21. DeAngelis DL, Kitchell JA, Post WM. 1985. The influence of naticid predation on evolutionary strategies of bivalve prey: conclusions from a model. *Am. Nat.* 126:817-42
22. Des Marais DJ, Strauss H, Summons RE, Hayes JM. 1992. Carbon isotope evidence for the stepwise oxidation of the Proterozoic environment. *Nature* 359:605-9
23. Dudley R, Gans C. 1991. A critique of symmorphosis and optimality models in physiology. *Physiol. Zool.* 64:627-37
24. Ehrlich PR, Raven PH. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18:586-608
25. Fischer AG. 1984. Biological innovations and the sedimentary record. In *Patterns of Change in Earth Evolution*, ed. HD Holland, AF Trendall, pp. 145-57. Berlin: Springer
26. Fox LR. 1981. Defense and dynamics in plant-herbivore systems. *Am. Zool.* 21:853-64
27. Fox LR, Morrow PA. 1981. Specialization: species property or local phenomenon? *Science* 211:887-93
28. Frazzetta TH. 1970. From hopeful monsters to bolyerine snakes? *Am. Nat.* 104:55-71
29. Futuyma DJ. 1983. Evolutionary interactions among herbivorous insects and plants. See Ref. 31, pp. 207-31
30. Futuyma DJ, Slatkin M. 1983. Introduction. See Ref. 31, pp. 1-13
31. Futuyma DJ, Slatkin M. 1983. *Coevolution*. Sunderland, Mass: Sinauer
32. Garland T Jr, Huey RB. 1987. Testing symmorphosis: does structure match functional requirements? *Evolution* 41:1404-9
33. Gould SJ. 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11:2-12
34. Gould SJ. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *J. Paleontol.* 62:319-29

35. Gould SJ. 1990. Speciation and sorting as the source of evolutionary trends, or "things are seldom what they seem." See Ref. 55, pp. 3–27
36. Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. London (B)* 205:581–98
37. Guensburg TE, Sprinkle J. 1992. Rise of echinoderms in the Paleozoic evolutionary fauna: significance of paleoenvironmental controls. *Geology* 20: 407–10
38. Hertz PE, Huey RB, Garland T Jr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or Boy Scouts? *Am. Zool.* 28:927–38
39. Hoffman A. 1989. *Arguments on Evolution: A Paleontologist's Perspective*. New York: Oxford Univ. Press
40. Howe HF. 1984. Constraints on the evolution of mutualisms. *Am. Nat.* 123:764–77
41. Kelley PH. 1992. Coevolutionary patterns of naticid gastropods of the Chesapeake Group: an example of coevolution? *J. Paleontol.* 66:794–800
42. Kitchell JA. 1986. The evolution of predator-prey behavior: naticid gastropods and their molluscan prey. In *Evolution of Animal Behavior: Paleontological and Field Approaches*, ed. MH Nitecki, JA Kitchell, pp. 88–110. New York: Oxford Univ. Press.
43. Kitchell JA. 1990. The reciprocal interaction of organism and effective environment: learning more about "and." In *Causes of Evolution: A Paleontological Perspective*, ed. RM Ross, WB Allmon, pp. 151–69. Chicago: Univ. Chicago Press
44. Knoll AH. 1992. The early evolution of eukaryotes: a geological perspective. *Science* 256:622–27
45. Lauder GV. 1981. Form and function: structural analysis in evolutionary morphology. *Paleobiology* 7:430–42
46. Losos JB. 1992. The evolution of convergent structure in Caribbean *Anolis* communities. *Syst. Biol.* 41:403–20
47. Margulis L. 1991. Symbiogenesis and symbiointicism. See Ref. 48, pp. 1–14
48. Margulis L, Fester R. 1991. *Symbiosis as a Source of Evolutionary Innovation: Speciation and Morphogenesis*. Cambridge, Mass: MIT Press
49. Maynard Smith J. 1976. What determines the rate of evolution? *Am. Nat.* 110:331–38
50. Maynard Smith J. 1989. The causes of extinction. *Philos. Trans. R. Soc. London (B)* 325:241–52
51. Maynard Smith J. 1991. A Darwinian view of symbiosis. See Ref. 48, pp. 26–39
52. McCune AR. 1982. On the fallacy of constant extinction rates. *Evolution* 36:610–14
53. McKinney FK, Jackson JBC. 1991. *Bryozoan Evolution*. Chicago: Univ. Chicago Press. 2nd ed.
54. McKinney ML. 1990. Classifying and analyzing evolutionary trends. See Ref. 55, pp. 28–58
55. McNamara KJ. 1990. *Evolutionary Trends*. Tucson: Univ. Ariz. Press
56. Pearson PM. 1992. Survivorship analysis of fossil taxa when real-time extinction rates vary: the Paleogene planktonic Foraminifera. *Paleobiology* 18:115–31
57. Reid DG. 1990. A cladistic phylogeny of the genus *Littorina* (Gastropoda): implications for evolution of reproductive strategies and for classification. *Hydrobiologia* 193:1–19
58. Ricklefs RE, Cox GW. 1972. Taxon cycles in the West Indian avifauna. *Am. Nat.* 106:195–219
59. Rosenzweig ML, Brown JS, Vincent JL. 1987. Red Queens and ESS: the coevolution of evolutionary rates. *Evol. Ecol.* 1:59–94
60. Rosenzweig ML, McCord RD. 1991. Incumbent replacement: evidence of long-term evolutionary progress. *Paleobiology* 17:202–13
61. Roughgarden J. 1983. The theory of coevolution. See Ref. 31, pp. 33–64
62. Schaeffer B, Rosen DE. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Am. Zool.* 1:187–204
63. Signor PW, Vermeij GJ. 1994. The plankton and the benthos: origins and early history of an evolving relationship. *Paleobiology* 20: In press
64. Simon L, Bousquet J, Levesque RC, Lalonde M. 1993. Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature* 363:67–69
65. Stanley SM. 1973. An explanation for Cope's Rule. *Evolution* 27:1–26
66. Stenseth NC, Maynard Smith J. 1984. Coevolution in ecosystems: Red Queen evolution or stasis? *Evolution* 38:870–80
67. Sterrer W. 1992. Prometheus and Proteus: the creative, unpredictable individual in evolution. *Evol. Cognition* 1: 101–29
68. Thayer CW. 1983. Sediment-mediated biological disturbance and the evolution

- of marine benthos. In *Biotic Interactions in Recent and Fossil Benthic Communities*, ed. MJ Tevesz, PL McCall, pp. 479–625. New York: Plenum
69. Turner JRG. 1983. Mimetic butterflies and punctuated equilibria: some old light on a new paradigm. *Biol. J. Linn. Soc.* 20:277–300
 70. Valentine JW, Awramik SM, Signor PW, Sadler PM. 1991. The biological explosion at the Precambrian-Cambrian boundary. *Evol. Biol.* 25:279–356
 71. Van Valen L. 1973. A new evolutionary law. *Evol. Theor.* 1:1–18
 72. Van Valen L. 1976. Energy and evolution. *Evol. Theor.* 1:179–229
 73. Van Valen L. 1983. How pervasive is coevolution? See Ref. 31, pp. 1–19
 74. Van Valkenburgh B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia: Carnivora): evolutionary interaction among sympatric predators. *Paleobiology* 17:340–62
 75. Van Valkenburgh B, Hertel F. 1993. Tough times at La Brea: tooth breakage in large carnivores of the Late Pleistocene. *Science* 261:456–59
 76. Vermeij GJ. 1973. Adaptation, versatility, and evolution. *Syst. Zool.* 22:466–77
 77. Vermeij GJ. 1982. Unsuccessful predation and evolution. *Am. Nat.* 120:701–20
 78. Vermeij GJ. 1983. Intimate associations and coevolution in the sea. See Ref. 31, pp. 311–27
 79. Vermeij GJ. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton: Princeton Univ. Press
 80. Vermeij GJ. 1989. Evolution in the long run. *Paleobiology* 15:199–203
 81. Vermeij GJ. 1990 (1989). The origin of skeletons. *Palaos* 5:585–89
 82. Vermeij GJ. 1991. When biotas meet: understanding biotic interchange. *Science* 253:1099–1104
 83. Vermeij GJ. 1993. *A Natural History of Shells*. Princeton: Princeton Univ. Press
 84. Vrba ES. 1980. Evolution, species and fossils: how does life evolve? *South Afr. T. Sci.* 76:61–84
 85. Vrba ES. 1983. Macroevolutionary trends: new perspectives on the roles of adaptation and incidental effect. *Science* 221:387–89
 86. Ward P. 1986. Cretaceous ammonite shell shapes. *Malacologia* 27:3–28
 87. Wells MJ, O'Dor RK. 1991. Jet propulsion and the evolution of the cephalopods. *Bull. Mar. Sci.* 49:419–32
 88. West K, Cohen A, Baron M. 1991. Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator-prey coevolution. *Evolution* 45:589–607
 89. Wilson EO. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95:179–93