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Author(s): Peter A. Abrams

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THE EVOLUTION OF PREDATOR-PREY INTERACTIONS: Theory and Evidence

Peter A. Abrams

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5 Canada; e-mail: abrams@zoo.utoronto.ca

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■ **Abstract** Recent theories regarding the evolution of predator-prey interactions is reviewed. This includes theory about the dynamics and stability of both populations and traits, as well as theory predicting how predatory and anti-predator traits should respond to environmental changes. Evolution can stabilize or destabilize interactions; stability is most likely when only the predator evolves, or when traits in one or both species are under strong stabilizing selection. Stability seems least likely when there is coevolution and a bi-directional axis of prey vulnerability. When population cycles exist, adaptation may either increase or decrease the amplitude of those cycles. An increase in the defensive ability of prey is less likely to produce evolutionary counter-measures in its partner than is a comparable increase in attack ability of the predator. Increased productivity may increase or decrease offensive and defensive adaptations. The apparent predominance of evolutionary responses of prey to predators over those of predators to prey is in general accord with equilibrium theory, but theory on stability may be difficult to confirm or refute. Recent work on geographically structured populations promises to advance our understanding of the evolution of predator-prey interactions.

INTRODUCTION

In this article, the term “predation” is used to describe an interaction in which individuals of one species kill and are capable of consuming a significant fraction of the biomass of individuals of another species. This definition includes finches that consume seeds, and the interaction between insect parasitoids and their hosts. However, it does not include most disease organisms and also does not include many herbivores. This definition was chosen because the interactions that fall under the definition can be modeled using a common mathematical framework. Most parasite-host relationships (which fall under some definitions of predation) require models where the number of infected hosts is the index of the abundance of the natural enemy. It is also necessary to take the longevity of infected hosts into account to determine parasite birth (transmission) rates. These properties lead to

quite different mathematical representations than those used for predators under the current definition. Even within this somewhat narrow definition of predation, however, there are very few species that are not engaged in some form of predator-prey interaction.

Given their major effects on fitness, traits that affect the ability to accomplish or avoid predation should therefore be under strong selection. Many current-day evolutionary biologists believe that predation has played a major role in determining patterns in the history of life on this planet, such as the increase in maximum complexity of organisms (32, 49, 66, 98). At the same time, the evolution of traits related to predation in both predator and prey has proven to be difficult to understand in theory, and difficult to study in the field. Many textbooks fail even to mention the evolution of traits related to predation, or at most, they devote a couple of pages to the subject (e.g. 45). The 33rd symposium of the British Ecological Society treated the subject of "Genes in Ecology" with only a passing reference in one chapter to the subject of predator-prey coevolution (22). Interpretations of temporal changes in predation-related characteristics of species have often been controversial (e.g. 61 vs. 76).

These difficulties have not prevented the growth of theory predicting the potential evolutionary trajectories of predator-prey interactions. Darwin (31) proposed that selection for catching various types of prey could lead to diversification of geographical races of predators. However, he did not discuss the simultaneous evolution of both species. Cott (30) may have been the first person (in 1940) to present the currently popular view of predator-prey coevolution as an arms race. In the following decades, most biologists who worked on the problem reverted to thinking about one-way evolutionary interactions between predator and prey. In the late 1960s and early 1970s, many biologists were concerned with explaining why predators did not evolve such a high efficiency that they drove their prey extinct (see Slobodkin's discussion of "prudent predation" in 90). Coevolution began to be mentioned more frequently beginning in the late 1960s. Some key works were Pimentel's verbal descriptions and laboratory experiments suggesting the possibility of a "genetic feedback mechanism" (74, 75) and a set of theoretical models of coevolution (including 65, 82, 83, 89). Dawkins & Krebs's (33) description of predator-prey coevolution as an arms race also helped to revive interest in the field.

Nevertheless, the empirical problems alluded to above have not yielded significantly to any advances in concepts or technology, and most of what we know comes from theoretical studies. This article reviews the questions asked, and both the assumptions and predictions made by previous theoretical treatments of the evolution of predator-prey interactions. It then reviews empirical evidence relating to both the assumptions and the predictions of the theory. In previous reviews of the evolution of predator-prey systems, there has been an excessive amount of interest in whether changes in the interaction of predator and prey represent coevolution in the narrow sense of Janzen's definition (60). Here evolutionary change in either species must evoke an evolutionary change in the other, which

then changes the original trait value of the first species. This complicated scenario can best be understood by building upon the simpler cases in which only one of the two interacting species undergoes significant evolutionary change. Most interactions in nature are asymmetrical, and there is some evidence that predator-prey interactions are often characterized by greater responses of prey to predators than vice versa. Vermeij (97, 98), for example, has argued forcefully that predators affect the evolution of their prey, but prey do not significantly affect the evolution of predators. Nevertheless, it is both unlikely and difficult to prove that two-way effects are nonexistent. Therefore, the question 'Is it coevolution?' is not considered in any detail here. This article considers the evolution of one party in the predatory interaction, as well as coevolution of both species.

A REVIEW OF PREDATOR-PREY MODELS

The evolution of traits related to predation cannot be understood without some understanding of the dynamics of interacting populations that do not exhibit any significant evolutionary change. The two standard models for predator-prey and parasitoid-host interactions are the Lotka-Volterra and Nicholson-Bailey models. In their simplest forms both models lack any density dependence in the growth of the victim population, which leads to nonpersistent dynamics (neutrally stable cycles in the case of Lotka-Volterra, and diverging cycles ending in extinction for the Nicholson-Bailey system). The density-dependent versions of these two models are thus the minimal representations of a predator-prey system. The Lotka-Volterra model for a prey population of size N and a predator population of size P may be written,

$$\begin{aligned}\frac{dN}{dt} &= rN \left(1 - \frac{N}{K}\right) - CNP \\ \frac{dP}{dt} &= P(BCN - D)\end{aligned}\tag{1a,b}$$

where r and K are the maximum per capita growth rate and carrying capacity of the prey; C is the capture rate per unit time per unit prey density by an average predator; B is the conversion efficiency of ingested prey into new predators; and D may be interpreted either as a per capita death rate or a per capita food requirement for maintenance and replacement of predators. The product, CN , represents the predator's functional response, i.e. the relationship between prey density, N , and the amount ingested by an average predator. The most common variant of equations (1a,b) is to replace this linear functional response with a type-2 (58) response. The latter is often described by the disk equation, $CN/(1 + ChN)$, where h is the amount of time required to capture a prey individual, during which further search for, or capture of prey is impossible. Equations (1a,b) always have a locally stable two-species equilibrium, provided the prey's carrying capacity is large enough

($K > D/(BC)$). If the type-2 response is substituted for the linear response in Equations (1a,b), then predator-prey cycles are possible when the predator is efficient (i.e. when the equilibrium prey density is low relative to its carrying capacity). Three other common modifications of these equations are: (a) a nonlinear relationship between amount eaten and per capita predator reproductive rate (i.e. a nonlinear numerical response); (b) a negative effect of predator density on the numerical or functional responses; and (c) nonlinear density-dependence of prey population growth.

The Nicholson-Bailey model and variants of it are difference equations that characterize population densities only at discrete intervals. Use of such models is most appropriate when reproduction occurs seasonally. The simplest case assumes that prey are eaten by predators continuously throughout the interval (i.e. season), but that predator numbers do not change within the interval. Then prey reproduction is based on the number of surviving prey multiplied by a per-individual birth rate that is reduced appropriately according to the density of prey (either at the beginning of the interval or averaged over the interval). The reproductive output of the predators is directly proportional to the number of prey eaten in the simplest case. A simple model for prey and predator numbers at time $t + 1$, given N_t prey and P_t predators at time t , is:

$$\begin{aligned} N_{t+1} &= N_t \text{Exp} \left(r \left(1 - \frac{N_t}{K} \right) - CP_t \right) \\ P_{t+1} &= BN_t (1 - \text{Exp}(-CP_t)) \end{aligned} \quad 2a,b.$$

Again, it is possible to modify these equations to incorporate other forms of density dependent prey growth, nonlinear predator functional or numerical responses, and direct effects of predator density on the predator's per capita growth rate. The dynamics of equations (2) are still not fully understood, although conditions for the existence of a locally stable equilibrium were published over 20 years ago (20). Relatively high values of r and C can produce cycles or chaotic dynamics (12, 62).

The time course of evolutionary change in any trait that affects parameters in the above equations (or analogous parameters in more detailed equations) will usually depend on the population densities and patterns of change in population densities of one or both species. Thus, there is no way to study the evolution of such traits independently of the population dynamics that the ecological interaction implies.

TRAITS AND EVOLUTIONARY MODELS OF THEIR DYNAMICS

Many traits affect prey mortality and predator population growth rates in a predator-prey interaction. These may be classified according to which parameters of a population-dynamical model they influence. A few basic parameters appear in almost all such models. For the predator, the universally present parameters

potentially affected by one or more traits are: (a) the individual's maximum capture rate of prey (C in Equations 1 and 2), and (b) the individual's per capita intake rate of prey required for zero population growth of the predator (B/D in Equation 1). In most cases, the relationship between prey abundance and the predator's intake rate (its functional response) is nonlinear, and predator traits may affect the shape of this relationship, for example, by changing handling time.

The shape of the relationship between intake rate and per capita growth rate (the predator's numerical response) may also be affected by the predator's traits. This relationship is assumed to be linear in both Equations 1 and 2, but it need not be. Any characteristics that increase the efficiency of conversion of food into new predators will affect the initial slope of the numerical response and may affect other aspects of its shape. A particular trait will often affect more than one parameter of the predator's population growth function. For example, larger jaw muscles in a predator that captures prey using its mouth may have the following effects: (a) greater maximum capture rate, because fewer prey escape following initial contact; (b) shorter handling time, because prey can be subdued or ingested more rapidly; (c) greater intake required for zero population growth, because larger muscles are energetically expensive, or offspring size or gestation period must increase. When predator abilities change with age, traits that affect life history parameters of necessity also affect predation-related parameters.

The traits of prey species may also be classified by the parameter(s) of a population dynamics model that are affected by those traits. The single parameter that is always present in predator-prey models is the predator's maximum per capita capture rate of prey (C in Equations 1 and 2). This is, of course, a function of prey traits as well as those of the predator. A lower maximum capture rate may be caused by traits that reduce the prey's chance of encountering a predator, of being detected if encounter occurs, or of escape following detection. Escape can often be brought about if the prey can discourage the predator from attacking by appearing dangerous, non-nutritious or unpalatable, or so proficient at escape that the attack would be futile. Life-history adaptations of prey to deal with high risk of predation may include faster progress through vulnerable stages or more general adaptations to high mortality (e.g. earlier reproduction and greater reproductive investment).

Most evolutionary models assume that there are pleiotropic effects of any trait that has an effect on capture rates. For the predator, traits that increase capture rates reduce some other component of fitness; for the prey, traits that decrease predation rates have costs. This assumption of tradeoffs or costs has empirical support from several detailed studies (for example, 25, 63). It is also a logical necessity in many (but not all) models, because without it traits would evolve to infinite values. In fact, some models (80, 89, and some models in 81) have solutions in which traits continue to increase indefinitely, although the system persists because adaptations in one species offset those in the other. Such models are not realistic (as Rosenzweig et al point out in 81). The exception to this argument for the necessity of costs is when an intermediate value of the trait produces the greatest

value of a predation-rate-enhancing trait in the predator, or of an anti-predator trait in the prey.

Understanding the evolution of a predator-prey interaction requires a description of the potential dynamics of one or more traits in one or both species through time. Because the genetics of such traits are generally largely or completely unknown, most recent models have adopted approaches that are largely phenotypically based. Here, no restrictions are placed on the values of the predation-related traits, and the strength of selection determines the rate of change of average trait values. Three approaches fall under this general description. The first are models in which the traits change according to quantitative genetic recursion equations (64; applied in 84) or approximation to these equations (15, 91; applied in 13, 14). The second approach assumes that populations consist of asexual clones, and mutations with small effects produce new clones having slightly different phenotypes. If the new clone has a higher fitness than the resident, it will invade and either replace it or coexist with it (73). This approach is used by Dieckmann & Law (36), Dieckmann et al (37), and Marrow et al (70). The third approach is one that can be applied only when the equilibrium is stable; it simply looks for strategies that cannot be invaded by other strategies (27). All of these approaches are often well approximated by the same model in which the mean values of continuous traits change at rates proportional to the derivative of individual fitness with respect to the individual's trait value (15, 36, 99). Predictions are usually (but not always) very similar to those of multilocus models in which many loci have similar, small, additive effects on a character (38). The preceding discussion and the rest of this chapter ignores the role of evolutionary forces other than selection (and to a limited extent, mutation). This is more a reflection of the lack of knowledge about the roles of gene flow and drift than evidence that they are unimportant. Although most of the models have been based on extremely simple population models like Equations 1 and 2, there have now been enough studies of different models that some of the general features of these simplified scenarios are becoming clear.

This review tries to synthesize the findings of these previous models and focuses on two types of questions. The first is how evolution or coevolution affects the stability of predator-prey systems. The second question asks what is the response of predation-related traits in one species of the predator-prey pair to an environmental change or a change in the characteristics of its partner in the interaction? These are the questions that have most commonly been addressed in studies of predator-prey systems.

Population cycles are a potential consequence of predator-prey interactions without any evolution, and both predatory and anti-predator traits have been shown to affect the stability of the ecological interaction (7, 9, 13, 14, 79, 88). If the evolutionary dynamics of the traits that determine predation rates are unstable, this will drive population cycles. The previous discussions of the ability of evolutionary change in predator-prey systems to drive cycles have ranged from the conclusion that cycles occur very seldom (88) to the conclusion that cycles are

almost inevitable (69). Neither of these extreme positions applies to the range of biologically plausible models that have been analyzed to date.

The second question concerned the response of traits to environmental change. The topics that have attracted the most attention to date are the responses of traits in one species to a change in the other species (2, 4, 5, 33, 34), and the response of traits to factors external to the predator and prey, such as enrichment of the prey's food source or changes in the predator's mortality rate (4, 56, 80). Here again, a variety of results have been obtained.

EVOLUTION AND STABILITY

Perhaps the most interesting questions about the effects of evolution of predation-related traits on stability are: Can evolution produce cycles in otherwise stable systems? (If so, under what conditions?); Can evolution dampen or eliminate cycles that occur in the absence of evolutionary change? (Again, under what conditions?); Do population cycles significantly change the mean values of adaptively evolving traits?

To answer the first question, we must start with a stable version of a system like Equations 1 or 2, add dynamics of one or more of the parameters in that population dynamical model, and determine whether the resulting expanded system is still stable. This has been done for the case of predator evolution in (7), for prey evolution in (71) and (14), and for coevolution of both species in (13, 36, 37, 46, 56, 69–71, 85, 89, 94, 96). The theoretical results obtained thus far suggest that, although evolution in one species can cause cycles, the most likely source of evolutionary instability is the interaction between evolutionary variables in both species. However, some rather special conditions must be met for this to occur.

Predator Evolution

Predator evolution alone is able to drive cycles in otherwise stable systems (7), but it appears to be relatively unlikely to do so. Cycles require that higher prey densities select for lower predator consumption rates and that the response to selection be very rapid. The optimal capture-rate parameter (C in Equations (1) or (2)) should often decrease in response to increased prey abundance. This is favored by a predator numerical response (per capita growth rate) that increases at a decreasing rate as prey densities become high. Under these conditions, it is advantageous to reduce costly traits that increase capture when prey are abundant or easily caught because increased food intake increases population growth by only a small amount. This decrease in predation when prey are abundant has a destabilizing influence on the system because it allows the prey population to continue growing when it is abundant. To produce population cycles, however, the evolutionary decrease in capture rates must be quite rapid, and no empirical examples give evidence of this mechanism.

Evolutionary stabilization of predator-prey systems with unstable population dynamics is also possible. When constraints on the predator's capture rates or reproductive rates are minimal, then increases in prey abundance should select for investment in costly capture-related traits; when prey are rare, the costs are likely to exceed the potential benefits of such traits. The result will be greater values of capture-related traits when prey are common and lower values of these traits when prey are rare. Both of these outcomes favor increased stability, because both push prey densities toward an equilibrium with intermediate densities.

Prey Evolution

The evolution of prey defensive traits is more likely to be a source of instability than is evolution of capture-related traits in the predator. Instability can take the form of population and trait cycles (as in 14) or of evolution that leads to extinction of the prey species (72). Each of these outcomes depends on the presence of a saturating functional response on the part of the predator (absent from many previous models of evolution in predator-prey systems). The cyclic outcome occurs via the following mechanism. As predators reduce the number of prey, they become less satiated, raising the risk of capture for prey individuals. This increases the selection for resistance on the part of prey, which leads to a reduced predator population and selection to reduce costly defensive traits. Given the appropriate time scale of responses, the time lag between changes in predator population and prey vulnerability will result in cycles. This requires relatively slow predator population dynamics and relatively rapid evolutionary change on the part of the prey, in addition to the nonlinear predator functional response. If this process occurs, then there is a positive feedback between cycle amplitude and relaxed selection on the prey's defensive trait. Greater vulnerability results in great amplitude population cycles, which imply that the predator is usually either rare or satiated. This further relaxes selection for defense.

If the process of positive feedback described in the preceding paragraph is not halted, population cycles continue to grow in amplitude, ending in extinction of one or both species (14). This runaway process requires that the prey be able to gain a growth rate advantage by decreasing defense, even when defense is already low. In the examples considered by Matsuda & Abrams (72), the predator population was assumed to be constant as the result of alternative resources other than the focal prey. A constant predator population prevents evolutionary or population cycles. In this case, prey evolution could cause a steady decrease in the prey population without any cycles. This again depends on a type-2 functional response and occurs because predators become less satiated as prey become more difficult to capture. This increases the risk, selecting for even greater defense. If the greater defense requires a reduced capture rate of the prey's own food (e.g. if vulnerability is based on time spent foraging), then the outcome can be evolution to vanishingly small population sizes of the prey species. In a stochastic system, extinction occurs rapidly under this scenario.

Prey evolution is not always destabilizing. As Abrams & Matsuda (14) noted, a linear predator functional response ensures that evolution of costly defensive traits in the prey will always promote stability. Stabilization is also possible with nonlinear functional responses (14, 59), provided that the nonlinearity is not too pronounced. Stabilization of an otherwise cyclic predator-prey system via evolution of the prey is also possible (14). The most important condition for this outcome is that the relationship between vulnerability and prey growth rate be negatively accelerating (i.e. have a negative second derivative). This is a very reasonable assumption for many prey traits. Predators have maximum capture rates, which can prevent capture rates from increasing further once prey are very easy to capture. Furthermore, prey are likely to have maximum growth rates that cannot be exceeded by becoming very vulnerable to predators. Given this sort of vulnerability-growth rate relationship, greater predator density in the course of a population cycle is likely to select for greater defense, which will dampen or eliminate the cycles.

Many possible scenarios for evolutionary change in predator or prey have yet to be examined in any detail. Different scenarios in the simple sorts of models discussed above can be produced by assuming that traits affect different pairs (or trios, etc.) of population dynamics parameters. For example, evolution in a predator with a type-2 functional response may produce both greater values of the per-individual capture rate C and higher values of the handling time, h . Alternatively, a tradeoff relationship could exist between handling time and per capita death rate or between handling time and efficiency of conversion of prey into predators. Abrams (2, 4) presented a fairly extensive list of possible relationships but did not explore these in the context of unstable population dynamics.

Coevolution

The vast majority of the studies touching on stability have assumed that both predator and prey are capable of significant evolutionary change. Most of these have found that predator-prey coevolution can lead to cycles in both traits and population densities. There have been enough studies with different assumptions that it is now possible to identify some of the key features responsible for stabilization or destabilization. Clearly, the cases of predator evolution and prey evolution are limiting cases of coevolution, so it must be possible for the outcomes described above to occur under genuine coevolution, provided the species have very unequal magnitudes of evolutionary change in their capture-related parameters. However, there are additional mechanisms whereby stability can be affected when both species undergo significant evolutionary change. The interaction of predator and prey traits in determining a capture rate seems to be the most important factor determining the stability of the entire system. Most studies in which cycles are a commonly observed outcome assume that the predator maximizes its rate of capture of the prey by matching the prey's phenotype. For a measurable trait, this means that the prey have a "bidirectional" axis of vulnerability; they can

reduce their risk by having a trait either larger than or smaller than an intermediate “most vulnerable” phenotype, where the latter is determined by the predator’s phenotype. The presence of this sort of bidirectional axis of vulnerability seems to be the primary reason for the occurrence of cycles in the models by Marrow et al (71, 72), Marrow & Cannings (69), Dieckmann et al (37), Dieckmann & Law (36), Gavrillets (46), and one set of models in Abrams & Matsuda (14). The mechanism for cycling in these studies can be described roughly as follows. If the prey’s phenotype is initially slightly larger than the “most vulnerable” value, it will continue to increase, and the predator’s phenotype will increase in response. When the prey phenotype becomes sufficiently extreme, its rate of change is slowed by the greater costs of increasing an already extreme trait. This allows the predator to catch up and surpass the prey phenotype. Immediately thereafter, there is strong selection for the prey to reduce its character value, and the predator phenotype then chases the prey phenotype back to low values of the trait. This is again followed by a decreased evolutionary rate of the prey when extremely small values of the trait incur heavy costs, and the predator is able to overtake the prey in phenotypic space, restarting the cycle. These evolutionary cycles occur in models with fixed population sizes, as shown by Gavrillets (46), and stability conditions appear to be changed relatively little by population dynamics (13).

A bidirectional axis of vulnerability is not sufficient to guarantee that cycles will occur. If there is sufficiently strong stabilizing selection based on the costs of extreme trait values in both species, then stable equilibria are likely (13). Stabilizing selection on the predator’s trait is especially likely to eliminate cycles (13). If it does so, there may be either one or two alternative stable equilibria (37). The possibility of alternative equilibria arises because the prey can reduce predation by being either larger or smaller than the phenotype that is most vulnerable to the predator. If there is stabilizing selection based on effects on other population growth parameters in each species, the number of equilibria will depend on whether the optimal traits based on stabilizing selection alone are similar or different. If similar, then alternative equilibria are likely because the prey can reduce risk by becoming larger or smaller in trait value, depending on initial conditions. If the optima in predator and prey are quite different, it is more likely that there is a single equilibrium with the difference in trait values being determined by the positions of these predation-independent optima. The efficiency of predators in reducing the prey population size is an important parameter determining the existence of cycling. If the efficiency is low, the predator will not be common enough to drive the prey population significantly away from the trait optimum attained in the absence of predators. If the predators are efficient, they reduce both their own and the prey’s population sizes. In the model of Dieckmann et al (37), this reduces the strength of selection on the predator, since its prey intake near equilibrium is going to be low (based on the low prey density), regardless of its phenotype. In models with a nonlinear functional or numerical response (unlike the models of Dieckmann et al), high predator efficiency usually leads to population dynamic cycles, which entrain cycles in the traits. Both Dieckmann et al (37) and Abrams

& Matsuda (13) showed that the prey must evolve with sufficient rapidity relative to the predator that their trait value can temporarily change more rapidly than that of the predator.

Several other models assume bidirectional axes of prey vulnerability. Van der Laan & Hogeweg (96) made this assumption in their model of predator-prey coevolution, which also exhibits cycles. Their model makes the rather unusual additional assumption that the phenotypic axis is circular. This would be the case if both species were potentially active for 24 hours and the adaptations for escape and capture were shifts in activity time. This seems to be at best a rare scenario. Doebeli's (39) is one of the few studies that argues for a strongly stabilizing role for coevolution when there is a bidirectional axis of vulnerability. He adopted a discrete generation model that is identical to the Nicholson-Bailey host-parasitoid model except for the presence of genetic variation in capture-related traits and sexual reproduction. Stabilization in this case means a reduced amplitude of cycles and/or longer persistence times, rather than a locally stable equilibrium. The Nicholson-Bailey model itself predicts rapid extinction due to divergent oscillations of parasitoid and host. In Doebeli's coevolutionary version of this model, a large number of loci (all assumed to have small additive effects) is required before indefinite persistence occurs. It is not clear to what extent genetic variation stabilizes systems that would persist in the absence of variation, such as the Nicholson-Bailey model with added density dependence, although Doebeli (39) presented some simulations showing that increased stability is possible for this case.

Of the papers that assume a bidirectional axis of vulnerability, there appears to be only one that did not observe cycles in traits and population densities. This is the study of Brown & Vincent (27). However, there are several potential explanations for the apparent stability described in that study. First, their analysis does not include any explicit evolutionary dynamics. Instead, they simply calculate equilibria that represent local fitness maxima for mutant types and use these to determine the traits and population densities in the final community. Because cycling is usually associated with equilibria where mean fitness is minimized for one of the species, this outcome may have simply been missed because of the lack of any explicit evolutionary dynamics. In addition, they presented calculations for only a limited range of parameters; thus, it could be that they happened to choose parameters that were stable. Finally, Brown & Vincent's model makes assumptions that differ from those of most other studies of coevolution: 1) new predator and prey types can always enter the system if their traits allow them to increase; and 2) the predator's growth is a decreasing function of the ratio of predator to prey density. The first assumption often requires the occurrence of mutations of large effect that can breed true. The second assumption is difficult to reconcile with more mechanistic consumer-resource models (48). While not impossible, neither assumption seems to be very general. Thus, in general, it appears that a bidirectional axis is a potent mechanism for generating coevolutionary cycles.

A bidirectional axis of vulnerability is not a requirement for the existence of cycles in the traits of predator and prey. Both Abrams & Matsuda (13) and Sasaki &

Godfray (85) have published models in which cycling can be caused by coevolution in spite of a unidirectional axis of prey vulnerability. Here, for each species, the direction of change in the trait that reduces (or increases) predator capture rates is independent of the phenotype of the other species. Both of these studies assumed an S-shaped relationship between the difference in trait values and the capture-rate parameter, corresponding to C in Equations 1 and 2. Abrams & Matsuda (13) assumed a continuous time model similar to Equation 1; here cycles with a unidirectional axis occur for a relatively narrow range of parameters. The presence of cycles was associated with an evolutionary equilibrium at which the mean trait value of prey represented a relative fitness minimum. In Sasaki & Godfray (85), the basic model was discrete, with many similarities to Equation 2. Here, the most common form of cycling was one in which the mean abilities of both species increased over a number of generations, followed by a crash in host resistance, which then produced a more gradual decrease in parasitoid attack ability. When attack ability was low enough, the increasing phase of the trait cycle began again. These cycles occurred for parameters where population densities would cycle in the absence of any evolutionary change. However, the amplitude of population cycles was often less in a model with coevolution than in a comparable model with no evolutionary change. Sasaki & Godfray (85) assumed that evolution occurred via competition among asexual clones, and this assumption appears to be important for the existence of the cycles that they observed. These depend on the invasion and increase of prey (hosts) with minimal defense when the majority of the prey have high levels of defense and the predators have highly developed attack traits. If the prey trait was polygenically determined in a sexual population, mutants with traits much less than the mean would not breed true.

Frank (44) provided another example of a predator-prey model with a unidirectional axis of prey vulnerability, where cycles in traits and population densities occur. Frank called his model a host-parasite model, but the population dynamics are described by difference equations that are analogous in form to Equation 1. This Lotka-Volterra form makes the model more appropriate as a description of predator-prey systems, although his discrete generation form may yield unrealistically large fluctuations or extinction when prey growth is high. In any case, Frank's model exhibits some examples of fluctuating traits and populations that probably involve mechanisms similar to those described for the model of Sasaki & Godfray's (85). It is unclear to what extent the very complex and chaotic fluctuations observed with inherently unstable population dynamics may be affected by the unrealistic aspects of the assumed linear density dependence in this difference equation system.

Saloniemi (84) appears to be the only other study in which cycles were observed in a model that did not assume a bidirectional axis for prey defensive traits. However, the cyclic outcomes appear to be due to a questionable model structure, which did not include the demographic consequences implied by the assumed stabilizing selection. As Abrams & Matsuda (13) showed, when these demographic effects are included, cycles never occur. This represents another case with a

unidirectional axis of prey defense, where coevolution is basically a force that promotes stability.

Most studies of predator-prey coevolution have considered single homogeneous populations of both species. However, many populations exist as arrays of semi-independent populations connected by dispersing individuals. Spatial clumping of parasitoids and hosts has been one of the main factors cited as stabilizing interactions between them (52). However, the clumping has generally been assumed to occur in models without any consideration of whether or not it is adaptive. Van Baalen & Sabelis (94) were the first to consider the movement strategies of predators and prey (parasitoids and hosts) as evolutionary variables. The main finding of their coevolutionary model was that very large differences in patch quality (measured by prey population size that could be supported in the absence of predators) were required for stability at a coevolutionary equilibrium; stability also required many patches of poor quality. Coevolution failed to stabilize the system when patches were similar in quality.

Extensions of the idea of patch selection as a component of predator-prey coevolution include Abrams (10) and van Baalen & Sabelis (95). Abrams (10) examined the stability of two-patch systems in which predators adaptively switched between two patches, each characterized by unstable population dynamics. Faster switching was always advantageous to the predator, but it often led to increased amplitude of the population cycles. Van Baalen & Sabelis (95) extended their earlier (94) work to examine the population dynamics that occurred when there was flexible and adaptive patch selection by both parasitoid and host in many-patch environments. They found that, in spite of chaotic population dynamics, conditions allowing coexistence of both species were broader than when both species had rigid patch selection behavior.

Conclusions Regarding Evolution and Stability

Several general conclusions can be drawn from studies of the impact of evolution on the stability of predator-prey systems. The first is that evolution in a predator's capture-related traits is most likely to be stabilizing. Even if it does not confer stability on a cycling system, by itself it is relatively unlikely to produce cycles in a system that would otherwise be stable. Prey evolution often increases the instability of a system that would cycle in the absence of evolutionary change; cycle amplitude may become larger, or stable cycles may become divergent, leading to extinction. However, prey evolution by itself seems relatively unlikely to destabilize otherwise stable systems and may stabilize some unstable systems. Coevolution of both species seems most likely to generate cycles when there is a bidirectional axis of vulnerability, meaning that prey can reduce their risk by increasing or decreasing trait values relative to a most-vulnerable form, which depends on the predator's phenotype. Even in this case, cycling requires additional conditions, including sufficiently rapid prey evolution relative to predator evolution, sufficiently weak stabilizing selection due to costs of the traits, and an intermediate level of predator

efficiency in converting consumed prey into new predators. Seger (1992) drew attention to the fact that parasite-host models had often predicted cycles, while most previous predator-prey models had not. This was largely a consequence of the gene-for-gene model of virulence and resistance that had been adopted in most previous parasite-host models and the unidirectional axis of attack and defense assumed by the few previous predator-prey models based on continuous traits. In both bidirectional and gene-for-gene models, the selectively favored direction of change in the predator's trait depends on prey's trait and vice versa. This is not the case for unidirectional axes such as speed vs. speed, or strength vs. armor. Switches in the direction of selection on the trait are required for evolution to generate cycles in an otherwise stable system.

EFFECTS OF ENVIRONMENTAL PARAMETERS ON TRAITS

Effects of Traits of Other Species

This section begins by considering the effect of an evolutionary shift in a predation-related trait in one species on the evolutionarily-favored trait value of its partner. This response should reveal much about the long-term evolution of both species. The types of models discussed above assume that a certain spectrum of trait values exists in one or both populations, but costs or tradeoffs entailed by the traits are fixed. On a longer time scale, novel mutations will arise, or changes in the genetic architecture will allow one species to reduce the costs of a given predation-related trait, and rapidly evolve to a new evolutionary equilibrium. The long-term course of evolution is determined by how each partner in the interaction responds to such changes in the other species. There has been remarkably little work on this particular question. The most comprehensive analyses appeared 10 or more years ago (2, 4). These papers assume that there is a stable population-dynamical equilibrium, and that each species has trait values that maximize individual fitness. As is clear from the preceding discussion of stability, neither of these assumptions is always valid. However, if they are, some rather general results can be obtained.

First consider the question, how does a predatory trait change in response to an evolutionary improvement in prey defense? Some authors have assumed that the predator's attack-related traits should always increase in response to an increase in the prey's defense (33). However, this is often not an adaptive response for predators whose traits are maintained by a balance between the benefits of catching more prey and the costs of greater trait development. One significant factor, often neglected in the absence of mathematical analysis, is the change in prey density as the result of its greater escape ability. Prey population size is likely to increase as its mean defensive trait increases. There are some exceptions to this statement if the defensive trait affects the prey's exploitation rate of its own biological resources. However, if we neglect this possibility, then the prey's

density response (increased population) will offset its decreased vulnerability. It thus becomes less clear whether there should be any change in selection on the predator's trait following the increase in prey defense. If the predator's per capita population growth rate is solely a function of its intake rate of prey, and if the capture rate can be factored into the product of a term dependent on the predator's trait and a term dependent on the prey's trait, then the prey trait has no effect on the evolutionary equilibrium of the predator's trait (2). Under these conditions, the increase in prey density exactly cancels the effect of the decreased capturability of individual prey, and there is no change in the selection pressure on the predator's trait. This simple result is unlikely to be literally true in any real system. The result is changed if the predator's density affects its per capita growth rate, if the predator and prey traits don't combine multiplicatively, or if the prey's trait affects other aspects of the interaction, such as handling time. Nevertheless, the existence of some compensatory response in prey density when the vulnerability of individual prey decreases is a relatively general phenomenon. Furthermore, there are many circumstances under which the predator's optimal capture ability decreases when the prey become better at evading capture. This outcome is likely if the ratio of the costs of increased capture ability to the benefits goes up as the capture trait increases (2).

The response of prey to an evolutionary improvement in the predator's ability to capture is more likely to be a decrease than an increase in its inherent vulnerability (2, 4). Increased predator capture ability may decrease predator population size if the predator is already overexploiting prey (i.e. the equilibrium prey density is below the most productive density). However, this decrease is generally smaller in magnitude than the original increase in predator capture ability that caused the decrease in density. This is more in accord with thinking based on the "arms race" analogy than is the normal predator response to increased prey defense. However, when the predator and prey traits combine additively to determine the per capita capture rate, then greater predator abilities will select for less defense in the prey whenever the prey are overexploited (4). In this additive case, the strength of selection for better escape/defense is proportional to predator population size, but independent of the predator's trait.

The analysis in Abrams (2, 4) suggests that the key factors determining the direction of response of predators to a change in prey, or vice versa, are: 1) the mathematical relationships between a measure of the predator's trait and the per capita capture rate, and the relationship between the prey's trait value and the capture rate; 2) the nonlinearity of the predators functional and numerical responses; and 3) whether the predator's population density affects its own per capita growth rate. Predictions of the directions of evolutionary response under different conditions are as yet untested. However, the asymmetry in predicted evolutionary responses resulting from prey density compensation supports the general finding that prey often evolve in response to the addition of predators, but predators are seldom observed to change (or inferred to have changed) in response to prey addition. Evidence is presented below.

The findings (2, 4) summarized above are based on an assumption that traits and populations reach a locally stable equilibrium point. This is clearly not generally valid because predator-prey cycles occur frequently in laboratory systems and at least occasionally in the field (43). There has been relatively limited exploration of the consequences of cycles for the nature of one species' response to a change in the other. However, it is clear that population dynamical cycles often result in evolutionary outcomes that differ significantly from those in stable systems. This is frequently true when individual fitness is nonlinearly related to the evolving character (9). For example, the scenario described above, in which the effect of prey density cancels the effect of a lower encounter rate, is usually not true when there are predator-prey cycles; in cyclic systems it is more common for predators to increase capture ability in response to decreased prey vulnerability (9).

Effects of Productivity

The final environmental parameter considered here is the productivity of the environment, reflected in carrying capacity, K , intrinsic (maximum) per capita population growth, r , or both r and K . Productivity is of interest because it is often easy to manipulate and has a significant effect on population dynamics. Frequently natural spatial gradients in productivity represent natural experiments. The so-called "paradox of enrichment" (predator-prey cycles caused by fertilization) (78) was the impetus for several early studies of predator-prey coevolution (79, 80, 89). Rosenzweig & Schaffer (80; p. 162) concluded that "Coevolution always opposes the destabilization induced by enrichment and, in case r and K vary proportionally, actually increases stability." However, this work assumes that population densities have their equilibrium values; this is not valid in the model Rosenzweig & Schaffer (80) considered because the equilibrium is unstable at high carrying capacities.

Several more recent studies have revisited the question of the effect of enrichment on both trait values and stability in an evolving predator-prey system. The results are both more varied and more interesting than the work of Rosenzweig & Schaffer (80) suggested. In the models of predator evolution in Abrams (7), greater carrying capacity always increases the probability that the system will cycle. In the event that it does cycle, the mean trait value is generally lower than the equilibrium value. When the system is stable, increasing the carrying capacity, K , can either increase or decrease the equilibrium value of the predator's trait. When there is an upper limit to the functional or numerical response, a decrease in the capture rate following increased K is more likely than an increased capture rate. In the case of prey evolution, the effects of increased productivity are discussed by Abrams (4) and Abrams & Matsuda (14). In stable systems, prey vulnerability usually decreases in response to increased K , but it often increases or has a unimodal response to an increased intrinsic growth rate, r (4). In unstable systems, it is likely that an increased carrying capacity will decrease prey investment in defense, since larger K implies cycles of greater amplitude, but generally causes a slight decline in average predator abundance (16). Both of these changes generally favor

decreased defense. However, if increased productivity acts primarily by increasing r , prey defense is likely to increase. This is because a greater r has little effect on cycle amplitude while significantly increasing mean predator density (17).

The consequences of increased productivity for the coevolution of traits in both species have apparently been addressed in only a single study since the work of Rosenzweig & Schaffer (80). Hochberg & van Baalen (57) studied the effects of productivity gradients in a metapopulation model with coupled predator and prey evolution within patches. The dispersal between patches did little to change the patterns of attack and defense abilities predicted by considering evolution independently in each patch. The population dynamical assumptions ensured that each patch in isolation would reach a stable equilibrium, so the effect of evolution on the paradox of enrichment was not addressed. In the model of Hochberg & van Baalen (57), higher productivity (in this case, greater maximum growth and equilibrium density) led to higher levels of both attack and defense in predator and prey, respectively. This result stems from the accelerating cost functions they assumed for each trait, and the linear relationship between predator intake rate and birth rate. These ensure that, for each species, higher density of the other selects for greater investment in predatory functions. Greater productivity increases both densities, leading to greater trait development in both species. Other studies have shown that a nonlinear numerical response of the predator often leads to a decrease in the optimal values of predatory traits with increased prey density (5). Thus, the uniform increase in predatory traits with increased productivity is likely to depend on specific assumptions of the model as acknowledged by Hochberg & van Baalen (57). They assumed an additive combination of trait values, but alternative assumptions are known to give different results (4), at least when the predator's trait is relatively constant.

The traits and dynamics of predator-prey systems respond in a number of ways to increases in the productivity of the environment. Higher productivity may destabilize systems more rapidly in evolving systems than in the absence of evolution, but it is also possible that the evolution eliminates or reduces the paradox of enrichment. The former outcome seems most likely to be associated with a dominance of the prey's evolutionary response, while the latter is driven by a greater possible evolutionary shift in the predator. In stable systems, the change in trait values with increased productivity is influenced by how traits combine in determining a capture rate and by the shapes of the functional and numerical responses of the predator. Work is as yet insufficient for general conclusions about the conditions required for different effects of productivity.

GAPS IN PRESENT-DAY THEORY

In assessing the articles summarized above, it is important to realize that neither the range of models considered nor the comprehensiveness of the analysis of those models is very great. Most models assume that the traits affect only the per capita

rate of successful attack of predator on prey (or parasitoid on host). Other traits that are important in most interactions include those determining the efficiency of conversion of prey into new predators, the amount of time required by the predator to handle captured prey, the amount of direct competition between predators, and the effect of prey availability on the strength of that competition. There has been limited consideration of some of these factors (e.g. see 83 for efficiency), but much remains to be explored. While there has been some work on patch selection by predator and prey in heterogeneous environments, more work is needed in this area. If the prey can escape by growing into larger, less vulnerable forms, then life history variables need to be considered, and the dynamics framework used in models (1) and (2) is not appropriate. Chase (28) has made a start toward considering this case by examining competition between a form that can grow to an invulnerable stage and one that cannot. One option for a stage-structured prey species is to have very high exposure to predation in early life-history stages in order to get through those stages rapidly, while another possible strategy is to reduce exposure and prolong the early stages (18, 77). Which strategy is favored by evolution will have a significant effect on population dynamics and the evolution of traits in the predator that influence their ability to capture later life-history stages of the prey.

Past theoretical work has also largely avoided consideration of evolution and coevolution when one or both species have two or more traits that influence predation rate. One exception to this is Hochberg's (55) analysis of the evolution of traits determining host exposure to attack by parasitoids and traits determining host ability to encapsulate (and thus kill) parasitoid eggs after they have been attacked. These two traits are obviously coupled, since concealment from parasitoids makes costly encapsulation abilities undesirable. Hochberg considers coevolution with a parasitoid having independent traits related to discovery of hosts and defenses of eggs against encapsulation. Unlike hosts, parasitoids generally have high values of both traits when hosts have significant defenses. There are cases similar to this one in other types of predator-prey systems. Endler (42) has broken the predation process down into the five sequential stages of detection, identification, approach, subjugation, and consumption. Clearly, traits influencing one stage will alter the selective value of traits at other stages. Traits to resist subjugation have no advantage to a prey individual that is not detected or is ignored because it is misidentified. It is possible that models with many traits will lead to different effects of coevolution on stability.

The influence of the genetics of trait determination on the course of coevolution is another area where little is known. Some early models with artificially simple one-locus-few-allele systems have been largely replaced by a quantitative genetic or simpler phenotypic description of character evolution. However, the consequences of asexual vs. sexual reproduction, assortative vs. random mating, and continuous vs. discrete traits have received relatively little attention. There are some cases where we know that the outcome was greatly affected by the genetic system of trait determination. For example, Doebeli (39) notes that, unlike multilocus sexual inheritance, asexual inheritance does not increase persistence in

the simple host-parasitoid models he examined. There is reason to believe that the genetic system will often have a major effect on dynamics when one or more potential evolutionary equilibria are characterized by disruptive selection on one or more traits. Under some circumstances (e.g. asexual inheritance and some cases of sexual inheritance and assortative mating), disruptive selection is likely to result in splitting of the lineage undergoing disruptive selection into two separately evolving lines (35, 73). However, under randomly mating sexual systems, this circumstance will result in a stable equilibrium or cycles, but no increase in the number of independently evolving units (13, 15).

Theory has understandably concentrated on the simplest systems in which there is a single specialist predator consuming a single prey species. Even in this rather special case, the two species have typically been left out of their food web context. A more complete model would include the resource(s) of the prey species and any higher level predators or parasites that attack the focal predator. These omissions are not trivial. It is possible to represent some of the effects of the prey's resource by simply introducing density-independent growth of the prey. However, this automatically eliminates the time lag that occurs when the density dependence must be generated by changes in the abundance of a resource. Furthermore, the types of costs of defensive traits are likely to be represented differently in these artificially simplified models. When there is no explicit representation of the resource, the cost of greater defense is almost always assumed to be either a reduced maximum growth rate or an increased susceptibility to intraspecific competition. However, defense frequently reduces feeding (67), and this affects both maximum growth rate and competition in ways that differ from the way they are normally incorporated into models of coevolution (1, 6). Models of simultaneous behavioral optimization by both predator and prey embedded in the middle of a four-species food chain have quite different properties than do models in which the top and bottom populations are not represented (6). Most predators feed on more than a single prey species, and most prey are consumed by several predators (29). Thus, understanding the consequences of the coupled evolution of a given predator and a given prey will usually require consideration of other interacting species. There has been limited analysis of coevolution in the context of systems with three or more species (5, 8, 11); these studies have revealed a variety of potential evolutionary indirect effects and new mechanisms for cycles. However, multispecies systems still represent *terra incognita* in both empirical and theoretical realms.

The past decade has been characterized by an increasing focus by population and community ecologists on the spatial context in which population interactions occur (51). This focus has not spread to theoretical studies of predator-prey coevolution, with a few exceptions (e.g. 56). Thompson (92, 93) has emphasized the general importance of spatial heterogeneity for coevolution, but most well-studied examples involve parasites and hosts rather than predators and prey. Ironically, one of the earliest theoretical studies of predator evolution was a simulation study of the evolution of exploitation rates in a metapopulation in which predator and prey within subpopulations could either cycle or reach a stable equilibrium depending

on the predator's capture rate (47). The main result of that study was that group selection on predators could reduce the values of otherwise cost-free traits that increased capture rates. This scenario for group selection has yet to receive any empirical confirmation, but this mechanism should operate to some extent in most metapopulations.

EVIDENCE

Connection between the above theory and the real world can be made in two ways: 1) demonstrations that key assumptions of the model are satisfied; and 2) demonstrations that predictions of the models actually occur in natural systems. Both issues are considered below.

The models reviewed above suggest the evolution of predation-related traits is largely determined by a small number of key assumptions. Thus, for example, if we knew whether most defensive traits could be characterized as bidirectional or unidirectional, we could reach some tentative conclusions about the probable stabilizing or destabilizing effects of coevolution. If we knew in more detail how trait values of the two species enter into an expression for the consumption rate, then we would have made a major step towards knowing how traits in each species should respond to evolutionary change in traits of the other species. The shapes of functional and numerical responses of predators are often key determinants of the stability of the coevolutionary system and of the direction of response of one trait to a change in a trait in the other species. Unfortunately, information about most of these key properties is generally lacking. For example, although more than ten theoretical papers have assumed a bidirectional axis of vulnerability, not one of these refers to an empirical study that has demonstrated such an axis. The most that has been done is to note that predators are generally size-selective and ignore both very large and very small prey items. This can be used as a justification for a bidirectional axis only if the range of size variation in prey species is known to be large enough so that safety via both large and small size within that species is possible. Such information should be obtainable, but it does not seem to have been noted in any published articles on predator-prey systems. It is known that functional responses in the laboratory are usually strongly saturating, but most theorists continue to adopt the simpler assumption of linear responses.

Unfortunately, population densities are usually impossible to assess from the fossil record, and experimental systems in which two species can be maintained for sufficiently many generations to observe evolution in both are generally limited to bacteria and phage, and other parasite-host systems among single-celled and smaller organisms. Few natural systems have been studied thoroughly enough and long enough to assess changes in both predation-related traits and population densities over periods of many generations. This has left a rather unfortunate gap between theory and experiment. This gap is most likely to be closed by studies

that are able to deduce some of the properties of the evolutionary interaction from measurements over one or a few generations.

Empirical work on the coevolution of competitors has been a much more active area than the study of predator-prey coevolution (see e.g. 50, 86, 87). This is probably because different questions have been asked about the two types of systems. In the case of competitors, there exist essentially no data or theory about how one competitor changes in response to an evolutionary innovation in the other. There is no interest in stability, since competition is unlikely to generate population cycles. Thus, the relatively difficult questions asked about predators and prey are not asked about competitors. However, there are many natural experiments in which two or more competitors occur in isolation or together. Thus, the central question in the evolution of characters related to competition has been how they change when another species is introduced or removed. This question is rather uninteresting in the case of predator-prey systems. Specialist predators cannot exist in the absence of their prey, so a sympatric-allopatric comparison is not possible. Prey do exist without predators, but it is not particularly significant that prey increase defenses when predators are introduced and decrease defenses when predators are absent (41).

One of the major problems in empirical studies of predator-prey relationships is that it is often difficult to find species pairs with both members having easily measurable traits influencing the interaction. There are many cases where predators have selected for more cryptic color patterns in their prey species (41). However, the predator traits involved in detecting cryptic prey are much more difficult to measure. The fossil record provides examples of change in morphological traits that affect predation (97), but many of the potential counter-adaptations of the predators (e.g. increased perceptual acuity) would have left no trace in the record.

The question of stability is exceptionally difficult to examine empirically. We lack long-term records of both traits and population densities for natural systems undergoing cycles. Laboratory host-parasitoid systems have produced some suggestive evidence that host evolution may have decreased the amplitude of cycles (75). This would be consistent with the theory of Abrams & Matsuda (14) if it were shown that there were strong stabilizing selection on the prey's trait. Because many species exist as metapopulations, one possible method for examining stability in a short-term study is to examine the variation in traits of similar but isolated pairs of predator and prey populations. Lively (68) has done this for a parasite-host system, which appears to undergo cycles. One of the most consistent results from previous models is the association of bidirectional axes of vulnerability with population/evolutionary cycles. It is conceivable that such an association could be demonstrated if we knew more about the relationship between traits and capture-rate parameters. Cycles in the asymmetry of the jaws of scale eating fish is a possible example (58a).

In spite of the long list of difficulties, there are some empirical connections with theory. A topic that has received considerable attention over the years is the question of whether there is a trend for one or the other party of the predator-prey relationship to become more successful over evolutionary time. Success is

difficult to define (3, 97), but it usually corresponds to the maximal rate at which a predator individual captures prey in some standardized circumstances. Evidence in some systems strongly suggests that one or the other party in a predator-prey interaction has increased its success in the interaction over time. Bakker's (19) analysis of locomotor traits in ungulates and their cursorial predators and of tooth wear in the ungulates suggests a decrease in the risk of mortality due to predators over the past 60 million years. Similarly, the fact that the shells of some species of snails became more heavily armored while their crab predators did not alter claw morphology suggests that those snail species have improved their defense over time (97). Endler (41; Table 5.1) reviewed several dozen examples of prey responding to selection by predators, but no cases of predators responding to prey (although there are some cases of herbivores responding to selection due to plant characteristics). These observations are consistent with the asymmetry in responses described above, in which prey density-compensation reduces any selective pressure on predators generated by better prey defense. However, there are alternative explanations (26), including the possibility that the predators may have responded with greater (unfossilized) perceptual or behavioral abilities. We still are uncertain whether predator lineages are on average less successful than prey lineages over evolutionary time. This asymmetry is certainly unlikely to characterize all interacting lineages, since predators are still very well represented among the earth's fauna.

The greatest progress in empirical studies of both predator-prey and parasite-host relationships seems likely to come from systems in which there is geographical variation in the interaction and in which key traits of both species can easily be measured. One of the more promising examples of such a system is the interaction between the garter snake, *Thamnophis sirtalis*, and the toxic newt, *Taricha granulosa*, studied by Brodie & Brodie (23–26). The newts produce a highly potent neurotoxin, tetrodotoxin, from skin glands, and *T. sirtalis* is the only predator able to survive consumption of the newt. Both species occur over a wide geographical range, and each species occurs in some areas where the other species is absent. There is genetically based geographic variation in the degree of resistance of the snake and geographic variation in the degree of toxicity of the newt. There is also within-population variation in the resistance of the snake. This is expected, since tetrodotoxin-resistance entails a cost in decreased locomotor performance by the snakes (25). The patterns of variation for the most part exhibit positive between-species correlations (more resistant snakes occur where newts are more toxic), but the correlation is not perfect, and good assays for newt toxicity have only recently been developed (26). Toxin-antitoxin traits are likely to combine additively in determining the ability of snakes to eat newts, since it is likely to be at least in part the difference in amounts of toxins and detoxifying substances that determines the prey's actual toxicity to the predator (2). This additive model suggests that predators should respond to higher levels of toxin by developing greater resistance to the toxin, resulting in a classic arms race scenario (2). This is supported by the observed geographic correlation of trait values.

The garter snake–newt system is unusual in that there is evidence of evolutionary change of each party brought about by the other. Another species pair in which there is a rapidly growing body of evidence for coevolution from between population comparisons is the interaction between *Drosophila* and its hymenopterous parasitoids in the genera *Asobara* and *Leptopilina* (63). Here again, there is a positive correlation between the virulence of the parasitoid (ability of eggs and larvae to survive within the host body) and resistance of the host (immune defenses against the early stages of parasitoids). Studies of geographical variation in predator-prey systems commonly find variability in prey traits based on presence or absence of predators, but they either do not find or are unable to study variation in the predators characteristics (e.g. 21, 40, 77).

The study of geographic variation is important for reasons beyond simply establishing or refuting the existence of coevolution. The work reviewed by Kraaijeveld & Godfray (63) has shown that resistance and virulence in the *Drosophila-Asobara tabida* interaction represents a unidirectional axis of ability. The study of geographic variation potentially allows measurement of the detailed shape of the relationship between predator and/or prey traits and the per capita consumption rate. Systems in which variation in both defense and attack abilities exists and can be measured are ideal for developing the quantitative descriptions required for population models. The studies of Henter (53) and Henter & Via (54) of variation in an aphid's vulnerability to a parasitoid, and of the parasitoid's ability to overcome those defenses, illustrate the type of measurements that are possible. The growing interest in studying geographically variable interactions (92, 93) should result in significant advances in our understanding of how evolution changes predator-prey systems.

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LITERATURE CITED

1. Abrams PA. 1984. Foraging time optimization and interactions in food webs. *Am. Nat.* 124:80–96
2. Abrams PA. 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. *Evolution* 40:1229–47
3. Abrams PA. 1989. The evolution of rates of successful and unsuccessful predation. *Evol. Ecol.* 3:157–71
4. Abrams PA. 1990. The evolution of antipredator traits in prey in response to evolutionary change in predators. *Oikos* 59:147–56
5. Abrams PA. 1991. The effects of interacting species on predator-prey coevolution. *Theor. Pop. Biol.* 39:241–62
6. Abrams PA. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *Am. Nat.* 140:573–600

7. Abrams PA. 1992. Adaptive foraging by predators as a cause of predator-prey cycles. *Evol. Ecol.* 6:56–72
8. Abrams PA. 1996. Evolution and the consequences of species introductions and deletions. *Ecology* 77:1321–28
9. Abrams PA. 1997. Evolutionary responses of foraging-related traits in unstable predator-prey systems. *Evol. Ecol.* 11:673–86
10. Abrams PA. 1999. The adaptive dynamics of consumer choice. *Am. Nat.* 153:83–97
11. Abrams PA. 2000. Character displacement of species that share predators. *Am. Nat.* In press
12. Abrams PA, Kawecki TJ. 1999. Adaptive host preference and the dynamics of host-parasitoid interactions *Theor. Pop. Biol.* 56:307–24
13. Abrams PA, Matsuda H. 1997. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. *Evol. Ecol.* 11:1–20, [reprinted with corrections from 1996, *Evol. Ecol.* 10:167–86]
14. Abrams PA, Matsuda H. 1997. Prey evolution as a cause of predator-prey cycles. *Evolution* 51:1740–48
15. Abrams PA, Matsuda H, Harada Y. 1993. Evolutionarily unstable fitness maxima and stable fitness minima in the evolution of continuous traits. *Evol. Ecol.* 7:465–87
16. Abrams PA, Namba T, Mimura M, Roth JD. 1997. Comment on Abrams and Roth: The relationship between productivity and population densities in cycling predator-prey systems. *Evol. Ecol.* 11:371–73
17. Abrams PA, Roth JD. 1994. The responses of unstable food chains to enrichment. *Evol. Ecol.* 8:150–71
18. Abrams PA, Rowe L. 1996. The effects of predation on the age and size of maturity of prey. *Evolution* 50:1052–61
19. Bakker RT. 1983. The deer flees, the wolf pursues: incongruencies in predator-prey coevolution. In *Coevolution*, ed. DJ Futuyma, M Slatkin, pp. 350–52. Sunderland: Sinauer
20. Beddington JR, Free CA, Lawton JH. 1978. Concepts of stability and resilience in predator-prey models. *J. Anim. Ecol.* 47:791–16
21. Benkman CW. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *Am. Nat.* 153:S75–S91
22. Berry RJ, Crawford TJ, Hewitt GM, eds. 1992. *Genes in Ecology*. Oxford: Blackwell Sci.
23. Brodie ED III, Brodie ED Jr. 1990. Tetrodotoxin resistance in garter snakes: an evolutionary response of predators to dangerous prey. *Evolution* 44:651–59
24. Brodie ED III, Brodie ED Jr. 1991. Evolutionary response of predators to dangerous prey: reduction of toxicity of newts and resistance of garter snakes in island populations. *Evolution* 45:221–24
25. Brodie ED III, Brodie ED Jr. 1999. Costs of exploiting poisonous prey: evolutionary tradeoffs in a predator-prey arms race. *Evolution* 53:626–31
26. Brodie ED III, Brodie ED Jr. 1999. Predator-prey arms races. *Bioscience* 49:557–68
27. Brown JS, Vincent TL. 1992. Organization of predator-prey communities as an evolutionary game. *Evolution* 46:1269–83
28. Chase JM. 1999. To grow or reproduce? The role of life history plasticity in food web dynamics. *Am. Nat.* 154:571–86
29. Cohen JE, Briand R, Newman CM. 1990. *Community Food Webs: Data and Theory*. Berlin: Springer Verlag
30. Cott HB. 1940. *Adaptive Coloration in Animals*. London: Methuen
31. Darwin CR. 1859. *The Origin of Species*. London: John Murray
32. Dawkins R. 1982. *The Extended Phenotype*. Oxford: Oxford Univ. Press
33. Dawkins R, Krebs JR. 1979. Arms races between and within species. *Proc. R. Soc. Lond. B* 202:489–511

34. 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
35. Dieckmann U, Doebeli M. 1999. On the origin of species by sympatric speciation. *Nature* 400:354–57
36. Dieckmann U, Law R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* 34:579–612
37. Dieckmann U, Marrow P, Law R. 1995. Evolutionary cycling in predator-prey interactions: population dynamics and the Red Queen. *J. Theor. Biol.* 176:91–102
38. Doebeli M. 1996. Quantitative genetics and population dynamics. *Evolution* 50:532–46
39. Doebeli M. 1997. Genetic variation and the persistence of predator-prey interactions in the Nicholson-Bailey model. *J. Theor. Biol.* 188:109–20
40. Downes S, Shine R. 1998. Sedentary snakes and gullible geckos: predator-prey coevolution in nocturnal rock-dwelling reptiles. *Anim. Behav.* 55:1373–85
41. Endler JA. 1986. *Natural Selection in the Wild*. Princeton, NJ: Princeton Univ. Press
42. Endler JA. 1986. Defense against predators. In *Predator-Prey Relationships*, ed. M Feder, G Lauder, pp. 109–34. Chicago: Univ. Chicago Press
43. Ellner S, Turchin P. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *Am. Nat.* 145:343–75
44. Frank SA. 1994. Coevolutionary genetics of hosts and parasites with quantitative inheritance. *Evol. Ecol.* 8:74–94
45. Futuyma DJ. 1998. *Evolutionary Biology*. Sunderland, MA: Sinauer. 3rd ed.
46. Gavrillets S. 1997. Coevolutionary chase in exploiter-victim systems with polygenic characters. *J. Theor. Biol.* 186:527–34
47. Gilpin ML. 1975. *Group Selection in Predator-Prey Communities*. Princeton, NJ: Princeton Univ. Press
48. Ginzburg LR. 1998. Assuming reproduction to be a function of consumption raises doubts about some popular predator-prey models. *J. Anim. Ecol.* 67:325–27
49. Gould SJ. 1977. *Ever Since Darwin: Reflections in Natural History*. New York: Norton
50. Grant PR. 1986. *Ecology and Evolution of Darwin's Finches*. Princeton, NJ: Princeton Univ. Press
51. Hanski I, Gilpin M. ed. 1997. *Metapopulation Biology: Ecology, Genetics, and Evolution*. New York: Academic Press
52. Hassell MP, May RM. 1973. Stability in insect host-parasite models. *J. Anim. Ecol.* 42:693–736
53. Henter HJ. 1995. The potential for coevolution in a host-parasitoid system. II. Genetic variation within a population of wasps in the ability to parasitize an aphid host. *Evolution* 49:439–45
54. Henter HJ, Via S. 1995. The potential for coevolution in a host-parasitoid system. I. Genetic variation within an aphid population in susceptibility to a parasitic wasp. *Evolution* 49:427–38
55. Hochberg ME. 1997. Hide or fight? The competitive evolution of concealment and encapsulation in parasitoid-host associations. *Oikos* 80:342–52
56. Hochberg ME, Holt RD. 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations. *Evol. Ecol.* 9:633–61
57. Hochberg ME, van Baalen M. 1998. Antagonistic coevolution over productivity gradients. *Am. Nat.* 152:620–34
58. Holling CS. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Entomol.* 91:293–320
- 58a. Hori M. 1993. Frequency dependent natural selection in the handedness of scale-eating cichlid fish. *Science* 260:216–19
59. Ives AR, Dobson AP. 1987. Antipredator behavior and the population dynamics

- of simple predator-prey systems. *Am. Nat.* 130:431–37
60. Janzen DH. 1980. When is it coevolution? *Evolution* 34:611–12
 61. Jerison H. 1973. *Evolution of the Brain and Intelligence*. New York: Academic
 62. Kaitala V, Ylikarjula J, Heino M. 1999. Dynamic complexities in host-parasitoid interaction. *J. Theor. Biol.* 197:331–41
 63. Kraaijeveld AR, Godfray HCJ. 1999. Geographic patterns in the evolution of resistance and virulence in *Drosophila* and its parasitoids. *Am. Nat.* 153:S61–S74
 64. Lande R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314–34
 65. Levin SA, Udovic JD. 1977. A mathematical model of coevolving populations. *Am. Nat.* 111:657–75
 66. Levy CK. 1999. *Evolutionary Wars*. New York: W. H. Freeman
 67. Lima SL. 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive and ecological perspectives. *Adv. Stud. Behav.* 27:215–90
 68. Lively CM. 1999. Migration, virulence, and the geographic mosaic of adaptation by parasites. *Am. Nat.* 153 (suppl.):S34–S47
 69. Marrow P, Cannings C. 1993. Evolutionary instability in predator-prey systems. *J. Theor. Biol.* 160:135–50
 70. Marrow P, Dieckmann U, Law R. 1996. Evolutionary dynamics of predator-prey systems: an ecological perspective. *J. Math. Biol.* 34:556–78
 71. Marrow P, Law R, Cannings C. 1992. The coevolution of predator-prey interactions: ESSs and Red Queen dynamics. *Proc. R. Soc. Lond. B* 250:133–41
 72. Matsuda H, Abrams PA. 1994. Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theor. Pop. Biol.* 45:76–91
 73. Metz JAJ, Geritz SAH, Meszèna G, Jacobs FJA, van Heerwaarden JS. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems*, ed. SJ van Strien, SM Verduyn Lunel, pp. 183–231. Amsterdam: KNAW Verhandeligen
 74. Pimentel D. 1961. Animal population regulation by the genetic feed-back mechanism. *Am. Nat.* 95:65–79
 75. Pimentel D, Stone FA. 1968. Evolution and population ecology of parasite-host systems. *Can. Entomol.* 100:655–62
 76. Radinsky L. 1978. Evolution of brain size in carnivores and ungulates. *Am. Nat.* 112:815–31
 77. Reznick DN, Bryga H, Endler JA. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–59
 78. Rosenzweig ML. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171:385–87
 79. Rosenzweig ML. 1973. Evolution of the predator isocline. *Evolution* 27:84–94
 80. Rosenzweig ML, Schaffer WM. 1978. Homage to the Red Queen. II. Coevolutionary response to enrichment of exploitation ecosystems. *Theor. Pop. Biol.* 14:158–163
 81. Rosenzweig ML, Brown JS, Vincent TL. 1987. Red Queens and ESS: the coevolution of evolutionary rates. *Evol. Ecol.* 1:59–94
 82. Roughgarden J. 1979. *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. New York: MacMillan
 83. Roughgarden J. 1983. The theory of coevolution. In *Coevolution*, ed. DJ Futuyma, M Slatkin, pp. 33–64. Sunderland: Sinauer
 84. Saloniemi I. 1993. A coevolutionary predator-prey model with quantitative characters. *Am. Nat.* 141:880–96
 85. Sasaki A, Godfray HCJ. 1999. A model for the coevolution of resistance and virulence in coupled host-parasitoid interactions. *Proc. R. Soc. Lond. B* 266:455–63

86. Schluter D. 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science* 266:798–801
87. Schluter D. 2000. The role of ecological character displacement in adaptive radiation. *Am. Nat.* In press
88. Seger J. 1992. Evolution of exploiter-victim relationships. In *Natural Enemies*, ed. M Crawley, pp. 3–26. Oxford: Blackwell
89. Shaffer WM, Rosenzweig ML. 1978. Homage to the Red Queen. I. Coevolution of predators and their victims. *Theor. Pop. Biol.* 14:135–57
90. Slobodkin LB. 1974. Prudent predation does not require group selection. *Am. Nat.* 108:665–78
91. Taper M, Case TJ. 1992. Models of character displacement and the theoretical robustness of taxon cycles. *Evolution* 46:317–34
92. Thompson JN. 1994. *The Coevolutionary Process*. Chicago: Univ. Chicago Press
93. Thompson JN. 1999. Specific hypotheses on the geographic mosaic of coevolution. *Am. Nat.* 153:S1–S14
94. Van Baalen M, Sabelis M. 1993. Coevolution of patch selection strategies of predators and prey and the consequences for ecological stability. *Am. Nat.* 142:646–70
95. Van Baalen M, Sabelis M. 1999. Nonequilibrium population dynamics of “ideal and free” prey and predators. *Am. Nat.* 154:69–88
96. Van der Laan JD, Hogeweg P. 1995. Predator-prey coevolution: interactions across different timescales. *Proc. R. Soc. Lond. B* 259:35–42
97. Vermeij GJ. 1987. *Escalation and Evolution*. Cambridge, MA: Harvard Univ. Press
98. Vermeij GJ. 1994. The evolutionary interaction among species: selection, escalation, and coevolution. *Annu. Rev. Ecol. Syst.* 25:219–36
99. Vincent TL, Cohen Y, Brown JS. 1993. Evolution via strategy dynamics. *Theor. Pop. Biol.* 44:149–76