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ADAPTATION AND SPECIES INTERACTIONS IN SIMPLE FOOD WEBS; *THE CASE OF PREDATOR SWITCHING*

ADAPTACIÓN E INTERACCIONES ENTRE ESPECIES EN TRAMAS TRÓFICAS SIMPLES; EL CASO DE DEPREDADORES QUE ALTERNAN LA DIETA

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ABSTRACT

Jesús Alberto León was one of the first biologists to begin incorporating adaptive change into models of interacting species. This article draws some general lessons about the implications of the dynamics of adaptation by examining a model in which a predator changes its relative consumption rates of two prey species, given that it cannot consume both at maximal rates. It begins by classifying traits that have important effects on the dynamics of food webs, and surveys various models of the dynamics of adaptively changing traits. The model of predator switching between two prey is used to show the importance of both the rules for, and rates of, adaptive change in foraging traits for determining the dynamics of the entire system. Contrary to intuition, dynamic switching can desynchronize the fluctuations in the prey species, and force the predators diet further from an 'ideal free' distribution of foraging time or effort. The article ends with a discussion of some of the broader implications of these theoretical results and a call for more empirical work to explore the actual dynamics of rapid modes of adaptive change.

RESUMEN

Jesús Alberto Léon fue uno de los primeros biólogos que incorporaron el cambio adaptativo en los modelos de especies interactuantes. Este artículo proporciona algunas conclusiones generales acerca de la dinámica de la adaptación, examinando un modelo en el que el deperedador cambia sus tasas relativas de consumo de dos especies de presa, dado que no puede consumir ambas presas a tasas máximas. Se comienza clasificando los caracteres que tienen efectos importantes sobre la dinámica de redes tróficas, y se revisan varios modelos de dinámica de caracteres adaptativos cambiantes. El modelo del depredador que alterna entre dos presas se usa para mostrar la importancia, tanto de las reglas como de las tasas del cambio adaptativo en caracteres de forrajeo, en la determinación de la dinámica del sistema completo. Contrario a lo intuitivamente esperado, el cambio de la dinámica puede desincronizar las fluctuaciones de las especies de presas, y desviar aún mas la dieta de los depredadores de la distribución "libre ideal" de tiempo o esfuerzo de forrajeo. Finalmente se discuten algunas de las implicaciones más generales de estos resultados teóricos, y se indica la necesidad de mas trabajo empírico que explore la dinámica real de los tipos rápidos de cambio adaptativo.

Keywords: Dynamics of adaptation, fitness gradient, habitat selection, ideal free distribution, predation, switching.

Palabras Clave: Dinámica de adaptación, gradiente de aptitud, selección de hábitat, distribución libre ideal, predación, alternancia.

INTRODUCTION

Much of past and current thinking in ecology assumes that species have fixed properties. The traits that determine the impact of an additional individual of one species on the per capita growth rate of another species are usually assumed to be constant. Thus, competition coefficients in models of competing species are usually assumed to be unchanging in ecological time, and predator functional responses in predator-prey models do not change their shape under the action of natural selection. This assumption of constancy is contradicted by a large and growing body of research in evolutionary biology that shows that; (1) ecologically important traits can change substantially under the influence of natural selection; and (2) such traits can change significantly on a time scale that is comparable to the time scale of population dynamics when selection is intense (Thompson 1998; Hendry and Kinnison 1999). Similarly, behavioral ecologists have shown that adaptive changes in foraging and mating behaviors can have large effects on interactions between species, and can lead to a bewildering variety of indirect effects (Werner and Anholt, 1993; Peacor and Werner, 1997; Abrams *et al.*, 1996). Maynard Smith (1969), was one of the first scientists to draw attention to the inadequacy of this assumption of fixed traits. I have argued elsewhere that ignoring such evolutionary changes can lead to wildly inaccurate predictions about how population densities will change following environmental changes (Abrams 1996). However, we are still far from understanding the range of circumstances under which inaccuracies will be significant. We are equally far from understanding the nature of those inaccuracies in those circumstances where they may be large in magnitude.

Jesus Alberto León was one of the early investigators of the consequences of relaxing the fixed-trait assumption in his 1974 paper entitled, *Selection in contexts of interspecific competition.* León, was considerably ahead of his time in this mathematical analysis of how population dynamics and adaptive evolution interacted to affect the dynamics of both traits and populations. His work consisted of two very different approaches. The first was a population genetic model based on discrete Lotka-Volterra competition, in which there was one locus in each species that affected carrying capacity and intrinsic growth rate. This was followed by a less detailed analysis based of fitness sets. Here, León was able to investigate a wider range of ecological assumptions, including traits that could affect competition coefficients as well as purely single-species growth characteristics. However, this case proved to be rather intractable, and neither case yielded a clear answer to the question of how evolution was likely to affect the stability of complex communities.

In the quarter of a century since León's 1974 paper, there has been considerable progress in understanding the coupled dynamics of pairs of interacting and adaptively changing species. Schluter (2000), reviews work on the coevolution of pairs of competitors, while Abrams (2000), summarizes recent work on predator-prey coevolution. There are a larger number of studies incorporating adaptive behavior into models, many of which are reviewed in Lima (1998). This work has been able to make progress by assuming simplified models of the dynamics of the adaptive characters. Most often, evolutionary models have been based upon the assumption that mean traits change at a rate proportional to the gradient of individual fitness, an approximation that follows from simple assumptions about traits determined by the additive effects of many loci. Behavioral models have usually been based on the idea that optimal or near-optimal behaviors are adopted instantaneously as population densities or conditions change (e.g., Fryxell and Lundberg, 1994; Abrams, 1984, 1992b). The dynamics of systems with more than two species has received far less attention than has the dynamics of species pairs. This article is a preliminary attempt to extend this work to larger sets of interacting species.

The first section below will present a general method of classifying traits that have important effects on the dynamics of food webs, and will survey the methods that have been used to model the dynamics of adaptively changing traits. The next section will concentrate on a particular type of 3-species food web with a single predator species and two prey species. It examines the consequences of different possible rules for, and rates of adaptive change in a trait that determines the predator's choice of prey. Both rules and rates have major effects on the dynamics of the three-species system of which the flexible predator species is a part. The article ends with a discussion of some of the broader implications of these theoretical results and some suggested directions for future research.

Types of traits and methods of modeling adaptive species food webs

In the context of a food web, the traits that are most important in determining population dynamics are those that affect the capture rate of foods (exploitation-related) and the vulnerabilities to predators (escape-related). Traits of each type can be classified by the specificity of their effects. Exploitation-related traits may increase the capture rate of as many as all, or as few as one, of the available prey types. Similarly, escape-related traits may affect vulnerability to many or few predator types. The different consequences of adaptive change in specific versus general traits have received relatively little attention. However, work by Matsuda et al. (1994, 1996) suggests that specific traits have a much greater possibility of promoting stability in food webs that consist of two trophic levels. In addition to their specificity, the costs of exploitation and escape traits play important roles in determining how they change over time as the result of adaptive processes. Traits that can exhibit adaptive variation must entail costs as well as benefits, or they would have been fixed at their maximum values. Many potential costs for foraging and anti-predator traits exist. For example, a trait that increased the capture rate of food-type-*x* could entail any or all of the following types of costs: (1) a decreased capture rate of one or several other foods; (2) an increased vulnerability to one or more predators; (3) an increased non-predatory mortality rate; (4) a decreased efficiency of converting food into new offspring. Each of these types of costs has different implications for coevolution (for example, see the analysis of predator-prey coevolution in Abrams (1986b). The complexity of such coevolutionary systems is magnified by the fact that a given demographic parameter, such as the per capita capture rate of prey *x* by predator *y*, is necessarily influenced by the characteristics of both of those species, and may often be affected by population sizes and trait values of other species in the web. Even when this parameter is independent of other species, there exists a huge range of possible ways that the predator's and prey's traits can combine to generate a per capita capture rate of prey by a searching predator. Additive and multiplicative combinations are the ones most commonly used by theorists when a single pair of traits is involved. However, these two alternatives do not even represent endpoints of a spectrum of possibilities (Abrams, 1990). Another important factor determining the dynamics of population-trait systems is the nutritional interaction of different food types in determining an organism's fitness. This is another area where Jesus Alberto León carried out path-breaking research (León and Tumpson 1975) that is likely to have important impacts on future work on the dynamics of adaptive traits.

As a result of the complexities outlined above, a dynamic system with both traits and population densities for a moderately species-rich food web, is often too complex to understand without the intuition that simpler models can provide. However, the intuition from models with only two species (and usually no more than one adaptive trait in each species) is likely to be insufficient in dealing with models having a large number of species. The intermediate steps – models with three or four species – have not been extensively studied. Nevertheless, there have been some advances for some types of food webs, and research on one of these webs will be reviewed below. All models having three or more species have the potential (lacking in two-species systems) of a trait that increases the fitness consequences of interactions with one species, while decreasing the fitness consequences of interactions with one or more other species on the same trophic level. This sort of trait is the focus of the work described below.

Previous models of 3- and 4-species webs with adaptive traits include: (1) models of food chains in which one or more species have traits that increase both feeding rate and vulnerability to predators (Abrams, 1984; 1992b); (2) models of two predators, a shared prey, and a trait that determines the relative vulnerability of the prey to each of the predators (Abrams, 2000a); (3) models of two prey, a shared predator, and the trait determining predator choice (e.g., Abrams, 1999; van Baalen *et al.*, 2001); such systems are the main focus of this article; (4) Systems with two predators and two or more prey with variation in choice traits of one or both predators (Lawlor and Maynard Smith 1975; Abrams 1986a; Matsuda *et al.*, 1994; 1996). There is not time to adequately review all of this work here, and the body of the article will concentrate on the third category of food webs in this list.

I have discussed the general issues of how to model adaptively variable traits in a number of previous articles (Abrams, 1992a; 1995; 1999; 2000c; Abrams *et al.*, 1993), and will only provide a brief discussion here. One frequently-used approach, derived from quantitative genetics (Taper and Case, 1992; Abrams *et al.*, 1993), assumes that the mean value of a trait in a population changes at a rate that is the product of two factors: (1) the gradient (slope) of individual fitness with respect to the value of that trait; and (2) a general rate term, which may be constant, or may be a function of the mean value of the trait. This type of model is known to provide a good approximation to the evolution of polygenic traits having a small enough additive genetic variance (Taper and Case, 1992; Abrams *et al.*, 1993), and for the evolution of traits determined by a single biallelic locus. It is quite reasonable that behaviors should also change more rapidly when the consequence of a small change in the behavior is a large change in fitness. (Similarly, behaviors are expected to change more slowly when fitness is insensitive to the behavior). The second factor determining the rate of change of the trait (the 'general rate term') represents the additive genetic variance in polygenic and single-locus genetic models (Abrams *et al.*, 1993; Taylor and Day, 1997). If the trait is constrained to lie above a minimum value and/or below a maximum, genetic variance must decrease as those extremes are approached. Similarly, behavior must cease changing in a given direction if the behavior is approaching a minimum or maximum value, even if the fitness gains of continuing to change (were that possible) would be substantial. Thus, a typical equation predicting the rate of change in the mean value of a trait, z is,

$$\frac{d\bar{z}}{dt} = v(\bar{z})\left.\frac{dr(z,\bar{z})}{dz}\right|_{z=\bar{z}} \tag{1}$$

where r is the expected per capita growth rate of individuals with trait z in a population whose average trait value is $\bar{z}$. The function $v(\bar{z})$ is a positive-valued function that approaches zero when the average trait approaches its extremes. If v is not constant, then it is likely to be a unimodal function of the average trait value. If z is constrained to lie between z_{min} and z_{max}, a reasonable form would be:

$$v(\bar{z}) = v_0(\bar{z} - z_{min})^p(z_{max} - \bar{z})^p$$

where p is a positive exponent, and v_0 is a positive constant. Another possible form is:

$$v(\bar{z}) = v_0 \exp\left[-\frac{g}{\bar{z} - z_{min}} - \frac{g}{z_{max} - \bar{z}}\right]$$

Here g is a small positive constant; smaller values make the rate function remain closer to v_o over a larger part of the range of the trait.

Eq. (1) assumes that the distribution of traits in a population can be adequately characterized by its mean. This is often reasonable in the case of polygenic traits determined by the additive combination of many loci of small effect. Such traits within populations are often well-described by a normal distribution of phenotypes, which is relatively insensitive to weak or moderate selective pressures. If this is not the case, the expression for per capita growth rate must often take into account more characteristics of the distribution, and it may be necessary to have equations describing the dynamics of each of a variety of different phenotypic classes to obtain an adequate description of the population.

It is likely that behavioral dynamics are far less constrained than are evolutionary changes, so that large magnitude shifts that increase fitness may occur, even when small shifts in the same direction are disadvantageous. (This is unlikely in quantitative genetic models.) There is usually no reason to assume that the distribution of behaviors in a population can be adequately characterized by its mean. It is also likely that behavioral variability is regenerated much more rapidly than genetic variability. A behavioral trait may be able to shift rapidly in an adaptive direction, even when its mean value in the population is very close to the minimum or maximum possible. Recombination may prevent the splitting of unimodal trait distributions in populations under disruptive selection (Felsenstein, 1979; Abrams *et al.*, 1993), but no analogous process should operate on behavioral traits. Nevertheless, it seems plausible that, as specified by Eq (1), behavior should change more rapidly when there is a greater gain in fitness with a unit change in the behavior. There are various ways that some of these phenomena can be incorporated into the equation for evolutionary trait dynamics specified by Eq (1). One way to reduce the loss of variation at extreme trait values implied by the v function discussed above, is to modify the right hand side of equation (1) above by the addition of the following term:

$$\alpha\left(1 - \frac{2(z - z_{min})}{(z_{max} - z_{min})}\right) \tag{2}$$

This term has the effect of pushing the trait value away from either of its limiting values. This may be maladaptive at times, but it prevents the trait from becoming 'stuck' near one of its extremes. It is also possible to introduce extreme phenotypes into the population at low rates, as another means of generating behavioral variants. In this case, it would be appropriate to have several equations with the form of Eq (1) to follow the dynamics of qualitatively distinct behavioral variants.

An entirely different behavioral dynamic has been utilized in several studies (Matsuda 1985; Matsuda et al. 1987; Abrams 1992b; Fryxell and Lundberg 1994; Krivan 1997; van Baalen *et al.* 2001). This assumes that traits are adjusted to optimal or near-optimal values without any time lag. In this case, it is sometimes assumed that individuals make errors, so that the behavior does not in general correspond exactly to the optimum. For example, behavior that is predicted to be a step function becomes an S-shaped function that can be adjusted to more or less closely approximate the step function. Fryxell and Lundberg (1994) examine a situation where the proportion of prey 2 encountered that are actually attacked should jump from 0 to 1 at a particular density of prey 1. However, their model assumes that the proportion of type 2 that are consumed can be described by:

$$N_1^x / (N_1^x + N_{1T}^x),$$

where N_1 is the population density of prey 1, and N_{1T} is the population density of prey 1 at which the inclusion of prey 2 in the diet is optimal. The exponent, x, is > 1, with larger values producing a function that is closer to the optimal step-function. Matsuda (1985) and Matsuda et al. (1987) used a similar function to describe switching behavior, but also allowed evolution in the parameters of this function. These models incorporate the observed fact that behavior does not achieve the exact optimum in most real systems, but it lacks the time lag in adaptive change that is present in models based on Eq. (1). There has been very little analysis to determine the difference in dynamics between models with this underlying concept of behavioral change and models of the fitness-gradient based dynamics described in the preceding paragraphs. Clearly there are many other elaborations and modifications that can be made, and it is unlikely that any single framework will provide an adequate description of all possible dynamics of behavioral change.

Models of one predator and two prey species with adaptive predator choice.

The traits that I consider here are those that increase the predator's capture rate of one prey species at the expense of a lower capture rate of the other prey. I also assume that the two prey species are nutritionally substitutable, so that the adaptive response to an increase in the density of a either of the two prey species is to increase the capture rate of that prey at the expense of the other. This response is typically known as predator switching (Murdoch, 1966). Nutritional interactions between the two prey types can lead to anti-switching, in which consumption decreases with abundance (Abrams, 1987); this type of behavior will not be considered here. I will also ignore the case where a less rewarding prey type should be dropped from the predator's diet if the more rewarding type is sufficiently abundant. Models of a two-prey-one predator food web that incorporate switching include Lawlor and Maynard Smith (1975), Tansky (1978), Teramoto *et al.* (1979), Matsuda (1985), Matsuda *et al.* (1987) Abrams (1987, 1999, 2000c), van Baalen *et al.* (2001), Abrams and Kawecki (1999) and van Baalen and Sabelis (1999). Perhaps the most common mechanism generating switching is the location of the two prey species in different places. It is also possible for switching to occur when the prey are located in the same place, provided that different search behaviors are more effective in capturing the different prey types. Although it is usually thought of as a behavioral phenomenon, switching can also take place on an evolutionary time scale. In this case, effective capture of each of the two prey types requires a different value of one or more morphological traits, or requires different traits whose development is negatively correlated. Switching has been widely regarded as a stabilizing force in population dynamics (Murdoch and Oaten, 1975), but this conclusion has been derived from a very limited set of models.

The work described here is an extension of Abrams (1999). That article analyzed a model in which the predator is characterized by a type-2 functional response, and its trait increases consumption of one prey species at the expense of a reduced consumption of a second prey. The trait is described by an equation with the general form of Eq. (1). If the predator is relatively efficient, the equilibrium point of this system is unstable. Abrams (1999) concentrated on the case where both prey occur in the same habitat, but require different search methods or morphologies. Although it is intuitively reasonable that switching would synchronize the dynamics of the two prey species, this frequently was not the case in the models described in Abrams (1999). The degree of synchrony of prey species, and, in fact, the dynamics of the entire system were highly sensitive to the rate at which switching occurs. As the rate function, v in Eq (1) is increased in a system where the two prey have identical growth functions and nutritional benefits to the predator, there are a series of transitions between synchronized and asynchronous dynamics of the two prey species. Asynchronous dynamics result in large differences between the densities of the two species at most points in time, even though their densities would always be equal, if switching were eliminated. Chaotic dynamics occur for a wide range of parameters when the two prey species differ in their growth functions. Surprisingly, switching from one prey to another can actually increase the difference between the densities of the two prey species and can increase the amplitude of cycles rather than being stabilizing.

Here I will examine a case that was only briefly introduced in Abrams (1999). The two prey species occur in different habitats, and the predator adaptively adjusts the amount of time it spends in one or the other habitat (T). The dynamics of the three species and the trait, T that defines switching can be described by the following equations:

$$\frac{dR_1}{dt} = i_1 + r_1 R_1\left(1 - \frac{R_1}{K_1}\right) - \frac{TC_1 R_1 N}{1 + h_1 C_1 R_1}$$

$$\frac{dR_2}{dt} = i_2 + r_2 R_2\left(1 - \frac{R_2}{K_2}\right) - \frac{(1-T)C_2 R_2 N}{1 + h_2 C_2 R_2}$$

$$\frac{dN}{dt} = N\left(\frac{TB_1 C_1 R_1}{1 + h_1 C_1 R_1} + \frac{(1-T)B_2 C_2 R_2}{1 + h_2 C_2 R_2} - D\right)$$

$$\frac{dT}{dt} = v_0 V(T)\left(\frac{B_1 C_1 R_1}{1 + h_1 C_1 R_1} - \frac{B_2 C_2 R_2}{1 + h_2 C_2 R_2}\right)$$

(3a-d)

Table 1.- Definition of Parameters in Eqs. (3).

Symbol	Definition
i_i	immigration rate of prey i
r_i	intrinsic growth rate, prey i
K_i	carrying capacity, prey i
C_i	per capita capture rate of prey i by a searching predator
h_i	handling time required to consume an individual of prey i
B_i	efficiency of converting consumed prey i into offspring
D	per capita death rate of the predator
v_o	scaling constant for the rate of adaptive change in T

The population densities of the two prey species are given by R_1 and R_2, the predator by N, and the mean proportion of time spent in the patch containing prey 1 by T. The parameters in the model are defined in Table 1. The switching rate parameter, v_o, defines how the probability of moving between the two patches (or two types of areas) changes with a given magnitude of difference between prey intake rates in the two patches. When the population dynamics without adaptive change reach a stable equilibrium, T approaches a value at which both prey species yield equal rewards to the predator. When $B_1 = B_2$, $C_1 = C_2$, and $h_1 = h_2$, this implies equal resource densities at equilibrium, even when their growth parameters, i, r, and K, differ considerably. However, this is not the case when the population dynamical system (equations (3a,b,c)) exhibits limit cycles, as it does when D is sufficiently small, given positive handling times (Abrams et al. 1998).

Fig. 1 shows the dynamics of both species over a series of different adaptive rates, under the assumption that the rate constant is modified by the function, $V(T) = \exp[-g/T - g/(1-T)]$ with $g = 0.01$. This function has a value close to one unless T is close to 0 or 1. Consequently, the rate constant, v_o, is not modified significantly until T approaches its upper or lower limits rather closely. Slow adaptation results in roughly synchronized cycles of the two prey species (as would be true with no adaptation), as shown in the middle panels of the figure. The prey species differ in population

Table 2.- Average and Minimum Population Sizes and Traits

A. Eqs. (3a-d)

	$v_o = 0.01$	$v_o = 0.1$	$v_o = 10$
Mean R_1	0.403	0.420	0.400
Min R_1	0.000295	0.000130	0.000564
Mean R_2	0.341	0.327	0.339
Min R_2	0.00233	0.000147	0.000937
Mean N	0.299	0.294	0.292
Min N	0.0268	0.0501	0.0730
Mean T	0.567	0.557	0.518

B. Eqs. (3a-d) with the addition of Eq. (2) to Eq. (3d)

	$v_o = 0.01$	$v_o = 0.1$	$v_o = 10$
Mean R_1	0.393	0.419	0.419
Min R_1	0.000704	0.000126	0.00130
Mean R_2	0.389	0.328	0.314
Min R_2	0.000839	0.000136	0.000473
Mean N	0.249	0.261	0.256
Min N	0.0269	0.0261	0.0314
Mean T	0.543	0.532	0.773

C. Eqs. (3a-c) with T determined by Eq. (4)

	$p = 2$	$p = 8$	$p = 20$
Mean R_1	0.404	0.407	0.407
Min R_1	0.000850	0.000784	0.000758
Mean R_2	0.360	0.339	0.333
Min R_2	0.000749	0.000756	0.000758
Mean N	0.245	0.264	0.274
Min N	0.0291	0.0276	0.0267
Mean T	0.618	0.685	0.720

densities near the peaks of the cycle because of their difference in growth rates. Moderate values of v_o (top panels of Fig. 1) result in chaotic fluctuations with some periods of near synchrony and other periods of great asynchrony in prey dynamics. Large values of v_o result in out-of-phase fluctuations in the densities of the two species (bottom panels of Fig. 1). The synchronized dynamics in the example shown in the figure are observed from $v_o = 0$ to approximately $v_o = 0.03$; chaotic dynamics or complex cycles occur from approximately $v_o = 0.031$ to approximately $v_o = 0.22$. The offset cycles shown at the bottom of figure 1 characterize all systems with $v_o \geq 0.23$, given the other parameters in Fig. 1. As v_o increases within this last range, the phase difference between the two prey populations increases. This highest rate of v_o is appropriate for modeling behavioral change. An exhaustive bifurcation analysis of this model has not been undertaken. Nevertheless, these same three categories of dynamics occur for many other parameter values that have been examined for Eqs. (3). If the current example is modified so that the products $C_i h_i K_i$ are sufficiently smaller than in this example, there is often a fourth category of dynamics at very high rates of adaptive change; here both prey fluctuate in almost perfect synchrony, with nearly equal population densities at all points in time. Abrams (1999, Fig. 6) illustrates a very similar model in which the two prey species have identical growth parameters, unlike the current example.

Although chaos does not occur in this case, there are roughly similar classes of dynamics in terms of the synchrony or asynchrony of the two prey types. The adaptive rate constant does not have an effect on the predator efficiency at which this system switches from a stable equilibrium point to sustained fluctuations.

The rate constant v_o clearly has a major impact on the form of the population dynamics when the internal equilibrium is unstable. Thus, evolutionary rate also has a significant effect on average and extreme population sizes of the three species involved. Table 2A presents the average and minimum values of the three populations as well as the average trait value T, for all three cases illustrated in Fig. 1. The average predator population size declines by a small amount as adaptation becomes more rapid, but the minimum predator population size increases substantially with the rate of adaptation. The rate of adaptation has small effects on the average population sizes of the two prey species, but it has a larger effect on the average value of the time allocation to prey type 1; T decreases by approximately 10% in going from $v_o = .01$ to $v_o = 10$.

Switching between habitats is more likely to be governed by behavior than by a genetically determined time allocation. Thus, the form of the dynamical equation governing T in many real systems may be quite different from Eq. (3d). Nevertheless, it is likely that switching will have some dependence on the difference in the rates of food intake in the two patches, and more detailed behavioral mechanisms may produce a dynamic very similar to Eq. (3d). The population and trait trajectories shown in Fig. 1 are highly dependent on the form of the model for behavioral change. If the modification represented by Eq. (2) is incorporated into Eq. (3d), this prevents the predator from becoming very highly specialized on either of the two prey species. This extra term changes both the range of rate parameters producing various types of dynamics, and the range of dynamic patterns that are possible. Assume, for example, that the parameter a in Eq. (2) is 0.01 (z_{min} is 0 and z_{max} is 1). The type of synchronized cycles shown for $v_o = 0.01$ in Fig. 1, now occur for approximately $v_o < 0.036$. For $0.036 < v_o < 1.5$, there are chaotic dynamics or complex cycles, with a general trend towards greater synchronization at more rapid adaptive rates. The out-of-phase cycles shown on the bottom of Fig. 1 do not occur for any parameters. Values of v_o larger than approximately 1.9 produce simple limit cycle dynamics where the two prey species are nearly synchronized, but differ significantly in densities when both prey approach their maximum densities. This synchronization is the opposite of what occurs if the term given by Eq. (2) is absent. Not surprisingly, larger values of the parameter a increase the range of parameters over which approximate synchronization of the two populations is observed. Table 2B shows how average and minimum values of variables are altered by the addition of Eq. (2) to the trait dynamics; changes in density and especially average trait value (compared to the system with Eq. (3d)) are quite substantial at high rates of adaptation, where the two prey cycle in phase rather than out of phase. This extreme sensitivity of population dynamics to the form of the trait-dynamic equation is unfortunate, because we currently have no idea whether behavioral models based on Eq. (1) alone, or Eq. (1) with the addition of Eq. (2), are reasonable representations of the behavior of real animals.

All of the models of switching predation discussed above have been based on the gradient dynamics equation for change in the trait (i.e. Eq. (1)). The other approach that has been used to model switching is that of instantaneous but imperfect (incomplete) switching (e.g. Matsuda et al. 1987). In the context of the two-patch model introduced in Eqs. (3), this approach implies that the proportion of time spent in habitat 1 (consuming prey 1) can be described by the following formula, where x_i is the food intake rate in habitat i:

$$T = \frac{x_1^p}{x_1^p + x_2^p} \tag{4}$$

A larger value of the exponent p makes T more closely approximate the step function that represents the optimal strategy. The predator's intake rate per unit time of prey i, x_i, is given by $b_i a_i R_i/(1 + a_i h_i R_i)$. The dynamics of Eqs. (3a,b,c) using this formula for T have been explored for a wide range of parameters, and an example otherwise identical to Fig. 1 is shown in Fig. 2. In all cases examined, the dynamics were simple limit cycles, and the difference between the densities of the two prey species decreased as the accuracy of the switching (the value of p) increased. However, the accuracy of switching (i.e. the magnitude of p) has very little effect on the dynamics or average densities of any of the species. It is especially significant that, for this set of parameters, the limiting case of very rapid adaptation (large v) in the fitness gradient model does not approach the dynamics based on representing T by equation (4), regardless of the value of its parameter p. Fitness gradient models based on Eqs. (1) predict that species often cycle out of phase with each other, whereas this apparently never occurs under the assumption that adaptation is instantaneous, but incomplete. Table 2C presents average population densities and T values for three different values of the exponent p. Averages frequently differ substantially from those for the fitness gradient models presented in Table 2A and 2B. In particular, the average proportion of time spent exploiting prey 1, T, is higher in these instantaneous adaptation models than in the fitness gradient models, except for the single case of a trait model with Eq. (2) and with a high rate constant for adaptive change. The accuracy of the switching (controlled by the parameter p) has far less effect on the form of the dynamics or on the average and minimum values of variables, than did the rate of adaptation (v_o) in the fitness-gradient models.

The issue that concerned León in his 1974 paper was whether evolution would stabilize ecological communities. It is becoming clear that the answer to this question depends crucially on the details of the community, the traits involved, the definition of stability, and the mode of adaptation (e.g., Abrams 2000b). The results in Table 2A show that more rapid adaptation increases the minimum predator population size, (greater stability), while decreasing the minimum size of prey 2, and either increasing or decreasing the minimum size of prey 1 (depending on how much v_o is increased). In none of the models discussed here does adaptive change greatly change the range of parameters producing limit cycles, although there is some reduction in the case of the 'instantaneous adaptation' models.

Other models of switching.

The general message, that the form of the trait dynamic equation is crucial to the dynamics of the entire system, has been borne out by several other models of two-prey-one-predator systems. Abrams (2000c) investigated the dynamics of a system in which individuals of a predator population of fixed size moved between different patches, each containing a distinct dynamic prey population. In the two-patch case, this is similar to Eqs. (3) modified so that the predator population size (N) is constant, while the intrinsic growth rates of the two prey species vary regularly (but not identically) through time. When there is no environmental variation, the predator equalizes the population densities of the prey types in different patches, and the system approaches a stable equilibrium. However, if there are asynchronous environmental fluctuations in the patches containing the different prey species, then the rate at which the predator redistributes between patches often has a large effect on both the total prey density and the difference in densities between patches. The average prey densities and predator fitness are frequently maximized when movement rates are intermediate. These moderate movement rates allow enough of a lag in consumer redistribution that prey in each patch periodically escape overexploitation. The larger prey populations result in a greater average predator intake rate. Prey densities and variation in density between patches may both increase by a large factor as the rate of predator movement (or the sensitivity of predator movement to differences in intake rates) increases.

Another two-prey-one-predator model with adaptive predator choice was investigated by Abrams and Kawecki (1999). This model was based explicitly on a two-host-one-parasitoid system. The discrete generation form that is appropriate to such models allows a wide range of complex dynamic behaviors, even when the parasitoid exhibits no adaptively flexible behavior. Provided the system reaches a stable equilibrium, the exact form of the model governing the dynamics of the parasitoid's choice-related trait frequently does not affect the ultimate population densities attained in a constant environment. However, cycles are extremely common in

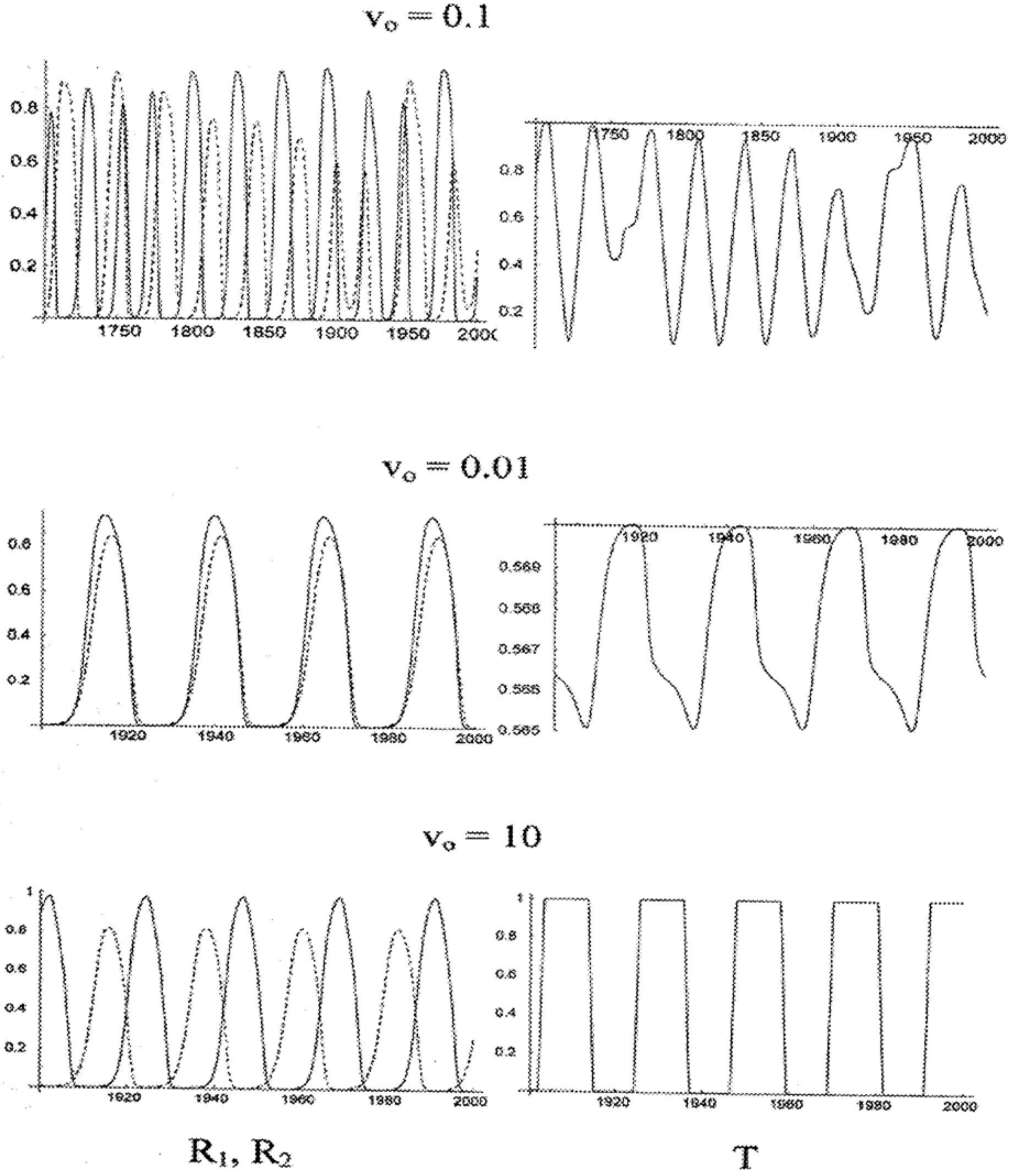

Figure 1. The dynamics of the system given by equations (3) for three different rates of adaptive change. Common parameter values are: $r_1 = 1$; $r_2 = 0.7$; $K_1 = K_2 = 1$; $C_i = 5$; $h_i = 1$; $i = 0.0001$; $D = 0.4$; $V(T) = \exp[-0.01/T - 0.01/(1-T)]$. The graphs on the left show patterns of change in population density vs. time, while those on the right show the proportion of time spent in habitat 1 as a function of time. Note that the *y*-axes on the right hand graphs have different scales. These represent the three types of dynamics that occur in this system as the rate constant of adaptive change (v_o) is increased.

laboratory populations of insect hosts and parasitoids. In addition, at least one form of behavioral switching leads to unstable equilibria for all possible prey growth rate parameters. The analysis of behavioral switching in Abrams and Kawecki (1999) assumed that the parasitoids have instantaneous and accurate knowledge of all of the conditions necessary to make a fitness-maximizing choice of attack rates. The attack rates on the two host types were negatively and linearly related, as would be true when the hosts occurred in different habitat patches. Two possible types of behavioral choice were considered. In the first, the parasitoids have a period before hosts become available during which they can fix their phenotype for the season (choose a habitat patch or specialized morphology). In this case, an individual's strategy remains the same over the course of the season, and individual fitness is maximized under this constraint. The second alternative is that the parasitoids adjust attack rates during the season. Here, if rates of encounter with healthy hosts of one type are higher, only that type will be attacked; when encounter rates are equal, each host is equally likely to be attacked. This second type of behavioral switching is appropriate when the parasitoid is capable of changing locations or behaviors rapidly throughout the season. The first type of switching always resulted in an unstable equilibrium with asynchronous dynamics of the two prey types. The second type of switching yielded stability and synchrony for some parameter values, but it frequently predicted asynchronous dynamics over a wider range of parameter space than did the comparable model with constant capture rates. Models of quantitative genetic evolution of relative capture rates also frequently produced asynchronous dynamics when the equilibrium with all species present was locally unstable.

There is very little basis for arguing that any one of the models discussed above is the best general description of switching in predators. It is clearly impossible for predator behavior to change instantaneously with prey densities. It is possible that with sufficiently rapid change in the predator, and a dynamic that prevents excessive specialization, the predictions using Eq. (3d) or Eq. (4) will usually be very similar. However, the fact that fitness gradient models often predict different dynamics than do the earlier models with instantaneous adaptation, argues for more investigation of the consequences of time lags in adaptation. The examples discussed above certainly do not exhaust the range of reasonable dynamical descriptions of switching behavior. It is likely that future experimental studies will suggest many possible dynamical rules that as yet have not been considered in any model. The models presented here and those reviewed here have only three species and only one trait. It seems likely that models with more species and traits will, if anything, have dynamics that are even more sensitive to the exact representation of the rules governing adaptive change in species' characteristics.

CONCLUSIONS

When Jesus Alberto León published his analysis of the coevolution of competing species in 1974, investigating the dynamics of systems of multiple differential equations was sufficiently arduous that it was seldom undertaken by biologists. León focused on single locus genetic models because that is the framework most previous investigations of coevolution had adopted, and behavioral ecology was then in its infancy. His work represented one mode of adaptation (evolution), and a particular mechanism within that mode. It was confined to an analysis of the existence and stability of equilibrium points. This was nevertheless a major advance in that it investigated the connections between adaptive processes and population dynamics. Studies in this area would no doubt have flourished sooner, had the methods to examine the dynamics of unstable dynamic systems been better developed at that time. Advances in computer hardware and software have now made extensive numerical work faster and easier by orders of magnitude. This will permit a much more extensive exploration of the wide variety of adaptive mechanisms that are likely to occur in nature. The work done thus far, some of which has been discussed above, indicates that the rates and rules governing adaptive change can be crucial in predicting dynamics, population sizes, and responses of systems to environmental perturbations.

Work that combines the dynamics of populations and their demographically-important characteristics is in its infancy. The examples described above are

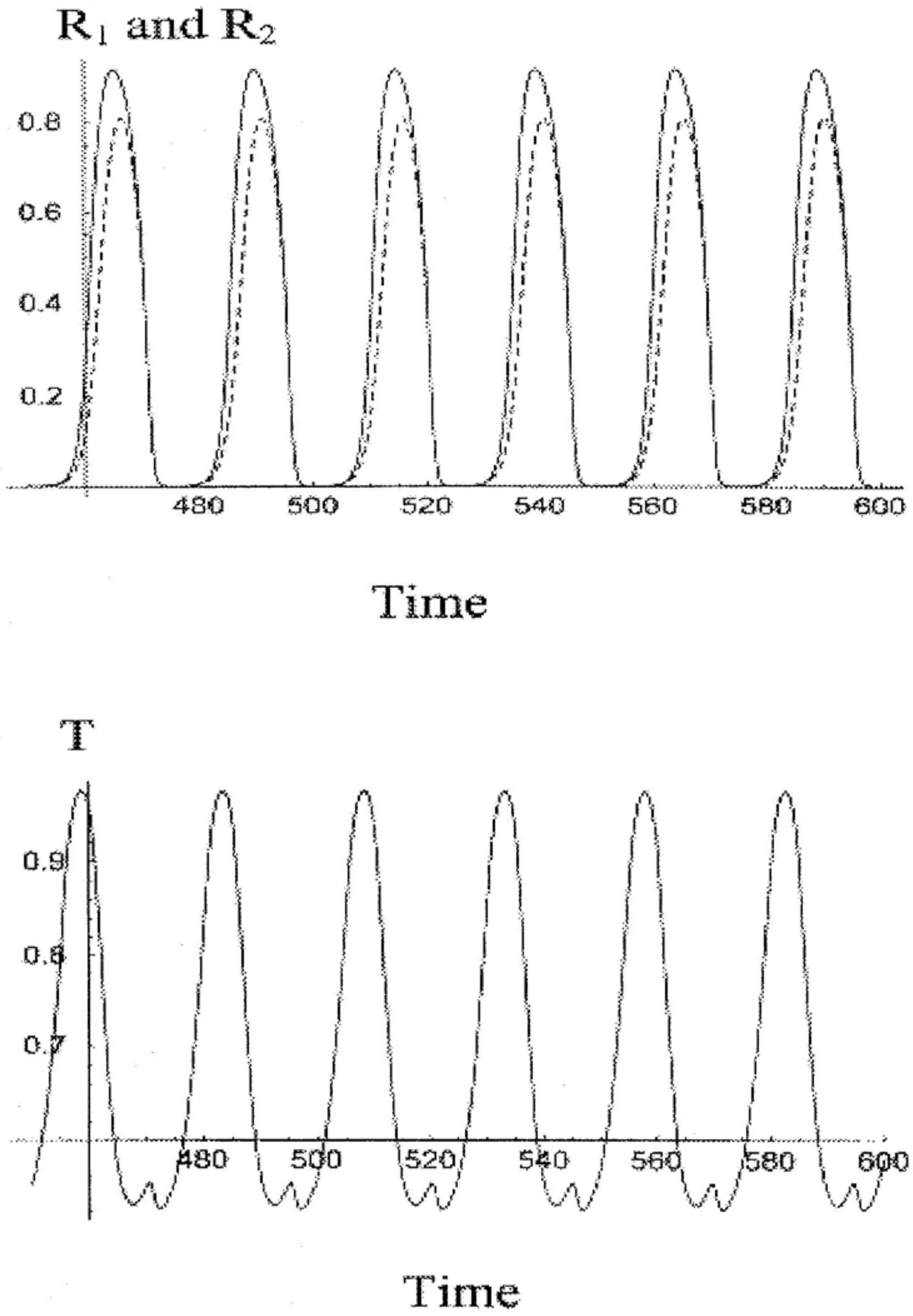

Figure 2. The dynamics of the system given by Eqs. (3a, b, and c) with T described by Eq. (4). This represents instantaneous but incomplete switching. The parameter values are the same as in Fig. 1, and the exponent in Eq. (4) is $p = 8$. The top panel shows the densities of the two populations, while the bottom panel shows the proportion of time individuals spend in habitat 1 as a function of time. As in Fig. 1, the solid line in the top panel describes R_1, the density of the faster-growing resource, while the dashed line is R_2.

highly speculative, inasmuch as we know almost nothing about the dynamics of ecologically important behavioral traits, and relatively little about the evolutionary dynamics of such traits. The results are perhaps most significant in that they justify the importance of actually investigating the dynamics of the behavior of real animals in a way that can lead to useful models. One of the major unknowns is how the dynamics of traits change as the trait values approach their extremes. In systems that cycle, this can have a surprisingly large effect on the nature of the population and trait cycles, and on the temporal mean values of both traits and populations. The next few decades should reveal how often the theoretical possibilities revealed above represent realistic possibilities in natural systems.

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