Dynamic versus Instantaneous Models of Diet Choice

Brian O. Ma, Peter A. Abrams,* and Chad E. Brassil

Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada

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abstract: We investigate the dynamics of a series of two-prey-one-predator models in which the predator exhibits adaptive diet choice based on the different energy contents and/or handling times of the two prey species. The predator is efficient at exploiting its prey and has a saturating functional response; these two features combine to produce sustained population cycles over a wide range of parameter values. Two types of models of behavioral change are compared. In one class of models ("instantaneous choice"), the probability of acceptance of the poorer prey by the predator instantaneously approximates the optimal choice, given current prey densities. In the second class of models ("dynamic choice"), the probability of acceptance of the poorer prey is a dynamic variable, which begins to change in an adaptive direction when prey densities change but which requires a finite amount of time to approach the new optimal behavior. The two types of models frequently predict qualitatively different population dynamics of the three-species system, with chaotic dynamics and complex cycles being a common outcome only in the dynamic choice models. In dynamic choice models, factors that reduce the rate of behavioral change when the probability of accepting the poorer prey approaches extreme values often produce complex population dynamics. Instantaneous and dynamic models often predict different average population densities and different indirect interactions between prey species. Alternative dynamic models of behavior are analyzed and suggest, first, that instantaneous choice models may be good approximations in some circumstances and, second, that different types of dynamic choice models often lead to significantly different population dynamics. The results suggest possible behavioral mechanisms leading to complex population dynamics and highlight the need for more empirical study of the dynamics of behavioral change.

Keywords: adaptive choice, behavioral dynamics, chaos, food web, indirect effects, optimal foraging, predation, stability.

* Corresponding author; e-mail: abrams@zoo.utoronto.ca.

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The question of how consumers choose resources has been of long-standing interest to ecologists. Most theory assumes that predators (consumers) will choose prey (resources) that maximize their long-term rate of energy gain when there are no nutritional requirements or costs that modify this goal (Pyke et al. 1977; Stephens and Krebs 1986). One of the first foraging problems considered by theorists was that of diet choice in situations where prey differ only in energy content and handling time and where prey items are encountered randomly within a homogeneous foraging area (Schoener 1971; Charnov 1976). The solution to the energy maximization problem in this case is to rank prey items based on the ratio of energy content divided by handling time and only include an item in the diet if the abundance of the higher-ranked items is below a threshold level. A wealth of empirical studies confirmed the broad outlines of this solution, but discrimination against items that should have been rejected was almost never perfect (Pyke 1984). However, few empirical studies have tried to determine what factors influence the time course of behavioral change when a low-quality prey is added to or dropped from the diet (but see Getty and Krebs 1985).

A number of theoretical studies have explored the population dynamical consequences of this diet choice rule, usually in the context of a one-predator-two-prey system (e.g., Gleeson and Wilson 1986; Fryxell and Lundberg 1994, 1998; Krivan 1996; Genkai-Kato and Yamamura 1999; Krivan and Sikder 1999; van Baalen et al. 2001). The majority of works suggest that adaptive diet choice leads to an increase in system stability relative to an indiscriminate generalist predator, where stability has been measured by the probability of local stability of the equilibrium (Gleeson and Wilson 1986; Fryxell and Lundberg 1994), by the range of parameters yielding permanence (i.e., populations bounded away from zero densities; Krivan and Sikder 1999), or by a decreased amplitude of population cycles (Gleeson and Wilson 1986; Krivan 1996; van Baalen et al. 2001). The comparisons of stability in systems with a specialist predator (that eats only the better prey type) or an adaptive generalist forager have been more equivocal. Fryxell and Lundberg (1994) found that local stability could be promoted by adaptive foraging on a

second, lower-quality food. However, this stabilization depended on the fact that diet choice in their model was imperfect (Fryxell and Lundberg 1994, van Baalen et al. 2001). Krivan and Sikder (1999) show that adaptive generalist systems are permanent less often than are specialist systems, while Krivan (1996) and van Baalen et al. (2001) suggest that the amplitude of oscillations may be lower in the adaptive generalist system than in the specialist system.

An assumption common to all of the models discussed in the previous paragraph is that foragers instantaneously adopt the new optimal diet or some approximation to it when prey densities change. In other words, the probability of consuming the poorer-quality prey at any point in time is purely a function of the current prey densities and is unaffected by previous food densities or the previous foraging strategy. This is also a common assumption in models of switching by predators (Tansky 1978; Matsuda 1985; Matsuda et al. 1986; Krivan 1997; van Baalen et al. 2001) and other models of behavioral choices (Abrams 1982, 1984, 1992). This assumption requires reevaluation because consumption behaviors cannot in general respond instantaneously to changes in food densities. If food densities change, organisms must be able to detect those changes before making any adaptive shift in foraging behavior. Sampling is inherently both time-consuming and stochastic, so that rapid behavioral change is likely to entail an increased frequency of errors. Once a decision to change has been made, attaining the new optimal diet may require training or learning both to recognize and to capture the new type of food. More general models of learning have predicted that changes in behavior require time and that shifts occur most rapidly when the attendant difference in fitness is greatest (Harley 1981; Boyd and Richerson 1985; Stephens and Clement 1998). In addition, recent work on population dynamic models with switching (Abrams 1999) has suggested that at least some models of dynamic behavioral change can result in very different system properties than do models with instantaneous change.

The purpose of this article is to explore the population dynamic consequences of modeling predator diet choice as a dynamic rather than an instantaneous process. In the class of dynamic models examined in greatest detail here, the probability that a randomly chosen predator individual will attack an individual of the poorer prey type increases or decreases in a continuous manner, with the rate and direction of change being determined by the fitness gained in making a switch. Alternative dynamic models are examined in somewhat less detail. The ability to make behavioral shifts is an adaptation to an environment where food densities vary over time. In the models we examine here, food density varies because of the inherently unstable interaction of predator and prey. There is abundant evidence that many natural predator-prey systems have sustained fluctuations in population densities (Royama 1992; Turchin and Taylor 1992; Ellner and Tuchin 1995; Kendall et al. 1998). It has also been shown that whether a population undergoes cycles often alters the qualitative effect of changes in environmental parameters on population densities and species interactions (Abrams et al. 1998). Our comparison of dynamic and instantaneous models of diet expansion concentrates on four major population-level consequences: the qualitative nature of population dynamics, the local stability of the equilibrium point, the average densities of the three species in the system, and the indirect interactions between prey species via their effects on a common predator.

Models

Our model of the ecological interactions follows the one-predator-two-prey model of Fryxell and Lundberg (1994):

$$\frac{dN_1}{dt} = m_1 + r_1N_1\left(1 - \frac{N_1}{K_1}\right) - \frac{c_1N_1N_3}{1 + h_1c_1N_1 + qh_2c_2N_2}, \tag{1a}$$

$$\frac{dN_1}{dt} = m_2 + r_2N_2\left(1 - \frac{N_2}{K_2}\right) - \frac{qc_2N_2N_3}{1 + h_1c_1N_1 + qh_2c_2N_2}, \tag{1b}$$

$$\frac{dN_3}{dt} = N_3\left(\frac{b_1c_1N_1 + qb_2c_2N_2}{1 + h_1c_1N_1 + qh_2c_2N_2} - d\right), \tag{1c}$$

where prey densities are N_1 and N_2 and the predator density is N_3. Growth of prey species i is logistic with intrinsic rate of increase r_i and carrying capacity K_i. In addition, there is immigration of prey into the system at an instantaneous rate m_i. Immigration prevents prey densities from reaching extremely low levels and is expected when (as is common) prey are more widely distributed than are their predators. The encounter rate per unit of prey density by a searching predator is given by c_i for prey species i. Predators have an instantaneous per capita death rate of d. We assume that prey 1 is more profitable than prey 2 ($b_1/h_1 > b_2/h_2$), where b_i is the energy content of prey i and h_i is the handling time of prey i. Predators always attack the more profitable prey, species 1, when encountered. However, the probability, denoted q, of attacking the poorer prey, species 2, can vary between 0 and 1. The formulation in equations (1) assumes that the population can be characterized by a single probability q, which im-

plies that all individuals in the population have a value of q that is close to the population mean. Alternatives to this assumption are considered below.

The behavioral scenario underlying the models assumes that an individual forager, characterized by an attack probability q, either samples the consequences of a short-term change in q or gathers information on prey densities and uses the result of that process to decide whether and how to change q for a longer period. The probability of making a long-term change in q, the magnitude of that change, or both increase with the fitness difference detected by the short sampling period. We assume that the population of predators is characterized by a small variance in values of q so that all individuals have attack probabilities close to the population mean q^*. The rate of sampling is not constant but decreases as the trait approaches either of its limiting values (0 and 1). There are several reasons for this decrease near extreme values. The most general is that the closer an individual's trait is to 0 (for example), the smaller is the maximum possible change in the direction of 0. A second reason is that some individuals in the trait distribution are likely to already have $q = 0$ when q^* is close to 0. Finally, it may be advantageous to reduce sampling when q is close to an extreme value. Because extreme values are the only possible optima, it is likely to be more important to determine the optimal direction of behavioral change (via sampling) when q is intermediate than when it is extreme.

This scenario can be described quantitatively by a model in which the rate of change of q is an increasing function of the change in individual predator fitness (W), given a unit change in the individual's probability of attack of the poorer prey, that is, the predator's fitness gradient with respect to q. Here we assume that change is simply proportional to dW/dq. This derivative is multiplied by a function V that reflects decreased sampling at extreme trait values; this function depends on the mean trait value and approaches 0 when q^* approaches 0 or 1. This yields the following general equation describing the rate of change in the mean trait:

$$\frac{dq^*}{dt} = V(q^*)\frac{dW}{dq}\bigg|_{q=q^*}. \tag{2}$$

Models based on equation (2) or other dynamic rules for the rate of change of q will be referred to as dynamic choice (DC) models. Equation (2) can be derived from quantitative genetics (see Lande 1976; applied in Iwasa et al. 1991; Taper and Case 1992; Abrams and Matsuda 1997*a*, 1997*b*). This form has also been proposed previously as a description of behavioral change in Abrams (1992, 1999), Abrams et al. (1993), and Taylor and Day (1997). The function V is biologically motivated, but it is also necessary to prevent q^* from becoming negative or exceeding 1 for some parameter sets. If the distribution of traits around the mean is assumed to be narrow enough, then the average fitness gradient experienced by individuals in the population can be approximated by the gradient of an individual possessing the mean trait q^* (Abrams et al. 1993). In the following, we drop the distinction between q and q^* because of this assumption.

In the most extensive set of the simulations reported below, the function V is given by

$$V(q) = 2^{2n}\nu q^n(1 - q)^n. \tag{3}$$

The parameter ν is the maximum of V (attained when $q = 1/2$) and is a general scaling factor for the rate of change in q. The parameter n describes how rapidly the function V decreases as q departs from 1/2; large values of n make behavioral change become slow when it is further from the extreme values of $q = 0$ or $q = 1$. The factor 2^{2n} is a constant that makes the maximum value of V independent of the shape parameter n. Our most extensive set of simulations assumes $n = 2$, which implies that the rate of change toward either extreme declines significantly when q is still some distance away from the extreme. Any positive exponent (n) in expression (3) means that moving away from an extreme trait value (close to 0 or 1) is always relatively slow, even when ν is large. This property reflects reduced behavioral sampling when conditions have favored one extreme value of q over a long time. An exponent $n > 1$ is likely to produce a particularly significant lag in the behavioral response and is thus a case that is particularly likely to differ from the instantaneous model. Combining the fitness expression implied by equation (1c) with equations (2) and (3) and assuming $n = 2$ yield the following dynamics of q:

$$\frac{dq}{dt} = 16\nu q^2(1 - q)^2\left\{\frac{c_2N_2[b_2(1 + c_1h_1N_1) - b_1c_1h_2N_1]}{(1 + h_1c_1N_1 + qh_2c_2N_2)^2}\right\}. \tag{4}$$

The quantity in braces is the slope of fitness (instantaneous per capita growth) with respect to q.

Under instantaneous adaptation, $q = 0$ or $q = 1$ depending on whether the density of the better quality prey N_1 is greater or less than the following threshold density:

$$\eta = \frac{b_2}{c_1(b_1h_2 - b_2h_1)}. \tag{5}$$

Because errors prevent perfect step functions from occur-

ring in real diet choice scenarios, and because the step function form of the optimal q creates problems for numerical integration, we will follow Fryxell and Lundberg (1994) in approximating this optimal step function by the following sigmoid function of N_1:

$$q = \frac{\eta^z}{\eta^z + N_1^z}, \tag{6}$$

where η is the threshold density of prey 1 from equation (5). The parameter z in equation (6) is a positive integer that determines closeness of the predator diet choice to the optimal step function; q approaches a step function as z becomes very large ($z \gg 1$). When z is small, a significant fraction of the poorer prey are ignored when they should be attacked, and similarly, many are attacked when they should be ignored. Equations (1) with expression (6) substituted for q will be referred to as the instantaneous choice (IC) model.

Methods

Numerical integrations of both DC and IC systems were carried out using a C++ implementation of a fourth-order Runge-Kutta method with adaptive step size (Press et al. 1992). Many calculations were replicated using the NDSolve function in Mathematica (Wolfram 1999). Nonequilibrium dynamics were classified based on the Lyapunov exponent, calculated using a C++ implementation of the method of Wolf et al. (1985). Periodic solutions were further classified according to their complexity; cycles were classified as complex if at least one variable exhibited two or more local maxima over the course of a cycle. If all variables had only a single local maximum over the cycle, they were classified as simple cycles. The arithmetic average densities over time were used to define the indirect interactions between prey species.

The full parameter space of this model is too large to examine exhaustively for either DC or IC model. Our approach was to carry out a very detailed analysis of a set of systems having common values for most parameters ($m_i = 0.005$, $r_i = 1$, $c_i = 5$, and $h_i = 2$ for $i = 1, 2$; $d = 0.4$) over a broad range of the parameters b_1, $K_1 = K_2 = K$, and two alternative values of b_2. These values represent a relatively high immigration rate, a relatively low half-saturation constant for the predator's functional response, and a relatively efficient predator. Such systems cycle over a wide range of carrying capacities and energy contents. The ranges of values for b_1 and K were 1.0–6 and 0–4, respectively. For the other parameter values that we adopted, values of $b_1 > 6$ and $K_i > 4$ lead to either extremely low equilibrium prey densities or cycles with extremely low minimum prey densities that would make them unlikely to persist in finite populations. The two alternative values of b_2 were chosen to lie on either side of the value at which prey 2 is just sufficiently rewarding to be included in the diet at the equilibrium point ($b_2 = dh_2$). Values that differ greatly from this threshold result in either constant inclusion or exclusion of prey 2 being the optimal strategy over most of the cycle, so diet choice becomes irrelevant. The key parameters determining the maximum rate of change of q in the two models were $\nu = 18.75$ and $z = 30$. These values were large enough so that significant increases in their magnitude had little effect on dynamics, but they were not so large as to cause problems in the numerical solution of the equations. We will refer to the above set of values as the standard parameter set. Dependence of the results on the standard parameters was examined for a more limited set of simulations using a variety of alternative parameter combinations. These alternative parameters and some alternative models are discussed below.

Results

Stability and Dynamics for Standard Parameters

Figure 1 summarizes the dynamics that occurred over the b_1-K parameter space for the standard set of other parameters. The initial set of simulations used a fixed set of initial conditions. We used a second set of simulations with random initial conditions to find alternative attractors and then mapped the regions where each attractor had a nonzero basin of attraction by continuing a given solution in both directions along each parameter axis. The four panels of figure 1 correspond to cases where the poorer prey is ($b_2 = 0.9$) or is not ($b_2 = 0.7$) included in the diet at the equilibrium point for both the IC and DC models. The form of the dynamics was classified as: predator extinction, locally stable point equilibrium with all three species, simple limit cycles, complex cycles, chaotic dynamics, and two alternative attractors. The alternatives in most cases were either two simple limit cycles or a stable point and a simple limit cycle. In some cases the largest Lyapunov exponent was very close to 0, making it impossible to determine whether the dynamics were chaotic or periodic given the length of our simulations; such cases are also distinguished in figure 1.

Some broad features of the division of parameter space into different dynamic regimes are similar for all panels in figure 1. At sufficiently low carrying capacities when the energy content of the better prey, b_1, is relatively low, there is a stable equilibrium point. A stable equilibrium also occurs at high b_1 for the entire range of carrying capacities examined. The high value of b_1 decreases the

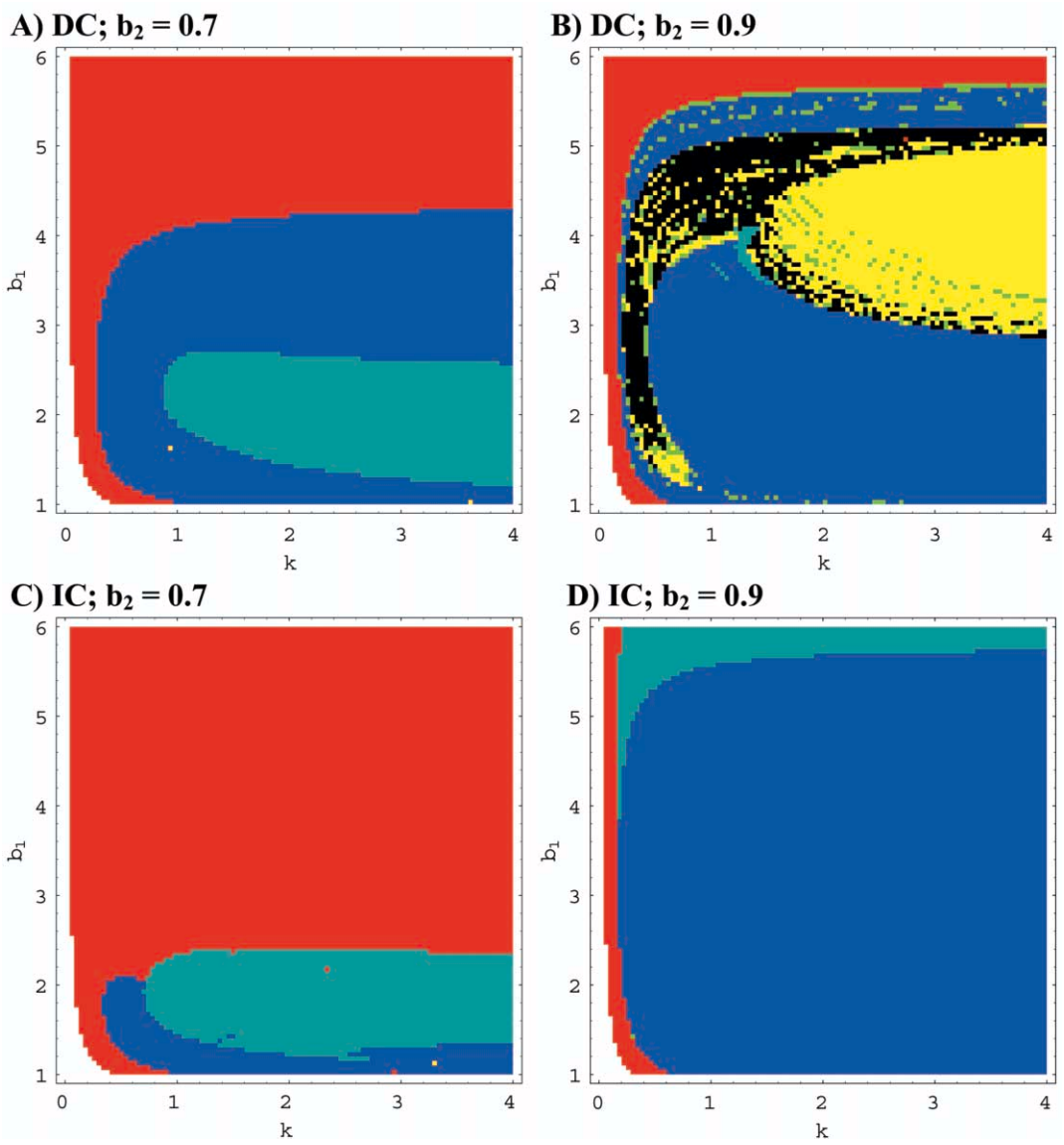


Figure 1: Qualitative form of the dynamics of the dynamic (DC) and instantaneous (IC) diet choice models for the standard parameter set: $r_1 = r_2 = 1$, $m_1 = m_2 = 0.005$, $h_1 = h_2 = 2$, $c_1 = c_2 = 5$, $d = 0.4$; DC model $\nu = 18.75$; IC model $z = 30$. The meaning of the colors is as follows: white, predator extinction; red, point equilibrium; dark blue, simple limit cycles; yellow, complex cycles; black, chaos; green, possibly chaotic (indeterminate maximum Lyapunov exponent); light blue (teal), regions with alternative attractors. *A*, DC model, $b_2 = 0.7$ ($b_2 < dh_2$). *B*, DC model, $b_2 = 0.9$ ($b_2 > dh_2$). *C*, IC model, $b_2 = 0.7$. *D*, IC model, $b_2 = 0.9$.

equilibrium density of that prey species sufficiently that immigration (which is stabilizing) becomes a major component of population growth. The size of this region of stability at high b_1 is affected by the form of the behavioral dynamics and by the energetic value of the poorer prey; the region is largest for the IC model when prey 2 is not in the equilibrium diet. If only the superior prey is present with the predator, the boundaries for different types of dynamics are very similar to those in figure 1*A*, except that the area with alternative attractors in figure 1 only has simple limit cycles in the one-prey system.

The broad similarities of IC and DC models in the locations of different dynamic patterns in parameter space were coupled with some significant differences in the locations of the boundaries between stable and unstable dynamics and many cases of significant differences in the

qualitative form of dynamics when there were cycles. Three of the most notable differences are discussed next.

Differences in Parameters Yielding Stable Equilibria. Stable equilibria were more common in the IC model than in the DC model (given the standard parameters) when $b_2 < dh_2$ but less common in the IC model than in the DC model when $b_2 > dh_2$. The increased stability in the IC model when prey 2 was relatively unrewarding was because the predator was unable to specialize as completely on the higher-quality prey as was possible in the DC model. Specialization is the optimal strategy when b_1 is relatively large and when $b_2 < dh_2$, and a specialist system with a large b_1 always cycles. However, the assumed imperfection in the strategy of the IC predator, together with the relatively large handling times and capture rates in this example, meant that even a small consumption of the less-rewarding prey reduced the consumption of the better prey significantly. This stabilized the system at large values of b_1 in the IC model when consuming prey 2 was maladaptive at equilibrium. In the DC model, q was able to approach 0 very closely, so that cycles in the better quality prey occurred over a wider range of parameters.

When $b_2 > dh_2$, the optimum strategy is to become a complete generalist at equilibrium. When b_1 is large enough, the equilibrium is stable as the result of the large relative contribution of immigration to prey growth, given the small equilibrium population size of prey 1. In the IC model, this equilibrium is locally but not globally stable. When cycles occur, the choice parameter q varies over nearly its entire range of 1–0, with significant times at intermediate levels when the density of prey 1 is close to its threshold. This prevents the system from remaining for long periods with low enough densities of both species that immigration dominates intrinsic prey population growth. In the DC model, behavioral dynamics slow down as q approaches 1, so the brief periods when q drops (because of a peak in the abundance of species 1) do not prevent the longer-term trend toward $q = 1$. This decreased relative stability of the IC model at high b_1 occurs for a wide range of alternative parameters.

Differences in the Presence and Nature of Alternative Attractors. The types of alternative attractors and the areas of parameter space yielding these alternative attractors differed markedly between the two behavioral models. One category of alternative attractors that occurs in the IC model for high values of b_1 when $b_2 > dh_2$ was discussed above. When $b_2 < dh_2$, there are different regions of parameter space with different types of alternative attractors in the IC and DC models. In the IC model, the alternatives are a (locally) stable equilibrium and a limit cycle having high amplitude closely synchronized fluctuations of both prey. In the DC model (when $b_2 < dh_2$), the alternatives are large amplitude and roughly synchronous fluctuations in both prey or smaller amplitude cycles with a lower mean density of the high-quality prey and a higher mean (close to the carrying capacity) of the poorer prey. When the poorer prey was part of the optimal equilibrium diet, alternative attractors in the DC model were found only for very narrow regions of parameter space that lay on the border of parameter regions that had significantly different dynamics (these do not appear in fig. 1*B*).

Differences in the Qualitative Form of the Population Dynamics. Complex cycles and chaos occurred almost exclusively in the DC model. For our standard parameter set, these dynamics were only common in the case where b_2 was sufficient for inclusion of prey 2 in the equilibrium diet ($b_2 \geq dh_2$). There were a few isolated cases of chaotic dynamics when b_2 was below the threshold for equilibrium diet inclusion, given the DC model and the standard parameter set, but these do not appear in figure 1*A*. Some other parameters (noted below) resulted in large parameter regions producing chaotic dynamics when the poorer prey's value fell below the threshold ($b_2 < dh_2$). The DC model produced more complex dynamics than did the IC model because of the interaction between population and behavioral dynamics in the former. In the IC model, behavioral choice is necessarily synchronized with changes in prey abundance, resulting in simpler dynamics. The (relative) lack of dynamic complexity produced by the DC model when $b_2 < dh_2$ can be attributed to the fact that, in this case, it is seldom adaptive to add the poorer prey to the diet, given the parameters used here. As a result, population cycles were mainly influenced by the interaction of the predator and the better prey species.

Figure 1*B* shows that under the DC model with $b_2 > dh_2$, chaos or complex cycles occur over a wide range of parameters. Figure 2 presents some examples of the actual differences in the time course of population densities. In the top and bottom panels, the DC model dynamics are complex cycles, while in the middle panel they are chaotic. All of the IC dynamics are simple cycles. In some cases (e.g., the top panel of fig. 2), there are relatively minor differences in cycle period and amplitude between the two models, but for other parameters, differences are often substantial (as in the middle and bottom pairs of graphs in fig. 2). It is clear from figures 1*B* and 1*D* that qualitative differences in dynamics between IC and DC models characterize a large fraction of b_1-K parameter space under the standard parameter set when $b_2 > dh_2$. Complex dynamics are common in systems with two different and unsynchronized oscillating components. In the DC model, the lag in the response of the behavioral variable q to changes in population density produces the more complicated dy-

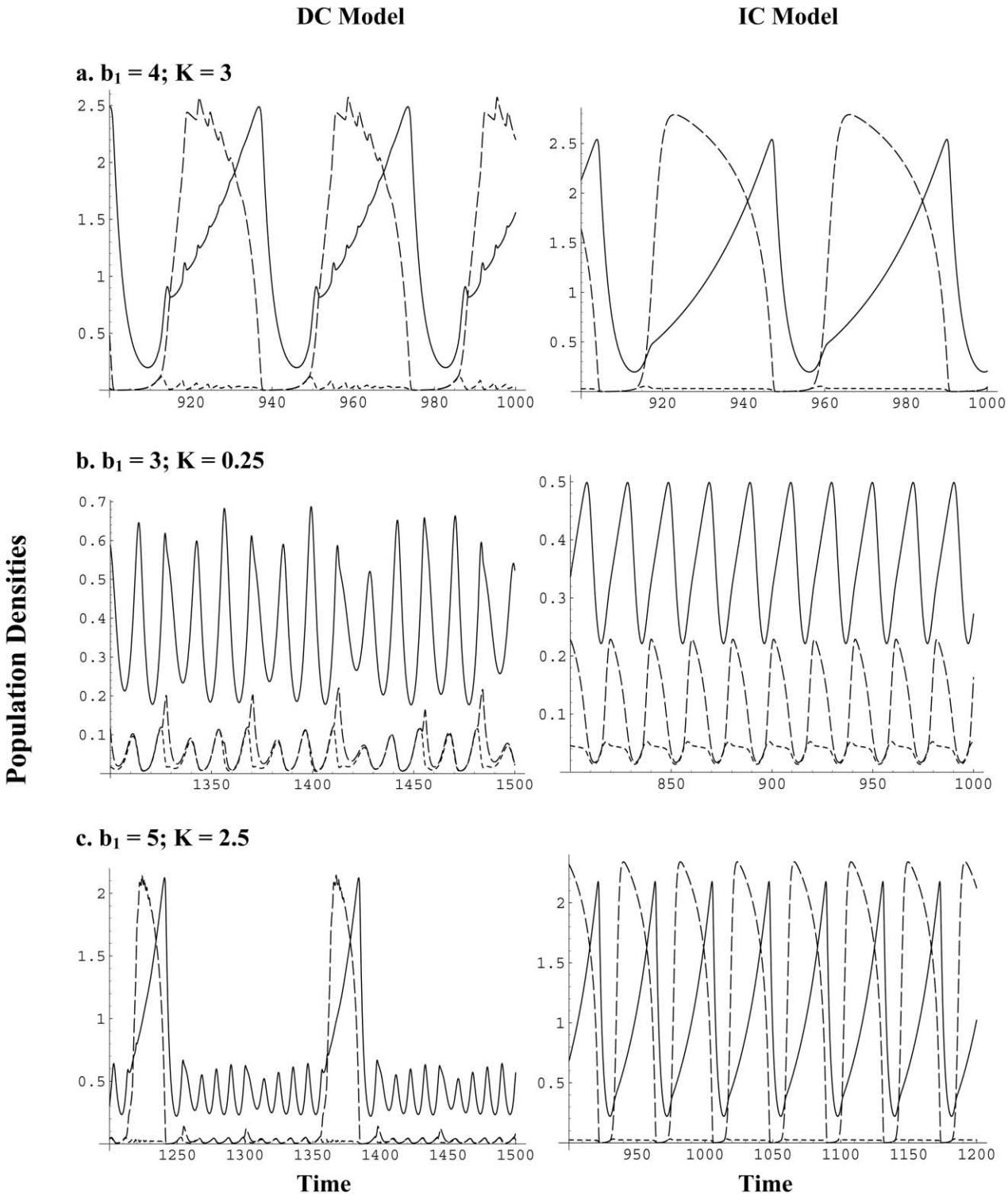


Figure 2: Samples of the dynamics of the DC and IC models for the standard parameter set: $r_1 = r_2 = 1$, $m_1 = m_2 = 0.005$, $h_1 = h_2 = 2$, $c_1 = c_2 = 5$, $b_2 = 0.9$, $d = 0.4$; $v = 18.75$ in the DC model; $z = 30$ in the IC model. The solid line denotes N_3, the long dashed line is N_2, and the short dashed line is N_1.

namics shown in the left-hand panels of figure 2. This lag can be pronounced in spite of the rapid maximum rate of behavioral change because the dynamics of q slow down when its value approaches 0 or 1.

Local Stability and Dynamics for Other Demographic Parameters

To what extent do the large differences between IC and DC model dynamics depend on the particular parameters we have explored? We examined a large set of randomly generated parameter combinations and also varied each parameter in the standard set individually to determine whether the major differences between DC and IC models described above were atypical. The results, summarized in table 1, suggest that although the two models do not always differ greatly, they do so for a wide range of parameters. The results for very low prey immigration rates are particularly significant because they show that chaotic dynamics can also occur when the poorer prey is not included in the equilibrium diet. When immigration rates were set to 10^{-9}, the percentage of b_1-K parameter space that produced complex cycles or chaos when $b_2 = 0.7$ was increased from a few isolated points to close to 30% of the b_1-K parameter space shown in figure 1. For most of the parameters examined, if the variation in the better prey is sufficient that it is repeatedly adaptive for the predator to switch from specialization to generalization (or vice versa), our DC model frequently predicts different (and often more complex) dynamics than does the instantaneous-choice model. On the other hand, dynamic choice is stabilizing relative to instantaneous choice when both prey immigration and the quality of the better prey are high.

The results in table 1 do not include the parameters involved in the scaling function V. We noted earlier that the dynamics were insensitive to the adaptive rate constant ν when it was large. The fraction of parameter space yielding chaos or complex cycles in figure 1*B* ($b_2 > dh_2$) was only slightly changed by increasing the rate constant ν fivefold to 93.75; the fraction of b_1-K parameter space producing complex cycles increased from 15.9% to 18.8%, while the fraction producing chaos changed from 12.2% to 12.5%. Chaotic dynamics occurred in a similar region of parameter space for the higher ν. Much lower rates of adaptive change did have a major impact on the nature of dynamics and the parameters where complex cycles or chaos occurred. For example, when $\nu = 2$, the area with a stable equilibrium in figure 1*B* was greatly reduced (from 12% to 5%) while the combined frequency of complex cycles and chaos increased (from 28% to 50%). Lower values of z ($z = 2$) in the IC model increased the area with local stability slightly but did not produce qualitatively different dynamics.

The exponent n in equation (3) determines the rate at

Table 1: Effects of changing parameters from those in the standard parameter set on the difference between the dynamics of DC and IC models

Parameter(s) changed	Difference in stable region	Difference in dynamic complexity within the unstable region[a]
Capture rates c_i	Qualitatively similar to figure 1 for larger or smaller c_i; similar small changes for IC and DC models	Smaller c_i increases size of chaotic region for DC models until c_i is significantly <1; increases in c_i have small effects in DC model
Handling times, h_i, differ rather than energy contents	Qualitatively similar to figure 1 with similar small changes for IC and DC models	Chaos in DC model often becomes complex cycles; differences in prey densities between DC and IC models are reduced
Predator demographic rates (multiplicative decreases in both b_i and d with similar increases in ν)	Qualitatively similar to figure 1	Slower rates reduce chaos and complex dynamics in DC model and often change chaos to complex cycles
Prey immigration m_i	Lower immigration removes stable region at high b_1 and reduces stable region in both models	Much lower m produces a modest reduction in the chaotic region for the DC model when $b_2 > dh_2$ but greatly increases chaos when $b_2 < dh_2$
Poorer prey profitability b_2	Minor effects unless b_2 is much larger, which reduces stable region	Probability of complex dynamics in the DC model is reduced as b_2 moves away from $b_2 = dh_2$
Symmetry of prey parameters (equality of r, K, c, m)	Quantitative but not qualitative change in both models, provided the better prey produces cycles	Small or moderate asymmetry often increases the range of chaotic dynamics in most DC models

[a] The IC model was not observed to exhibit complex cycles or chaos under any of these parameter changes.

which behavioral dynamics slow as they approach a limiting value of the trait. Increasing this exponent to 3 or 4 had only small effects on parameter ranges that produced particular types of dynamics. However, reducing n sufficiently produced very significant changes in the form of the dynamics of the DC model. These lower values reduce the lag in the response of q to population densities when q is close to 0 or 1. If the DC simulations in figure 1 are altered so that $n = 1$, the categories of dynamics shown in figure 5 result. The distribution of different types of dynamics over parameter space is similar to the results in figure 1 ($n = 2$) when $b_2 = 0.7$, except there is a region of complex cycles and a few cases of chaos when b_1 is relatively low. The results for $b_2 = 0.9$ have much less chaos and a larger region of alternative attractors (one of which is a complex cycle) than for the corresponding parameters when $n = 2$.

This case ($n = 1$) and smaller values of n required a modification of the trait dynamic equation (3) to prevent q from becoming negative or >1 when adaptive change was rapid. This was accomplished by adding a function, $\varepsilon/q^2 - \varepsilon/(1 - q)^2$, to the equation for dq/dt. Here, ε is a very small constant (on the order of 10^{-6} or less). This function pushes the trait away from its limiting values but has insignificant effects on dynamics when the trait has an intermediate value. Adding such a function to the original model for $n = 2$ has no significant effect on the pattern of dynamics over parameter space provided ε is small enough. This function also allows us to examine the dynamics when $n = 0$. Here, there is no slowing of behavioral change until q is extremely close to 0 or 1, and then the slowing only affects the dynamics when selection favors a value more extreme than the current one. Results (not shown) for $n = 0$ reveal fewer cases of chaos or complex cycles than when $n = 1$ or $n = 2$. However, complex cycles still occur over significant ranges of parameters, even at quite high rates of behavioral change ($\nu \gg 10$). Complex cycles occur for cases with b_2 above and below the threshold for equilibrium diet inclusion. Thus, although n can have a large effect on dynamics, all values of n that we examined lead to significant differences between IC and DC models.

Mean Population Densities and Indirect Interactions for the Standard Parameters

The difference in dynamics between IC and DC models might be of little consequence if this difference had little effect on the population densities of the three species or on how those densities changed with removal or addition of other species in the system. However, as suggested by figure 2 and as detailed below, when the models differ in the qualitative form of their dynamics, they also frequently differ significantly in population densities and the indirect effects between prey species that those densities imply. Here we return to the DC model analyzed in greatest detail, characterized by $n = 2$.

Mean Densities. The mean densities of the two prey under the IC model are similar to those under the DC model for a significant fraction of b_1-K parameter space when $b_2 < dh_2$. The qualitative form of the dynamics is often similar across models in this case. There are large differences in densities between the two types of models when $b_2 > dh_2$, corresponding to large differences in the type of dynamics. Usually the density of prey 2 is lower in the DC model than in the IC as the result of greater consumption of prey 2 in the DC model. This reduces consumption (and hence overexploitation) of prey 1, allowing the predator to achieve higher densities in the DC model. Transitions between chaotic and periodic dynamics result in a complicated pattern of change in average densities over b_1-K parameter space in the DC model. Figure 3 summarizes the difference between the mean population densities under the two models. This difference was scaled relative to the mean of the densities in the two models and was expressed as a percent; that is, $100(N_{i,\mathrm{DC}} - N_{i,\mathrm{IC}})/[0.5(N_{i,\mathrm{DC}} + N_{i,\mathrm{IC}})]$. Figure 3 shows the areas of parameter space in which one or more of the species differed by at least 20% or by at least 50% between the IC and DC models. Large differences clearly characterize a large fraction of the parameter space. Minimum densities also differed significantly between IC and DC models for the parameters shown in figure 3, with the DC model generally having a higher minimum density of prey 1 (which always has a lower mean abundance than prey 2).

Indirect Interactions. Prey affect each other indirectly via both the predator's population density and the predator's behavior (i.e., q). Indirect interactions between the two prey species were quantified by comparing the mean prey density in a predator-prey system with only one prey species present with the mean density when both prey were present. Effects were measured by the percent change of the mean population density of the focal prey following the addition of the second prey species after allowing the system to reach its final dynamics. The indirect effects were designated by an ordered pair whose first element was the sign of the change in the mean density of the first (superior prey) species following introduction of the second (inferior prey); the second element was the sign of the change in the second following introduction of the first. Effects were classified as zero if they were less than a small threshold value (1% or 5%). Table 2 summarizes the percentages of parameter space with each possible type of indirect effect in the two models, using the 1% threshold. Figure 4 shows

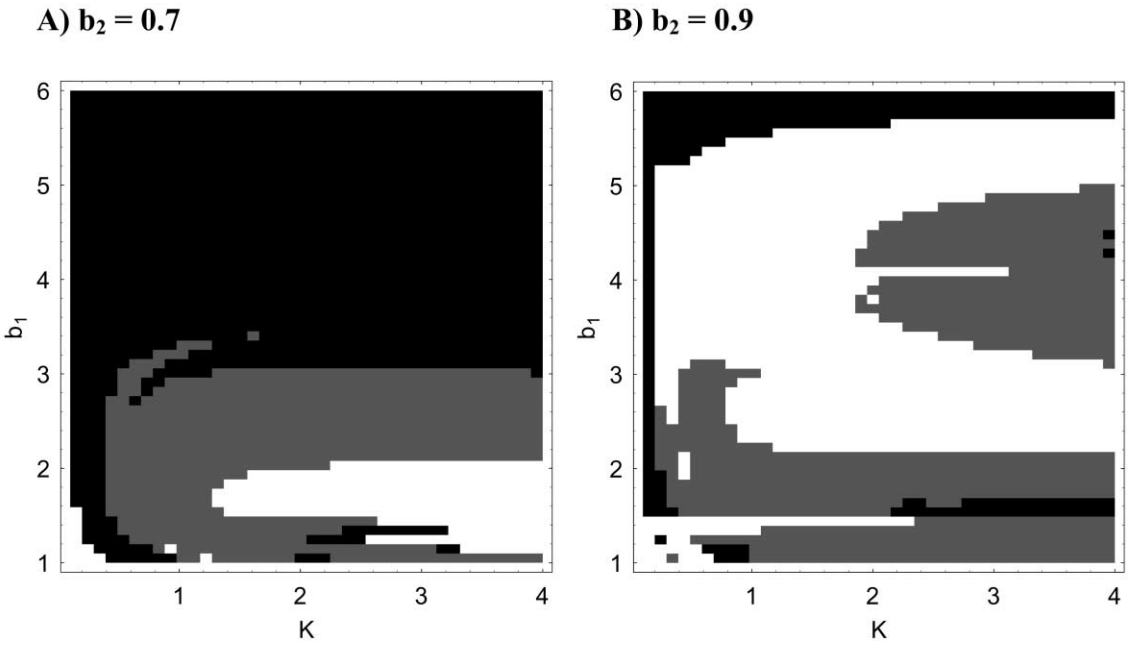


Figure 3: Areas of parameter space where the average density of at least one of the three species differed between DC and IC models by either 20% or 50%, assuming the standard parameter set. Black represents zero or small difference in the average densities, gray represents a ≥20% difference, and white represents a ≥50% difference between models for at least one species.

areas of parameter space with different types of interaction for both the IC and DC models (with a 5% threshold for a nonzero interaction).

One of the most conspicuous differences between the two models is the much greater percentage of parameter space yielding (+, −) interactions in the DC model where the better prey benefits from the presence of the poorer prey. This occurs when $b_2 > dh_2$, that is, when the poorer prey are adequate for predator subsistence. Here the modest increase in N_1 is due to the increased amplitude of cycles in the two-prey system; larger cycles often increase mean prey density in predator-multiprey systems (Abrams et al. 1998). The poorer quality prey typically experiences a large decrease in density due to the presence of the better prey in both DC and IC models. This occurs because the poorer prey experiences a greater predator population when the more nutritious prey 1 is present. The same parameters that result in (+, −) interactions in the DC model often produced (−, −) interactions in the IC model; here, prey 2 generally has a small negative effect on prey 1. The close coupling of the two prey populations entailed by the IC model tends to result in stronger apparent competitive interactions than in the DC model. If we restrict attention to indirect effects that cause a >40% change in the density of one of the two prey, there are still many regions of parameter space with significant effects when $b_2 = 0.9$ (i.e., $b_2 > dh_2$). Here the IC model predicts that ~30% of parameter space will have significant indirect interactions, whereas the DC model predicts that ~65% of parameter space will have significant indirect interactions.

Alternative Rules for Behavioral Dynamics

It is clear that at least one rule for behavioral dynamics frequently produces population dynamics that differ greatly from the analogous models in which the behavior continuously approximates the optimal behavior for current prey densities. However, it is not clear whether the dynamic rule that was investigated here represents a good approximation to many (or any) real predators. There are many models that can equally validly claim to represent plausible predator choice behavior. A similarly detailed analysis of a large number of such models requires several additional articles. However, we have carried out less extensive sets of simulations for a range of alternative models and report on some of the results for two classes of models here.

The first alternative model assumes that the predator uses the optimal threshold formula (or the approximation given by eq. [6]) but uses an estimate of the density of prey 1, which lags behind the actual value. This makes

Table 2: Percent of b_1-K parameter space producing different indirect effects between prey

Indirect interaction[a]	DC		IC	
	$b_2 = .7$	$b_2 = .9$	$b_2 = .7$	$b_2 = .9$
(0, 0)	58.0	.3	15.5	.3
(+, +)	…	1.0	…	.8
(−, −)	35.8	15.0	8.7	65.8
(0, −)	…	5.6	2.2	5.0
(−, 0)	6.2	…	48.3	…
(0, +)	…	…	…	…
(+, 0)	…	…	25.3	…
(+, −)	…	78.1	…	27.8
(−, +)	…	…	…	.3

[a] The first sign gives the effect of adding prey 2 on the density of prey 1; the second sign gives the effect of adding prey 1 on the density of prey 2. The standard parameter set was assumed, and a <1% difference resulted in a zero effect.

diet choice a dynamic variable but assumes no role for the fitness gradient in determining the rate of change. Because information gathering is time-consuming, one would expect that estimates of the prey density should lag behind the actual density. The model simply assumes that E_1, the estimate of N_1, changes at a rate proportional to the difference between N_1 and E_1. In other words,

$$\frac{dE_1}{dt} = \nu(N_1 - E_1), \tag{7a}$$

$$q = \frac{\eta^z}{E_1^z + \eta^z}, \tag{7b}$$

where η is given by equation (5). The dynamics of this model are quite similar to those of the instantaneous model provided that the rate constant ν is sufficiently large. We examined how much of a lag (i.e., how small a value of ν) is required for the dynamics to depart significantly from the dynamics predicted by the instantaneous model. Figure 6 illustrates the change in dynamics as the rate parameter ν is varied, assuming our standard parameter set with $K = 1$ and $b_1 = 2.5$. Significant differences between the population dynamics in the instantaneous and lagged models in this example begin to appear when ν is on the order of 1. The value $\nu = 0.5$ (top panels of fig. 6) produces population dynamics that differ markedly from those of the IC model, which produces dynamics that are almost indistinguishable from those in the bottom panels (fig. 6) when $\nu = 50$. When $\nu = 2$ (second pair of panels), there is little lag between the switch in the optimal q (from 1 to 0 or 0 to 1) and the switch in the actual value of q. When $\nu = 10$, the lag is invisible on the graph, but the pattern of fluctuation in q still differs significantly from the pattern observed when $\nu = 50$ (or with the IC model). Values of ν on the order of 10 or more yield distributions of dynamics over the standard parameter space that are very similar to figure 1*D* (i.e., similar to the IC model).

The second alternative dynamic framework investigated here assumes that an individual can instantaneously change from $q = 0$ to $q = 1$, and the rate of these transitions depends on the change in fitness produced. However, unlike the previous models, individuals in the population do not all have nearly identical trait values. There are two predator phenotypes, the specialist with population size P_s and the generalist with population P_g, and each phenotype can switch to the other when it is adaptive to do so, yielding

$$\begin{aligned}
\frac{dP_s}{dt} &= P_s\left(\frac{b_1c_1N_1}{1 + h_1c_1N_1} - d\right) \\
&\quad - MP_s\left\{\exp\left[\nu\left(\frac{b_1c_1N_1 + b_2c_2N_2}{1 + h_1c_1N_1 + h_2c_2N_2} - \frac{b_1c_1N_1}{1 + h_1c_1N_1}\right)\right]\right\} \\
&\quad + MP_g\left\{\exp\left[\nu\left(-\frac{b_1c_1N_1 + b_2c_2N_2}{1 + h_1c_1N_1 + h_2c_2N_2} + \frac{b_1c_1N_1}{1 + h_1c_1N_1}\right)\right]\right\}, \\
\frac{dP_g}{dt} &= P_g\left(\frac{b_1c_1N_1 + b_2c_2N_2}{1 + h_1c_1N_1 + h_2c_2N_2} - d\right) \\
&\quad - MP_g\left\{\exp\left[\nu\left(-\frac{b_1c_1N_1 + b_2c_2N_2}{1 + h_1c_1N_1 + h_2c_2N_2} + \frac{b_1c_1N_1}{1 + h_1c_1N_1}\right)\right]\right\} \\
&\quad + MP_s\left\{\exp\left[\nu\left(\frac{b_1c_1N_1 + b_2c_2N_2}{1 + h_1c_1N_1 + h_2c_2N_2} - \frac{b_1c_1N_1}{1 + h_1c_1N_1}\right)\right]\right\}.
\end{aligned} \tag{8}$$

This has the same functions describing transitions between types as a recent model of switching between habitats (Abrams 2000*b*). The exponential terms result in transitions between the two phenotypes, whose rates increase with an increasing fitness gain from making the transition. The model assumes that each behavioral type produces offspring that initially have its own behavioral phenotype. The parameter M is the per capita rate of switching from specialist to generalist (or vice versa) when the food intake rates of the two strategies are equal. The parameter ν adjusts the sensitivity of the switching rate to the difference in rewards; a large ν means that even a small difference in food intake rates will be sufficient to increase the rate of switching greatly over the baseline rate given by M. No cost of switching is included in the model. Results corresponding to the parameter space in figure 1 are shown in figure 7. Some areas of chaotic dynamics are observed, but chaos is less common than in the monomorphic model illustrated in figure 1. However, when $b_2 = 0.9$, complex cycles occur over a wider range of parameter space than in the comparable model shown in figure 1*B*, and the zone of stable equilibria at high values of b_1 is not present in

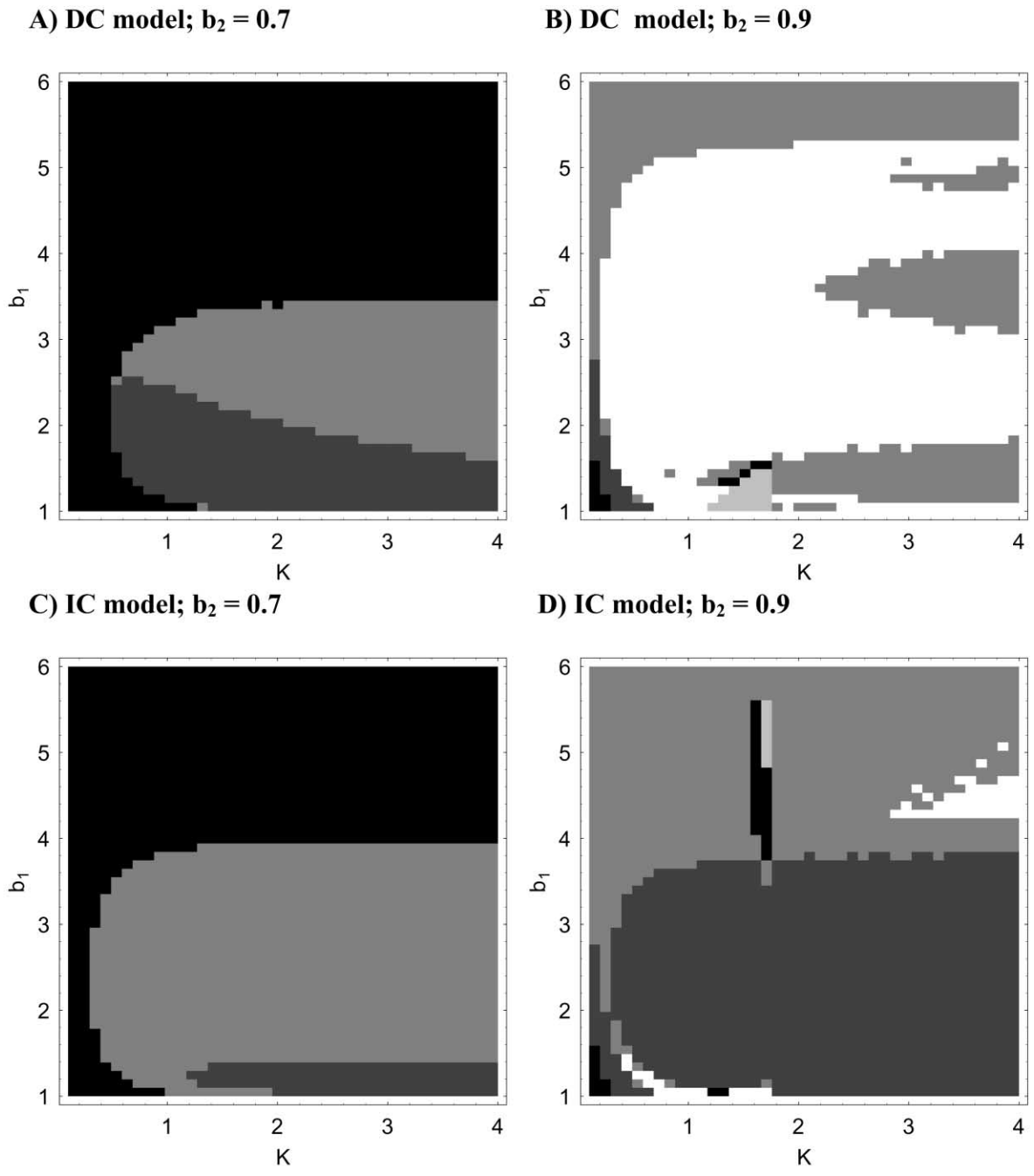
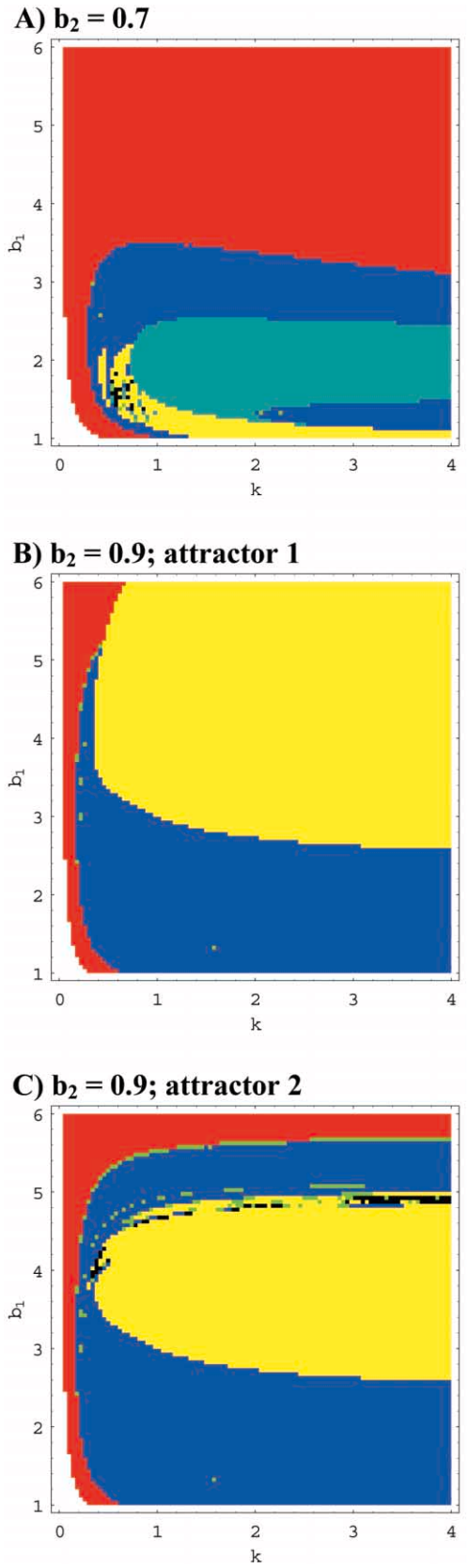


Figure 4: Regions of b_1-K parameter space with different forms of indirect interactions between the two prey species under the standard parameter set for DC and IC models. A >5% difference in average density of one prey following addition of the other prey species constituted a significant interaction. The shadings have the following meanings: black, $(0, 0)$; dark gray, $(-, -)$; medium gray, $(-, 0)$ or $(0, -)$; light gray, $(+, 0)$ or $(0, +)$; white, $(+, -)$ or $(-, +)$.

figure 7*B*. The case of $b_2 = 0.7$ can produce complex cycles (at low b_1), unlike the monomorphic model. Although these details differ from the monomorphic model based on equation (4), the general locations of alternative attractors (in the case of $b_2 = 0.7$) and complex dynamics (in the case of $b_2 = 0.9$) are similar for these two quite different models.

Combining this quick survey of two alternative dynamic



models of behavior with our original DC model shows that there are some circumstances when the IC model can provide a good approximation to dynamic models. However, the lag inherent in all dynamic models of behavior can produce more complicated dynamics than predicted by the IC model for at least some ranges of parameters in all of the models we have examined. In addition, there are significant differences between the dynamics of all three classes of dynamic model examined here: those based on equations (4), (7), and (8).

Discussion

The differences between instantaneous and dynamic behavioral models documented here suggest that instantaneous models should not be relied upon to accurately predict the impact of adaptive behavior on population dynamics. This message is certain to apply to many other situations involving behavioral choice beyond the simple two-prey systems considered here and in Abrams (1999). Bernstein et al. (1988, 1991) also argue that behavioral dynamics can affect population dynamics, using a simulation model of patch choice by predators. However, the present results also suggest that there are behavioral mechanisms and/or parameter ranges where an instantaneous approximation may be quite accurate and that different plausible dynamic models often make different predictions. Thus, we clearly need to find out more about the actual dynamics of adaptive behavioral decisions within populations. Do individual predators pass through a phase with intermediate preferences when the density of better prey is changed through the threshold value for the inclusion of poorer prey? How much does preference vary between individuals in a population experiencing the same prey densities? How much is sampling behavior reduced when a particular strategy (here specialization or generalization) has been adaptive for a long time? What is the relationship between the fitness gradient and the rate of change of behavior? (Is it linear, as assumed here, or does it have a more complex form?) Answers to these sorts of questions could narrow (or perhaps expand) the range of biologically plausible models of behavioral dynamics. It

Figure 5: The dynamics of the DC model given the standard parameter set but with $n = 1$, that is, less slowing of the rate of change in q as q approaches its limiting values of 0 or 1 than in figure 1. *A* is the attractor for $b_2 = 0.7$. *B* and *C* show the alternative attractors for the case of $b_2 = 0.9$ because there are several qualitatively different pairs of attractors over the parameter space where alternatives exist. An additional function is added to prevent the value of q from exceeding its biological bounds ($\varepsilon = 10^{-6}$). The color coding of the dynamics is identical to that used in figure 1.

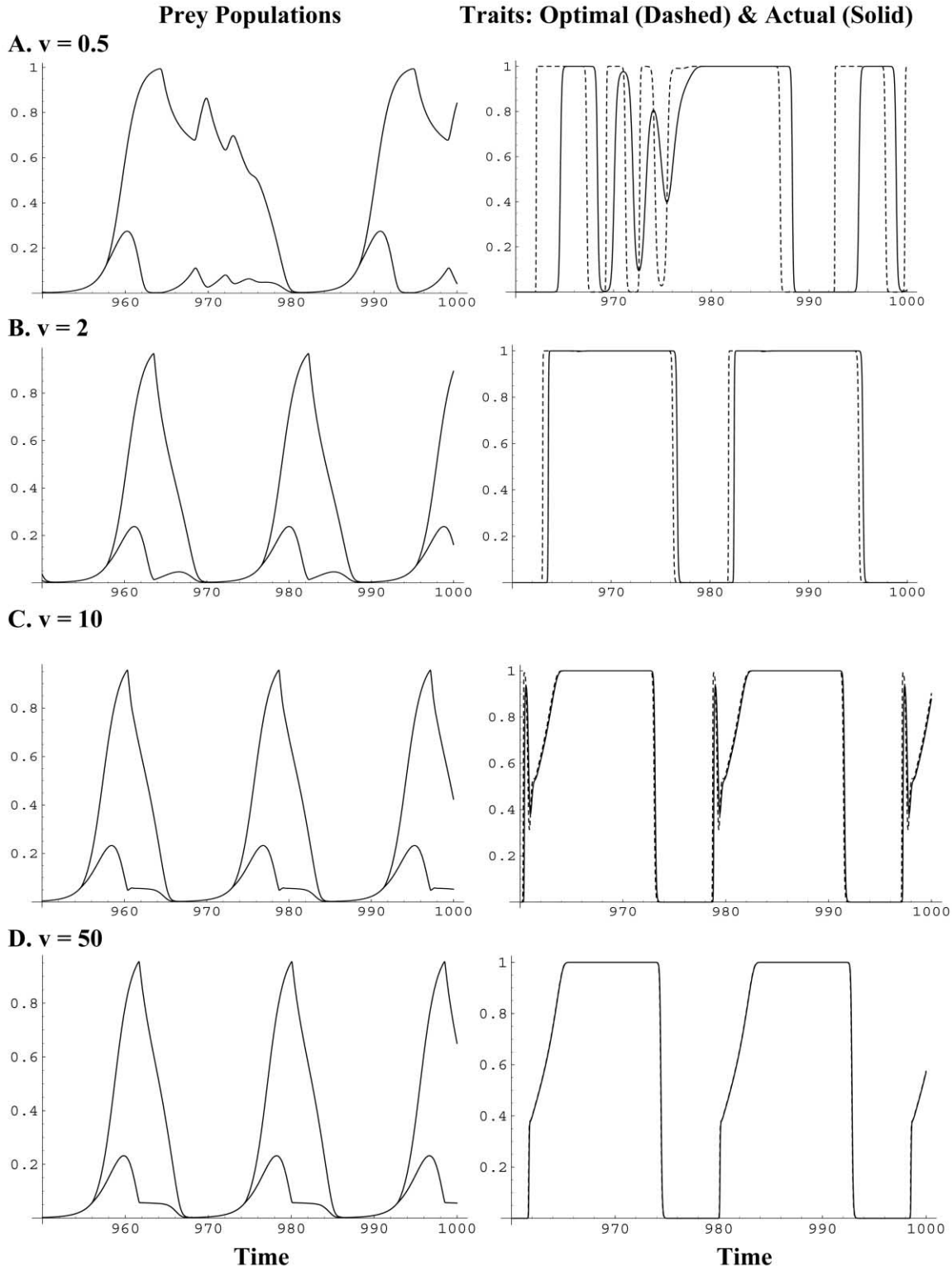


Figure 6: Four examples of the dynamics of the model with a delayed estimate of the density of the better prey; equations (1) combined with equations (7). The left-hand panels show the prey populations over time, with the lower line denoting the more rewarding prey (species 1). The right-hand panels show both the value of q in the model (*solid line*) and the optimal q (*dashed line*) at every instant in time. The parameter values are $r_i = 1$, $K_i = 1$, $m_i = 0.005$, $b_1 = 2.5$, $b_2 = 0.9$, $h_i = 2$, $c_i = 5$, $d = 0.4$. Adaptive rates larger than $\nu = 50$ produce population and trait dynamics indistinguishable from those for $\nu = 50$.

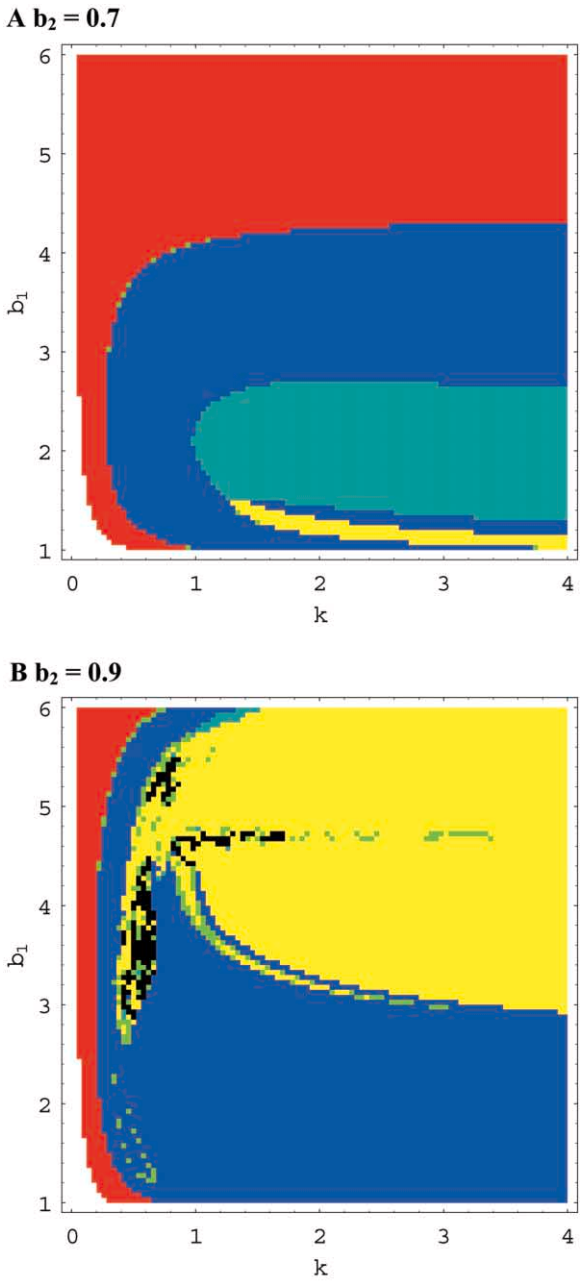


Figure 7: Dynamics produced by the dimorphic model (eqq. [8]). The population dynamic parameters are identical to those in figure 1, with results for $b_2 = 0.7$ and $b_2 = 0.9$. The switching between types is described by the parameters $M = 0.005$ and $\nu = 20$. The color coding for different types of dynamics is identical to that used in figures 1 and 5.

has long been known that foraging behaviors do not respond instantaneously to changes in food conditions (Tinbergen 1960; review in Krebs and Inman 1994). Nevertheless, we do not have the types of empirical information that would be required to describe the time course of changes in behavior, given different sorts of temporal changes in food abundance.

The present work also highlights the lack of theory regarding the interaction of population dynamics and behavioral dynamics. We have only considered the effects of behavioral dynamics on the final population dynamics in an otherwise constant environment. Models in which behavior shifts because of altered environmental conditions and analyses of the effects of behavioral dynamics on transient population dynamics are needed. There are also many ecological scenarios involving adaptive behavioral shifts for which there are no investigations of the impact of behavioral flexibility, even in the case of instantaneous shifts. The consequences of dynamic behaviors need to be explored in simple extensions of the present model, such as one in which prey species compete for resources. One would expect that rules governing behavioral dynamics would be especially likely to affect system behavior in larger food webs in which two or more species simultaneously attempt to adapt to each other's behaviors and population densities. The few previous analyses of such scenarios (e.g., Abrams 1992; Abrams and Matsuda 1993) have assumed (or adopted behavioral rules that ensure) that behaviors reach an equilibrium with respect to each other and with respect to population densities. It is unlikely that this will always occur in natural systems. The growing recognition that effectively instantaneous behavioral change can have a large impact on population dynamics (Abrams 1982, 1984, 1995; Fryxell and Lundberg 1998; Lima 1998; Houston and McNamara 1999; Peacor and Werner 2001; Bolker et al. 2003) argues for a similar recognition that the dynamic rules by which behaviors change are also critical in understanding ecological communities. The scarcity of theory dealing with behavioral dynamics in a community ecological context contrasts with a relative abundance of theory on the population dynamical implications of different rates and forms for the evolutionary dynamics of traits in ecological communities (e.g., Abrams et al. 1993; Van der Laan and Hogeweg 1995; see reviews in Abrams 2000*a*, 2001).

Earlier work based on IC models (Fryxell and Lundberg 1994; Van Baalen et al. 2001) had suggested that a predator with adaptive diet choice was likely to create more stable dynamics than a generalist predator. However, neither of those studies included immigration of the prey. Our results show that the IC model is more likely to exhibit sustained cycles than is the standard DC model (eq. [4]) when prey immigration is high and $b_2 > dh_2$. Under these conditions, the standard DC model predicts that the predator becomes a complete generalist, which cannot occur under the IC model. Thus, contrary to earlier suggestions by Fryxell and Lundberg (1994) and van Baalen et al. (2001), systems with diet choice can be less stable than those with inflexible

generalist predators. This result serves as a warning against overgeneralization regarding the stabilizing or destabilizing effects of diet choice. Clearly, much more information on the actual forms of population growth functions and behavioral dynamics is needed before the stability question can be addressed adequately.

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Literature Cited

Abrams, P. A. 1982. Functional responses of optimal foragers. American Naturalist 120:382–390.

———. 1984. Foraging time optimization and interactions in food webs. American Naturalist 124:80–96.

———. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. American Naturalist 140:573–600.

———. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. American Naturalist 146:112–134.

———. 1999. The adaptive dynamics of consumer choice. American Naturalist 153:83–97.

———. 2000*a*. The evolution of predator-prey systems: theory and evidence. Annual Review of Ecology and Systematics 31:79–105.

———. 2000*b*. The impact of habitat selection on the heterogeneity of resources in varying environments. Ecology 81:2902–2913.

———. 2001. Modeling the adaptive dynamics of traits involved in inter- and intra-specific competition: an assessment of three methods. Ecology Letters 4:166–175.

Abrams, P. A., and H. Matsuda. 1993. Effects of adaptive predatory and anti-predator behavior in a two prey–one predator system. Evolutionary Ecology 7:312–326.

———. 1997*a*. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. Evolutionary Ecology 11:1–20.

———. 1997*b*. Prey adaptation as a cause of predator-prey cycles. Evolution 51:1742–1750.

Abrams, P. A., H. Matsuda, and Y. Harada. 1993. Unstable fitness maxima and stable fitness minima in the evolution of continuous traits. Evolutionary Ecology 7:465–487.

Abrams, P. A., R. D. Holt, and J. D. Roth. 1998. Apparent competition or apparent mutualism? shared predation when populations cycle. Ecology 79:201–212.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1988. Individual decisions and the distribution of predators in a patchy environment. Journal of Animal Ecology 57:1007–1026.

———. 1991. Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and the structure of the environment. Journal of Animal Ecology 60:205–225.

Bolker, B. M., M. Holyoak, V. Krivan, L. Rowe, and O. J. Schmitz. 2003. Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114.

Boyd, R., and P. J. Richerson. 1985. Culture and the evolutionary process. University of Chicago Press, Chicago.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist 110:141–151.

Ellner, S., and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. American Naturalist 145:343–175.

Fryxell, J. M., and P. Lundberg. 1994. Diet choice and predator-prey dynamics. Evolutionary Ecology 8:407–421.

———. 1998. Individual behaviour and community dynamics. Chapman & Hall, New York.

Genkai-Kato, M., and N. Yamamura. 1999. Unpalatable prey resolves the paradox of enrichment. Proceedings of the Royal Society of London B, Biological Sciences 266:1215–1219.

Getty, T., and J. R. Krebs. 1985. Lagging partial preferences for cryptic prey: a signal-detection analysis of great tit foraging. American Naturalist 125:39–60

Gleeson, S. K., and D. S. Wilson. 1986. Equilibrium diet: optimal foraging and prey coexistence. Oikos 46:139–144.

Harley, C. B. 1981. Learning the evolutionarily stable strategy. Journal of Theoretical Biology 89:611–633.

Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behaviour. Cambridge University Press, Cambridge.

Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences. II. The "handicap" principle. Evolution 45:1431–1442.

Kendall, B. E., J. Predergast, and O. Bjørnstad. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns of population cycles. Ecology Letters 1:160–164.

Krebs, J. R., and A. J. Inman. 1994. Learning and foraging: individuals, groups, and populations. Pages 46–65 *in* L. A. Real, ed. Behavioral mechanisms in evolutionary ecology. University of Chicago Press, Chicago.

Krivan, V. 1996. Optimal foraging and predator-prey dynamics. Theoretical Population Biology 49:265–290.

———. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. American Naturalist 149:164–178.

Krivan, V., and A. Sikder. 1999. Optimal foraging and predator-prey dynamics. II. Theoretical Population Biology 55:111–126.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

Matsuda, H. 1985. Evolutionarily stable strategies for predator switching. Journal of Theoretical Biology 115:351–366.

Matsuda, H., K. Kawasaki, N. Shigesada, E. Teramoto, and L. M. Ricciardi. 1986. Switching effect on the stability of the prey-predator system with three trophic levels. Journal of Theoretical Biology 122:251–262.

Peacor, S., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences of the USA 98:3904–3908.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in C: the art of scientific computing. 2d ed. Cambridge University Press, Cambridge.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15: 523–575.

Pyke, G. H., R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.

Royama, T. 1992. Analytical population dynamics. Chapman & Hall, London.

Schoener, T. W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2:369–404.

Stephens, D. W., and K. C. Clement. 1998. Game theory and learning. Pages 239–260 *in* H. K. Reeve and L. A. Dugatkin, eds. Game theory and animal behavior. Oxford University Press, Oxford.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Oxford University Press, Oxford.

Tansky, M. 1978. Switching effect in prey-predator system. Journal of Theoretical Biology 70:263–271.

Taper, M., and T. J. Case. 1992. Models of character displacement and the theoretical robustness of taxon cycles. Evolution 46:317–334.

Taylor, P., and T. Day. 1997. Evolutionary stability under the replicator and the gradient dynamics. Evolutionary Ecology 11:579–590.

Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie 13: 265–343.

Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. Ecology 73:289–305.

van Baalen, M., V. Krivan, P. C. J. van Rijn, and M. W. Sabelis. 2001. Alternative food, switching predators, and the persistence of predator-prey systems. American Naturalist 157:512–524.

Van der Laan, J. D., and P. Hogeweg. 1995. Predator-prey coevolution: interactions across different timescales. Proceedings of the Royal Society of London B, Biological Sciences 259:35–42.

Wolf, A., J. B. Swift, H. L. Swinney, and J. A. Vastano. 1985. Determining Lyapunov exponents from a time series. Physica D 16:285–317.

Wolfram Research. 1999. Mathematica 4.0. Wolfram Research, Champaign, Ill.

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