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Dynamic versus Instantaneous Models of Diet Choice

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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.

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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 Síkder (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 Turchin 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):

\[
\frac{dN_1}{dt} = m_1 + r_1 N_1 \left( 1 - \frac{N_1}{K_1} \right) - \frac{c_1 N_1 N_3}{1 + h_1 c_1 N_1 + q_1 h_1 c_1 N_2}, \tag{1a}
\]

\[
\frac{dN_2}{dt} = m_2 + r_2 N_2 \left( 1 - \frac{N_2}{K_2} \right) - \frac{q_2 c_2 N_2 N_3}{1 + h_2 c_2 N_1 + q_2 h_2 c_2 N_2}, \tag{1b}
\]

\[
\frac{dN_3}{dt} = N_3 \left( \frac{b_1 c_1 N_1 + q b_1 c_1 N_2}{1 + h_1 c_1 N_1 + q h_2 c_2 N_2} - d \right), \tag{1c}
\]

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:

\[
\frac{dq^*}{dt} = V(q^*) \frac{dW}{dq} \bigg|_{q=q^*}.
\]

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 1997a, 1997b). 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

\[
V(q^*) = 2^{a \nu} q^n (1 - q^*^n).
\]

The parameter \( \nu \) 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 \( 2^n \) 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 \( n \) 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 \( q^* \):

\[
\frac{dq^*}{dt} = 16 \nu q^{1-1} \left( 1 - q^* \right)^q \left( c_1 N_1 [b_1 (1 + c_1 h_1 N_1) - b_1 c_1 h_1 N_1] \right) \left( 1 + b_1 c_1 N_1 + q h_2 c_2 N_2 \right)^{2}.
\]

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:

\[
\eta = \frac{b_1}{c_1 (b_2 h_2 - b_2 h_1)}.
\]

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 \( N_i \):

\[
q = \frac{\eta^*}{\eta^* + N_i^z},
\]

where \( \eta \) 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). Non-equilibrium 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 \((m_i = 0.005, \ r_i = 1, \ c_i = 5, \ h_i = 2 \ for \ i = 1, 2; \ d = 0.4)\) over a broad range of the parameters \( b_1, K_1 = K_2 = K_3 = K_4 \) 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 \( K_2 > 4 \) 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 non-zero 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: \( r_1 = r_2 = 1, m_1 = m_2 = 0.005, b_1 = b_2 = 2, c_1 = c_2 = 5, d = 0.4; \) DC model \( \rho = 18.75; \) IC model \( x = 30. \) 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, \( \rho = 18.75; \) B, DC model, \( \rho = 18.75; \) C, IC model, \( b_1 = 0.7. \) D, IC model, \( b_1 = 0.9. \)

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 1A, 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. Spe-
cialization is the optimal strategy when \( b_1 \) is relatively large
and when \( b_2 < dh_2 \). The DC model was more stable
when \( v < dh_2 \). 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.

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 prey 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 (be-
cause of a peak in the abundance of species 1) do not
prevent the longer-term trend toward \( q = 1 \). This de-
creased 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 At-
tractors.** The types of alternative attractors and the areas
of parameter space yielding these alternative attractors dif-
fered 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 \( b_1 < dh_2 \), there are different regions of pa-
rameter 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 \( b_1 < dh_2 \)), 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, al-
ternative 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. 1B).

**Differences in the Qualitative Form of the Population Dy-
namics.** Complex cycles and chaos occurred almost exclu-
dively in the IC 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 \( b_2 < dh_2 \). 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, be-
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, pop-
ulation cycles were mainly influenced by the interaction
of the predator and the better prey species.

Figure 1B 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 1B and 1D that qualitative
differences in dynamics between IC and DC models char-
terize 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 unsynch-
nized 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: $r_1 = r = 1$, $m_0 = m = 0.005$, $h_1 = h = 2$, $c = c = c = 5$, $b_1 = 0.9$, $d = 0.4$, $v = 18.75$ in the DC model; $z = 30$ in the IC model. The solid line denotes $N_0$, the long dashed line is $N_p$, and the short dashed line is $N_f$. 
dynamics 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 $10^{-5}$, the percentage of $b_1$-$K$ parameter space that produced complex cycles or chaos when $b_1 = 0.7$ 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 $v$ when it was large. The fraction of parameter space yielding chaos or complex cycles in figure 1B ($b_2 > dh_1$) was only slightly changed by increasing the rate constant $v$ 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 similar region of parameter space for the higher $v$. 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 $v = 2$, the area with a stable equilibrium in figure $1B$ was greatly reduced (from 12% to 5%) while the combined frequency of complex cycles and chaos increased (from 28% to 50%). Lower values of $v$ ($v = 2$) 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>
<thead>
<tr>
<th>Parameter(s) changed</th>
<th>Difference in stable region</th>
<th>Difference in dynamic complexity within the unstable region*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Capture rates $c_i$</td>
<td>Qualitatively similar to figure 1 for larger or smaller $c_i$; similar small changes for IC and DC models</td>
<td>Smaller $c_i$ increases size of chaotic region for DC models until $c_i$ is significantly &lt;1; increases in $c_i$ have small effects in DC model</td>
</tr>
<tr>
<td>Handling times, $h_o$, differ rather than energy contents</td>
<td>Qualitatively similar to figure 1 with similar small changes for IC and DC models</td>
<td>Chaos in DC model often becomes complex cycles; differences in prey densities between DC and IC models are reduced</td>
</tr>
<tr>
<td>Predator demographic rates (multiplicative decreases in both $b_i$ and $d$ with similar increases in $v$)</td>
<td>Qualitatively similar to figure 1</td>
<td>Slower rates reduce chaos and complex dynamics in DC model and often change chaos to complex cycles</td>
</tr>
<tr>
<td>Prey immigration $m_i$</td>
<td>Lower immigration removes stable region at high $b_i$ and reduces stable region in both models</td>
<td>Much lower $m$ produces a modest reduction in the chaotic region for the DC model when $b_i &gt; dh_i$ but greatly increases chaos when $b_i &lt; dh_i$</td>
</tr>
<tr>
<td>Poorer prey profitability $b_i$</td>
<td>Minor effects unless $b_i$ is much larger, which reduces stable region</td>
<td>Probability of complex dynamics in the DC model is reduced as $b_i$ moves away from $b_i = dh_i$</td>
</tr>
<tr>
<td>Symmetry of prey parameters (equality of $r, K, c$, $m$)</td>
<td>Quantitative but not qualitative change in both models, provided the better prey produces cycles</td>
<td>Small or moderate asymmetry often increases the range of chaotic dynamics in most DC models</td>
</tr>
</tbody>
</table>

* 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 \( b_2 \) 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, \( \epsilon q^2 - \epsilon/(1 - q)^2 \), to the equation for \( dq/dt \). Here, \( \epsilon \) 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 \( \epsilon \) 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 \( b_2 - K \) parameter space when \( b_2 < dh_{p_2} \). 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 \( b_2 > dh_{p_2} \), 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 \( b_2 - K \) 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, \( 100(N_{i,DC} - N_{i,IC})/[0.5(N_{i,DC} + N_{i,IC})] \). 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
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

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**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 \( \geq 20\% \) difference, and white represents a \( \geq 50\% \) difference between models for at least one species.
Table 2: Percent of $b_1$-K parameter space producing different indirect effects between prey

<table>
<thead>
<tr>
<th>Indirect interaction</th>
<th>DC $b_1 = .7$</th>
<th>DC $b_1 = .9$</th>
<th>IC $b_1 = .7$</th>
<th>IC $b_1 = .9$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(0, 0)</td>
<td>58.0</td>
<td>.3</td>
<td>15.5</td>
<td>.3</td>
</tr>
<tr>
<td>(+, +)</td>
<td>...</td>
<td>1.0</td>
<td>...</td>
<td>.8</td>
</tr>
<tr>
<td>(−, −)</td>
<td>35.8</td>
<td>15.0</td>
<td>8.7</td>
<td>65.8</td>
</tr>
<tr>
<td>(0, 0)</td>
<td>6.2</td>
<td>5.6</td>
<td>2.2</td>
<td>5.0</td>
</tr>
<tr>
<td>(0, +)</td>
<td>...</td>
<td>...</td>
<td>48.3</td>
<td>...</td>
</tr>
<tr>
<td>(+, 0)</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>(−, −)</td>
<td>...</td>
<td>78.1</td>
<td>...</td>
<td>27.8</td>
</tr>
<tr>
<td>(−, +)</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>.3</td>
</tr>
</tbody>
</table>

* 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.

The model assumes that $E_i$, the estimate of $N_i$, changes at a rate proportional to the difference between $N_i$ and $E_i$. In other words,

$$\frac{dE_i}{dt} = \nu(N_i - E_i), \quad (7a)$$

$$q = \frac{\eta_p}{E_i + \eta_p}, \quad (7b)$$

where $\eta$ is given by equation (5). The dynamics of this model are quite similar to those of the instantaneous model provided that the rate constant $\nu$ is sufficiently large. We examined how much of a lag (i.e., how small a value of $\nu$) 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 $\nu$ 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 $\nu$ 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 $\nu = 0$ (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 $\nu$ on the order of 10 or more yield distributions of dynamics over the standard parameter space that are very similar to figure 1D (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

$$\frac{dP_s}{dt} = \rho \left( \frac{b_1 c N_s - d}{1 + h c N_s} \right) - M P_s \left[ \exp \left\{ - \left( \frac{b_1 c N_s + b_2 c N_g}{1 + h c N_s + h c N_g} - \frac{b_1 c N_s}{1 + h c N_s} \right) \right\} \right]$$

$$+ M P_s \left[ \exp \left\{ - \left( \frac{b_1 c N_s + b_2 c N_g}{1 + h c N_s + h c N_g} + \frac{b_1 c N_s}{1 + h c N_s} \right) \right\} \right],$$

$$\frac{dP_g}{dt} = \rho \left( \frac{b_1 c N_g + b_2 c N_s}{1 + h c N_s + h c N_g} - d \right)$$

$$- M P_g \left[ \exp \left\{ - \left( \frac{b_1 c N_g + b_2 c N_s}{1 + h c N_s + h c N_g} - \frac{b_1 c N_g}{1 + h c N_g} \right) \right\} \right]$$

$$+ M P_g \left[ \exp \left\{ - \left( \frac{b_1 c N_g + b_2 c N_s}{1 + h c N_s + h c N_g} + \frac{b_1 c N_g}{1 + h c N_g} \right) \right\} \right].$$

This has the same functions describing transitions between types as a recent model of switching between habitats (Abrams 2000b). 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 model assumes that an individual can instantaneously switch from the specialist to generalist (or vice versa) when the 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 $b_1 = 0.9$, complex cycles occur over a wider range of parameter space than in the comparable model shown in figure 1B, 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 $(−, +)$.

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 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 $r_i = 1$, $K_i = 1$, $m_i = 0.005$, $h_i = 2.5$, $h = 0.9$, $h = 2$, $c = 5$, $d = 0.4$. Adaptive rates larger than $v = 50$ produce population and trait dynamics indistinguishable from those for $v = 50$. 

A. $v = 0.5$ 

B. $v = 2$ 

C. $v = 10$ 

D. $v = 50$
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Figure 7: Dynamics produced by the dimorphic model (eqq. [8]). The population dynamic parameters are identical to those in figure 1, with results for \( b_1 = 0.7 \) and \( b_2 = 0.9 \). The switching between types is described by the parameters \( M = 0.005 \) and \( r = 20 \). 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 2000a, 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 \( b_2 > dh_y \). 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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