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Consequences of behavioral dynamics for the population dynamics of predator-prey systems with switching

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Abstract This article explores how different mechanisms governing the rate of change of the predator's preference alter the dynamics of predator-prey systems in which the predator exhibits positive frequency-dependent predation. The models assume that individuals of the predator species adaptively adjust a trait that determines their relative capture rates of each of two prey species. The resulting switching behavior does not instantaneously attain the optimum for current prey densities, but instead lags behind it. Several mechanisms producing such lags are discussed and modeled. In all cases examined, our question is whether a realistic behavioral lag can significantly change the dynamics of the system relative to an analogous case in which the predator's switching is effectively instantaneous. We also explore whether increasing the rate parameters of dynamic models of behavior results in convergence to the population dynamics of analogous models with instantaneous switching, and whether different behavioral models produce similar population dynamics. The analysis concentrates on systems that undergo endogenously generated predator-prey cycles in the absence of switching behavior. The average densities and the nature of indirect interactions are often sensitive to the rate of behavioral change, and are often qualitatively different for different classes of behavioral models. Dynamics and average densities can be very sensitive to small changes in parameters of either the prey growth or predator switching functions. These differences suggest that an

understanding of switching in natural systems will require research into the behavioral mechanisms that govern lags in the response of predator preference to changes in prey density.

Keywords Apparent competition · Choice behavior · Predation · Population cycles · Positive frequency dependence · Predator switching

Introduction

Most models of interacting species that have incorporated flexible behaviors have assumed that those behaviors instantaneously attain, or approximate, the optimal behavior, given current conditions (e.g., Holt 1983; Abrams 1984, 1992b; Matsuda et al. 1987; Fryxell and Lundberg 1994; Krivan 1996, 1997; Bernstein et al. 1999; Krivan and Sikder 1999; Van Baalen et al. 2001, Krivan and Eisner 2003). If conditions and population densities reach a stable state, this is usually a good approximation, assuming that transient dynamics are not of interest. However, most environments are seasonal, all are subjected to some level of stochastic perturbations, and many appear to undergo endogenously generated fluctuations (Ellner and Turchin 1995; Kendall et al. 1998). Indeed, such fluctuations are the primary reason why behavioral flexibility is favored. Under these circumstances, the relative speeds of environmental change and adaptive change in characters should influence the dynamics of both the characters and the population sizes of the organisms in question.

Many studies of behavioral choice have noted a lag between when the environment changes and when the behavior reaches a state that is appropriate for the new conditions (e.g., Tinbergen 1960; Pietrewicz and Kamil 1979; Bergelson 1985; Getty 1985; Lawrence 1985; see reviews in Krebs and Inman 1994 and Dukas 1998). The importance of learning (a time-consuming process) in determining choice behavior was discussed by Staddon

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(1983, chapter 9). It is known that adaptive changes in foraging behaviors can have large consequences for interactions between species, and can lead to a bewildering variety of indirect effects (Werner and Anholt 1993; Abrams et al. 1996; Peacor and Werner 1997; Bolker et al. 2003; Werner and Peacor 2003). However, very few of these trait-mediated indirect effects have been examined theoretically using models that lack a stable equilibrium and that incorporate non-instantaneous change in the behavioral trait or traits.

The present article will examine the importance of behavioral lags in determining the dynamics of, and indirect effect in, a system in which a predator exhibits adaptive, flexible choice between two prey species. This choice entails positively frequency-dependent predation, and is known as switching (Murdoch 1969). Switching is adaptive when a tradeoff prevents the predator from maximizing its consumption of both (or all) prey types simultaneously (Murdoch and Oaten 1975; Oaten and Murdoch 1975; Abrams 1987). Switching is important in determining the ability of prey species to coexist (Roughgarden and Feldman 1974; Comins and Hassell 1976), and in altering the predator-mediated indirect effect between prey that do coexist (Holt 1984; Abrams and Matsuda 1996). Empirical studies have often noted that switching is not an instantaneous process (Tinbergen 1960; Bergelson 1985; Hughes and Croy 1993). However, it has been modeled as instantaneous in a range of studies, including Tansky (1978), Teramoto et al. (1979), Matsuda (1985), Matsuda et al. (1987), Abrams (1987), Van Baalen and Sabelis (1999), Post et al. (2000), and Van Baalen et al. (2001). It is desirable to know whether the dynamics in these models are significantly affected by this assumption.

Switching is often measured by documenting how the average preference of a number of predator individuals changes in response to the relative abundance of their prey. Most of the theoretical studies listed in the previous paragraph have assumed, implicitly or explicitly, that predator individuals have the same preference at a given point in time. However, a given pattern of change in preference over time that is measured at the population level may be produced by two different mechanisms. All individuals can gradually shift their prey preference in a similar manner, or individuals can change from one specialization to the other, but do so at different times. It is not known whether these two mechanisms produce different predator-prey dynamics.

In one study that incorporated behavioral dynamics, Abrams (1999) assumed that prey choice was a continuous variable that was similar for all predator individuals, and adopted a model of behavioral change based on an analogy to the adaptive evolution of continuous traits. That study showed that such a mechanism for change could produce very different population and trait dynamics than a similar model with instantaneous change. In addition, the type of dynamics and indirect effects between prey was very sensitive to the absolute rate of change. However, that study left several important

questions unanswered. First, Abrams (1999) only examined a single type of behavioral model, which assumed that, once an individual became highly specialized, it required a long time to alter its behavior. Because of the lack of studies of behavioral dynamics, it is unclear whether that particular assumption is widely applicable. This calls for analyses of other models based on alternative assumptions about the mechanisms underlying behavioral change. Second, because Abrams (1999) did not explicitly compare the length of the lag in switching to the timescale of population dynamics, it is unclear whether the lags that caused major differences in dynamics in those models were unrealistically long. Finally, that study concentrated on the relatively uncommon situation in which the different prey species have identical growth functions. It is therefore important to examine other potential models that produce behavioral lags before concluding that the behavioral dynamics that produce them need to be included in models and studied in natural systems.

Here, we compare the population dynamics produced by several different rules governing the change in predator choice behavior, to determine which, if any, allow behavioral change to be approximated as being instantaneous at the population level. We also determine whether different mechanisms of switching produce significantly different population dynamics and indirect effects between prey. We compare several different models with continuous change at the individual level to models in which an individual can instantaneously change from being a specialist on one prey type to being a specialist on another type, although the population exhibits a lag. We also investigate the consequences of the assumption made in Abrams (1999) that the rate of change of the behavior slows once the predator has become very specialized. In all of the models studied, we explicitly examine the lag in the actual choice variable compared to the optimal value of that variable. Our goal is to examine a wide range of possibilities to determine whether different plausible rules for the dynamics of choice can alter population dynamics, rather than exhaustively analyzing parameter space for any single model.

Before considering cycling models with switching, we note the outcomes expected in models that have a stable equilibrium. When a 1 predator:2 prey system has a stable equilibrium and there is no switching (e.g., Holt 1977), decreasing the intrinsic growth rate of one prey species increases the population density of the other prey species, by causing a decrease in the predator population. (Increasing the intrinsic growth rate of one prey species has the opposite effects.) In a stable system with switching and a linear tradeoff between the predator's attack rates on two prey, there is no effect of changing the intrinsic growth rate of one prey on the density of the other (Holt and Kotler 1987). If there is direct predator density dependence, mutualistic effects may also occur (Holt 1977, 1984; Abrams and Matsuda 1996), but such density dependence is not considered in the models we

analyze here. A non-linear tradeoff in which a generalist strategy is favored at all points in time results in apparent competition in stable systems, but the magnitude of the competitive effect is much lower than in systems without switching (Abrams 1987; Abrams and Matsuda 2003).

Models

Population dynamical assumptions

We consider a model in which individuals of one predator species search for two prey species within a single habitat where the two prey types are homogeneously distributed. Because it is assumed to exhibit satiation, the predator is assumed to have disk equation (Holling 1959) functional response. The prey species have logistic growth with a small amount of outside immigration. Immigration of prey prevents population cycles from having unrealistic amplitudes. In addition, because prey can occur in habitats where their density is too low to support the predator, they are likely to be more widely distributed than their predators, and immigration from other areas is likely. The restoration of offshore populations of the Japanese sardine during the 1970's via immigration from coastal areas is a potential example (Matsuda et al. 1992). Here, we investigate two types of models. In the first, the individuals in the population all have a similar prey choice, but this choice trait changes continuously over time within individuals. Continuous change is often expected when learning to recognize a previously-ignored prey type requires practice. In the second type of model, individuals may specialize on either prey type, and may switch from being a complete specialist on one type to being a complete specialist on the other without any intervening stages.

In the first type of model (monomorphic predators), the attack rates on the two prey types are assumed to be linearly related, and both are determined by a single trait, denoted z . The attack rate on prey 1 is C_1z , and that on prey 2 is $C_2(1-z)$. The dynamics of the predator, with population N , and the two prey species, with populations R_1 and R_2 , are given by:

$$\begin{aligned} \frac{dR_1}{dt} &= i_1 + r_1R_1 \left(1 - \frac{R_1}{K_1}\right) \\ &\quad - \frac{C_1(z)R_1N}{1 + h_1C_1zR_1 + h_2C_2(1-z)R_2}, \\ \frac{dR_2}{dt} &= i_2 + r_2R_2 \left(1 - \frac{R_2}{K_2}\right) \\ &\quad - \frac{C_2(1-z)R_2N}{1 + h_1C_1(z)R_1 + h_2C_2(1-z)R_2}, \\ \frac{dN}{dt} &= N \left(\frac{B_1C_1(z)R_1 + B_2C_2(1-z)R_2}{1 + h_1C_1(z)R_1 + h_2C_2(1-z)R_2} - D \right). \end{aligned} \quad (1a-c)$$

The parameters in the system are:

- r_j , the intrinsic growth rate of prey j ;
- K_j , the carrying capacity of prey j ;
- i_j , the immigration of prey j into the system;
- C_j , the per capita capture rate of prey j by a searching predator individual having maximum specialization on prey j ;
- h_j , the handling time for an item of prey j ;
- B_j , the energy (or limiting nutrient) content of an individual of prey j ;
- D , the per capita death rate of the predator;
- z is a trait which determines the prey preference; note the linear relationship and the possibility of complete specialization on either prey.

Equations 1 are supplemented by an equation for the dynamics of the mean value of the trait z . Because we assume individuals have a narrow range of trait values, and because the fitness of a predator with a given z does not depend directly on the mean trait, we do not need to distinguish between an individual's z and the population mean. The model of trait dynamics is based on the following propositions:

1. The rate of change in the mean choice behavior increases when there is a greater rate of change in the instantaneous rate of increase with a unit change in the behavior (we refer to this as a 'fitness gradient', but it is based on an instantaneous rather than lifetime measure of fitness);
2. When the mean choice trait is close to an extreme value ($z=0$ or 1) random sampling of different behaviors tends to push its value away from that extreme;
3. The rates of adaptive sampling or the responsiveness of behavior to a given fitness gradient may decrease as the choice trait approaches an extreme value.

Proposition 1 is based on the observation that the rate of change in a learned behavior increases with the amount of the reward (Staddon 1983; Dukas 1998). When the difference in rewards from alternative behaviors is very small, it will be difficult to detect, which also tends to make the rate of change decrease when the fitness gradient becomes small. Trait dynamics based on a fitness gradient have been shown to arise from several behavioral processes (Boyd and Richerson 1985; Taylor and Day 1997), and have been incorporated into several previous models of behavioral dynamics (Abrams 1992a, 1999; Ma et al. 2003). Proposition 2 is based on the fact that, when most individuals have a limiting or nearly limiting behavior, random sampling must cause change to a more intermediate value. Proposition 3 is based on the fact that behavior only becomes very extreme when that extreme has been optimal for some time: under these circumstances, it would be adaptive to decrease sampling. Proposition 3 is also appropriate when adaptation is based on variation that becomes depleted when the trait value becomes extreme. These propositions are reflected in the following basic model:

$$\frac{dz}{dt} = v(z)\phi\left(\frac{\partial W(z)}{\partial z}\right) + \mu(z) \quad (1d)$$

where W denotes the instantaneous per capita growth rate of individuals with trait z . It is important to note that W is not lifetime fitness, but rather the instantaneous probability of birth minus the probability of death, which reflects the current food intake rate. Thus, it is possible for an individual's trait to change repeatedly during its lifetime.

Describing trait dynamics using Eq. 1d assumes a narrow distribution of trait values within the population (Abrams et al. 1993). If there were a broad distribution of trait values, an integral of $\partial W/\partial z$ over the distribution would be required to describe the rate of change of the mean. The scaling function, v , relates the fitness gradient to the amount of change produced in the character; it reflects the amount of adaptive behavioral sampling and flexibility. This function may simply be a constant, or it may be a unimodal function of the mean trait value. The function ϕ relates the fitness gradient to the amount of change in the character produced per unit time. It must be an increasing function with a value of zero when its argument is zero. Finally, the function μ reflects sampling, following from proposition 2 above. The function μ has a positive value when z is close to 0 and a negative value when z is close to 1. One role that this function serves is to keep the trait from crossing the biologically defined bounds of 0 or 1; this is necessary if v does not approach 0 when the mean trait approaches 1 or 0. The model studied in Abrams (1999) assumed that ϕ was the identity function, that $\mu=0$, and that v approached zero when z approached either 0 or 1. The latter two assumptions resulted in long time lags between when the relative abundances of prey types shift and when a specialized individual responds significantly to that change. These lags were lengthened by the lack of prey immigration in the models of Abrams (1999), as noted in the discussion below.

The second type of model investigated here (dimorphic predators) assumes that individuals are able to instantaneously switch, but the population exhibits a lag. The model has the following form:

$$\begin{aligned} \frac{dR_1}{dt} &= i_1 + r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - \frac{C_1 R_1 N_1}{1 + h_1 C_1 R_1}, \\ \frac{dR_2}{dt} &= i_2 + r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - \frac{C_2 R_2 N_2}{1 + h_2 C_2 R_2}, \\ \frac{dN_1}{dt} &= N_1 \left(\frac{B_1 C_1 R_1}{1 + h_1 C_1 R_1} - D\right) \\ &\quad + N_2 m \left(\frac{B_1 C_1 R_1}{1 + h_1 C_1 R_1} - \frac{B_2 C_2 R_2}{1 + h_2 C_2 R_2}\right) \\ &\quad - N_1 m \left(-\frac{B_1 C_1 R_1}{1 + h_1 C_1 R_1} + \frac{B_2 C_2 R_2}{1 + h_2 C_2 R_2}\right), \end{aligned}$$

$$\begin{aligned} \frac{dN_2}{dt} &= N_2 \left(\frac{B_2 C_2 R_2}{1 + h_2 C_2 R_2} - D\right) \\ &\quad - N_2 m \left(\frac{B_1 C_1 R_1}{1 + h_1 C_1 R_1} - \frac{B_2 C_2 R_2}{1 + h_2 C_2 R_2}\right) \\ &\quad + N_1 m \left(-\frac{B_1 C_1 R_1}{1 + h_1 C_1 R_1} + \frac{B_2 C_2 R_2}{1 + h_2 C_2 R_2}\right). \end{aligned} \quad (2)$$

The function $m(\Delta)$ describes the probability of making a transition from the current feeding type to the other type as a function of the difference, Δ , between the food intake rate of the other type and the current food intake rate; m is always positive, and increases as its argument increases. In our analysis, we use the following function to describe the per capita rate of making a transition from type j to type i :

$$\begin{aligned} m &\left(\frac{B_i C_i R_i}{1 + h_i C_i R_i} - \frac{B_j C_j R_j}{1 + h_j C_j R_j}\right) \\ &= M \exp\left(\lambda \left(\frac{B_i C_i R_i}{1 + h_i C_i R_i} - \frac{B_j C_j R_j}{1 + h_j C_j R_j}\right)\right), \end{aligned} \quad (3)$$

where M represents the per capita transition rate when food intake rates of both types are equal, thus reflecting sampling behavior. The other rate constant in this model is λ , which is a positive constant whose magnitude determines the sensitivity of transition rates to the difference in food intake rates between types. Movement increases at an accelerating rate with the difference between the fitness of the two types.

Because we are interested in comparing the consequences of instantaneous and non-instantaneous choice, we contrast the dynamics of both types of systems described above with those of comparable systems in which the optimum choice trait or optimum distribution of predators into the two specialist types instantaneously approximates the optimal value for current prey densities. In the monomorphic model, the optimal z may be approximated by the following formula:

$$z_{\text{opt}} = \frac{(R_1)^u}{(R_1)^u + \left(\frac{B_2 C_2 R_2}{B_1 C_1 - C_1 C_2 R_2 (B_1 h_2 - B_2 h_1)}\right)^u}, \quad (4)$$

where u is a large positive constant ($u=30$ in most of the following). This function approximates the step function describing the optimal z as a function of prey densities. Note that the expression simplifies considerably when the two prey have equal profitability ($B_1/h_1 = B_2/h_2$): the second term in the denominator is then $[B_2 C_2 R_2 / (B_1 C_1)]^u$. Equal profitability is assumed in most of our numerical analyses. The corresponding approximation to the optimal value of Z (i.e., the fraction of individuals specialized on prey 1) in the dimorphic model is:

$$Z_{\text{opt}} = \frac{I_1^u}{I_1^u + I_2^u} \quad (5)$$

where I_i is the current food intake rate of a specialist on prey i , $I_i = B_i C_i R_i / (1 + C_i h_i R_i)$, and u is again a large positive constant.

The type-2 functional response in Eqs. 1 and 2 is known to be capable of generating population cycles. We are interested in systems that display cycles, because they usually make the relative abundances of the two prey types change over time, which is what makes behavioral switching advantageous. The local stability conditions for Eqs. 1 or 2 are quite complicated, but when there is a non-zero handling time and density dependence in prey growth is not too strong, then an efficient predator will generate cycles. Efficiency can result from a low per capita death rate, D , or high attack rates, C_i . Because we are interested in comparing the consequences of different mechanisms for switching, we use a common set of parameters in each model.

Monomorphic models with instantaneous optimization

Instantaneous optimization models simply substitute the expression for z_{opt} given by Eq. 4 for z in Eqs. 1. Stable systems must be characterized by equal intake rates of both prey when the B , h , and C parameters are equal. When the two prey cycle, equality of intake rates can only be maintained when both prey have similar intrinsic growth rates, r . Given a large difference in growth rates, the predator population, when it is low, cannot control the growth of the faster growing prey, so that prey can reach quite high densities before the predator's own increased population is able to reduce the faster growing prey to a density similar to that of the slower growing species. Figure 1 presents some examples showing how the dynamics of the instantaneous monomorphic model change as a function of the disparity in growth rates of the two prey, when there are predator-prey cycles. (A brief description of numerical methods is included in the legend for Fig. 1.) When there is little difference between the growth rates of the two prey species, they have approximately synchronized cycles with approximately equal abundances (given similar growth functions). When the difference in growth rates becomes greater, the slower growing prey has a much smaller average abundance, and its increase phase lags behind that of the faster growing prey. The top part of Fig. 1 shows how the long-term average densities of both prey change when the intrinsic growth rate of prey 2 is varied from nearly zero to twice that of prey 1. This part of Fig. 1 reveals that changes in the intrinsic growth rate of prey 2 have relatively little impact on the mean density of prey 1. The change in the average R_1 caused by a decrease (for example) in r_2 may be either positive or negative, but is generally small. The mean density of prey 2 is also relatively insensitive to its own intrinsic growth rate until that becomes very small. The patterns of dynamics versus relative prey growth are sensitive to the efficiency of the predator and its demographic rates. A less efficient predator produces less extreme cycles, and is thus better

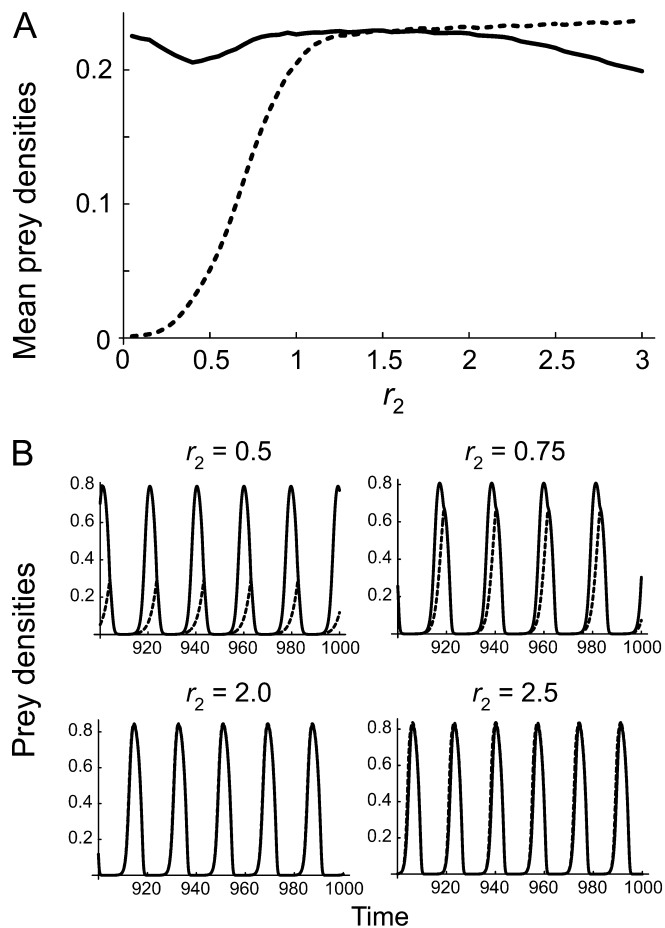


Fig. 1 Average prey densities as a function of r_2 (A); and sample population dynamics (B) for different values of r_2 in a model with instantaneous switching. In both panels, the *solid line* denotes prey species 1 and the *dashed line* denotes prey species 2. The parameters are: $r_1 = 1.5$, $K_i = 1$, $h_i = 1$, $b_i = 1$, $D = 0.3$, $C_i = 5$, $i_i = 0.0001$, and $u = 30$. Slight wiggles in the lines for average population sizes are because the timespan used to average densities was not an integer multiple of the cycle period, and cycle period differed with r_2 . In B, the slight differences between the two prey when $r_2 = 2$ are not visible because of the small scale of the graph. Numerical integration in this and subsequent figures was carried out using Mathematica 5.0 (Wolfram 2003). The initial conditions for each integration were the final conditions of the integration with the previous value of r_2 ; this procedure was carried out by both increasing and decreasing the value of r_2 to determine whether there were alternative attractors

able to maintain equality of intake rates from the two prey. Slower predator dynamics make the predator's fluctuations less extreme, and again lead to approximate equality of intake rates over a wider range of relative prey growth rates.

The parameter u in Eq. 4 reflects the accuracy of switching, with smaller values of u implying a more generalized diet for any given relative abundance of prey. Simulations with values of u close to 1 (less accurate switching) increase the synchrony between the two populations, but they also increase the negative indirect effect on the prey characterized by the lower growth rate (see Abrams and Matsuda 2003).

Monomorphic models with trait dynamics

The class of monomorphic models with behavioral change governed by Eq. 1d can differ in the presence and nature of the three component functions, ϕ , v , and μ . The previous work employing a special case of Eq. 1d (i.e., Abrams 1999) assumed that ϕ was the identity function, μ was 0, and v had a form that approached 0 as the trait approached either 0 or 1. The demographic model in that paper assumed 0 immigration of prey. Here, we explore three alternative sets of assumptions about these functions, examining the behavioral and population dynamics entailed by each set. To compare models, we concentrate on a single set of values for most parameters; the dependence of results on these values is discussed at the end of the section.

First monomorphic model

We begin with the simplest set of assumptions. The function ϕ is the identity function, so the rate of change of the character is proportional to the fitness gradient. The function v is a positive constant, V_0 , which describes how rapidly the behavior changes for a given fitness gradient. The function μ is very small unless the trait is very close to one of its limiting values: here it has the form $\epsilon/z - \epsilon/(1-z)$, where ϵ is a very small positive constant (0.00001 in the examples illustrated here). This function prevents the trait from going below 0 or above 1, but otherwise has little effect unless the fitness gradient is extremely small: behavioral change towards an extreme value only slows when the trait approaches that extreme closely, and behavioral change away from an extreme value is not changed significantly. Figure 2 shows both the average densities over a range of values of r_2 and examples of the time course of the two prey species at specific values of r_2 , for an example otherwise comparable to that in Fig. 1. Figure 2 shows that a given increase in r_2 may have a positive or negative effect on the density of prey species 1, depending on the initial and final values of r_2 . Both complex cycles (in which adjacent maxima of a given variable have different values) and chaotic dynamics occur for some values of r_2 (chaos was determined by computing Lyapunov exponents). The average densities differ in several ways from those shown for the corresponding instantaneous model in Fig. 1. In Fig. 2, but not Fig. 1, increasing r_2 increases the mean density of prey 1 and decreases the mean density of prey 2 when the two intrinsic growth rates are initially similar. Increasing r_2 has a much stronger negative effect on the density of prey 1 when r_2 is initially significantly greater than r_1 than it does in Fig. 1. The very low density of prey 2 when $r_2 < 0.25$ in Fig. 2 suggests that exclusion would occur for these parameters in a finite population without external input of individuals. This was not the case in the instantaneous model.

One reason for the difference between models is that, when change in the trait is proportional to the fitness

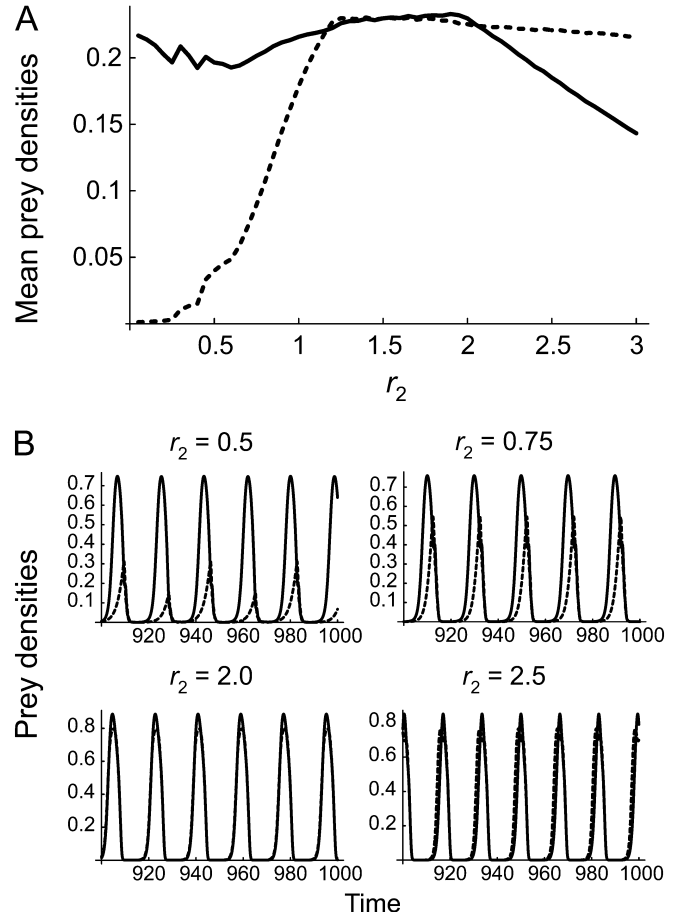


Fig. 2 The average densities of the two prey species as a function of r_2 in a switching model with dynamics based on the first monomorphic model (A), and examples of the corresponding temporal dynamics of the prey (B). As in Fig. 1, prey species 1 is denoted using a solid line, and prey species 2 using a dashed line. Parameters are: $r_1 = 1.5$, $K_i = 1$, $\epsilon = 0.00001$, $h_i = 1$, $b_i = 1$, $D = 0.3$, $C_i = 5$, $i_i = 0.0001$, $V_0 = 15$

gradient, change becomes very slow when both prey are rare; the cycles generated by the predator ensure that there are long periods when both prey are rare. The effects of these periods of low densities of both prey can be seen in Fig. 3, which shows both the prey densities, the value of z given by Eq. 1d, and the corresponding instantaneous optimum value of z (dashed line in the top panel). The longest lags in the response of the trait z , relative to the optimum (e.g., from approximately time 975 to 983), occur when both prey have very low densities, so the fitness gradient is very small. However, lags are not confined to situations with low densities of both prey. Each time there is a switch in the most rewarding prey, the difference in rewards is initially small. Thus, when prey 2 briefly becomes more abundant (e.g., near time 991.5), the lag in the consumer's response has a considerable impact on prey dynamics, in spite of the fact that both prey densities are relatively high and the lag is relatively short.

The lag in the behavioral response is reduced when the adaptive rate constant V_0 is larger. However, significant

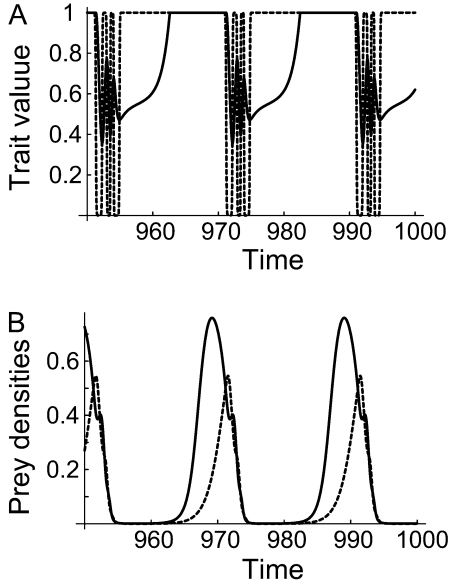


Fig. 3 **A** A comparison of the currently ‘optimal’ value and the actual value of the choice trait z in the example shown in Fig. 2 for $r_2=0.75$. The actual value is given by the *solid line*, while the current optimum is the *dashed line*. **B** The corresponding prey densities: prey 1 is the *solid line* and prey 2 is the *dashed line*

differences between this model and the instantaneous adaptation model occur over a wide range of adaptive rates. The value adopted in Figs. 2 and 3 ($V_0=15$) represents a biologically realistic value for behavioral change. It implies that the trait can change from 0.1 to 0.9 in 0.384 time units, given the parameters used in Figs. 2 and 3, when prey densities are fixed at $R_2=0$ and $R_1=1$. Given the per capita death rate of $D=0.3$ used in these figures, 10.88% of the population alive at the beginning of this time period would have died by the end. The behavioral timescale is thus significantly faster than the population dynamical scale, although some real behaviors are no doubt capable of much more rapid change. Significant differences between the instantaneous and non-instantaneous models are still present when the rate constant for behavioral change is increased an order of magnitude from its value in Figs. 2 and 3 (to $V_0=150$). A more efficient predator (lower D) or greater intrinsic growth rates of both resources increase the difference between instantaneous and dynamic models of this first type in the simulations we have run.

Second monomorphic model

The second monomorphic model is comparable to that used by Abrams (1999). The scaling function v is assumed to decrease significantly as the trait approaches either extreme value and to decrease the rate of change in either direction when the predator is relatively specialized. Here, we use one of the two functions employed in Abrams (1999):

$$v(z) = V_0 \exp \left[\frac{-s}{z(1-z)} \right] \quad (6)$$

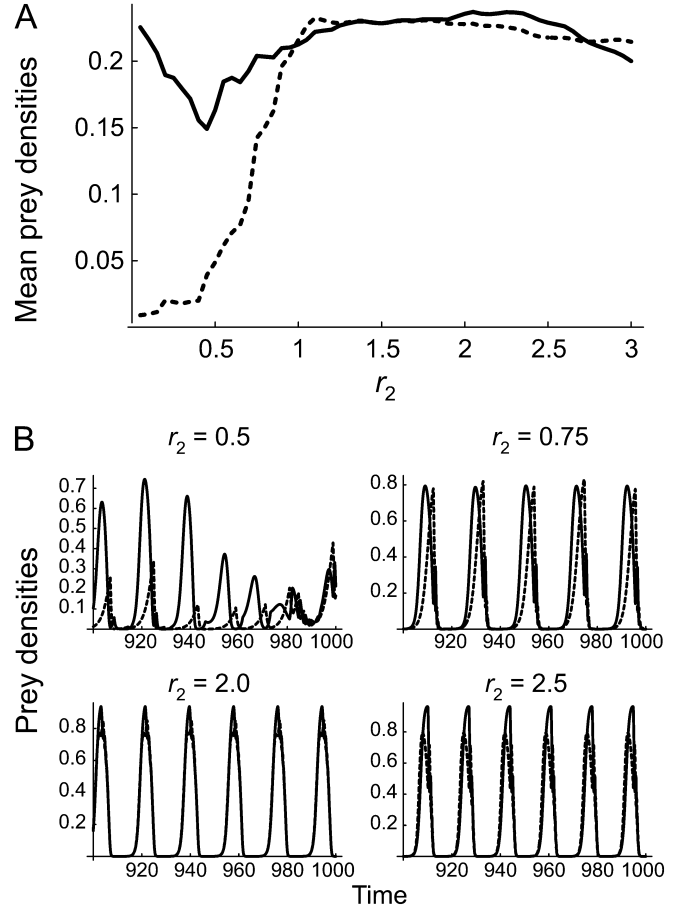


Fig. 4 Mean prey densities (**A**) and population dynamics (**B**) corresponding to different intrinsic growth rates, r_2 , in the second monomorphic model based on the scaling function, Eq. 6 with $s=0.2$ and $V_0=150$. Other parameters are as in Figs. 1 and 2. The *solid line* denotes prey 1 and the *dashed line* denotes prey 2

where s is a small positive constant. This function approaches 0 as z approaches 0 or 1.

The model with this scaling function produces dynamics that are quite different from the comparable instantaneous model. These dynamics are characterized by greater asynchrony in the prey populations. Figure 4 shows some examples of the population dynamics and the average density as a function of r_2 for a system comparable to those shown in Figs. 1 and 2. The erratic changes in mean densities with the intrinsic growth rate of prey 2 when $r_2 < 1$ result from abrupt shifts between qualitatively different types of dynamics, e.g., cyclic versus chaotic. The four specific examples shown in the bottom half of the figure include an example of chaotic dynamics ($r_2=0.5$), which is much more common in this model than in Fig. 2. The extremely low density of prey 2 when $r_2 < 0.25$, seen in Fig. 2, does not occur in this case. Figure 5 shows the difference between the temporal changes in the choice trait, z , and the changes in the corresponding optimal z at any given instant. The qualitative pattern of changes in actual and optimal traits is similar, but the scaling function produces a

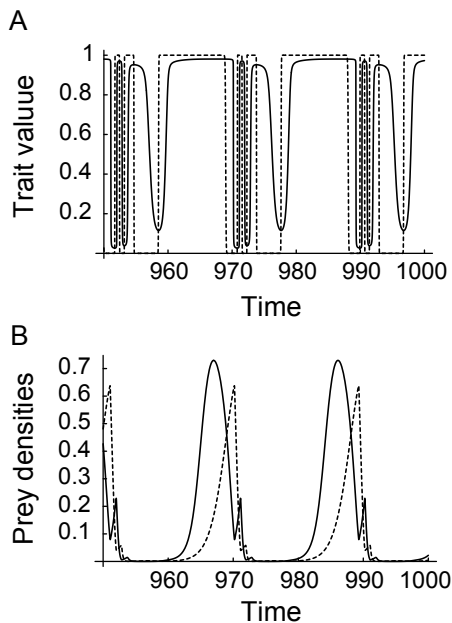


Fig. 5 The dynamics of the choice trait (A) and the prey species (B) when the predator's behavior changes according to the second monomorphic model, as in Fig. 4. The parameter values are identical to those in Fig. 4, except $r_2 = 0.7$. The scaling function, v , is given by Eq. 6, and has a parameter $s = 0.2$. In A, the actual trait is the *solid line* and the current optimum is the *dashed line*. In B, prey 1 is the *solid line* and prey 2 is the *dashed line*

behavioral lag that is usually in the order of one time unit or less.

The effect of increasing the rate constant, V_0 , by an order of magnitude (to 1,500) is surprisingly small. This decreases the amount of time that z has intermediate values, but it does not greatly reduce the lag between a shift in the optimal z and the actual z . This is because the greater specialization caused by a high V_0 when a particular extreme is optimal counteracts the effect of a high V_0 once the optimal z has shifted to the other extreme value.

Third monomorphic model

The final monomorphic model examined here differs from the first one (Fig. 2) in having a nonlinear function ϕ relating the fitness gradient to the rate of behavioral change. Specifically, we assume that ϕ is given by the gradient cubed. This sort of relationship is expected if the detectability of a given difference in densities is nonlinearly related to the difference. It makes change slower when the gradient is small. Results will not be presented here, but the difference between the instantaneous and dynamic models was increased by this change in the form of ϕ . This increase appears to be due to the greater lag in adaptive change that occurs when both prey populations are rare.

Instantaneous dimorphic models

These models assume that individuals consume either prey 1 or prey 2, but not both at any point in time. The

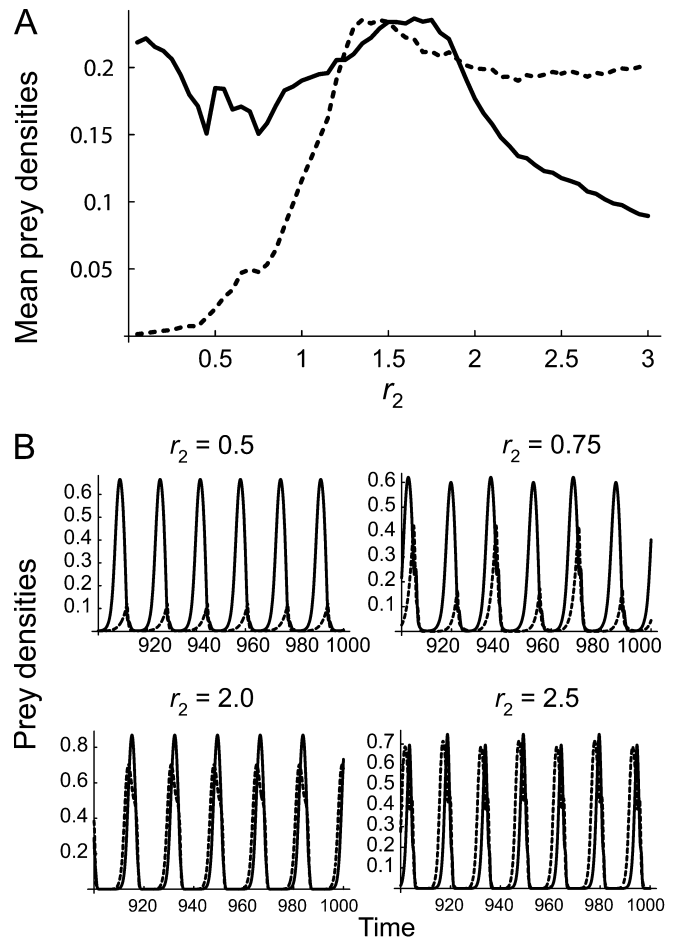


Fig. 6 The mean prey densities (A) and dynamics (B) produced by the dynamic, dimorphic predator model, Eqs. 2 and 3, for the parameter values used in Fig. 1. The parameters specific to the dimorphic model are $M = 0.05$ and $\lambda = 30$. As before, prey 1 is denoted by the *solid line*, and prey 2 is denoted by the *dashed line*

proportion of individuals of type 1 (consuming prey 1) is given by Eq. 5. The dynamics produced by this model are almost identical to those produced by the instantaneous monomorphic model (see Fig. 1), so they will not be illustrated here. This is not surprising, given that the optimum strategy at most points in time in the monomorphic model is to be a specialist, so there is little actual difference between the two.

Dynamic dimorphic models

The dimorphic model based on Eqs. 2 differs from the corresponding instantaneous model in that shifts between the two phenotypes occur more slowly, with the rates depending on the parameters M and λ , and the difference in intake rates between the two specialist types. Figures 6 and 7 continue our comparison of models using a standard parameter set, and show that the dynamics of the dimorphic model differ substantially from those of all monomorphic models. The mean densities of the two prey change with r_2 in a manner that differs from the pattern in

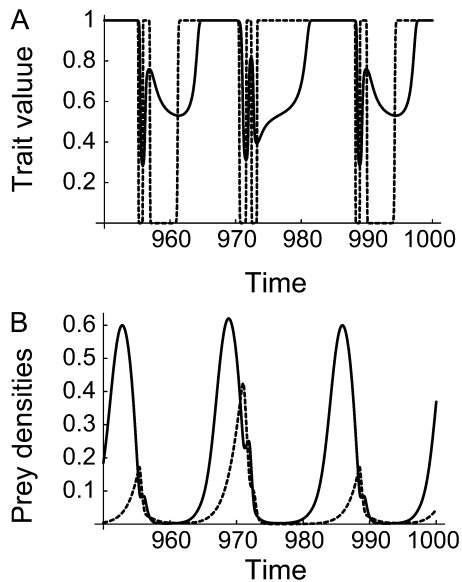


Fig. 7A, B The dynamics and lags in a dynamic dimorphic model based on Eqs. 2 and 3, using the same parameters as in Fig. 6 with $r_2=0.7$. **A** shows the proportion of individuals consuming prey 1 (*solid*) and the optimum proportion given current densities (*dashed*). **B** shows the population dynamics of the two prey corresponding to the dynamics of relative predator numbers shown in **A** (prey 1 is the *solid line* and prey 2 is *dashed*)

previous graphs. Like the other dynamic models, the density of one prey is more sensitive to the growth rate of the other prey than is true in the instantaneous model. Figure 6 differs from Fig. 2 in having generally larger effects of a given change in the growth rate of prey 2 on the mean density of prey 1. It differs from Fig. 4 in exhibiting a much larger negative effect of increased r_2 on R_1 when $r_2 \gg r_1$. The advantage of the slower-growing prey when both prey have similar growth is more pronounced in Fig. 6 than in either Fig. 2 or Fig. 4. It is difficult to define what constitutes an equal rate of switching for models as different as the monomorphic and dimorphic models used here. However, the qualitative differences between Figs. 2 and 6 are found across a range of other rate constants for both models. The change in the distribution of the two predator types over time, given in Fig. 7, shows that, as in the monomorphic models, there is a significant delay in completing the process of switching when both prey are rare.

The dimorphic model has two rate constants, M and λ , and more rapid shifts can be produced by increasing either one. Increasing M by as much as 5-fold (to 0.25) had very little effect on the results shown in Fig. 6. Large increases in λ caused major problems in numerical integration, but moderate increases (e.g., from 30 to 40) did little to change the outcomes shown in Figs. 6 and 7.

Dependence of dynamics on parameter values

The comparison of the different models presented above is of course dependent on parameter values and

functional forms for the components of the model. Some of the results may also depend on initial conditions. A complete exploration of the dynamics of even one model would require a huge amount of numerical work. Here, we only note some of the factors that are important in producing the patterns shown. All of the models considered yield very similar equilibrium points when the system is stable. Sufficiently larger values of the predator per capita death rate, D , or smaller values of the attack rates, C_i , stabilize the system. Even before the equilibrium is locally stable, however, such changes reduce the differences between models by reducing the amplitude of cycles. The immigration rate of prey can have a significant effect on dynamics. Higher immigration rates increase the minimum population densities of the prey, and therefore reduce the length of the periods when both prey are at low densities and adaptive change is very slow. This makes the dynamics produced by all models more similar to each other. In general, factors that promote synchrony in the prey dynamics lessen the difference between models. Thus, having a high minimum capture rate of both prey, regardless of z , reduces the difference between the dynamics of different models.

Are all types of switching adaptive?

Thus far, we have not shown that switching based on any of the above models is adaptive relative to the absence of switching. This is a reasonable question, particularly for the ‘second monomorphic model’ in which switching individuals can get stuck consuming the less rewarding prey for significant periods of time. We have simulated many cases of competition between a species with a fixed value of z and each of our behaviorally flexible populations. In almost all cases, the inflexible consumer species declined towards extinction. The one exception to this generalization that we observed was when the two prey had identical growth functions and the ultimate dynamics of the system was perfectly synchronized cycles of both resources. This case eventually resulted in both switching and non-switching consumers being characterized by a constant $z=0.5$. Thus they were competitively equivalent. Competition between different types of switching consumers is mentioned in the Discussion below.

Discussion

The impact of behavioral dynamics on population dynamics and indirect interactions

Although the cases presented here certainly do not exhaust the range of potential models, they show that models with instantaneous optimization may give misleading predictions regarding systems in which behav-

ioral change is dynamic. The differences between instantaneous and dynamic models of behavior include qualitative differences in the type of non-equilibrium dynamics, differences in average densities and coexistence conditions, and differences in the sign characterizing the indirect interactions between prey. All of the dynamic models we considered (Figs. 2, 4, and 6) predicted a greater sensitivity of the mean density of one prey to the growth rate of the other than did the instantaneous model (Fig. 1). However, for particular parameters, the dynamic models of behavior can predict similar population dynamics: both predict closely correlated cycles when the two prey are characterized by similar growth and vulnerability parameters. However, all of the dynamic models investigated here produce dynamics that differ significantly from those produced by instantaneous models over significant ranges of parameter values when there were high amplitude population fluctuations and a moderate or large disparity in the intrinsic growth rates of the two prey species. Furthermore, the dynamic models all differed in some important respects from each other. For example, the model with slow change in highly specialized individuals (Fig. 4), was much more likely to predict chaotic dynamics than the other dynamic models. The corresponding monomorphic and dimorphic dynamic models shown in Figs. 2 and 6 have some similarities, but also significant differences. For example, the dimorphic model (Fig. 6) predicts stronger indirect interactions, and a much larger population size advantage for the slower growing prey when both intrinsic growth rates are similar.

The set of parameters we illustrated in the figures here was not chosen to maximize the difference between different models of switching. While we could not explore parameter space completely, our simulations suggest that increasing prey immigration sufficiently reduced the differences between dynamics produced by different models. Reducing the demographic rates of the predator, while keeping the rate of adaptive change constant (reducing B and D by equal proportions and increasing ν or λ by the inverse of that proportion) also resulted in much smaller differences between different types of models. Thus, assuming instantaneous behavioral change may be an adequate approximation in many cases. However, our results argue that this cannot be assumed without knowing a lot about the rates of population and behavioral change.

The results obtained here for the ‘second monomorphic model’ differed in one major respect from those obtained by Abrams (1999), who employed a model that was identical except that it did not include immigration of prey from outside the system. The system without immigration often displayed asynchronous dynamics of the two prey when they had identical growth functions. The lack of immigration allowed cycles of very high amplitude, characterized by long periods where both prey were very rare. In these cases, the lack of random behavioral change meant that the predator’s choice trait

would remain at the value it had when both prey crashed until one of the prey recovered: because this value usually differed from $z=0.5$, the periods of relative constancy in z promoted asynchrony between prey. Such asynchrony of prey with identical growth functions occurred over a narrower range of rate parameters, ν , in the simulations of our ‘second monomorphic model’ than in Abrams (1999) because prey immigration reduced these long periods of behavioral stasis. Asynchrony was also greatly reduced for prey with identical growth functions when there was a significant amount of random behavioral change, as in the ‘first monomorphic model’.

We have quantified the indirect interaction between prey by determining how the average density of one prey species is changed by an increase in the intrinsic growth rate of the other prey. In systems with both switching and population cycles, this interaction differs from that in stable systems, where there is no effect of changing r_i on R_j given switching with a linear trade-off (Holt 1984; Holt and Kotler 1987). One of the characteristics of all of the models considered here is that a favorable change in the growth conditions for one prey species (e.g., increased r_2) can cause a decrease in its own density, and may also cause an increase in the density of the other prey species. The conditions for these two outcomes are not identical. Further, the plots of the density of each prey species as a function of r_2 presented above are often multi-modal. This makes it problematical to describe the indirect interaction between a pair of prey by using a simple pair of + or – signs.

Cycling and stable systems differ in their indirect effects, regardless of the model of behavioral change. In all of the cycling systems we have illustrated, the sign of the effect of a decrease (or an increase) in r_2 on R_1 depends on the initial and final values of r_2 . However, the indirect interaction between prey species also differs significantly between instantaneous and dynamic models of behavior, and between the different types of dynamic model that we have investigated. This suggests that it is important to know something about how behavior changes over time to predict the impact of factors affecting the growth of one prey species on the density of the other. This is significant because there have been almost no studies of the nature of behavioral dynamics. For most systems where switching has been studied, we do not know whether individuals that become very specialized take longer to detect a change in the density of an alternate prey. Similarly, we do not know how prey choice changes when both (or all) prey species have low densities. We often do not know whether individuals must change their prey choice gradually (as in the monomorphic model) or can switch completely in an instant (as in the dimorphic model). The relative rates of change in behavior, prey populations, and predator populations have apparently not been studied in systems with switching. All of this calls for more empirical work.

There are some common features of the various dynamic models of change when compared to a similar

instantaneous model. The indirect effects in dynamic models are generally larger in magnitude than those in instantaneous models. For most initial and final values of r_2 , the change in the density of prey 1 that is produced is greater in the dynamic models than in the instantaneous models of switching. This can be explained by the lower correlation in the densities of the two prey species in the dynamic models of behavior. When prey densities are perfectly correlated (true for all models when $r_1 = r_2$), the effects of r_2 on predator density are offset by the splitting of the predator's foraging effort across the two prey. When the prey often have quite different densities at a given point in time, the latter effect is reduced. When the two prey initially have the same intrinsic growth rate ($r_1 = r_2 = 1.5$ in the figures), then decreasing r_2 has the somewhat paradoxical effect of reducing the density of prey 1 in the dynamic models: this is particularly pronounced in the dimorphic model (Fig. 6). This is also explained by the larger asynchrony in prey dynamics when their growth rates differ by a greater amount. The asynchrony again reduces the benefit gained from splitting the predator's foraging effort.

Abrams and Matsuda (2003) analyzed models in which switching is instantaneous, but becomes greatly reduced (the predator becomes a generalist) when both prey densities are low. The dynamics produced by this type of model have several similarities with those illustrated here. In particular, when prey species differ in their intrinsic growth rates, their cycles tend to become asynchronous. This is because the predator becomes generalized when both prey species have low densities, which makes the slower growing prey much later in its recovery following a decline in predator numbers. As a result, when two prey initially have similar growth rates, increasing or decreasing the growth rate of one prey decreases the mean density of the other.

Empirical evidence

Although the dynamics of switching itself have not received much attention, the long-term population dynamics of systems in which switching almost certainly occurs have been studied at least once. Bonsall and Hassell (1997, 1999) explicitly investigated apparent competition in an experimental arena in which a parasitoid was able to move across a barrier that separated containers, each with a different host species. Almost any sort of adaptive foraging by the parasitoid should have led to switching in this experimental setup, and there should have been a close-to-linear trade-off due to the habitat separation. Yet, contrary to the expectation based on stable models, apparent competition occurred in this system, and led to the exclusion of the slower-growing of the two prey species. The initial dynamics before exclusion illustrated in Bonsall and Hassell (1997) appear to show asynchronous oscillations in the two prey species.

The models we have analyzed argue that the population dynamics of systems with switching differ

greatly depending on some features that, to our knowledge, have never been measured. However, the dynamics can also be changed greatly by relatively small changes in the form of the population growth model; e.g., adding a small amount of prey immigration, compared to no immigration, as in Abrams (1999). Thus, it is premature to make predictions about the dynamics or indirect interactions in specific natural systems. The current results do, however, argue that it is important to find out more about behavioral dynamics if one wants to understand systems with switching predators.

Extensions of the models

One of the limitations of the models considered here is that only two prey species are present. It is possible to extend these models to represent a system with three or more prey. However, a much greater range of trade-offs is possible in this case, as well as a much broader range of options for constructing a scaling function. In many cases, the Lagrange Multiplier approach used in Matsuda et al. (1996) can be used to extend the two-prey model to situations with more prey species.

We have modeled the predator population based on the assumption that all individuals have a similar trait value. This is expected when individuals with initially different trait values rapidly converge on a similar strategy. We have checked this for the system studied here, and rapid convergence does occur for the cycling systems we have simulated. However, we have not considered the possibility of between-individual variation in the trade-off function or other population parameters. If present, such variation may significantly change the nature of switching within the population as a whole.

We have assumed that both prey occur in the same habitat, so that switching entails different search techniques. Many cases of switching in nature are likely to involve prey species that occur in different habitats, so that simultaneous search for both species cannot occur. Limited results for switching in two-habitat models are presented in Abrams (1999, 2000). The dimorphic models considered here are applicable to a two-habitat form of switching. Thus, it is clear that differences between instantaneous and dynamic models will also be found when switching is based on the location of prey different habitats.

There are likely to be constraints on the parameters of the switching function. In particular, a population that rapidly switches when the abundances of foods change must have a way to detect those changes. In general, this requires that individuals frequently sample the less abundant prey to estimate its abundance. Thus it is reasonable that forms that are able to switch rapidly may also have relatively high minimum consumption rates of the less abundant prey: i.e., they cannot specialize as completely on the better prey as would a form that had

less rapid switching. Such consumption may be maladaptive, but could be maintained by the advantage of more rapid switching. Preliminary results (Abrams and Matsuda, unpublished data) suggest that polymorphisms involving types with different strategies on this rate versus accuracy trade-off occur frequently.

Behavioral dynamics in a broader context

There has been much less work on the methods for incorporating behavior into models of interacting populations than there has been on incorporating evolution into such models. Coevolutionary models have included a full range of genetic mechanisms from single locus-two allele models, to models based on quantitative genetic recursions. The standard approach for incorporating adaptive behavior into models of interacting species has been to assume that species either adopt or approximate the behavior that is optimal for current conditions (e.g., Matsuda 1985; Matsuda et al. 1987; Abrams 1992b; Fryxell and Lundberg 1994; Krivan 1997; Van Baalen et al. 2001). We have shown this to be potentially misleading for the case of simple switching between two prey species, and it is even more likely to be misleading in systems where two or more interacting species must each adjust their behavior based on the behavior of individuals of the other species. Although it is unlikely that any single framework will provide an adequate description of all possible behavioral dynamics, there is clearly a need to explore a wider range of behavioral models than has been studied to date. This exploration will be more fruitful with more empirical studies to provide information on what factors actually determine the nature of behavioral dynamics.

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