Evolutionary Ecology Research, 2005, **7**: 53–71

Individual behaviour, space and predator evolution promote persistence in a two-patch system with predator switching

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ABSTRACT

Predator switching is often assumed to be a stabilizing force in predator–prey interactions. Recent models, however, have shown that predator switching can have a destabilizing effect on populations, creating cycles or even extinctions of predators and prey. However, most of these models have been traditional top-down mathematical models that do not incorporate individual variability or evolution. We explored the influence of predator switching on predator–prey stability, persistence and evolution using an individual-based, spatially explicit model of predators switching between two prey patches. We also created difference equation models for comparison with the simulations. We found that individual variability among predators, and selection acting on switching thresholds, helped in maintaining stability and persistence in our predator–prey system. Predators that estimated prey density (with error) or had 'short memories' produced more stable population dynamics than predators with perfect knowledge of prey density or had 'long memories'. The threshold prey density at which switching occurred evolved in the predator population to be greater than the predicted optimal density. This result led to undermatching of predators to their resources and tended to increase predator–prey stability. Furthermore, multiple switching thresholds could be maintained in the predator population at the same time. These results suggest that in an ecological system with individual predators switching between prey species, predator switching may help stabilize predator–prey interactions.

Keywords: evolution, individual-based model, memory, optimal foraging, predator switching, undermatching.

INTRODUCTION

A predator is said to 'switch' if its relative attack rate on a prey species increases faster than does that prey's relative abundance (Murdoch and Oaten, 1975). Predator switching has traditionally been argued both to have a stabilizing effect on predator–prey interactions and to permit the co-existence of strongly competing prey species (Roughgarden and Feldman, 1975). Murdoch (1977), for instance, used a Lotka-Volterra type of model to show that a predator

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that switched between habitats could stabilize otherwise unstable predator–prey dynamics, provided switching predators had transit time during which they did not forage. Turchin and Hanski (1997) proposed that predator switching by generalist predators explains the latitudinal gradient in the amplitude of vole cycles in Fennoscandia (amplitudes decline as one moves southward, where generalist predators are more diverse and numerous). Recent mathematical models of predator switching have shown that although predator switching can be stabilizing in some circumstances, switching does not stabilize populations in others (Fryxell and Lundberg, 1994; Křivan, 1996, 1997; Abrams, 1999, 2000; Křivan and Sikder, 1999; P.A. Abrams and H. Matsuda, unpublished manuscript). This body of theory, however, has not considered the potential influence of individual variability or evolution in switching behaviour on population dynamics. Many studies of predator–prey and host–parasitoid systems have shown that individual variation can be stabilizing (for a review, see Hassell, 2000), but the dynamical consequences of variation in switching are unexplored. Moreover, if such variation has a heritable basis, switching behaviour can evolve. The evolution of foraging traits was found by Abrams (1997) to influence the population dynamics of predator–prey systems, but to date little attention has been paid to how evolution in switching itself can influence dynamics. In turn, the population dynamics of the interacting species (e.g. stable *vs* unstable) could potentially influence the direction of evolution in switching.

In this paper, we examine the impact of individual variation and evolution of switching on predator–prey dynamics. As a point of departure, we use a recent 'top-down' model by van Baalen *et al.* (2001) in which a special case of predator switching was explored by assuming that a preferred prey type occurred in one patch and an alternative prey type in a second patch. They assumed that the alternative prey type existed at a fixed density, that predators 'knew' the optimal preferred prey density at which to switch between patches (and could do so instantaneously and without cost), and that predators had a type II functional response in each patch. They found that the predator and preferred prey did not reach a point equilibrium, but persisted in a limit cycle.

Different assumptions, however, might alter the results of van Baalen *et al.* (2001). Most prior work on switching, including that of van Baalen *et al.* (2001), has been cast in a differential equation format, which assumes that population sizes are sufficiently large to be treated as continuous variables. Given unstable dynamics, densities are low, and this assumption becomes biologically questionable. Explicitly incorporating individual-level processes can strongly influence ecological and evolutionary dynamics. For instance, a tri-trophic host–parasitoid model examined by Wilson *et al.* (1998) incorporating demographic stochasticity in a spatially explicit model found that stochasticity had marked effects on the persistence of the system, compared with continuous state-space models. The influence of individual variability and demographic stochasticity on predator–prey systems with switching has not to date been addressed theoretically.

Empirical work suggests that individual variability may be important in predator–prey systems. When the distribution of consumers among prey patches is examined, one frequently observes more consumers in patches with fewer resources than predicted by optimal foraging theory (Kennedy and Gray, 1993). This 'undermatching' of consumers to resources in real communities suggests that the consumers may not be switching between patches at the optimal density. Our results will show that individual variability can lead to such undermatching.

Persistence in systems with predator switching should be influenced by realistic factors such as demographic stochasticity, constraints on individual behaviour and the co-existence of alternative foraging strategies (i.e. genetic polymorphisms in predator behaviour). To begin exploring how these complications affect population dynamics, we created a spatially explicit, individual-based predator switching model and examined the interplay of population and evolutionary dynamics. To facilitate comparison of our individual-based model results to more analytical models, we also constructed and analysed a simple difference equation model of the predator–prey system, and a second difference equation model with a vector of predator metabolic states.

We use this suite of models to answer several specific questions: (1) How do rules for patch sampling by predators influence persistence of predator–prey systems? (2) If the prey density at which predators switch between patches is allowed to evolve, do predators evolve to the threshold predicted by optimal foraging theory? (3) How does this evolution in turn affect population dynamics? (4) Does evolution generate a system that has a monomorphic switching strategy, or do polymorphisms arise?

METHODS

Our simulation model assumes two patches with a preferred prey type in one patch and an alternative prey type in the other patch. Prey remain within their own patches and are assumed not to evolve. Each patch is described by a lattice of cells, among which predators can move (within and between patches). Thus, both predators and prey are represented as individuals. Predators could be optimal foragers, fixed non-optimal foragers, or be forced to sample prey patches before making foraging decisions. By permitting mutations to arise in the model foraging parameters, genetic variation is introduced in the predator population, which can then be acted upon by selection.

Prey in the preferred prey patch have logistic growth and are relatively more nutritious to predators; prey in the alternative prey patch have fixed density and are lower in quality. The carrying capacity of the preferred prey patch is the total number of cells in the patch. Predators in a patch can either move randomly to an adjacent cell within that patch, or move between patches by jumping from the cell in one patch to the cell in the other patch with the same coordinate location. The patches can thus be thought of as being one on top of the other; predators are in effect foraging in a stratified environment with two strata (e.g. insectivorous birds foraging in distinct foliage layers in a forest).

Optimally foraging predators move from the preferred prey patch to the alternative prey patch when the average density of the preferred prey falls below a threshold density. This threshold density is calculated using the equation derived by van Baalen *et al.* (2001), using a model structurally similar to the one we explore:

$$N_s = \frac{C_A A}{C_N + A(C_N T_A - C_A T_N)} \tag{1}$$

Here, N_s is the optimal preferred prey density to switch between patches, A is the alternative prey density, C_N is the nutritional value of the preferred prey, C_A is the nutritional value of the alternative prey, T_N is the handling time of the preferred prey and T_A is the handling time of the alternative prey. Handling time is the number of time-steps that a predator is *not* allowed to move after consuming a prey item, including switching between patches. When the density of preferred prey, denoted N_t, exceeds the threshold N_s (equation 1), optimally switching predators move from the alternative prey patch to the preferred prey patch; when

$N_t < N_s$, optimally switching predators move to the alternative prey patch. Predators that do not forage optimally move between patches at prey densities other than that given by equation (1).

To address ecological questions, we assumed that there was no mutation, so fresh recruits had the same switching rule as did their parent. To examine evolution, we permitted the prey density at which newborn predators switched between patches (the switching threshold) to deviate from parental values due to mutation; selection could then occur due to differential reproduction based on foraging success. The individual-based model is described in more detail in the Appendix, and Table 1 lists the parameters.

Table 1. List of 15 parameters used in the individual-based model, and the values used in most runs of the model

Parameter	Description	Value in simulation
X	Number of cells in x-axis of each patch	50
Y	Number of cells in y-axis of each patch	50
r	Growth rate of preferred prey	0.021
C_N	Nutrition value of preferred prey	1.0
C_A	Nutrition value of alternative prey	0.1
T_N	Handling time of preferred prey	1
T_A	Handling time of alternative prey	1
I_N	Initial density of preferred prey	0.4
A	Density of alternative prey	0.4
I_S	Initial density of switching predators	0.02
I_W	Initial predator fitness value	1.0
R	W value above which predators reproduce	3.0
M_R	Cost of reproduction subtracted from W	2.0
B_R	Initial W value of newly born predator	1.0
M_S	Metabolism cost subtracted from predator W	0.04

Difference equation model

To illuminate the results of the individual-based simulation model with analytic results, we constructed a related difference equation model with constant predator mortality. The model is similar to the differential equation model of van Baalen *et al.* (2001), except that prey have exponential growth in the model of van Baalen *et al.* but logistic growth in ours:

$$\begin{aligned} N_{t+1} &= N_t\left[1 + r\left(1 - \frac{N_t}{K}\right)\right] - f_N(N_t, A)P_t \\ P_{t+1} &= P_t[1 + C_N f_N(N_t, A) + C_A f_A(N_t, A) - d] \end{aligned} \tag{2}$$

Here, P_t is predator density at time t, r is the preferred prey growth rate, K is the carrying capacity of the preferred prey patch, d is the predator mortality rate, and f_N and f_A are the functional responses of predators in the preferred prey and alternative prey patches, respectively. When $N_t > N_s$ (equation 1), predators forage exclusively in the preferred prey patch; when $N_t < N_s$, predators forage exclusively in the alternative prey patch. The functional response within the preferred prey patch is:

$$f_N(N_t, A) = \begin{cases} \dfrac{N_t}{1 + T_N N_t} & N_t > N_s \\ 0 & N_t < N_s \end{cases} \tag{3}$$

and the functional response within the alternative prey patch is:

$$f_A(N_t, A) = \begin{cases} 0 & N_t > N_s \\ \dfrac{A}{1 + T_A A} & N_t < N_s \end{cases} \tag{4}$$

Difference model with predator metabolism

The individual-based model contains individuals that must build up a reserve of energy (R) before reproducing, and individuals that die only after going several time-steps without finding prey. These characteristics of the model may have important effects on the dynamics of the system, but are not reflected in the difference equation model described in equations (2–4). To incorporate delayed reproduction and starvation into a more detailed deterministic analogue of the individual-based model, we created a second difference equation model that includes a vector of predator density in metabolic state j (denoted by $\mathbf{P_t}$), and a transition matrix among those states (denoted $\mathbf{M_t}$):

$$N_{t+1} = N_t\left[1 + r\left(1 - \frac{N_t}{K}\right)\right] - f_N(N_t, A)P_t' \tag{5}$$

$$\mathbf{P_{t+1}} = \mathbf{M_t}\,\mathbf{P_t}$$

Here, P_t' is the total predator population summed across metabolic states $\left(P_t' = \sum_j P(j)_t\right)$, and all other parameters and variables are as in equation (2). For a given metabolic state, j, predators have a probability of finding or not finding prey items. Predators in state j that do not find a prey item are moved to metabolic state $j-1$. Predators that do find a prey item are moved to metabolic state $j+i$, where i is the increase in metabolic state brought about by consuming that prey item. If $N_t > N_s$, predators forage exclusively in the preferred prey patch. Consequently, the fraction of predators in state j that find a prey item and move to state $j+i$ is determined by the functional response of predators in the preferred prey patch:

$$\frac{N_t}{1 + T_N N_t} \tag{6}$$

The fraction of predators in state j that do not find a prey item and therefore move to state $j-1$ is one minus equation (6). $\mathbf{M_t}$ is the matrix of transitions defined by equation (6) and one minus equation (6) for each metabolic state in vector $\mathbf{P_t}$. Thus, the density of predators in a given state j in the next time-step, $(P(j)_{t+1})$, is the fraction of predators currently in state

$j - i$ that find a prey item and move to state j, plus the fraction of predators currently in state $j + 1$ that fail to find a prey item and are reduced to state j:

$$P(j)_{t+1} = P(j-i)_t \left(\frac{N_t}{1 + T_N N_t}\right) + P(j+1)_t \left(1 - \frac{N_t}{1 + T_N N_t}\right) \tag{7}$$

Predators in state $j > j_R$ (where j_R is the reproduction threshold) reproduce by increasing the density of predators in state j_B (metabolic state at birth), and by reducing the parent to state $j - j_M$ (where j_M is the metabolic cost of reproduction). Only predators in state $j = 1$ are removed from $\mathbf{P}_t$, and the density removed is the density in $P(1)_t$ times the probability of not finding a prey item:

$$P(1)_t \left(1 - \frac{N_t}{1 + T_N N_t}\right) \tag{8}$$

When $N_t < N_s$, predators forage exclusively in the alternative prey patch and equations (6), (7) and (8) are the same except that N_t is replaced by the density of alternative prey, A; T_N is replaced by handling time in the alternative prey patch, T_A; and because the metabolic value of alternative prey is less than for the preferred prey, i is replaced by i', ($i' < i$). Consequently, the transition probability of equation (6) becomes the functional response of predators in the alternative prey patch, and the transition probability of equation (7) is one minus the functional response in the alternative prey patch.

Persistence

We used the above difference models to examine stability and persistence, to facilitate interpreting the dynamics produced by the individual-based model. The difference model of equation (5) is too complex for standard local stability analyses; stability and persistence were instead examined by numerical simulation. If densities of predators or prey in the numerical simulations fell below a threshold of 10^{-6}, they were considered extinct. Persistence of predators and prey in the individual-based model, denoted by δ, was determined by calculating the fraction of 25 independent model runs in which both the predator and prey populations persisted (contained at least one individual) for 10,000 time-steps. Persistence was examined for various combinations of prey growth rate, handling time and patch size.

Non-optimal switching and patch sampling

In the above simulations, all predators switch when the preferred prey density shifts past a threshold determined from an optimality model. In effect, this assumes that predators have perfect knowledge of prey abundance. In reality, however, predators will not have perfect knowledge of prey abundance and will frequently switch patches at a non-optimal prey density. The degree of non-optimal behaviour lies on a continuum, with predators that randomly move between patches at one extreme, and predators that sample the prey patch thoroughly enough to have an accurate estimate of prey density at the other extreme. We examined versions of the individual-based model with predators that moved randomly between patches, or predators that sampled the preferred prey patch to assess prey density.

Patch sampling was modelled by giving predators a memory of past encounters with prey in the preferred prey patch. More recent encounters were weighted more heavily in the estimator (adapted from the model of Hirvonen *et al.*, 1999) with the estimated density of prey in the preferred prey patch (defined as π) set equal to:

$$\pi = \left(\frac{1 - e^{-a}}{1 - e^{-(m+1)a}}\right) \sum_{v=0}^{m} e^{-av} I_v \tag{9}$$

Here, a is a devaluation parameter, m is the memory window of the predator (e.g. the number of previous encounters it remembers) and I_v is the index of whether or not prey was found v time-steps earlier. If a prey item was found, $I_v = 1$, otherwise $I_v = 0$. When a predator's estimate of the preferred prey density falls below N_s, the predator switches to the alternative prey patch and stays there for G time-steps. The probability of persistence of the predator–prey system was determined as before over a range of a, m and G values. For a given value of m, large a values describe a 'short memory' with rapid discounting of past experience, whereas small a values correspond to a 'long memory'.

Evolution

The above studies dealt with ecological questions, and provide a necessary backdrop for understanding the impact of evolution in switching. To examine evolution, we allowed the foraging parameters N_s and a in the individual-based model to undergo mutation and selection. To examine selection on the switching criterion with perfect knowledge, we initially randomly assigned each predator an N_s' value ($0 < N_s' < 1$). At reproduction, each offspring had the same expected N_s' value as its parent, but was perturbed by a random mutation taken from a normal distribution centred at zero with a standard deviation of 4×10^{-4}. Selection arose because predators with different N_s' could survive and reproduce at different rates. We ran the model 20 times for every value of prey growth rate and patch size examined. We calculated mean N_s' after 10,000 time-steps for each individual run, and then used those means to calculate the mean N_s' and 95% confidence interval at each prey growth rate and patch size examined. We repeated this process, but assuming that predators had to sample patches to estimate prey density, and allowing both N_s' and a to evolve. (Because we were examining the evolution of two parameters, in these final simulations we calculated the average N_s' and a after the model had run for 20,000 time-steps.)

At high prey growth rates, some predator populations evolved into a polymorphic state with multiple co-existing switching values. To examine if the multiple switching values were stable, we performed an invasibility analysis for a sample predator population with high prey growth rate that evolved two switching densities. We then performed an invasibility analysis using the optimal N_s value for the initial condition.

Finally, we compared the stability of the predator–prey system with predator populations undergoing selection on N_s' to optimally foraging predator populations without selection. A sample time-series was created for predator and prey abundance with a population of predators with fixed N_s, compared to a population facing selection on N_s'. In the population of predators undergoing evolution, mutation on N_s' was allowed to occur for 1000 time-steps and was then stopped so that predators with different N_s' values competed against each other without mutation on N_s'.

RESULTS

The difference equation model without the vector of predator states (equation 2) has an equilibrium with predators foraging exclusively in the preferred prey patch, which a Jacobian matrix analysis shows to be stable to small perturbations over a wide range of parameter values. The alternative prey, and therefore predator switching, are not necessary for persistence. In the differential equation model of van Baalen *et al.* (2001), on which equation (2) is based, an unstable equilibrium between prey and predators was always found, and switching was necessary for persistence. The difference between equation (2) and the model of van Baalen *et al.* (2001) is that prey were assumed to have exponential growth in the latter, while prey had logistic growth in equation (2). This introduces a stabilizing force of density dependence via prey recruitment, as in classical predator–prey theory (e.g. Rosenzweig and MacArthur, 1963).

However, adding variability in the form of a vector of predator metabolic states (equation 5; hereafter, the matrix model) creates a lag in predator reproduction and starvation that causes the equilibrium to be unstable. In the absence of alternative prey, the predator population goes extinct. Allowing predators to switch to the alternative prey, however, produces limit cycles and allows persistence of the predator–prey system (Fig. 1a). Lags in reproduction and starvation tend to induce instability in the individual-based model as well, and the predator population also goes extinct if switching to alternative prey is not allowed. The individual-based model produces very similar phase plane diagrams as generated by the matrix model (Fig. 1b).

The predator and prey populations of the matrix model persist at all but the lowest prey growth rates (Fig. 2). In contrast, the predator–prey system of the individual-based model only persists at relatively high prey growth rates, and because of the incorporation of explicit space and demographic stochasticity, large patch sizes also foster persistence (Fig. 2). Higher prey growth rates support larger predator populations, thereby decreasing the importance of demographic stochasticity in the individual-based model. Larger patch sizes also support larger predator populations, which again decrease the influence of demographic stochasticity and thereby lead to higher probabilities of persistence, δ.

Non-optimal predators

Although demographic stochasticity tended to decrease persistence in the individual-based model, stochasticity in other features of the system acted to *increase* persistence. In the matrix model, predators that moved randomly between patches had an unstable equilibrium and quickly went extinct. Over a range of parameters in the individual-based model, however, populations of randomly moving predators had a high probability of persistence (Fig. 3). Non-optimal switching predators could not persist in the matrix model because, at low preferred prey numbers, predators did not preferentially switch to the alternative prey patch, and therefore did not allow the preferred prey to increase when rare. In the individual-based model, however, preferred prey could increase when rare because spatial-explicitness of the model and stochastic movement of individual predators created a probability of escape from predation. Thus, stochasticity and spatial localization of interactions created a partial refuge for the preferred prey. The probability of escape from predation was enhanced at high alternative prey handling times, since larger handling times caused a larger proportion of the predators to be ‘stuck’ in the alternative prey patch at each time-step.

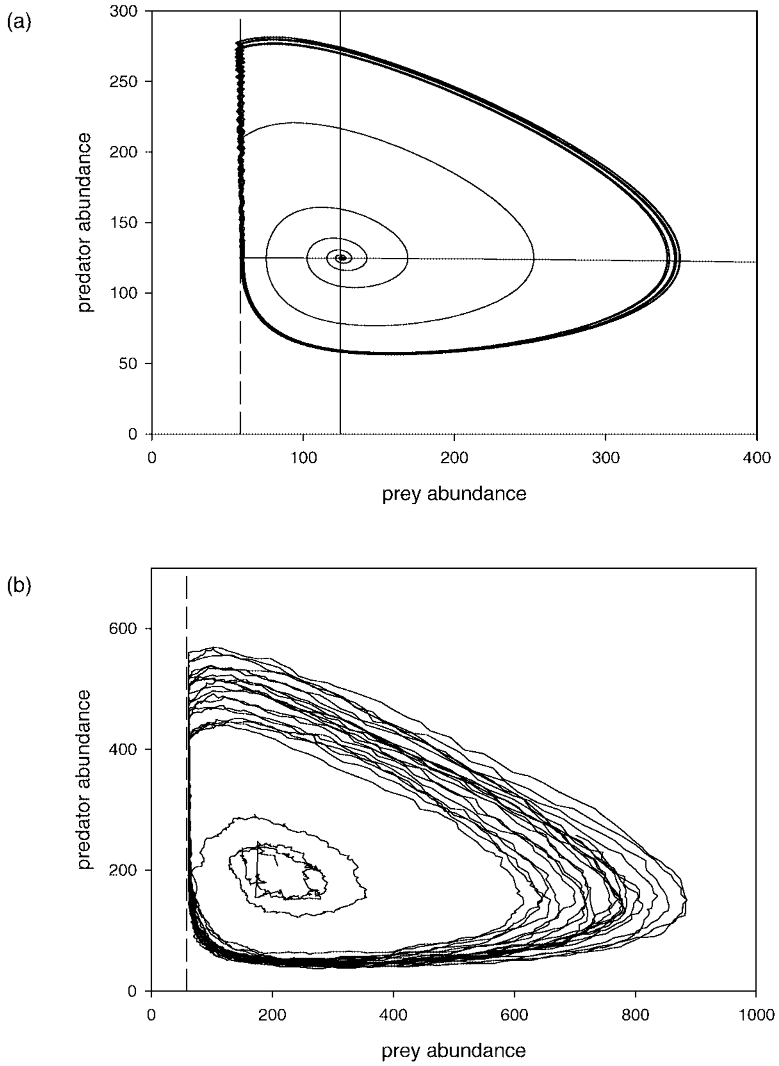

Fig. 1. Phase plane of optimally switching predator abundance versus preferred prey abundance. The dashed line is the optimal prey switching abundance. (a) Difference equation model (equation 5) with vector of predator metabolic states. The solid lines are the predator and prey zero-growth isoclines. The initial prey and predator abundances ($I_N = I_S = 125$, respectively) are a slight deviation from the equilibrium. $i = 25$, $i' = 2$, $K = 2500$. (b) Individual-based model with the same parameters as (a) except initial prey and predator abundances ($I_N = I_S = 225$, respectively) and $C_A = 0.08$. Note the difference in scales between (a) and (b). $r = 0.05$, and all other parameters as in Table 1.

Patch sampling

Predators that sample the patch to assess prey density more closely approximate the behaviour of optimally switching predators than do randomly moving predators, but still contain among-predator variability in the density at which individual predators switch

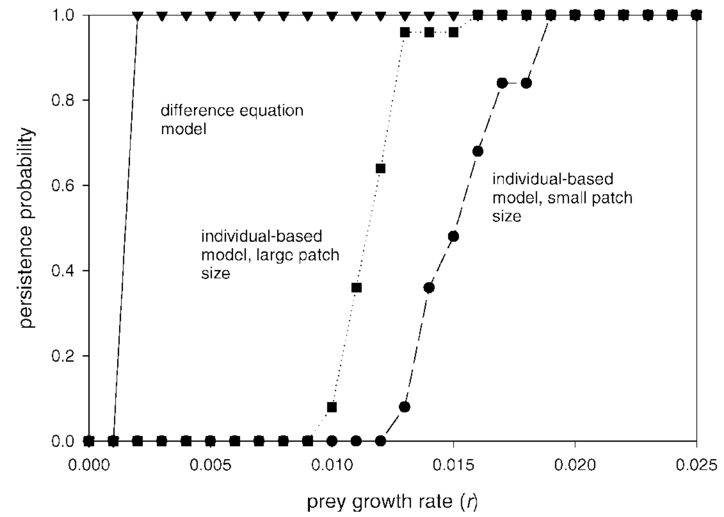

Fig. 2. Probability of persistence of the predator–prey system with optimally switching predators. Persistence of predators and prey in the difference equation model (equation 5; ▼), in the individual-based model with patch size X = Y = 70 (■), and in the individual-based model with patch size X = Y = 50 (●), over a range of preferred prey growth rates. $C_A = 0.08$, and all other parameters as in Table 1 and Fig. 1.

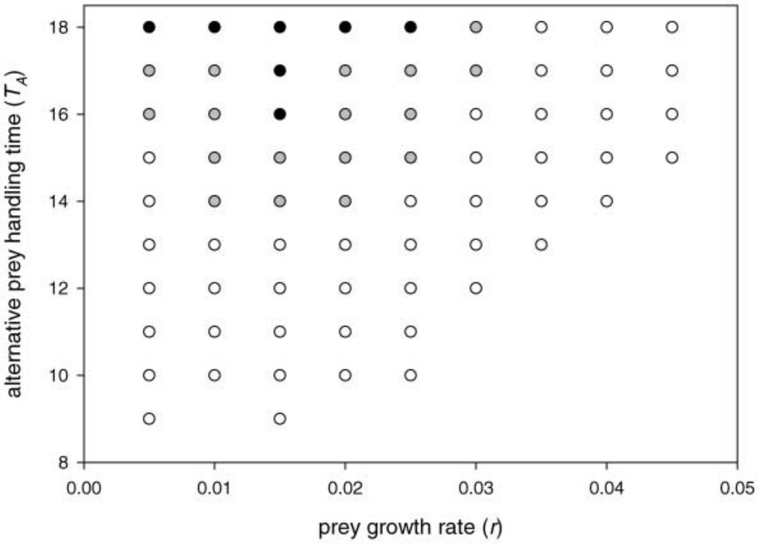

Fig. 3. Probability of persistence of predators randomly moving between patches, over a range of preferred prey growth rates and alternative prey handling times. Open circles are the probability of persistence, $0 < \delta < 0.75$. Grey filled circles are the probability of persistence, $0.75 \leq \delta < 1.0$. Solid circles are the probability of persistence, $\delta = 1.0$. The greatest persistence occurred at intermediate prey growth rates and high handling times. $C_A = 0.05$, $M_S = 0.01$, $I_S = 0.02$. All other parameters as in Table 1.

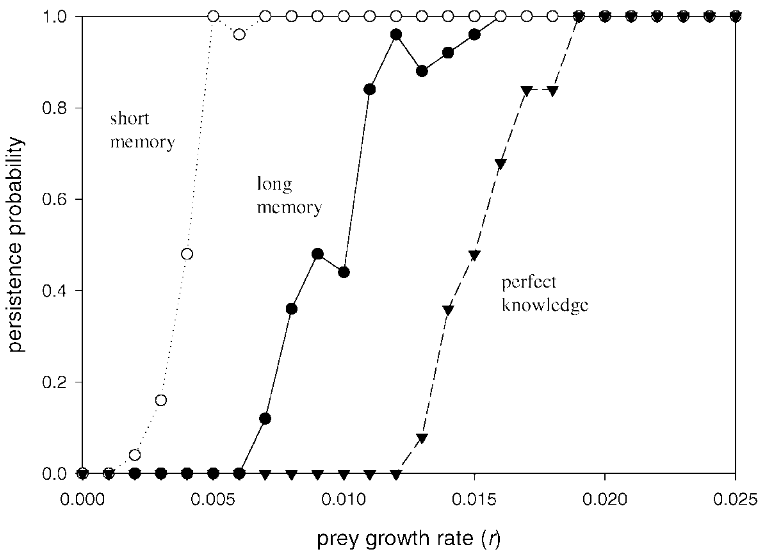

Fig. 4. Probability of persistence of the predator–prey system over a range of preferred prey growth rates with predators that sampled the prey patch with a short memory ($a = 1.0$; ○), predators that sampled the prey patch with a long memory ($a = 0.1$; ●), and predators with perfect knowledge of prey densities (▼). $G = 10$, $m = 15$, and all other parameters as in Table 1.

patches. Populations of patch sampling predators with both high and low a values had a greater probability of persistence than did populations of optimally switching predators with perfect knowledge of prey density (Fig. 4). Although all of the patch-sampling predators had the same switching threshold (equation 1), each predator had a different foraging history, and thus a potentially different estimate of the actual prey density. Thus, instead of a threshold of prey density that determined switching *en masse*, there was a gradual switching by predators over a range of prey densities. This among-predator variability in switching had a stabilizing effect on the system, smoothing the switching response, and thereby increasing δ over a range of prey growth rates.

The value of a in the predator population also influenced persistence. Populations of predators had a higher probability of persistence if a was high (i.e. predators had a short memory) than if a was low (i.e. predators had a long memory) (Fig. 4). Populations of predators with long memories more nearly approximated the switching threshold produced by predators with perfect knowledge of prey density, and were therefore closer to the optimally switching predators in persistence probability. Populations of predators with short memories made more mistakes in estimating prey density, thereby switching between patches at a larger range of actual prey densities, which smoothed the switching response and promoted persistence. In this model, a long memory is beneficial to the foraging success of the individual predator, but a short memory stabilizes the population dynamics of the system. Changing the memory window (m), and time-steps in the alternative prey patch (G), altered the probability of persistence, but did so only slightly relative to the impact of a.

Evolution

Evolution of predator switching density (N_s') in predator populations both with and without patch sampling resulted in mean N_s' values that diverged from the optimal N_s predicted by equation (1). The mean N_s' resulting from selection almost always exceeded the predicted optimum.

Populations of predators with perfect knowledge of prey density evolved N_s' values that were significantly greater than N_s (Fig. 5a). The switching densities favoured by selection

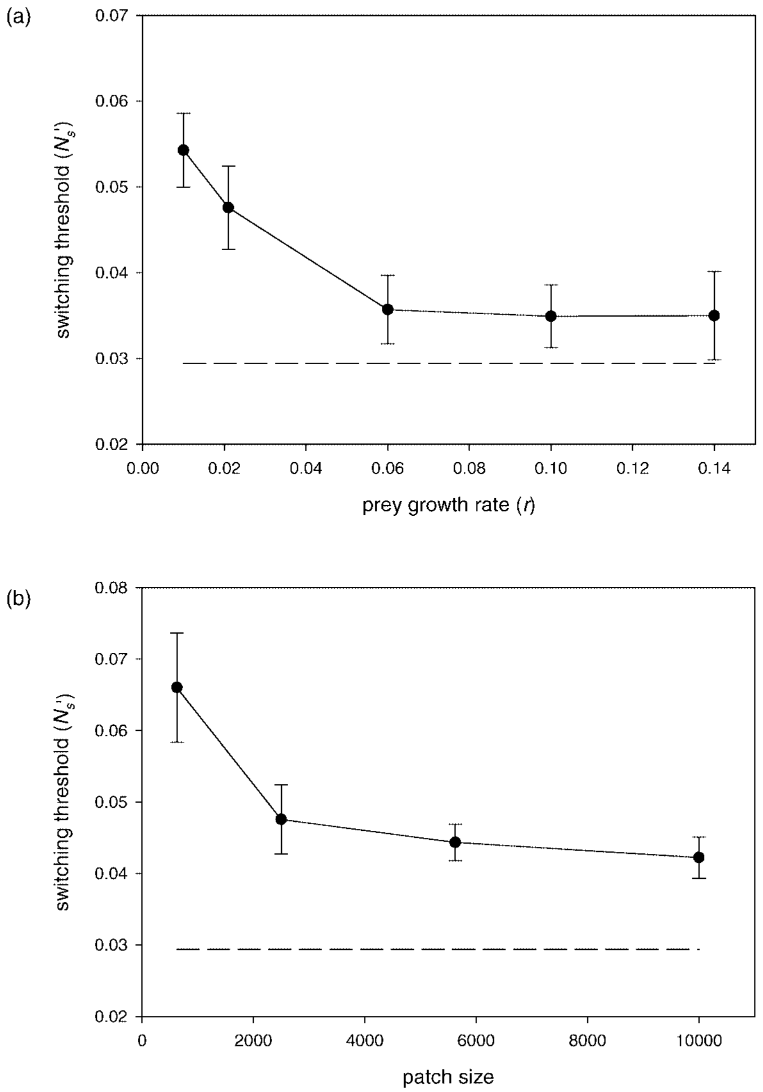

Fig. 5. Means and 95% confidence intervals for prey switching density selected for in predator–prey systems with different (a) preferred prey growth rates and (b) patch sizes. The dashed line is the predicted optimal switching density. Deviations from the optimal switching density are greatest at small prey growth rates and small patch sizes. All parameters as in Table 1.

were largest at low prey growth rates, and were closer to N_s as prey growth rate increased. A similar pattern occurred for the mean N_s' of predators foraging in different size patches (Fig. 5b); the smaller the patch size, the higher the mean N_s' selected for in the predator population. As demographic stochasticity increased with decreasing prey growth rates and patch sizes, selection favoured N_s' values increasingly larger than N_s. At low prey growth rates and small patch sizes, prey were replenished very slowly. When prey density was low, slow prey replenishment increased the probability of a predator in the preferred prey patch going several time-steps without encountering a prey item. As a result, N_s' values larger than N_s were favoured by selection. As prey growth rate and patch size increased, prey replenishment increased, and the N_s' values favoured by selection were nearer to N_s. However, even at the highest prey growth rates and largest patch sizes tested, stochasticity was still important to the system, and the N_s' values that evolved were still larger than N_s.

When both N_s' and a faced selection, the mean N_s' was again significantly larger than N_s (Fig. 6). The mean a value that evolved was approximately the same under all three prey growth rates ($a \sim 0.1$). Thus, predators evolved a long memory rather than a short memory. As before, slow prey replenishment selected for values of N_s' larger than N_s. The addition of patch sampling and selection on a acted to increase the stochasticity predators faced at low prey density, and led to selection for mean N_s' values that were relatively much larger than N_s.

In some runs of the model with high prey growth rate and no patch sampling, multiple N_s' values in the predator population appeared to co-exist. Figure 7 shows an example of a predator population with an emergent evolved polymorphism in switching. In this example, predators with relatively large N_s' values co-exist with predators with relatively small N_s'

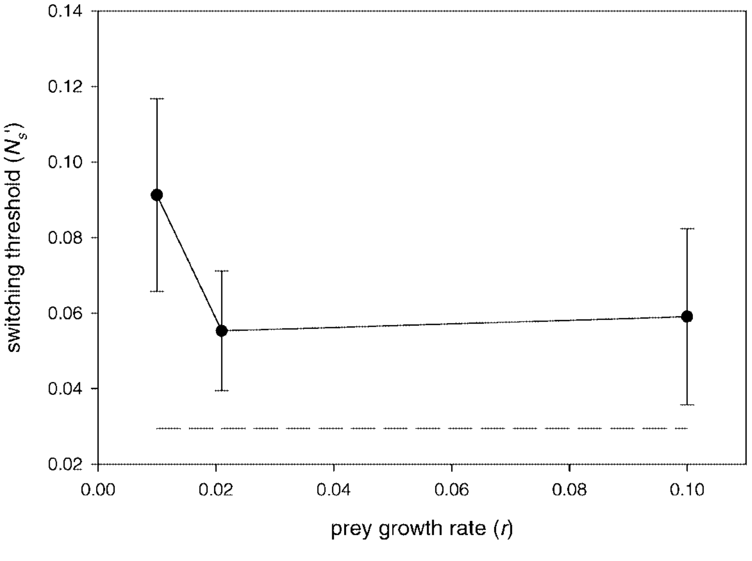

Fig. 6. Means and 95% confidence intervals for prey switching density selected for over a range of prey growth rates. Predators in the system sampled the prey patches and faced selection on a. The dashed line is the optimal switching density. $G = 10$, $m = 15$, and all other parameters as in Table 1.

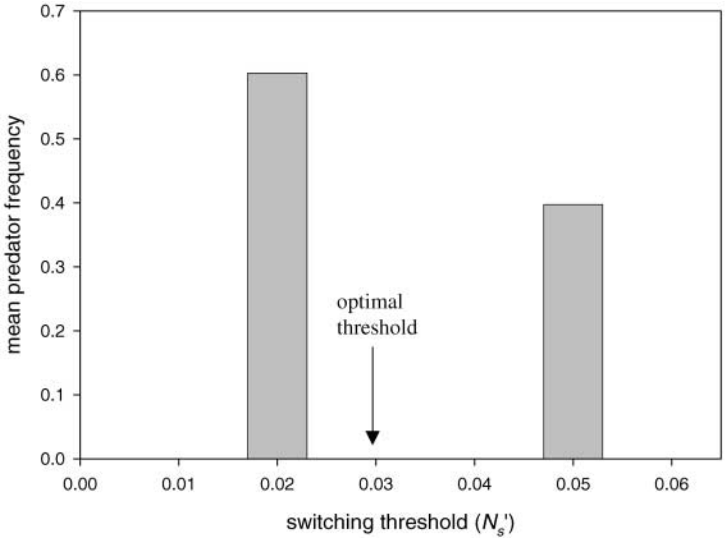

Fig. 7. Histogram of predator switching densities in a sample model run with high prey growth rate ($r = 0.1$). All other parameters as in Table 1. Two switching densities were maintained in the population throughout the simulation. Selection and mutation on switching density occurred for 5000 time-steps, then mutation was stopped and selection alone occurred on the switching densities. The histogram shows the mean frequency of predators in the population using each switching density. The mean frequency was found by determining the frequency of predator types in the population at 10,000 time-steps, and every 1000 time-steps afterwards, for a total of 10 samples. The frequencies in those 10 samples were then averaged to give the mean frequency.

values. Numerical invasion analysis showed in this and similar examples that predators with either switching density could increase when rare. Furthermore, predators with the optimal N_s value were able to out-compete predator populations with either the large or the small N_s' value, when alone. However, when predators with both the large and the small N_s' values co-existed in the same population, predators with the optimal N_s could not invade the population, and were able to be invaded by predator populations containing a mixture of both the large and small N_s' values. Co-existence in this system involves the interplay of unstable dynamics and non-linear functional responses, known as the Armstrong-McGhee effect (see Abrams and Holt, 2002). Predators with a large N_s' value did not remain in the preferred prey patch long enough, and predators with a small N_s' value stayed in the preferred prey patch too long, relative to the optimality criterion. Consequently, both predators with large and small N_s' values were at a disadvantage relative to the other at some point in the cycle of preferred prey densities.

We also found that evolution on N_s' tended to increase the stability of the predator–prey system. Time-series of predator and prey abundance for a sample model run shows that predator and prey populations in systems with selection on N_s' produced considerably smaller amplitude cycles than observed in systems with fixed N_s (Fig. 8a,b). This occurred because the evolved increase in N_s' made predators leave the preferred prey patch at higher prey densities, thus increasing the refuge for preferred prey at low density and thereby increasing system stability.

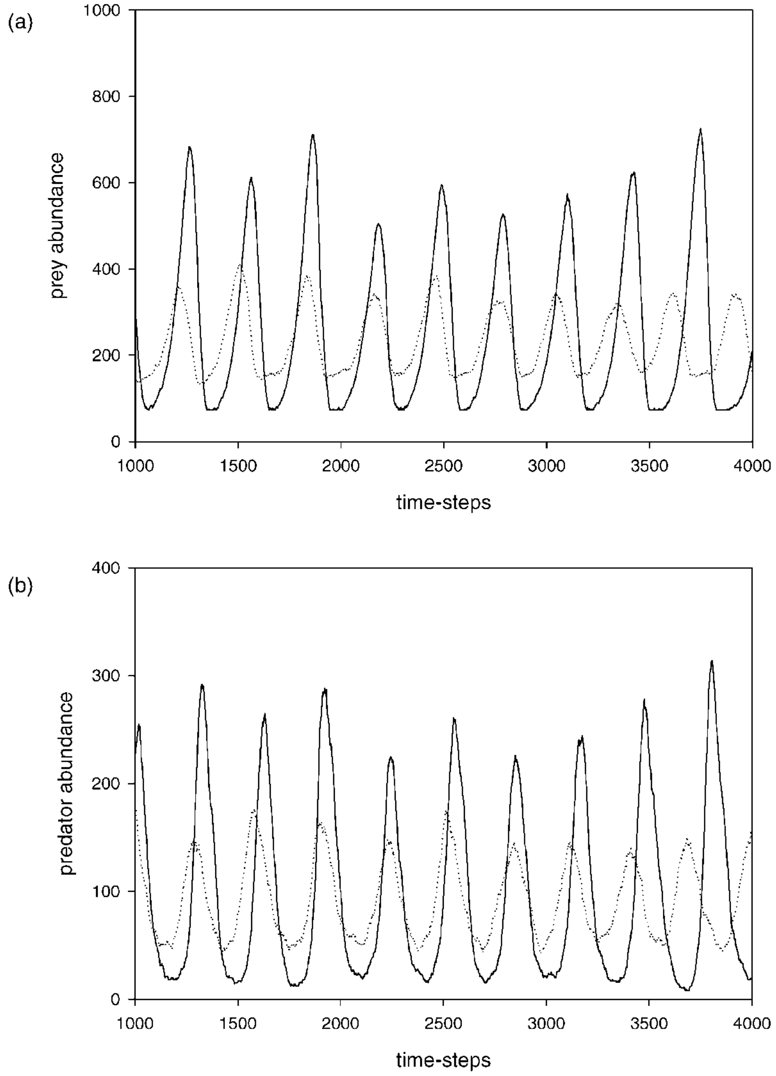

Fig. 8. (a) Time-series of preferred prey abundance with a predator population that faced selection and mutation on switching density for the first 1000 time-steps, and selection without mutation afterwards (dashed line), and a predator population with fixed switching density (solid line). (b) Time-series of predator abundance from the same model run, with predators that faced selection (dashed line) and predators with fixed switching density (solid line). The populations of predator and prey in the system undergoing selection have smaller amplitude cycles than the populations with fixed switching density. All parameters as in Table 1.

DISCUSSION

As noted in the Introduction, recent mathematical models of predator switching have shown that switching may frequently act to destabilize populations (Fryxell and Lundberg, 1994; Křivan, 1996, 1997; Abrams, 1999, 2000; Křivan and Sikder, 1999; Abrams and Matsuda, unpublished manuscript).

As predator switching is likely to be a common phenomenon in ecological systems, what role do our results suggest that predator switching might play in real communities of predator and prey?

The difference equation model without a vector of predator states (equation 2) may be a reasonable model of a predator–prey system if both predator and prey populations are relatively large, predator and prey reproduction is relatively fast, prey have density-dependent interactions, and predators face a constant probability of death. If these conditions are met, the model predicts that the predator and preferred prey may approach a stable equilibrium with predators rarely switching to the alternative prey, and consequently appearing to specialize on the preferred prey. The conditions of equation (2) are fairly restrictive, however; the addition of more realistic reproduction and starvation assumptions in the matrix model (equation 5) results in predators switching to alternative prey and limit cycles. Realistic assumptions of individual behaviour, stochasticity and space in the individual-based model also result in predator switching and limit cycles. Switching may be destabilizing, generating population cycles for instance, yet still be vital for population persistence.

Non-optimal predators

The matrix model predicts that predators that move randomly between patches are not expected to persist in a predator–prey system. However, if there is a substantial amount of stochasticity in a predator's ability to find prey in a patch and alternative prey is difficult to handle, the individual-based model suggests that predators that randomly move between patches may be able to persist. Similarly, the results of the individual-based model predict that a population of predators that must sample a prey patch to determine the density of prey will have smaller cycles and be more likely to persist if the predators have 'short memories' and make errors in estimating prey density. Predators that are good at estimating prey density may produce large population cycles and be less likely to persist. Nonetheless, because the ability to accurately estimate prey density benefits the individual predator, a 'good memory' is likely to be selected for in the predator population. Constraints on predator learning may thus indirectly facilitate persistence in predator–prey systems.

Evolution and undermatching

Selection on predator switching density meant that predators evolved switching thresholds larger than the predicted optima; as a consequence, predators were frequently in a patch not predicted to be the optimal patch. This result was observed when stochasticity played an important part in predator–prey interactions, such as when prey growth rate was low or patch size was small. Traditional optimal foraging models often do not take demographic stochasticity into consideration, and therefore may miss pervasive reasons to expect deviations from classical theory. Such a deviation occurs when predators spend more time in a poor prey patch than predicted by theory. The ecological implications of this result can be examined within the framework of the ideal free distribution (IFD). The evolution of N_s' values that were greater than N_s in the individual-based model meant that, on average, predators with the N_s' switching rule spent more time in the alternative prey patch than did predators with the optimal N_s switching rule. In IFD theory, a pattern of observing more individuals in the 'poor patch' and fewer individuals in the 'rich patch' than predicted by the IFD is called 'undermatching' (Kennedy and Gray, 1993). Undermatching has been found to occur in several empirical experiments testing IFD theory (Kennedy and Gray, 1993). The phenomenon of undermatching has been suggested to occur due to violations of IFD theory, including imperfect knowledge of resource density by consumers, unequal competitive ability, competitive interference and travel costs (Kennedy and Gray, 1993; Ranta *et al.*, 1999). We have found in our model, however, that even when predators have perfect knowledge of prey density, equal competitive abilities, insignificant competitive interference and no travel costs, predators still evolve to spend more time in the poor patch (alternative prey patch) than predicted. Predators that do not violate the assumptions of IFD theory may nonetheless evolve to undermatch their resources due to the stochasticity of resource replenishment. The results of evolution in the individual-based model suggest that undermatching is more likely to occur when prey growth rate is low, patch size is small, and the interaction between predators and prey is stochastic. Deviations from the assumptions of IFD theory, such as imperfect knowledge of prey density by patch sampling predators, may lead to undermatching. Nonetheless, our results suggest that violations of IFD assumptions may not be a necessary prerequisite for undermatching to occur.

Multiple co-existing switching densities

An unexpected result of allowing switching density to undergo mutation and selection was the potential for multiple N_s' values to co-exist in some predator populations. The ability of multiple switching behaviours to co-exist is reminiscent of the results of McPeek and Holt (1992), who found that species with multiple dispersal strategies could co-exist over several patches even in the absence of differences in mortality or patch utilization ability. They found that low-dispersing species and high-dispersing species could co-exist by partitioning high and low carrying-capacity patches, so that each type competed mostly with itself. A similar mechanism may allow multiple switching densities to co-exist in our model. Predators that evolve to leave the preferred prey patch early are at an advantage at some points in the prey cycle, while predators that stay in the preferred prey patch are at an advantage at other points; behaviour thus generates partitioning of the patches both spatially and temporally. This appears most likely to occur when the prey growth rate is relatively large. Peter Abrams (e.g. Abrams and Holt, 2002; Abrams *et al.*, 2003) has recently championed the importance of temporal variation in permitting the co-existence of multiple consumers. Our model provides another example of this same mechanism: the moderate instability of the system permits co-existence of alternative switching strategies. Thus, most of our results help reinforce the emerging perspective that variability among individuals may be an essential feature promoting persistence and stability in many natural populations (Lomnicki, 1988).

ACKNOWLEDGEMENTS

We would like to thank Manojit Roy, Michael Barfield, Peter Abrams and Gary Belovsky for insightful comments. This work was supported by an NSF Graduate Research Fellowship and a Self Fellowship to T.K, and the University of Florida Foundation.

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APPENDIX 1

The simulation model is spatially explicit, and individual-based; the simulation code was programmed in Objective-C using the Swarm Toolkit downloaded from www.swarm.org. We simulated preferred prey logistic growth by calculating the number of individuals to be added to the preferred prey patch at each time-step, and then placing those prey items randomly throughout the patch before predators moved. Only one prey item, one predator, or one prey item and a predator, could be in a cell at a time;

the density of predators or prey in a patch is the number of predators or prey in the patch divided by the total number of cells in that patch.

A predator that lands in a cell with a prey item consumes the prey. If the prey item is in the preferred prey patch, the prey is removed from the simulation, and the cell is empty until recruitment recurs. In the alternative prey patch, the prey item is instantaneously renewed at the same location; thus, the density of the alternative prey is fixed, as assumed in van Baalen *et al.* (2001). Reproduction and mortality both reflect the history of prey consumption, as encapsulated in an internal metabolic state variable (denoted W). If a predator consumes a prey item, the nutritional value of the prey item (C_N or C_A) is added to that predator's value for W. A metabolic cost (M_S) is removed from the W value of each predator each time-step in both patches. If W reaches zero, the predator dies. C_A was set low enough so that predators that foraged exclusively in the alternative prey patch faced certain extinction. If W reached a reproduction threshold (R), a birth occurred, and a reproduction cost (M_R) was subtracted from W of the parent predator. All newborn predators were given the same initial W value (denoted B_R; $B_R < M_R$).