

ON THE INTERPLAY OF PREDATOR SWITCHING AND PREY EVASION IN DETERMINING THE STABILITY OF PREDATOR–PREY DYNAMICS

TRISTAN KIMBRELL* AND ROBERT D. HOLT

*Department of Zoology, University of Florida, P.O. Box 118525, Gainesville,
Florida 32611-8525, USA*

ABSTRACT

Traditionally, predator switching has been assumed to be a stabilizing force in ecological systems. Recent work, however, has shown that predator switching can be either stabilizing or destabilizing. Most models of predator switching, to date, assume that prey are behaviorally passive and do not respond to predators. We allowed prey to respond behaviorally to predators, so as to avoid capture, in order to explore how this ecologically realistic addition modified the impact of predator switching upon population stability and persistence. We used an individual-based, spatially explicit model that described local interactions between predators and prey, with a probability that prey would “sense” predators in adjacent cells and move away from the predators. We compared the individual-based model to a simple difference equation model. We found that intermediate prey sensitivity in the individual-based model allowed the highest probability of persistence of the predator–prey system. By allowing prey sensitivity, and the prey density threshold at which predators switch between prey, to evolve, we found that the evolution of sensitivity acted to stabilize the predator–prey system. We also found that at large prey growth rates, polymorphism in switching strategies can be stable in the predator population. These results suggest that prey behavior, coupled with predator switching, can have a large impact on the stability, persistence, and heterogeneity of predator–prey systems.

INTRODUCTION

A venerable topic in community and population ecology is understanding how the diversity and complexity of natural communities contributes to the overall stability and persistence of ecological systems. One idea, which dates at least back to MacArthur (1955), is that a multiplicity of trophic links between predators and prey tends to promote the resilience of natural communities. The idea that diversity promotes stability is intuitively appealing. Yet traditional models of interacting predators and prey in which average interaction strengths are strong typically reveal that increasing the number of predator and prey species is, if anything, destabilizing (May, 1973).

*Author to whom correspondence should be addressed. E-mail: kimbrell@ufl.edu

One obvious limitation in traditional theoretical models addressing the stability–complexity issue is that the models typically have assumed that predators have rigid feeding patterns, rather than flexible behaviors. One kind of flexible behavior that may contribute to community stability is predator switching among alternative prey. Formally, a predator is said to “switch” if attacks are frequency-dependent, so its relative attack rate increases faster than the relative abundance of the prey species (Murdoch and Oaten, 1975). Predator switching can be either passive or active, depending on whether switching occurs as a result of predator familiarity with the more frequent prey type, or as a “choice” made by the predator to increase fitness (Morgan and Brown, 1996). Empirical examples of switching typically involve prey that live in different habitats (e.g., Royama, 1970; Murdoch and Oaten, 1975), so that switching arises because of predator movement between habitats, or time allocated to searching for prey in distinct spatial arenas. Thus the topic of switching in population and community ecology is closely related to the core issue of patch and habitat selection in behavioral ecology.

Predator switching has traditionally been believed to have a stabilizing effect on both predator and prey populations, and to permit the coexistence of prey species that otherwise might exhibit competitive exclusion (Roughgarden and Feldman, 1975). However, the switching expressions that were commonly used were not derived from individual-level theory such as optimality models (Holt, 1983). More recently, there has again been interest in the potential for adaptive behavior in general, and switching in particular, to be a potent stabilizer of otherwise unstable species-rich food webs (e.g., Kondoh, 2003). Recent mathematical models of predator switching have shown that predator switching can be stabilizing in some situations, but in fact does not stabilize populations in many others (Fryxell and Lundberg, 1994; Krivan, 1996, 1997; Abrams, 1999, 2000; Krivan and Sikder, 1999; Abrams and Matsuda, 2004).

One striking feature of this recent literature—and the theme we explore here—is that although the predator is assumed to show adaptive behaviors, the prey are assumed to be behaviorally passive. If prey can behaviorally respond to predators, so as to avoid capture, how does this modify the impact of predator switching upon population stability and persistence? Stated like this, it is clear that there is an under-appreciated game aspect to the issue of switching and predator–prey stability.

We will not attempt to address this question in general, but rather examine the influence of prey behavior on a particular model of switching behavior. In order to examine individual variation and evolutionary dynamics of switching behavior, we (Kimbrell and Holt, in press) have recently developed an individual-based model (IBM) of interactions between a predator and two prey species; each of the prey is restricted to a different habitat, and the predator can move between them. This model is based on a differential equation formulation in van Baalen et al. (2001), who derived criteria for when it is optimal for predators to switch habitats. There are several reasons it is sensible to use individual-based models. Prey and predator often encounter each other as discrete individuals in small neighborhoods, which in general makes it more likely that stochasticity and variation among individuals will have consequences at the population level (Chesson, 1978). It is well known that individual variation can be stabilizing in predator–prey and host–parasitoid systems (review by Hassell, 2000), but the dynamical

importance of such variation among predators in switching is unexplored. IBMs permit one to examine quite readily the consequences of a wide range of assumptions about the details of individual behavior, and the impact of variation among individuals. Moreover, if such variation has a heritable basis, switching behavior can evolve; IBMs provide a natural way to represent mutational input of variation for addressing evolutionary questions.

However, as in the other switching models mentioned above, in Kimbrell and Holt (in press) we also assumed that the prey were behaviorally passive. In the current paper, we relax this assumption by allowing prey to move so as to avoid predators within patches. The model is thus a predator–prey foraging game as predators “play the field,” making decisions to move among patches based upon average rates of return; also, prey can behaviorally avoid predators, possibly at some cost to themselves in terms of reproduction. The overall dynamics of the system thus reflects the interplay of predator and prey behavioral decisions and results in approximate evolutionarily stable strategy (ESS) solutions.

Here, we address several questions. We start with a “canonical” individual-based model with predator switching, which we have shown (Kimbrell and Holt, in press) can promote persistence, particularly at low prey growth rates. We compare the IBM to a related difference equation model based on van Baalen et al. (2001) and Kimbrell and Holt (in press). We then ask a series of questions about the importance of prey behavior. What are the consequences of incorporating different magnitudes of prey escape responses? How does the magnitude of prey escape influence the ESS switching threshold for the predator? If the prey escape response itself can evolve, how does such evolution influence persistence of the predator–prey interaction, and how is such evolution impacted by movement costs? In the absence of prey movement, polymorphism in switching can be stably maintained in the predator population (Kimbrell and Holt, in press). How does prey movement (with and without prey evolution) influence the maintenance of such a behavioral polymorphism?

METHODS

Our simulation model assumes two patches with a preferred prey type in one patch and an alternative prey type in the other patch. Each patch is a lattice of cells, among which predators can move (within and between patches), but each prey species remains within its own patch. The preferred prey is more nutritious to the predator and has logistic growth. The alternative prey is less nutritious, has constant density, and has no dynamics or evolution. Predators have perfect knowledge of prey density in each patch, and can either move randomly to an adjacent cell within a 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 one on top of the other; predators are in effect foraging in a stratified environment with two strata (e.g., depth zones in a lake). 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 simulate preferred prey logistic growth by calculating the number of individuals to be added to the preferred prey patch each time-step, and then placing those prey items randomly throughout the patch before predators move. Only one prey item, one predator, or one prey item and a predator, can 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. When all of the cells in the preferred prey patch are full of prey, the carrying capacity (denoted J) has been reached and no more prey can be added to the 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 (so the density of the alternative prey is fixed, as assumed in van Baalen et al. (2001)). A prey item that is renewed in a cell that already contains a predator cannot be consumed by that predator.

Both reproduction and mortality reflect the history of prey consumption, as encapsulated in an internal metabolic state variable (denoted W). If a predator consumes a preferred prey item or an alternative prey item, the nutritional value of the item (C_N or C_A , respectively) 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 is set low enough that predators that forage exclusively in the alternative prey patch face certain extinction. As a consequence, the preferred prey patch can be thought of as a source, and the alternative prey patch as a sink. Furthermore, when both preferred and alternative prey are present in their respective patches, preferred prey density is lower than when alternative prey is not present. Thus, the preferred prey faces apparent competition from the alternative prey (Holt, 1977). If W reaches a reproduction threshold (R), a birth occurs, and a reproduction cost (M_R) is subtracted from W of the parent predator. All newborn predators are given the same initial W value (denoted B_R ; $B_R < M_R$).

When a predator is adjacent to a preferred prey item, the prey item has a sensitivity (denoted s) to the predator. The value of s is the probability that the prey item will attempt to move one cell away from the predator. If a predator is not present, the prey item stays in its cell. If the prey item "senses" the predator and tries to move, but there are no free cells for the prey to move to, or the prey is adjacent to the patch boundary, the prey item does not move. Initially, s did not evolve in the prey population; therefore, we included no cost of movement.

One value of IBMs is that they permit the evaluation of analytical expressions for optimal and ESS behavior developed in simpler systems. van Baalen et al. (2001) develop a simple optimality criterion for predator switching. The optimal prey threshold density (denoted N_s) at which predators switch patches (derived by van Baalen et al., 2001), can be modified to include a term for prey sensitivity (which for the moment is assumed to be fixed):

$$N_s = \frac{C_A A}{(1-s)[C_N + A(C_N T_A - C_A T_N)]} \quad (1)$$

Here, A is the alternative prey density (assumed fixed), 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 not being able to switch between patches. When the density of preferred prey, denoted N_p , exceeds the threshold (eq 1), optimally switching predators move from the alternative prey patch to the preferred prey patch; when $N_t < N_s$, predators move to the alternative prey patch. If a few predators and prey are in the preferred prey patch, and N_t is the actual density of prey in the patch, N_t is also approximately the probability that a given cell adjacent to a predator contains a prey item. Because the prey can move, the density of prey that predators actually experience in the patch is $N_t(1-s)$. As a consequence, as s increases, the preferred prey density at which predators switch to the preferred prey patch increases (eq 1). When $s = 1$, eq 1 is undefined; this is reasonable because at $s = 1$, predators will not be able to catch any preferred prey, therefore predators should never switch to the preferred prey patch, and the optimal switching density should be undefined. Equation 1 assumes that prey sensitivity, and the ability of prey to move away from predators when a predator is sensed nearby (prey catchability), are constant with changing prey and predator densities. Consequently, eq 1 is probably most accurate as an approximation at relatively low prey and predator densities when interference between conspecifics is minimal.

To compare the IBM to a non-IBM, we analyzed a difference equation model based on the differential equation model of van Baalen et al. (2001) and the difference equation model of Kimbrell and Holt (in press). The difference equation model has the form:

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

Here, P_t is predator density, r is the prey intrinsic growth rate, K is carrying capacity, d is predator mortality, $f_N(N_t, A)$ is the functional response of predators in the preferred prey patch, and $f_A(N_t, A)$ is the functional response of predators in the alternative prey patch. The functional response in the preferred prey patch is defined as:

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

and the functional response in the alternative prey patch is:

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

Thus, when $N_t > N_s$ as defined by eq 1, predators forage exclusively in the preferred prey patch; and when $N_t < N_s$, predators forage exclusively in the alternative prey patch. We analyzed the model using standard local stability analysis, and used the results to qualitatively compare the difference equation model to the individual-based model.

To analyze the IBM, we began by estimating the predator and prey isoclines for the model. We found the predator isocline by holding preferred prey density constant over a range of prey values, allowing the predator population to go to equilibrium, and then estimating the mean predator density over the next 100 time-steps. We then did the reverse to find the preferred prey isocline. To determine the effect of prey sensitivity on the persistence of the predator-prey system, we ran the model without prey or predator evolution, but with different prey sensitivities, over a range of preferred prey growth rates. The probability of persistence of predators and prey in our model was determined by calculating the fraction of 25 model runs in which both the predator and prey persisted for 10,000 time-steps. This also allowed us to examine how prey and predator abundance was affected by prey sensitivity. We did this by creating time-series of predator and prey abundance at different prey sensitivities.

By permitting mutations to arise in the model foraging parameters, genetic variation is introduced that can be acted upon by selection to allow evolution in both predator and prey parameters. We examined the consequences of evolution in the predator switching threshold and in the probability of preferred prey moving away from predators.

To examine selection on the switching criterion, we randomly assigned each predator a switching prey "value," N'_s ($0 < N'_s < 1$). If the number of preferred prey N_t falls below $N_t = N'_s J$, that predator moves to the other patch. At reproduction, each offspring has the same expected N'_s value as its parent, but perturbed by a random mutation taken from a normal distribution centered at zero with a standard deviation of 4×10^{-4} . Selection arises because predators with different N'_s can survive and reproduce at different rates. We ran the model 20 times at four different prey sensitivities. 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 sensitivity examined.

We next kept the optimal switching threshold (eq 1) from evolving, and allowed sensitivity to evolve in the prey population. We began by assigning each prey item $s = 0.0$. We then allowed s to evolve by calculating the number of prey items to be added at a time-step, randomly choosing the same number of prey items from the existing prey population, and then adding new prey items with the same s values as the chosen prey items, except perturbed by a random mutation drawn from a normal distribution centered at zero with standard deviation of 0.1. The s value used in equation 1 to determine the switching threshold for predators was found by determining the mean s value in the prey population each time-step; thus, the switching threshold changed as sensitivity evolved, but the switching threshold itself did not evolve. A movement cost for prey (denoted m) was incorporated by precluding prey items from being chosen to reproduce with a probability of m ($0 < m < 1$) after they last moved. Thus, the logistic equation was used to determine the number of prey items to be added to the prey patch, and if a prey item that moved the previous time-step was randomly chosen to reproduce, it had a

probability m of not being allowed to reproduce and a different prey item randomly chosen in its place. If $m = 0.0$, there is no cost of movement. We followed the evolution of s for 10,000 time-steps in populations with different movement costs.

Allowing prey sensitivity to evolve while predator switching threshold is held constant, or allowing switching threshold to evolve while holding sensitivity constant, gives the rational reaction set for the prey or predator—the optimal strategy for the prey or predator, given a fixed strategy by the predator or prey. We next allowed both individual prey sensitivity and predator switching thresholds to evolve simultaneously. Because both strategies are allowed to evolve, this gives the approximate ESS solution for both predator and prey strategies. We ran the IBM 20 times at three different prey movement costs. We calculated the mean N_s' and mean s after 10,000 time-steps for each individual run, and then used those means to calculate the mean N_s' , mean s , and 95% confidence intervals for both means at each prey movement cost.

RESULTS

The predator and prey isoclines for the difference equation model (Fig. 1A) and the individual-based model (Fig. 1B) are both nonlinear and qualitatively similar. However, the equilibrium for the difference equation model is locally stable over a wide range of parameters (Appendix), but the IBM produces limit cycles over almost all parameters tested. Two likely reasons the IBM produces limit cycles is because the model includes both satiating functional responses and a time lag with the metabolic accrual of resource prey to reproduction. Both of these factors can lead to time delays in density dependence, generating population cycles.

Changing the prey growth rate (r), and sensitivity (s) of the prey to predators in the IBM had a large impact on population dynamics and thus predator–prey persistence. As r increased, the probability of persistence increased for almost all values of s . However, intermediate values of s led to the greatest probability of persistence of the system. The predator–prey system had low probability of persistence at low values of s (Fig. 2A). The probability of persistence increased with increasing values of s , until a threshold was reached and there was zero probability of persistence ($s = 0.9706$, Fig. 2A). The probability of persistence increased with s , until the value of s reached produced an optimal prey switching threshold (eq 1) that was equal to 1.0. A switching threshold greater than 1.0 results in predators never switching to the preferred prey patch and going deterministically extinct in the alternative prey patch.

In contrast to the IBM, the difference equation model showed no interaction between s and r in determining stability and persistence of the predator–prey system (Fig. 2B). The values of s that produce stability are the same regardless of the value of r (except for $r = 0$, which results in predators always becoming extinct). Furthermore, in the IBM, prey sensitivities that produce an optimal switching threshold (eq 1) greater than 1.0 result in a zero probability of system persistence. In the difference equation model, however, persistence ceases to occur when the value of s results in a negative equilibrium density of predators (Fig. 2B). This occurs at a lower value of s in the difference

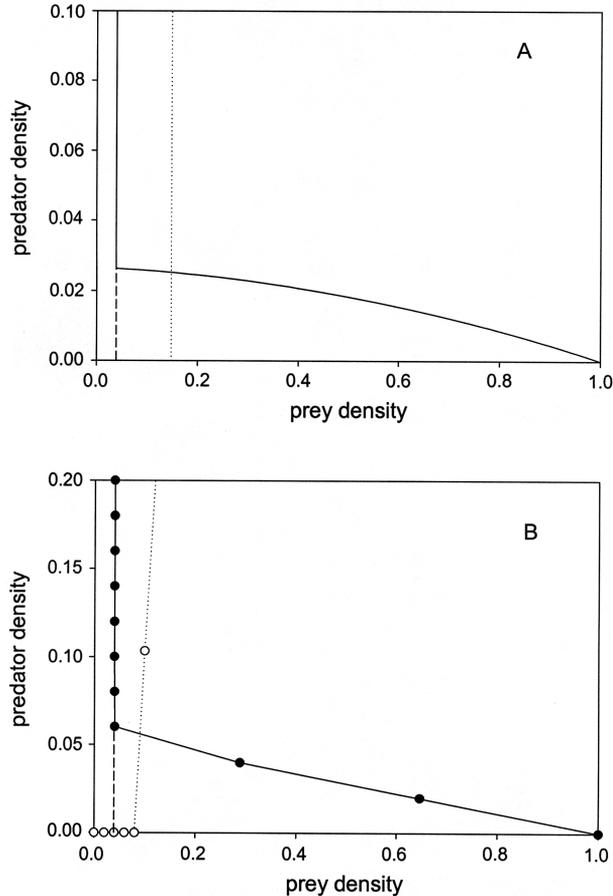


Fig. 1. Predator and prey isoclines for (A) difference equation model and (B) individual-based model. The solid line is the prey isocline, dotted line is the predator isocline, and the dashed line is the predator switching threshold. (A) $K = 1$, $C_N = 1.0$, $A = 0.4$, $T_N = T_A = 1.0$, $r = 0.02$, $d = 0.1$, $s = 0.25$. Parameters in (B) the same as (A), except $J = 2500$, $M_S = 2.0$, $B_R = 1.0$.

equation model than does an optimal switching threshold greater than 1.0. As a consequence, the IBM allows persistence of the predator–prey system at values of s at least as large or larger than the difference equation model.

To illustrate the influence of prey sensitivity on predator–prey dynamics, we followed predator and prey abundance in a sample run of the IBM, while changing prey sensitivity every 2,000 time-steps (Fig. 3). At values of $s = 0.0$ through $s = 0.5$, both predator and prey populations display large cycles. Increasing s to 0.75, both predator and prey cycles decrease in amplitude (but do not entirely disappear). Finally, increasing

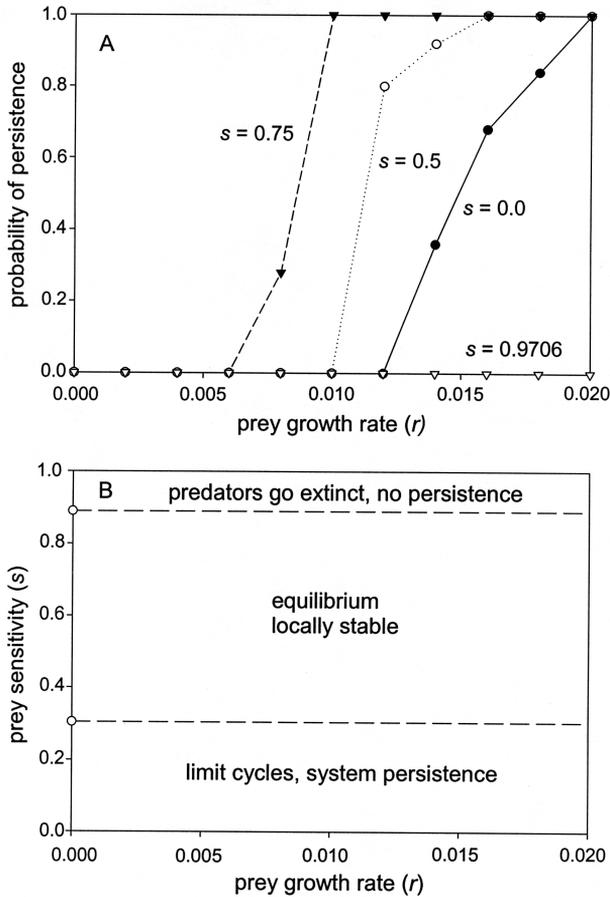


Fig. 2. (A) Probability of persistence of the IBM predator–prey system with different prey sensitivities (s) over a range of prey growth rates. Systems with $s = 0.75$ (filled triangles) have the highest probability of persistence over a wide range of prey growth rates, followed by systems with $s = 0.5$ (open circles), $s = 0.0$ (filled circles), and $s = 0.9706$ (open triangles), which become extinct. (B) Persistence and stability of the difference equation model at different values of s and r . All other parameters as in Fig. 1.

s to a value that produces a switching threshold greater than 1.0 results in predators going extinct and prey increasing logistically to J . The size of the cycles produced by changing s values correlates with the probability of persistence over different s values found in Fig. 2A. The reason is that extinction in our IBM is most likely to arise in population “troughs” of large cycles.

It is interesting to note in Fig. 3 that at $s = 0.75$, the prey density remains above the predators’ optimal switching threshold (eq 1) at all time-steps. Thus, the predator remains in the preferred prey patch at all time-steps, and in effect, specializes on the

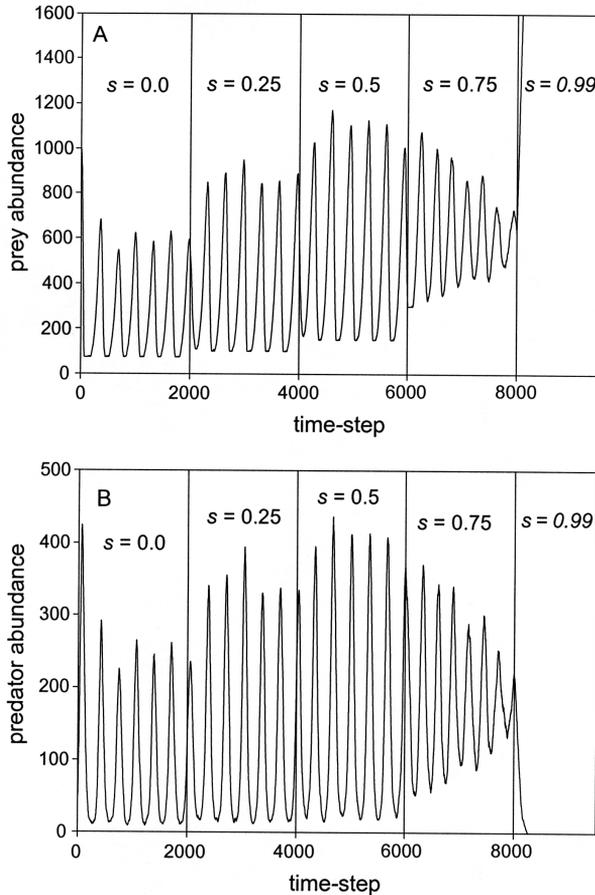


Fig. 3. Time-series of (A) prey abundance and (B) predator abundance in the IBM, while changing prey sensitivity every 2,000 time-steps. The amplitude of cycles in both predator and prey populations correlates with the probability of persistence in Fig. 2A. All other parameters as in Fig. 1.

preferred prey. This does not occur, however, when the predator switching threshold is allowed to evolve. The switching threshold evolved by predators increased as s was increased (Fig. 4). As a consequence, at large values of s , predators no longer specialized on the preferred prey, but instead switched to the alternative prey when preferred prey abundance fell to low values. Permitting predator behavioral response in this case fosters the maintenance of trophic generalization. Furthermore, the switching thresholds that evolved in the predator population were different than the predicted optimal thresholds (Fig. 4). At low s values, predators evolved switching thresholds larger than the predicted optima, and at high s values, the evolved thresholds were lower than predicted. As discussed below, at high s values, prey density tends to be high and prey interfere as

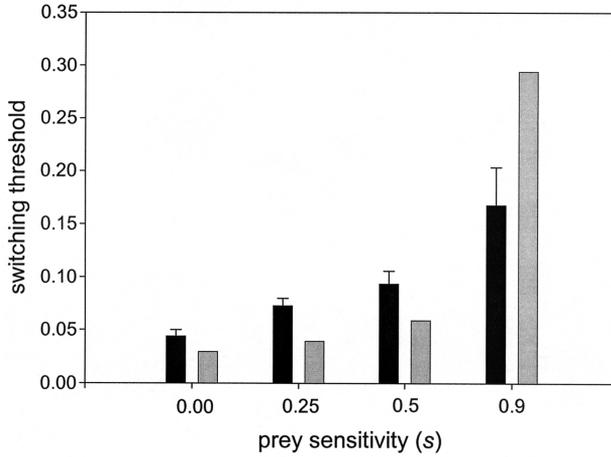


Fig. 4. Means and 95% confidence intervals for prey switching density selected for predator-prey systems with different prey sensitivities (black bars), and predicted optimal switching densities from eq 1 (gray bars). All other parameters as in Fig. 1.

they attempt to escape predation. This interference actually increases the predator attack rate, and therefore makes switching less advantageous.

When prey s values were allowed to evolve, the cost of movement for prey was important in determining the rate and target of evolution (Fig. 5). When $m = 0.0$, s values in the prey population quickly evolved to approximately 0.9. It is intriguing that in the

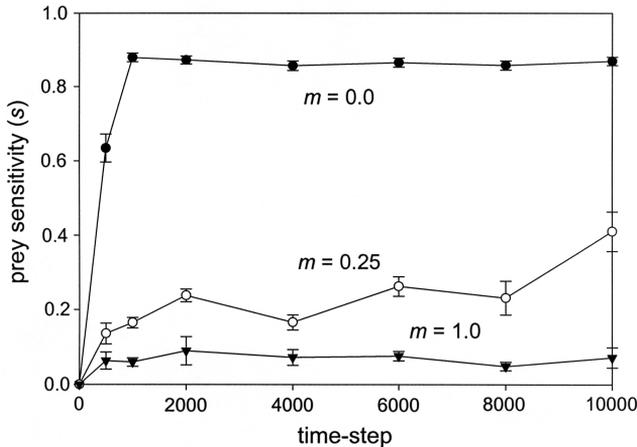


Fig. 5. Mean and 95% confidence intervals for prey sensitivity evolving through time in three different prey populations with different movement costs. With no cost of movement, $m = 0.0$ (filled circles), sensitivity quickly evolves to a large value in the prey population. $m = 0.25$ (open circles), sensitivity more slowly evolves to an intermediate value. $m = 1.0$ (filled triangles), sensitivity evolves to a much lower value in the population. All other parameters as in Fig. 1.

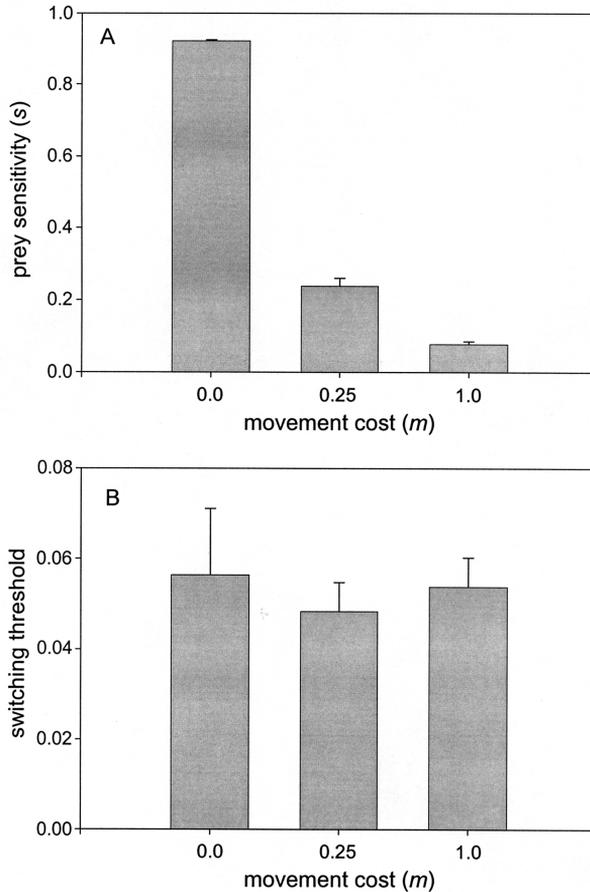


Fig. 6. Evolution of (A) prey sensitivity and (B) predator switching threshold, under three different movement costs. Prey sensitivity evolves to approximately the same level as when switching threshold does not evolve, but switching threshold evolves to lower levels than when prey sensitivity does not evolve. All other parameters as in Fig. 1.

absence of movement costs, the system did not converge to $s = 1.0$. The reason appears to be that as s increases, the strength of selection decreases and there continues to be mutational input of individuals with suboptimal values. Increasing the value of m resulted in the prey population evolving significantly lower sensitivity (Fig. 5). Movement costs can clearly influence the range of prey escape behavior arising in this model.

Allowing simultaneous evolution of prey sensitivity and predator switching threshold had a larger influence on predator switching than on prey sensitivity. Prey sensitivity (Fig. 6A) evolved to approximately the same values as occurred in Fig. 5 with different movement costs but no predator evolution. Predator switching thresholds, however,

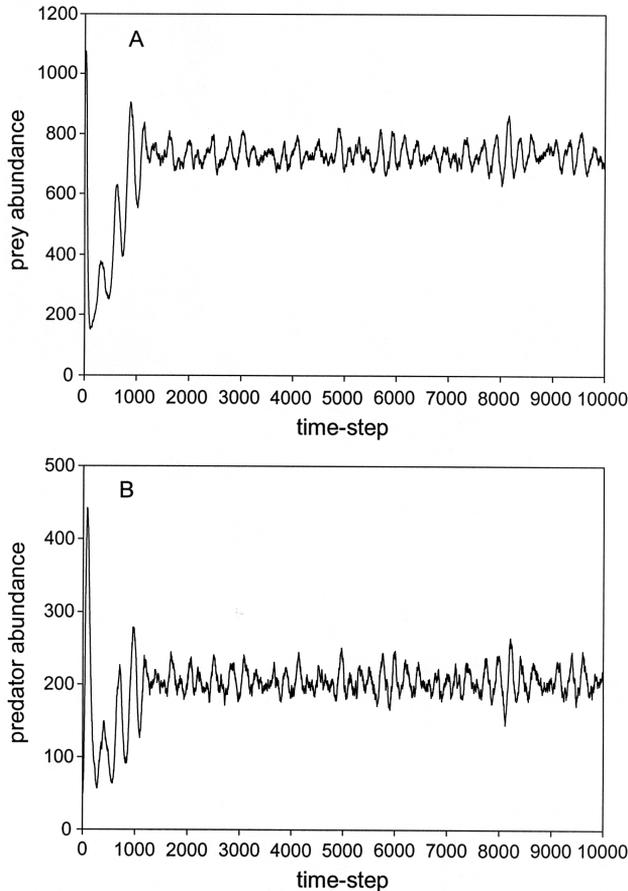


Fig. 7. Time-series of (A) prey and (B) predator abundance, as prey sensitivity and predator switching threshold evolve simultaneously and no cost of movement ($m = 0.0$). Both prey and predator cycles have amplitudes that are relatively smaller than the amplitude of cycles when prey sensitivity and switching threshold are fixed in the predator–prey system. All other parameters as in Fig. 1.

evolved to very different values when prey sensitivity evolved (Fig. 6B) than when prey sensitivity was held constant (Fig. 4). When we held prey sensitivity constant and allowed predator evolution, the evolved switching thresholds increased with increasing sensitivity (Fig. 4). But when prey sensitivity was allowed to evolve, predator switching thresholds evolved to approximately similar values regardless of the evolved sensitivity in the prey population (Fig. 6B). Thus, the similar, evolved switching thresholds that occur in Fig. 6B must be due to the evolution of sensitivity in the prey population. When we set $m = 0.0$ and allowed sensitivity and switching to evolve at the same time, the amplitude of cycles in both the prey and predator populations was relatively small (Fig. 7A,B) compared to the amplitude of cycles in Fig. 3. Simultaneous evolution of

prey movement and predator switching threshold can act to stabilize the predator–prey system if movement cost is low enough.

At high prey growth rates, a polymorphism in switching values (one high, one low) can coexist in the predator population (Fig. 8). This heterogeneity in switching evolution occurs even when selection is allowed to act on prey sensitivity. The value of s in the prey population appears to determine whether the lower or higher switching strategy is relatively more frequent in the predator population (Fig. 8). The stable coexistence of

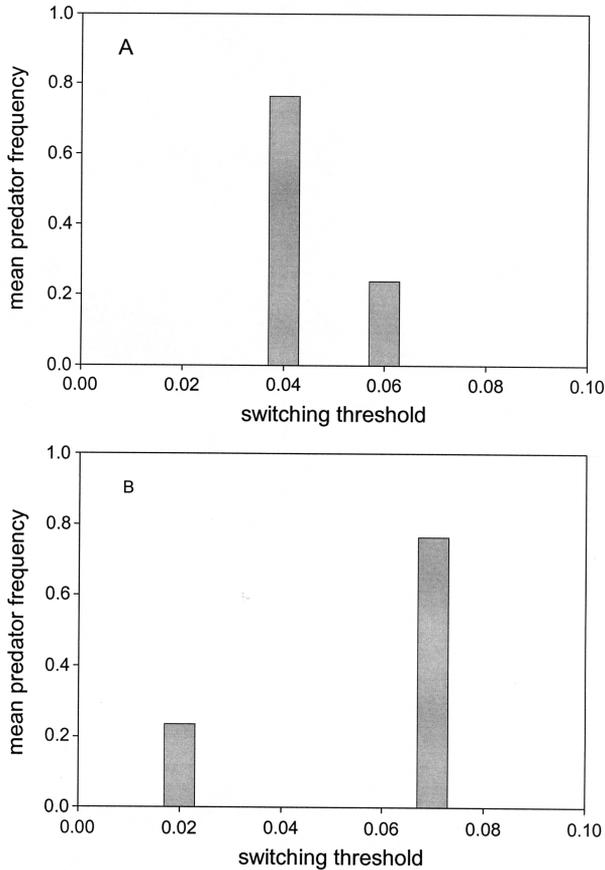


Fig. 8. Histograms of predator switching densities in two sample populations with high prey growth rate ($r = 0.1$), and sensitivities of (A) $s = 0.1$, and (B) $s = 0.2$. All other parameters as in Fig. 1. Two switching densities were maintained in each population throughout the simulations. Selection and mutation occurred for 5,000 time-steps, then mutation was stopped and selection alone occurred. The histogram shows the mean frequency of predators in each population using each switching density. The mean frequency was found by determining the frequency of predator types in a population at 15,000 time-steps, and every 1,000 time-steps afterwards, for a total of 10 time-steps. The frequencies in those 10 time-steps were then averaged to give the mean frequency.

alternative switching strategies in the predator population is a surprising result that seems to arise due to the stochasticity and localized interactions of the model. We intend to examine this in more detail in a follow-up work.

DISCUSSION

The classic Rosenzweig and MacArthur (1963) paper on stability of predator–prey interactions presented a simple graphical approach to analyzing the stability of interactions between predator and prey. This familiar model predicts that as prey become better at avoiding being eaten, limit cycles should decrease in amplitude, or disappear entirely. Thus, evolution on prey traits to withstand predators enhances the stability of predator–prey interactions (as long as the predator does not become so ineffective that it becomes extinct). Brown et al. (1999) found that the predator–prey dynamics of a system with prey that respond to predators by increasing vigilance and thereby becoming more difficult to catch, was most stable when prey were responsive to predators, but not perfectly responsive.

It is reasonable to equate prey avoiding being eaten in the Rosenzweig and MacArthur (1963) model, and increasing vigilance in the Brown et al. (1999) model, to prey movement away from predators in our models. The difference equation model agrees well with Rosenzweig and MacArthur (1963) and Brown et al. (1999); predator–prey dynamics become more stable as s increases, until s becomes so large that equilibrium predator density is negative and predators go extinct. In the individual-based model, intermediate values of s also produce the greatest stability; however, the predator–prey system persists at larger values of s than does the system in the difference equation model. Furthermore, the prey growth rate does not influence persistence or stability of the difference equation model at different values of s , but is important in the probability of persistence of the IBM.

We believe that the results from our IBM differ from those found in the difference equation model because of the incorporation of space and stochasticity in the IBM. The importance of the prey growth rate in determining persistence in the IBM and not the difference equation model reflects the stochasticity and explicit incorporation of individuals in the IBM. At low prey growth rates, predator and prey population density was low in the IBM, and demographic stochasticity frequently led to extinction. Demographic stochasticity did not occur in the difference equation model, and therefore prey growth rate did not influence persistence.

The explicit incorporation of space in the IBM may explain how the differences in prey sensitivity influenced persistence in the difference equation model and IBM. At large values of s , the optimal prey switching threshold is relatively large, ensuring that predators switch to the preferred prey patch at high prey abundance. At high prey abundance, however, the preferred prey patch in the IBM is nearly full with prey, and prey no longer have a refuge to move to when a predator is sensed nearby. The lack of refuge space when prey density is high allows predators to efficiently attack prey. The difference equation model does not explicitly incorporate space, and as a consequence,

extinction of predators occurs at lower values of s in the difference equation model than in the individual-based model. Thus, our results do not match the predictions of the difference equation model because the IBM includes space competition by prey at high prey abundances, which directly interferes with predator avoidance behavior. This result is similar to findings by Holt (1987), who explored simple models for competition for refuges, which usually led to stabilizing density dependence.

At high prey sensitivity, the predator is poor enough at attacking the preferred prey that prey abundance is always above the predator switching threshold. As a consequence, the predator never switches to the alternative prey patch, and in essence, becomes a specialist on the preferred prey. This is not the optimal ESS, however, as was determined by holding prey sensitivity constant and allowing the predator switching threshold to evolve. When facing selection, the switching threshold evolves to be higher than the predicted optimal threshold (eq 1) at low values of s , and lower than the predicted threshold at high values of s . At low values of s , predators efficiently attack prey, resulting in large amplitude cycles with the prey population reaching low densities. The stochasticity of discrete individuals at low abundance selects for predators to switch to the alternative prey patch at a higher preferred prey density than predicted by eq 1. At high s values, however, predators cannot drive prey to such low densities. Prey at high densities have less refuge space, thereby increasing the attack efficiency of predators, and selecting for a switching threshold in the predator population that is lower than expected. Adding a term to eq 1 incorporating the lack of refuge space would lower the predicted optimal switching threshold and make the fit with the evolved switching threshold better when prey sensitivity is high, but would also make the fit at low prey sensitivity worse. An equation for the optimal switching threshold must take into account not only prey refuge space at high prey density, but also the stochasticity of discrete individuals at low prey density.

As expected, when the predator switching threshold is held constant and prey sensitivity is allowed to evolve, the cost of movement experienced by prey determines the prey sensitivity that evolves in the population. The sensitivity that evolves in the prey population then determines the stability of the predator–prey system. In accordance with the earlier simulations in which we arbitrarily set constant prey sensitivities in the prey population, the evolution of a higher prey sensitivity results in greater stability of the system than does the evolution of a lower sensitivity.

Allowing prey sensitivity and the predator switching threshold to evolve simultaneously indicates the importance of incorporating genetic variability and evolution in the “rules” that determine “strategy” (e.g., move or stay still) in this foraging game. Mutation plays two roles in this model. First, it produces variation that allows populations to move towards the ESS. Second, for populations near an ESS, mutation creates non-adaptive variation—such recurrent variation can then be important for population dynamics, and even influence the nature of the ESS in the first place. Natural populations can hold substantial loads of mildly deleterious mutations; our results suggest that this non-adaptive variation is not just “noise,” but could have important implications for population stability and adaptive evolution. While prey sensitivity evolved to the same

level as occurred when the switching threshold was held constant, switching thresholds evolved to a lower level than when prey sensitivity was held constant. The evolution of lower switching thresholds suggests that genetic variation and evolution in prey sensitivities in the prey population allowed a lower switching threshold to be the ESS. Nevertheless, the evolution of prey sensitivity and switching threshold resulted in predator and prey cycles that had relatively much smaller amplitudes than if evolution had not occurred. Thus, the evolution of prey movement, and the coevolutionary response to that evolution by predators, may tend to stabilize predator–prey interactions.

The finding that multiple switching densities can coexist in the individual-based model suggests that predators using different foraging strategies can partition the preferred prey in some manner. This result is similar to work by McPeck and Holt (1992), who found that low and high-dispersing species could coexist when they partitioned high and low carrying-capacity patches. The coexisting foraging strategies in our model partition the preferred prey patch temporally and spatially, with one predator strategy leaving the preferred patch earlier and at relatively higher prey density than the other predator strategy. As the preferred prey cycles in abundance, each predator strategy is at an advantage relative to the other strategy at some points in the prey cycle, and at a disadvantage at other points, effectively partitioning the patches and allowing coexistence. We hope to examine this issue in detail in future studies.

ACKNOWLEDGMENTS

We thank Peter Abrams and Michael Barfield for useful thoughts on the work, and Joel Brown for insightful comments on the manuscript. R.D.H. thanks NSF and the University of Florida Foundation for support. T.K. thanks NSF for a Graduate Research Fellowship.

REFERENCES

- Abrams, P.A. 1999. The adaptive dynamics of consumer choice. *Am. Nat.* 153: 83–97.
- Abrams, P.A. 2000. The impact of habitat selection on the spatial heterogeneity of resources in varying environments. *Ecology* 81: 2902–2913.
- Abrams, P.A., Matsuda, H. 2004. Consequences of behavioral dynamics for the population dynamics of predator–prey systems with switching. *Popul. Ecol.* 46: 13–25.
- Brown, J.S., Laundre, J.W., Gurung, M. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80: 385–399.
- Chesson, P. 1978. Predator–prey theory and variability. *Annu. Rev. Ecol. Syst.* 9: 323–347.
- Fryxell, J.M., Lundberg, P. 1994. Diet choice and predator–prey dynamics. *Evol. Ecol.* 8: 407–421.
- Hassell, M.P. 2000. *The spatial and temporal dynamics of host–parasitoid interactions.* Oxford University Press, New York, 200 pp.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Ecol.* 12: 197–229.
- Holt, R.D. 1983. Optimal foraging and the form of the predator isocline. *Am. Nat.* 122: 521–541.
- Holt, R.D. 1987. Prey communities in patchy environments. *Oikos* 50: 276–290.

- Kimbrell, T., Holt, R.D. Individual behavior, space, and predator evolution promote persistence in a two-patch system with predator switching. *Evol. Ecol. Res.*, in press.
- Kondoh, M. 2003. Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299: 1388–1391.
- Krivan, V. 1996. Optimal foraging and predator-prey dynamics. *Theor. Popul. Biol.* 49: 265–290.
- Krivan, V. 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator-prey dynamics. *Am. Nat.* 149: 164–178.
- Krivan, V., Sikder, A. 1999. Optimal foraging and predator-prey dynamics, II. *Theor. Popul. Biol.* 55: 111–126.
- MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533–536.
- May, R.M. 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ, 235 pp.
- McPeck, M.A., Holt, R.D. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* 140: 1010–1027.
- Morgan, R.A., Brown, J.S. 1996. Using giving-up densities to detect search images. *Am. Nat.* 148: 1059–1074.
- Murdoch, W.W., Oaten, A. 1975. Predation and population stability. *Adv. Ecol. Res.* 9: 1–131.
- Rosenzweig, M.L., MacArthur, R.H. 1963. Graphical representation and stability conditions of predator-prey interactions. *Am. Nat.* 97: 209–223.
- Roughgarden, J., Feldman, M.W. 1975. Species packing and predation pressure. *Ecology* 56: 489–492.
- Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). *J. Anim. Ecol.* 39: 619–668.
- van Baalen, M., Krivan, V., van Rijn, P.C.J., Sabelis, M.W. 2001. Alternative food, switching predators, and the persistence of predator-prey systems. *Am. Nat.* 157: 512–524.

APPENDIX

The equilibrium for the predator and prey in the difference equation model occurs at $\hat{N} > N_s$, therefore we simplify the following equations by assuming $f_A(N_r, A) = 0$. The equilibrium for prey and predators is thus:

$$\hat{N} = \frac{d}{(1-s)[C_N - dT_N]}$$

$$\hat{P} = \frac{r \left(1 - \frac{\hat{N}}{K} \right) (1 + \hat{N} T_N (1-s))}{(1-s)} \quad (\text{A1})$$

To determine if the equilibrium is locally stable, we form the Jacobian matrix (**J**) at the equilibrium:

$$\mathbf{J} = \begin{bmatrix} r \left(1 - \frac{2\hat{N}}{K} \right) - f_N'(\hat{N}, A) \hat{P} & -f_N(\hat{N}, A) \\ \hat{P} \left[C_N f_N'(\hat{N}, A) \right] & 0 \end{bmatrix} \tag{A2}$$

Here, f_N' indicates the derivative of the functional response. We use the eigenvalues (λ) of \mathbf{J} to determine if the equilibrium is stable. We set $\lambda' = \lambda + 1$, and have the condition that the equilibrium is stable if $|\lambda'|^2 < 1$ for each eigenvalue. Thus, the equilibrium is locally stable if the following inequality is true:

$$|\lambda'|^2 = r \left(1 - \frac{2\hat{N}}{K} \right) + \left[\frac{(1-s)}{1+T_N \hat{N}(1-s)} - \frac{T_N \hat{N}(1-s)^2}{(1+T_N \hat{N}(1-s))^2} \right] \hat{P}(d-1) < 0 \tag{A3}$$