

Nonequilibrium Population Dynamics of “Ideal and Free” Prey and Predators

Minus van Baalen* and Maurice W. Sabelis

Institute for Biodiversity and Ecosystem Dynamics, Section Population Biology, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands

Submitted February 5, 1998; Accepted January 15, 1999

ABSTRACT: Aggregated spatial distributions of prey and predators promote stability of the otherwise unstable Nicholson-Bailey model. Nevertheless, when both predators and prey choose patches in an ideal free way, sufficiently aggregated distributions will only arise if patch quality (e.g., reflected in prey fecundity) is very heterogeneous. This requirement profoundly limits the possibilities for simultaneous population dynamical and evolutionary stability. However, stability is not necessary for coexistence. Under cyclic or chaotic dynamics, the rate at which species change their distributions becomes important. Here we consider two endpoints of a continuum of rates. The first is “rigid” selection of patch types based on the expected long-term distribution of conditions. The second is “flexible” selection based on current conditions. We carried out systematic surveys of the population-level consequences of coevolutionarily stable patch-selection strategies for different combinations of rigid and flexible strategies of predator and prey. First, if both prey and predators have rigid strategies, the evolutionary end result is either a stable population dynamical equilibrium or diverging cycles eventually leading to extinction. Second, for the case with rigid prey and flexible predators, the persistence boundary in parameter space is shifted from the boundaries obtained for rigid predators. The mechanism underlying persistence is different in that the flexible strategies of the predators destabilize the equilibrium, while the evolutionary response of the rigid prey leads to reduced cycles. Third, if both prey and predators are flexible, simulations lead either to chaotic fluctuations or to extinction (but not to stable equilibria, nor to limit cycles), and the conditions for coexistence are much wider than those under rigid patch selection. These simulations suggest that information constraints on adaptive patch choice have a major impact on predator-prey persistence under nonequilibrium conditions. We discuss how these predictions can be tested by field observations on expan-

sions and contractions in dietary range (or habitat range) in relation to population fluctuations.

Keywords: predator-prey interactions, aggregation, foraging behavior, evolutionarily stable strategy, coevolution.

In spatially structured predator-prey systems, patch selection may have profound effects on population dynamics as well as on subsequent evolution. The effect on population dynamics has been analyzed extensively in the framework of discrete generation models without intrageneration dynamics, the so-called Nicholson-Bailey type models (Hassell and May 1973, 1974; May 1978; Chesson and Murdoch 1986). In such models, predators and prey select patches instantaneously and do not pay the cost of traveling from patch to patch. Here we will consider the consequences of optimal patch choice for predator-prey dynamics within this Nicholson-Bailey framework, thus ignoring continuous time versions that take within-generation dynamics into account (Murdoch and Stewart-Oaten 1989).

Hassell and May (1973) have shown that strong aggregation of predators in patches of high prey density may stabilize an otherwise unstable ecological equilibrium of prey and predators. The “aggregative response” to prey density may therefore have a key role in explaining the coexistence of prey and predators (Hassell 1978, 1984). A fundamental question is whether such stabilizing spatial patterns are produced by the adaptive behavior of prey and predators.

Aggregative behavior of predators may be explained by optimal foraging theory (Hassell and May 1973; Cook and Hubbard 1977; Hubbard and Cook 1978; Brown 1998; Sih 1998). Explicit combinations of population stability analysis and optimal foraging theory were analyzed by Comins and Hassell (1979) and Sutherland (1983). Both studies were based on the assumption that optimal patch choice of a population of predators will lead to an “Ideal Free Distribution” (Fretwell and Lucas 1970), in which no individual predator can gain by moving to another patch. Where predators aggregate, local competition for prey will

* To whom correspondence should be addressed. Present address: Université Pierre et Marie Curie, Institut d'Écologie, URA 258, Bâtiment A, 7ème Etage, Case 237, 75252 Paris CEDEX 05, France; e-mail: mvbaalen@snv.jussieu.fr.

cause foraging efficiency to decrease. Optimal foraging strategies will lead predators away from patches where competition severely reduces foraging efficiency, and the degree of aggregation of the predator decreases (Comins and Hassell 1979; Sutherland 1983). If both predators and prey select patches optimally, the conditions for simultaneous ecological and evolutionary stability appear to be rather narrow (van Baalen and Sabelis 1993). However, a stable equilibrium is not a prerequisite for predators and prey to coexist. This requires analysis of the interdependence of evolution and nonequilibrium dynamics, as studied by Godfray et al. (1992), Fryxell and Lundberg (1993, 1997), Holt (1997), and Abrams and Matsuda (1997) for a variety of systems. The main question of the present article is whether adaptive patch choice can promote the persistence of prey and predators even under nonequilibrium conditions (see also Holt 1997).

One way of studying the effects of Ideal Free Distributions is to substitute them into the parameters of the population dynamical model and analyze the dynamics, as was done in van Baalen and Sabelis (1993). However, by using fixed parameters, it is implicitly assumed that spatial distributions are density independent. In some cases, this will be a reasonable assumption, for instance, where prey and predators can distinguish among patches of different types but cannot detect the densities of prey and predators within patches. Yet, in other cases, prey or predators are able to assess, and react to, the actual distribution of one or even both trophic levels. If prey or predators are "flexible," they can select the best patches based on information about the distribution of patch profitabilities. Then, spatial distributions will become density dependent: whether or not to enter a particular patch will depend on the overall degree of competition and, thus, on global densities of prey and predators.

Though simultaneous Ideal Free Distributions can result from both rigid and flexible patch-selection strategies, there is a crucial difference. If patch-selection strategies are rigid, population distributions will only change over evolutionary time, whereas if patch-selection strategies are flexible, spatial distributions will change also at the ecological timescale (within generations and from one generation to the next). Equilibrium densities and distributions are the same for these cases, but the dynamics around this equilibrium can be quite different, as we will show. Abrams and Kawecki (1998) analyze a similar Nicholson-Bailey type model with two prey species to show that the time scale of adaptive prey choice may have profound dynamical consequences.

To simplify the model as much as possible, we will assume a discrete-time setting in which prey and predators have a short time window to select their patches before they actually start to interact. That is, if they have flexible

strategies, they are allowed to assess all the patches (and assess the distributions of prey and predators) before choosing. Based on this knowledge, any individual will settle in the patch offering the highest reward. Since all individuals behave similarly, the population will eventually settle (actively) at an Ideal Free Distribution, and the actual interaction takes place.

The analysis is thus based on the bold assumption that populations can achieve Ideal Free Distributions for given conditions. One may ask whether this assumption is realistic, as in reality individuals are never "ideal" or "free." However, it has been shown that, even if individuals are either informationally or behaviorally constrained, the population may still achieve Ideal Free Distribution (Kacelnik et al. 1992). Whether such constraints acting on both trophic levels may prevent simultaneous Ideal Free Distributions is, as far as we are aware, still an open problem (Abrams and Matsuda [1997] discuss an example where mutual adaptation gives rise to cycles). In this article, we avoid bringing in mechanistic detail in the patch-selection strategies because it will impose arbitrary constraints and, therefore, cause equally arbitrary outcomes. We will assume that mechanisms underlying the individuals' patch-selection strategies are sufficiently sophisticated to result in Ideal Free Distributions.

Even in our simple framework, flexible patch selection complicates an explicit stability analysis considerably. Since the parameters that specify population distributions become functions of density, a local stability analysis will incorporate the derivatives of these functions with respect to density, which leads to very complicated expressions. As discontinuous changes may also have to be taken into account (which changes occur when patches change status from unprofitable to profitable), a global stability analysis is not feasible. We therefore carried out computer simulations to explore the consequences of simultaneous Ideal Free Distributions on nonequilibrium dynamics of predator and prey. To investigate the effect of density dependence, we considered three cases: patch-selection strategies of prey and predators are rigid; the prey have a rigid patch-selection strategy, while the predators have a flexible patch-selection strategy; and both prey and predators have flexible patch-selection strategies. These three cases reflect different possibilities in the order of settling on a patch: random arrival, the prey arrive before the predators, and prey and predators arrive simultaneously.

As in van Baalen and Sabelis (1993), we will assume that both prey and predators choose only once per generation. That is, at the beginning of the season, there is a short phase where all individuals are allowed to sample their environment and select a patch to settle (using the information that is available to them, depending on the case); but once they have settled, they are not allowed to

leave. This implies that we exclude within-generation changes from our analysis. Neither do our assumptions lead to across-generational responses; for example, predator decisions in generation t are not based on the prey distribution as it was in generation $t - 1$.

Křivan (1997) carried out an analysis similar to ours for simultaneous Ideal Free Distributions in continuous-time Lotka-Volterra predator-prey systems. He showed that such adaptive patch-selection behavior could render persistent the otherwise neutrally stable dynamics. We extend this analysis to show that adaptive patch choice can promote persistence in the strongly unstable setting of Nicholson-Bailey predator-prey dynamics in discrete time.

Population Dynamics

The numerical analyses we carried out are based on the model of van Baalen and Sabelis (1993),

$$N_{t+1} = N_t \sum_{i=1}^n \alpha_i \lambda_i e^{-a\beta_i P_t}, \quad (1a)$$

$$P_{t+1} = N_t \left[1 - \sum_{i=1}^n \alpha_i e^{-a\beta_i P_t} \right], \quad (1b)$$

where N_t and P_t represent populations of prey and predators in generation t . This model is identical to Hassell and May's (1973) model, except that prey fecundity, λ_i , varies from patch to patch. The parameter measuring predator searching efficiency, a , disappears when population densities are appropriately scaled and will be omitted in what follows. The parameters α_i and β_i are the fractions of prey and predators that move into patch i ($i = 1, \dots, n$; $\sum \alpha_i = \sum \beta_i = 1$). Van Baalen and Sabelis (1993) derived these parameters from the outcome of the patch-selection game played by prey and predators. These parameters were constant in van Baalen and Sabelis (1993) because equilibrium conditions were assumed. If every prey and every predator has its individual patch-selection strategy, a pair of CoESSs (coevolutionarily stable strategies; Maynard Smith and Price 1973; Maynard Smith 1982) specifies a pair of simultaneous Ideal Free Distributions (Fretwell and Lucas 1970) because only then it is true that no mutant can do better than a resident.

The simultaneous Ideal Free Distributions follow from the per capita fitness being equal in all patches for both prey and predators, that is, from

$$\lambda_i e^{-\beta_i P} = K, \quad (2a)$$

$$\frac{\alpha_i N (1 - e^{-\beta_i P})}{\beta_i P} = L, \quad (2b)$$

where K and L are the average fitness of prey and predators, respectively. Under conditions of ecological equilibrium, K and L will equal unity (van Baalen and Sabelis 1993). Explicit expressions for coevolutionarily stable patch-selection strategies can then be derived. Suppose that there are n patches in which prey fecundity is larger than 1. Under conditions of ecological stability, these patches will receive population densities of

$$\beta_i P = \ln \lambda_i, \quad (3a)$$

$$\alpha_i N = \frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i, \quad (3b)$$

as follows from equations (2a) and (2b) after setting $K = L = 1$. (Notice that a positive fraction requires $\lambda_i > 1$: under equilibrium, only patches in which the prey can reproduce are included in the simultaneous Ideal Free Distributions.) Summation of equations (3a) and (3b) over all n patches gives the equilibrium densities of predator and prey; the Ideal Free Distributions under equilibrium conditions can then be expressed explicitly:

$$\beta_i = \frac{\ln \lambda_i}{\sum_{j=1}^n \ln \lambda_j}, \quad (4a)$$

$$\alpha_i = \frac{\frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i}{\sum_{j=1}^n \frac{\lambda_j}{\lambda_j - 1} \ln \lambda_j}. \quad (4b)$$

When the distributions of prey and predators follow from their adaptive choices, the only parameters that remain are those that characterize the environment, that is, the patch qualities λ_i . The problem is thus to determine how the distribution of patch qualities λ_i relates to the dynamical behavior of the model. Van Baalen and Sabelis (1993) carried out a local stability analysis assuming that distributions (eqq. [4a], [4b]) are constant in ecological time. They assumed simple environments, consisting of two types of patches, a single high-quality patch in which prey fecundity is λ_H and $(n - 1)$ identical low-quality patches in which prey fecundity equals λ_L . The results, captured in figure 1, suggest that only if there are many (but not too many) marginal patches, rigid patch-selection may lead to ecological stability. Notice how fast the region of stability shrinks as quality of the marginal patches in-

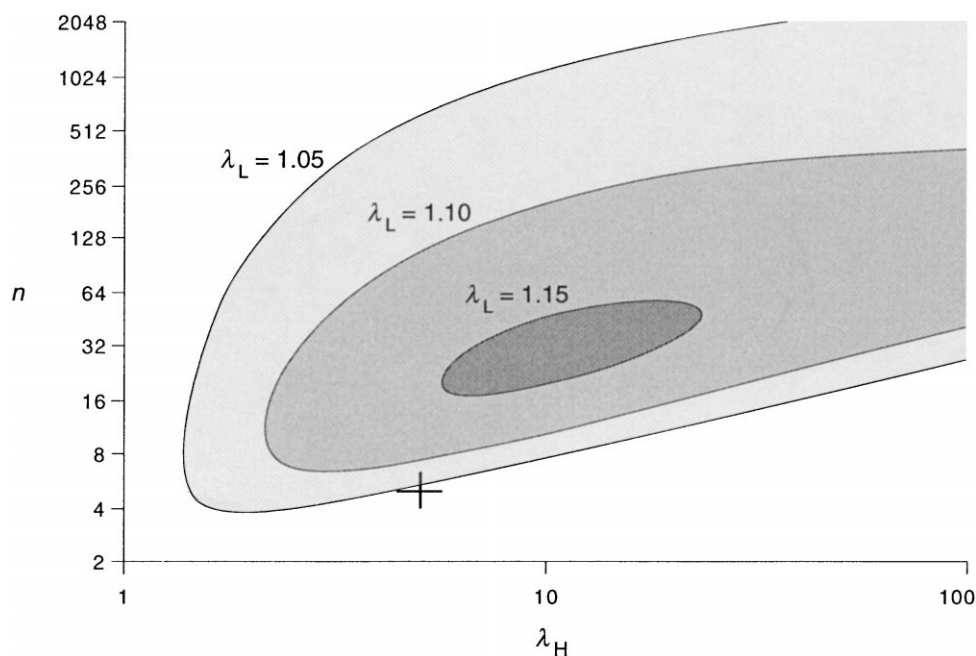


Figure 1: Domains of simultaneous ecological and evolutionary stability, when both prey and predator have rigid (density-independent) patch-selection strategies. The environment consists of one high-quality patch in which prey fecundity is λ_H , and $n - 1$ low-quality patches in which prey fecundity is λ_L . Plus sign denotes the combination of parameters chosen for some of the simulations. Source: van Baalen and Sabelis 1993.

creases. This implies that the low-quality patches should be really marginal, barely allowing for self-replacement of the prey. In source-sink terminology (Holt 1997), low-quality patches are sources, but only very weak ones.

Case 1: Rigid Patch Selection

First, we will investigate nonequilibrium dynamics assuming that individual prey and predators have rigid patch-selection strategies and thus extend van Baalen and Sabelis's (1993) analysis outside the region of ecological stability. The patch-selection strategies are first assumed to be equal to those expected under equilibrium conditions. After assessing the dynamical consequences, we will explore how the optimal patch-selection strategies change under the dynamical regime in the unstable domain.

In an environment with one high-quality patch ($\lambda_H = 5$) and four low-quality patches ($\lambda_L = 1.05$), the ecological equilibrium is unstable (this combination of parameters is located just outside of the region of stability; see fig. 1). However, the oscillations do not diverge indefinitely but approach an invariant loop (the discrete-time equivalent of the limit cycle). Hence, we can already infer that persistence of prey and predators is not restricted to conditions of stable ecological equilibria.

Figure 2 captures the results of a systematic exploration

of parameter space. The coefficient of variation of 500 prey generations is plotted (after a transient of 500 generations) for different combinations of λ_H and n ; λ_L is fixed at either 1.05, 1.1, or 1.15 (in figs. 2A, B, and C, respectively). There is a central region in which the coefficient of variation is 0; this corresponds with ecological stability. This region is surrounded by a region of increasing fluctuations, which turn out to be limit cycles. Eventually, the cycles become so large that extinction is inevitable (in the white area in the figure at least one of the populations reaches a density lower than 10^{-6} of its equilibrium density).

Thus, if the number of low-quality patches becomes either too low or too large, the stable equilibria give way to limit cycles and then to extinction. This pattern comes as no surprise if one realizes that, in either case, one type of patch starts to dominate, and the dynamics will approach those of the unstable Nicholson-Bailey model, which always ends in extinction. A similar argument holds if prey fecundity in the high-quality patch increases because then the prey will aggregate more and more in the high-quality patch, and the dynamics approach that of the Nicholson-Bailey model. These results, however, depend on the assumption that optimal distributions do not change if populations start to cycle, which is not true, as we will show now.

With the transition from an equilibrium to a cycling

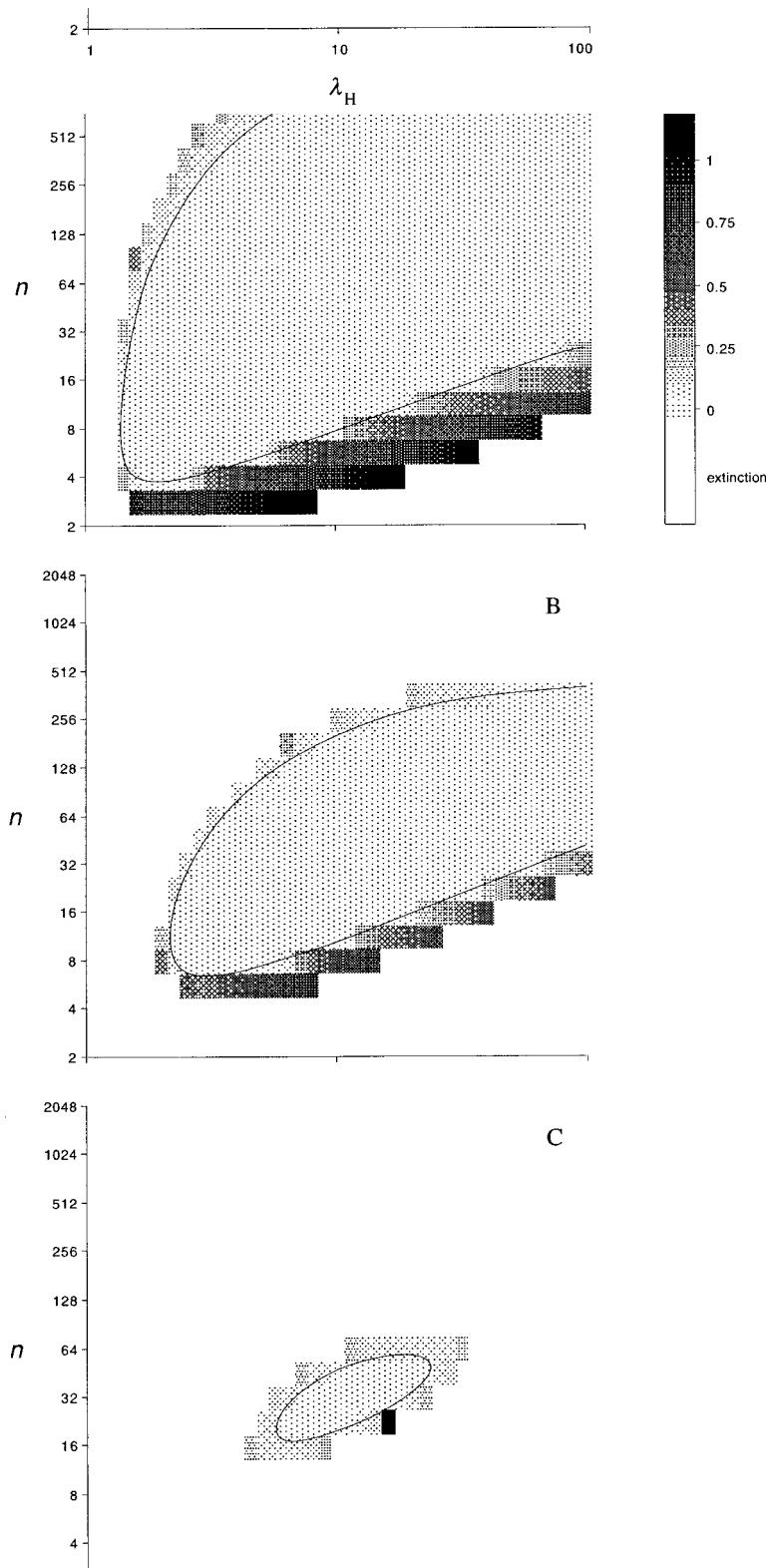


Figure 2: Parameter surveys of the dynamics that result when prey and predators are constrained to rigid patch-selection strategies. White indicates extinction, shading indicates the coefficient of variation of prey density in an environment consisting of one high-quality patch in which prey fecundity equals λ_H and $(n - 1)$ and marginal patches in which prey fecundity equals (A) $\lambda_L = 1.05$, (B) $\lambda_L = 1.1$, and (C) $\lambda_L = 1.15$. The stability boundary from the local stability analysis is superposed on each graph. The coefficient of variation is calculated from prey generations 501 to 1,000. Extinction was assumed when prey or predator density decreased below 10^{-6} times equilibrium density.

predator-prey interaction, optimal patch-selection strategies will change. Even if individuals are limited to a rigid patch-selection strategy, coevolutionarily stable patch-selection strategies will deviate from those expected under equilibrium (eqq. [4a], [4b]) because they should be optimal for a time average of the conditions as they vary over the limit cycle. Such time averages are likely to differ from equilibrium values when predator-prey populations cycle or fluctuate otherwise (Armstrong and McGehee 1976, 1980; Hofbauer and Sigmund 1988; Abrams and Roth 1994).

The appropriate fitness measure should thus incorporate density fluctuations. Consider resident predator-prey dynamics to be on its attractor with a period T (i.e., $T = 1$ for a point equilibrium, T is finite for a periodic attractor, and T is infinite for a quasiperiodic or a chaotic attractor). In that case, a mutant faces a fully specified environment (N_t^* , P_t^* , α_t^* , and β_t^* , with $t = 1, \dots, T$). For each generation t , the reproductive success of the mutant predator (F_t) is then given by the arithmetic mean over patches of the per capita reproductive success (ϕ_{it}) in the patches; that is,

$$F_t = \sum_{i=1}^n \beta_i \phi_{it}, \quad (5)$$

with

$$\phi_{it} = \frac{\alpha_t^* N_t^* (1 - e^{-\beta_t^* P_t^*})}{\beta_i^* P_t^*}. \quad (6)$$

Expected reproductive success over the generations $t = 1, \dots, T$ is then found as G , the geometric mean over the cycle of the arithmetic mean over the patches:

$$G = \sqrt[T]{F_T F_{T-1} \dots F_2 F_1} \quad (7)$$

(or the appropriate limit if T is infinite). This is the appropriate fitness measure for a mutant predator: if G exceeds unity, the mutant invades; if it is less, the mutant will go extinct. (An analogous fitness measure can be derived for mutant prey. A formal derivation of G is given in app. A; see McPeck and Holt [1992] and Holt and McPeck [1996] for more discussion on the concept of fitness in spatially extended discrete-time systems.)

If the predators are constrained to a rigid patch-selection strategy (i.e., β_i is constant for all t), optimization requires solving complicated expressions. In appendix A, it is shown that in an environment with two types of patches (such that a strategy β specifies the probability to select the high-quality patch and $[1 - \beta]/[n - 1]$ is the probability to select a given low-quality patch), the evolution-

arily stable patch-selection strategy (ESS) β^* should satisfy $dG/d\beta = 0$ for $\beta = \beta^*$, or

$$\frac{1}{T} \sum_{t=1}^T \frac{\phi_{Ht} - \phi_{Lt}}{\beta^* \phi_{Ht} + (1 - \beta^*) \phi_{Lt}} = 0, \quad (8)$$

where ϕ_{Ht} and ϕ_{Lt} denote per capita fitness in high- and low-prey-density patches, respectively. Thus, the average difference in profitability, weighed by per generation average fitness, should be 0. This weighing is necessary because a given fitness difference ($\phi_{Ht} - \phi_{Lt}$) counts more when overall fitness is low (i.e., during population crashes). Unless $T = 1$ (stable equilibrium), there is no easy way to solve this equation.

Equation (8) can be used to derive a “selection differential,” measuring the change in fitness that is associated with a small change in patch-selection strategy (eq. [A8]). On the basis of this information, the ESS can then be found iteratively. The results of this computationally rather intensive procedure are striking: the region of limit cycles surrounding the region of ecological stability disappears altogether and populations go extinct (results not shown). The reason for this result is the following: in a fluctuating environment, avoiding patches with high variance in per capita fitness becomes part of the optimal patch-selection strategy (see app. A) because the geometric mean is very sensitive to occasional low values. This variance is highest in the high-prey density patches. Consequently, when populations start to fluctuate, it pays predators to distribute their search more evenly. As a similar argument holds for the prey, for which high variance in predation risk decreases profitability, less aggregated distributions of prey and predators result. A runaway process occurs as fluctuations increase in amplitude and increased variance favors even less aggregated patch-selection strategies. The net result is, thus, that if the ecological equilibrium becomes unstable, spatial distributions of both prey and predator become more even, destabilizing the interaction even more. In this model, limit cycles are therefore not among the evolutionary outcomes.

Case 2: Rigid Prey and Flexible Predators

Suppose the prey are still limited to a rigid patch-selection strategy, but the predators have more elaborate behavioral repertoire that enables them to select the best patches depending on the circumstances. Then, as average fitness (L_t) varies when populations fluctuate, the predators’ spatial distribution, β_{it} , will vary in time as well. A first thing to notice is that, depending on the circumstances, flexible predators may avoid some of the patches, because if

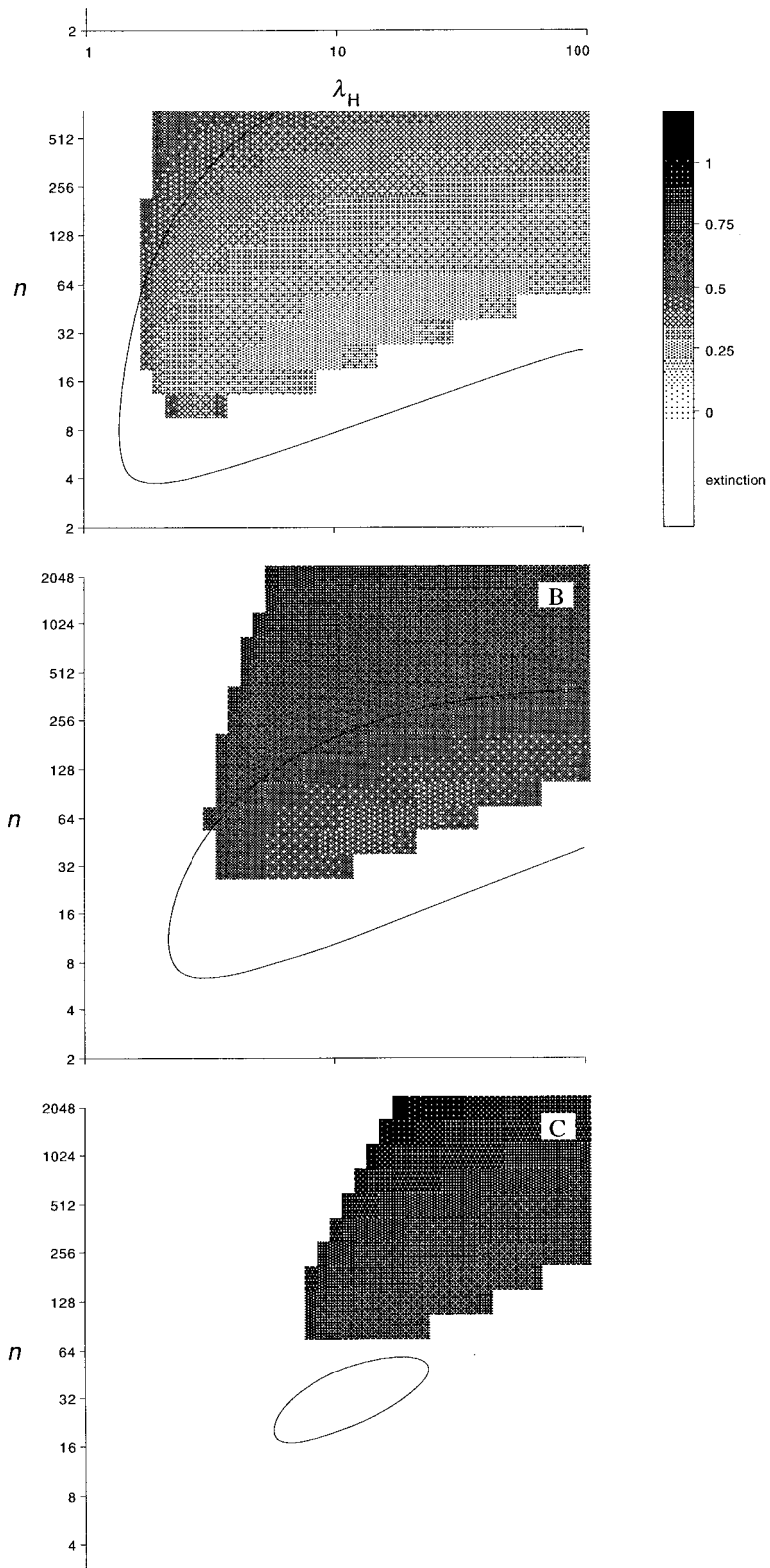


Figure 3: Parameter surveys of dynamics that result when predators adopt a flexible patch-selection strategy and prey are constrained to a rigid patch-selection strategy. See figure 2 legend for explanation.

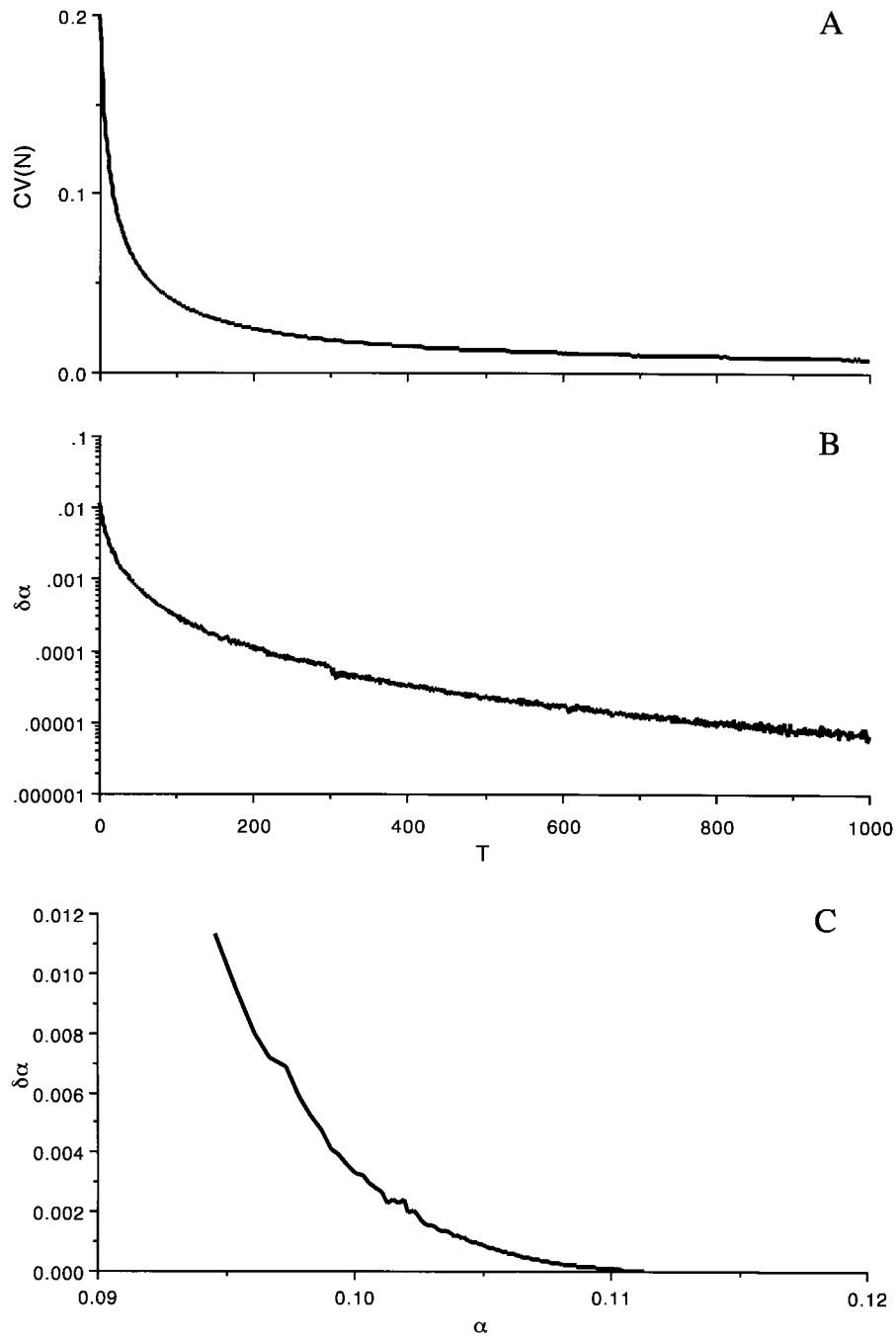


Figure 4: Evolution toward reduced cycle amplitude when the rigid patch-selection strategy of the prey evolves and the predators have a flexible patch-selection strategy. The results were obtained by repeating 1,000 times a cycle consisting of running a simulation for 1,000 generations, calculating the selection differential $\delta\alpha_H = df/d\alpha_H$ operating on α_H over the last 500 generations as outlined in appendix A, and adjusting α_H according to the selection differential using $\alpha_H \rightarrow C\alpha_H(1 - \alpha_H)\delta\alpha_H$. A, Relative amplitude (i.e., coefficient of variation CV_N) versus repeat number T ; B, selection differential $\delta\alpha_H$ versus T ; C, selection differential $\delta\alpha_H$ versus α_H . Parameters: $\lambda_H = 5$, $\lambda_L = 1.05$, $n = 20$, $C = 1$.

$$\alpha_i N_t < L_t, \quad (9)$$

patch i does not contain enough prey even in absence of competition with other predators. The Ideal Free Distribution is therefore implicitly specified by

$$\frac{\alpha_i N_t (1 - e^{-\beta_i P_t})}{\beta_i P_t} = L_t \quad (\beta_i > 0),$$

$$\alpha_i N_t < L_t \quad (\beta_i = 0). \quad (10)$$

Unfortunately, this set of conditions cannot be solved explicitly, so we have to resort to numerical approximations.

First, we investigate the consequences of flexible predators while the prey are still distributed according to the Ideal Free Distribution under equilibrium conditions. Then, numerical simulations reveal that ecological stability disappears altogether. Yet, even though stable equilibria do not occur, coexistence occurs in part of parameter space (fig. 3); this coexistence is in the form of limit cycles. Compared with the conditions of persistence of rigid prey and predators, roughly four times as many low-quality patches are necessary to prevent extinction.

Two opposing mechanisms are involved in determining the region of coexistence. Whenever patches are avoided by the predators, some of the prey are offered a refuge, which is, in principle, a stabilizing mechanism. To produce the fluctuations, there must also be a destabilizing mechanism. As Hassell (1984) and Murdoch and Stewart-Oaten (1989) have noted, much of the stabilizing effect of density-independent aggregation of the predators can be attributed to the fact that average searching efficiency is low when predator density is high. Flexible predators will counter this reduction in foraging efficiency as best as they can. Thus, though the active, adaptive “aggregative response” of predators to prey density may contribute to persistence, it is actually a destabilizing mechanism.

The results presented in figure 3 are based on the assumption that the prey adopt the patch selection that is optimal under equilibrium conditions. As noted before, the optimum will change when populations fluctuate. If we allow the prey to evolve (on a timescale much larger than the period of the cycles) we observe a consistent trend toward reduced amplitude of the fluctuations (fig. 4A). This decrease in temporal variability is accompanied by a stronger aggregation of the prey in the high-quality patch and a rapidly decreasing selection differential (fig. 4B). Hence, the approach to 0 amplitude is not exponential but subexponential, which implies that the rate of approach to equilibrium slows to 0 before the equilibrium has been reached (fig. 4C). It can be seen in figure 4A that the fluctuations have not disappeared, even after a long time. If the system would be brought at equilibrium, then

nonequilibrium conditions stop influencing the selection process, and the system will jump back to the Ideal Free Distribution with its unstable dynamics. The unstable dynamics will cause renewed selection for distributions that are more aggregated than the Ideal Free Distribution (that leads to reduced fluctuations), and the process starts all over again.

Case 3: Flexible Prey and Flexible Predators

To the prey, the profitability of a particular patch depends on the balance between patch quality and the risk of predation. A prey individual will therefore gain if it is able to respond to changes in abundance and distribution of the predators. An interesting situation results when prey and predators both can adopt flexible patch-selection strategies. In this section, we will merely assume that these abilities will cause predators and prey to be distributed according to simultaneous Ideal Free Distributions at any given generation.

The simultaneous Ideal Free Distributions of predator and prey can be calculated for any combination of densities N_t and P_t . Then, the α_i and β_i will become functions of the global densities of prey and predators. According to equation (2), patch i will receive

$$\beta_i P_t = \ln \lambda_i - \ln K_t, \quad (11a)$$

$$\alpha_i N_t = L_t \frac{\lambda_i}{\lambda_i - K_t} (\ln \lambda_i - \ln K_t), \quad (11b)$$

prey and predators, provided that it is sufficiently profitable, which is the case if

$$\lambda_i > K_t. \quad (12)$$

If the prey would avoid such a patch, so would the predators. However, in absence of predators, net prey fitness would be larger than average and the patch would attract more and more prey. Eventually, the patch becomes sufficiently profitable for predators to follow. The risk of predation will rise until net prey fitness is the same as in other patches.

The problem is to determine which patches are visited and which patches are ignored. This can be done using a simple procedure. Assume that prey and predators are distributed over the k best patches (this time in terms of patch quality, reflected in λ_i). Calculate average fitnesses K_t and L_t and check whether the next best patch is sufficiently profitable. If so, the prey will also include the next best patch, which means that the procedure has to be repeated for $k + 1$ patches. Eventually, no remaining

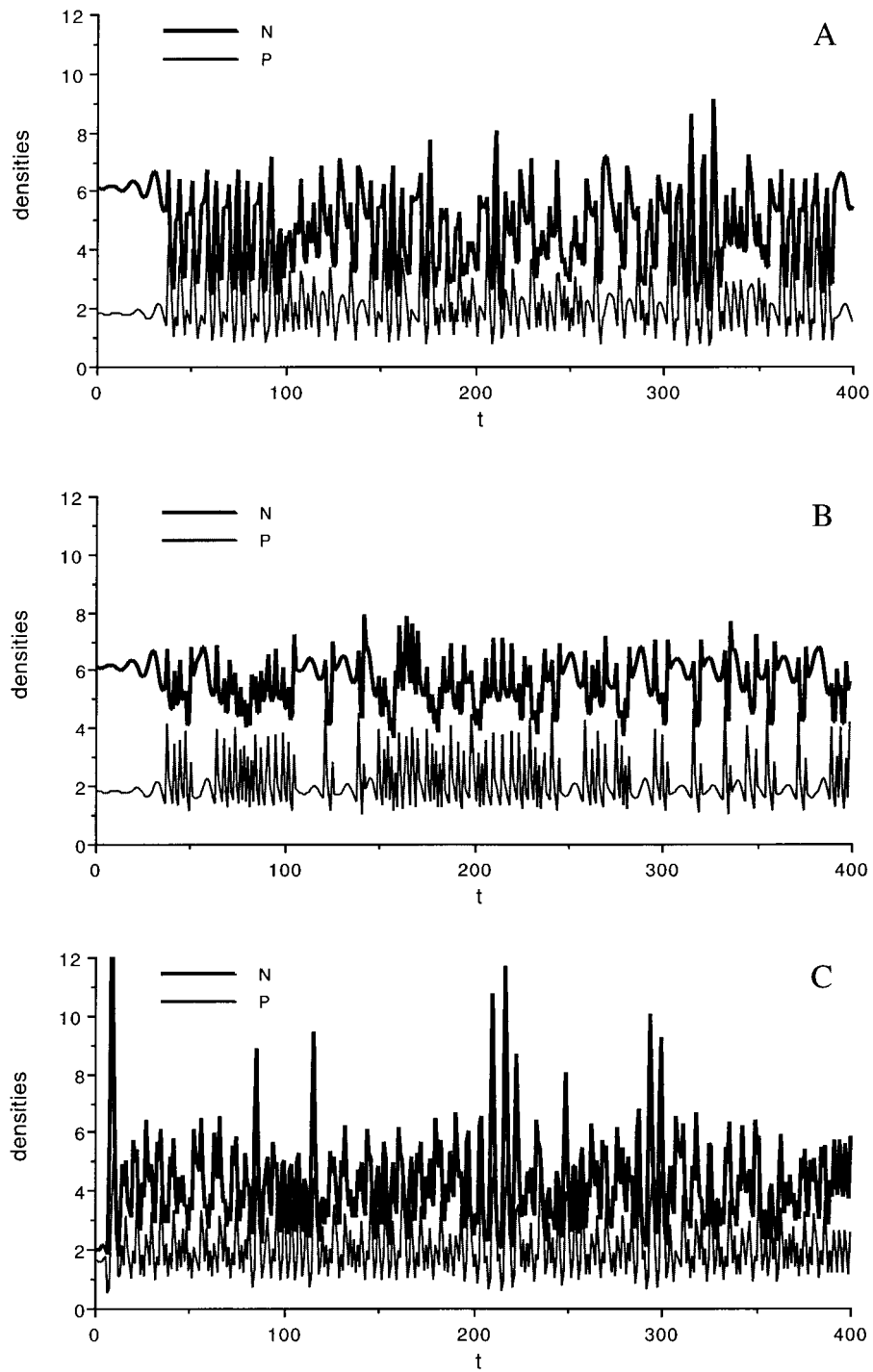


Figure 5: Population dynamics of prey and predators when they are distributed according to density-dependent simultaneous Ideal Free Distributions. The environment consists of one high-quality patch ($\lambda_i = 5$) and (A) four marginal patches ($\lambda_i = 1.05$), (B) four marginal patches ($\lambda_i = 1.05$) and five barren patches ($\lambda_i = 0.9$), and (C) five barren patches ($\lambda_i = 0.9$) and no marginal patches.

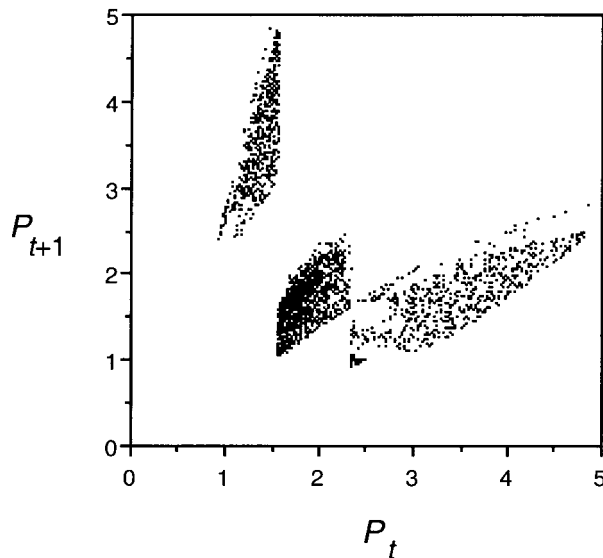


Figure 6: Predator densities in successive generations. Parameters: one high-quality patch with $\lambda_i = 5$, four marginal patches ($\lambda_i = 1.05$), and five barren patches ($\lambda_i = 0.9$).

patches are sufficiently profitable for the prey. (See app. B for a more formal treatment.)

Simultaneous optimal patch selection thus transforms another parameter from Hassell and May's (1973) model into a density-dependent function: the number of patches n . For example, when predator density is high, the prey population will decline, which implies that average prey fitness K_i is less than unity. The population distribution will then comprise more patches, which means that some prey are forced to choose patches where they have little chance to survive, even in absence of predation. Conversely, if predators are rare, prey and predators will be found only in the high-quality patches. Thus, the range of patches over which the populations distribute themselves expands and shrinks when populations fluctuate.

Simultaneous flexible patch selection may have dramatic population dynamical consequences. Take again the benchmark environment with one high-quality patch ($\lambda_i = 5$) and four marginal patches ($\lambda_i = 1.05$). The introduction of behavioral flexibility of prey and predators drastically destabilizes the equilibrium and causes the system to enter the chaotic domain (see fig. 5A). Now, patches never visited under equilibrium conditions (by prey or predator) may play an important role in population dynamics. Figure 5B shows that the addition of five outright barren patches ($\lambda_i = 0.9$), not even allowing self-replacement (i.e., sinks sensu Holt 1997), results in markedly less extreme fluctuations (though equally chaotic). Figure 5C shows that even if the four marginal patches ($\lambda_i = 1.05$)

are removed, predator and prey may coexist. This shows most clearly that the persistence of predator-prey systems can be promoted by the addition of refugia that the prey would avoid under equilibrium conditions.

In the recurrence map for the predators (fig. 6), three distinct clusters can be discerned, corresponding to the consequences of the populations residing in one, five, or 10 patches. (The fact that there are clusters of points rather than lines is indicative for a chaotic attractor.) Within each cluster, the regression line has a positive slope, but overall, the regression line has negative slope. Thus, at high predator densities, foraging success is low, which may be one of the mechanisms contributing to persistence.

The phase planes resemble projections of strange attractors, which are the hallmark of chaos. However, to prove that the dynamics are chaotic, it must be shown that the dominant Lyapunov exponent is larger than 0 (Metz 1990; Hastings et al. 1993). Such an analysis is beyond the scope of this article. Nor have we tried to prove that the system is truly permanent (Hofbauer and Sigmund 1988). It suffices here to show that flexible patch selection of prey and predators can destabilize an ecological equilibrium and may lead to complicated dynamics.

A systematic survey of environments with a single "good" patch and many "bad" patches (fig. 7A–C) shows that the range of parameters resulting in coexistence (for at least 1,000 generations) is large and does not resemble at all the region of ecological stability for density-independent population distributions. The darker shading indicates that the dynamics tend to become more extreme when either prey fecundity in the high-quality patch increases or when the number of patches increases. This makes intuitive sense. However, a surprising result is the transition from coexistence to extinction that occurs if prey fecundity in the high-quality patch becomes too high or the number of patches becomes too small. Instead of being bordered by a region of increasing variability, as one might expect, the region of coexistence abruptly gives way to the region of extinction.

A time series (fig. 8) provides an indication of what is happening. If a parameter combination is chosen just outside the region of coexistence, the populations quickly start to fluctuate chaotically, just as in the other simulations, and this might very well go on indefinitely. However, after a few hundreds of generations the oscillations suddenly blow up, and within a few cycles the populations are extinct. What underlies these suddenly appearing divergent cycles still has to be elucidated (Hastings and Higgins 1994; McCann and Yodzis 1994). In any case, these results constitute a warning: even if fluctuating densities do not approach zero for a long time span, it is no guarantee that they never will.

It is striking how large the region of coexistence is, in

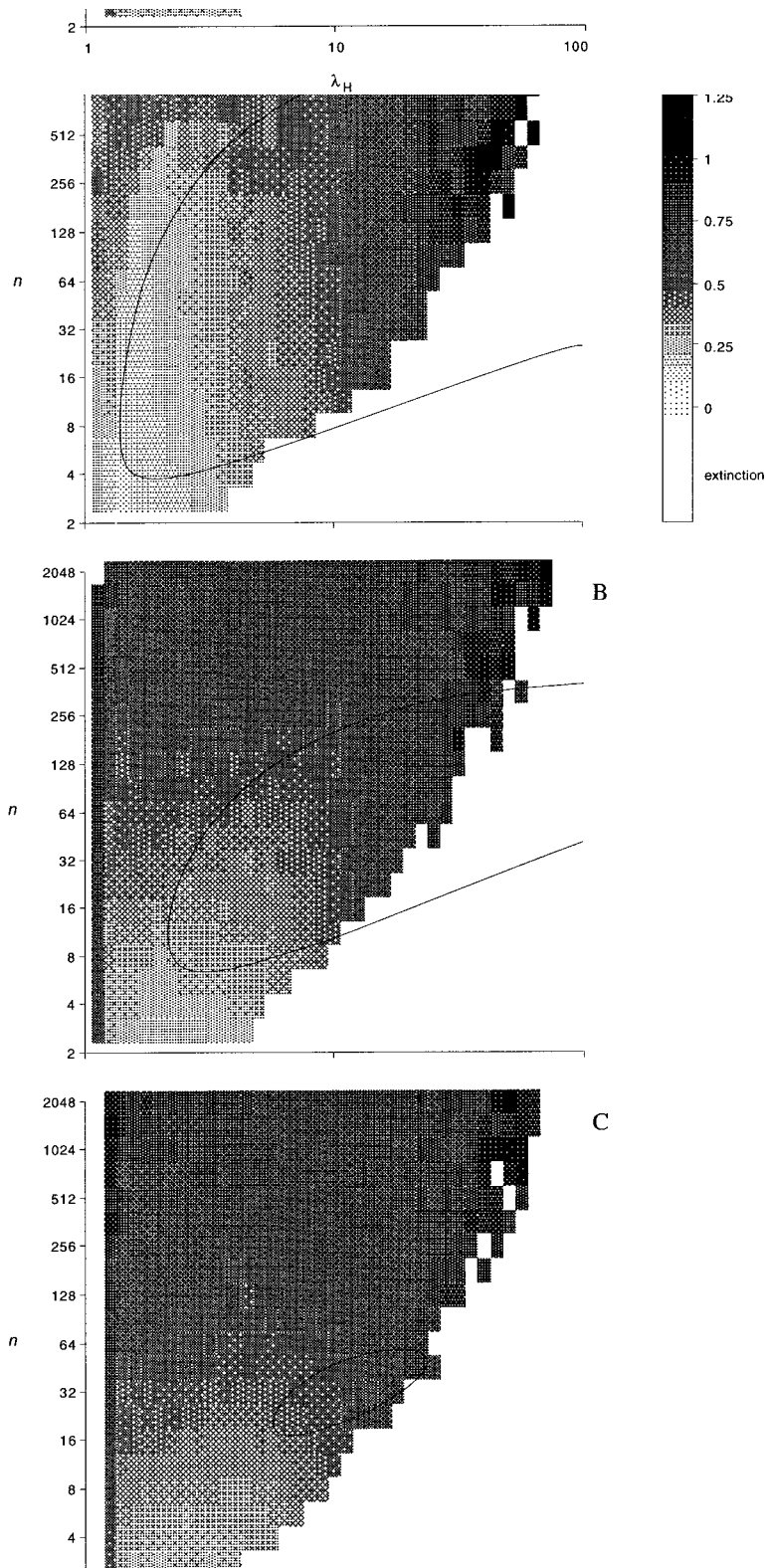


Figure 7: Parameter surveys of dynamics that result when both prey and predators adopt flexible patch-selection strategies. See figure 2 legend for explanation.

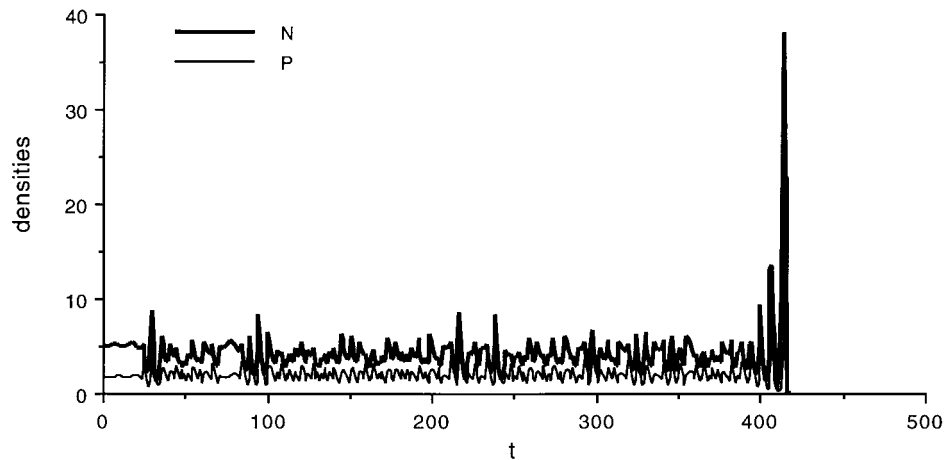


Figure 8: Postponed extinction. Flexible prey and predators are distributed according to simultaneous Ideal Free Distributions over one high-quality patch ($\lambda_i = 5$) and three low-quality patches ($\lambda_i = 1.05$).

comparison with the results from the previous sections. Moreover, the shape of the region of coexistence does not seem to be very dependent on the quality of the marginal patches (cf. fig. 7). Whether extinction occurs depends most strongly on prey fecundity in the high-quality patch and on the number of low-quality patches. Figure 9 shows that coexistence occurs in a large part of parameter space even if low-quality patches do not allow for self-replacement. In this case, under conditions of ecological equilibrium, all prey and all predators will be found in a single patch. The only difference with the unstable Nicholson-Bailey model is the addition of refugia, where the prey can only hope to survive bad times. The region of coexistence specified in figure 9 closely resembles those of the other simulations (fig. 7), which suggests that this kind of refuge-mediated persistence is rather robust. That persistence is promoted by the addition of enough refugia may not come as a surprise. Explaining the shape of the region of coexistence remains a challenge, however.

Discussion

Integration of ecology and evolution not only allows to test whether current ecological theories are compatible with the theory of natural selection but can also lead to hypotheses for situations that are just too complex to tackle using the toolbox of population dynamical models alone. The present article, which addresses the population dynamical consequences of density-dependent population distributions, provides an example.

The incorporation of density-independent spatial distributions into the Nicholson-Bailey model already complicates the analysis considerably, as many combinations of parameters must be considered. Replacing these parameters by arbitrary functions of density increases the number of possibilities even more while, in addition, the mathematical analysis becomes very difficult. Yet it is important to consider density-dependent spatial distributions because the stabilizing effect of aggregation by prey and predators seems to hinge on the assumption of arbitrary, density-independent spatial distributions. Density-independent aggregation implies that average foraging efficiency decreases when predator density increases (Hassell 1984; Murdoch and Stewart-Oaten 1989; Pacala et al. 1990; Hassell et al. 1991; Godfray and Pacala 1992; Ives 1992a, 1992b). Thus, ecological stability might be an artifact caused by the mathematical modeler, who, by clumping the predators, hinders them from searching efficiently.

Evolutionary models can be used to replace arbitrary distributions by distributions that are derived from the assumption that patch-selection strategies of prey and predators are molded by natural selection. In this way, van Baalen and Sabelis (1993) demonstrated that, with density-independent population distributions, the conditions for simultaneous ecological and evolutionary stability are quite narrow. The results presented in this article suggest that if spatial distributions are density dependent, ecological stability may even disappear completely. Interestingly, nonequilibrium persistence may occur under a much wider range of environmental conditions.

When prey and predators adopt flexible patch-selection

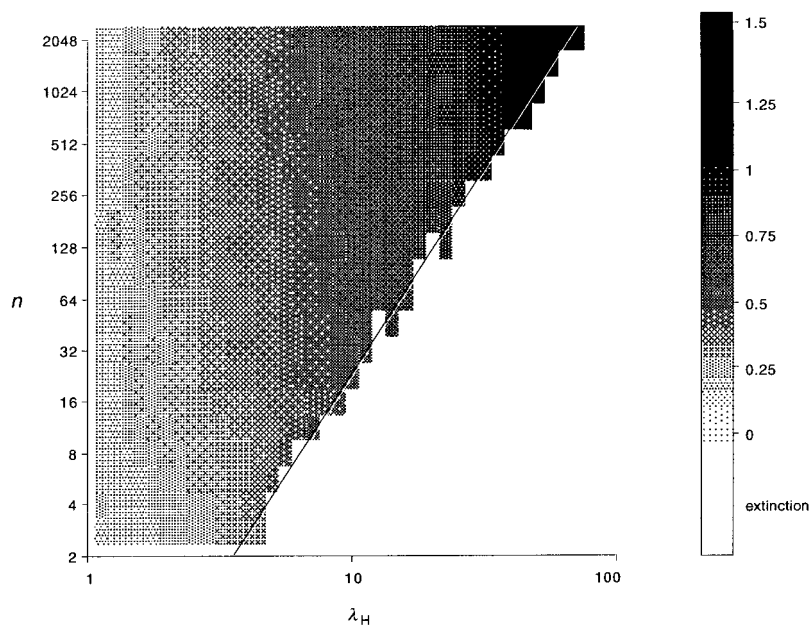


Figure 9: Parameter surveys of dynamics that result when both prey and predators adopt flexible patch-selection strategies in environments with one high-quality patch and many barren patches, not even allowing for self-replacement ($\lambda_L = 0.9$). See figure 2 legend for explanation. Superposed is the line $\log_2 n = 7.85 \log_{10} \lambda_H - 3.35$ (fitted by eye) that separates the region of coexistence from the region of extinction.

strategies, spatial distributions will expand and shrink when populations cycle. If predator density is high, it pays prey to select low-quality patches that they would avoid under other circumstances (a similar effect was demonstrated by Křivan (1997) for simultaneous Ideal Free Distributions in continuous-time Lotka-Volterra predator-prey systems). The simulations for this case show that active hide-and-peek is a destabilizing, yet persistence-promoting mechanism. The reason is that predator searching efficiency is negatively density dependent: when predator density is high, the prey spread over a larger number of patches, which reduces searching efficiency. Such reduced efficiency is not a consequence of the fixed aggregation pattern imposed by the mathematical modeler, but it results because part of the prey population seeks refuge in the marginal patches.

That low-quality refuges can help to promote persistence is in itself not a new finding. In fact, the effect has long been known (Hassell 1978; Chesson and Warner 1981; see also Holt and Hassell 1993; Hochberg and Holt 1995). Nor is the fact that natural selection may favor utilization of such low-quality refuges (Holt 1997) a new finding. Our analysis is new in that it suggests that persistence may be promoted not only by passive dispersal (of the kind normally assumed in metapopulation models;

see Holt 1997) but also by active dispersal (i.e., habitat selection). What we want to point out here in particular is that the ecological/evolutionary end result may depend sensitively on the flexibility of the individuals' responses to their environment.

In general, we found the effect to be weaker if the prey are constrained to rigid patch-selection strategies. Population dynamics thus sensitively depend on the way spatial distributions arise, that is, on the precise way individuals select patches. Comparison of the consequences both of rigid and of flexible patch selection of the prey suggests that it can make a large difference if the prey have "up-to-date" information about density and distribution of their predators, or if they can only base their decisions on expectations. Thus, whether prey move into the patches first or whether they move in simultaneously may lead to different types of population dynamics (see also Křivan 1997).

Combination of ecological and evolutionary analysis may lead to new insight and testable predictions. Instead of assuming a homogeneous environment, the present analysis takes into account underlying environmental variability. Thus, it generates hypotheses about patterns of habitat use, and these may be subject to observational or experimental tests. For many insect predator-prey systems,

the world consists of a few oases (the prey insect's preferred host plants) in the midst of a desert of marginal (low-quality host plants) and outright barren patches (i.e., all space not normally considered to be a "patch" at all). It may be difficult to decide whether observed spatial distributions of predators and prey are sufficiently close to an Ideal Free Distribution, because measuring net fitness is a laborious task. However, the prediction that the number of patches occupied by a predator-prey system should

expand and shrink with population fluctuations is definitely testable.

Acknowledgments

We thank P. Abrams, J. Bruin, J. Clobert, R. Holt, P. Lundberg, K. Nagelkerke, A. de Roos, and an anonymous referee (as well as the anonymous referees of a previous draft) whose comments were of great help in improving this article.

APPENDIX A

Evolution of Patch-Selection Strategies

Let population dynamics of resident prey and predators be on its attractor, and let this attractor have period T (i.e., be a point equilibrium if $T = 1$, a limit cycle if T is finite, a quasiperiodic or chaotic attractor if T is infinite). The environment that is faced by a mutant is then fully specified by N_t^* , P_t^* , α_{it}^* , and β_{it}^* , with $t = 1, \dots, T$.

Now consider a mutant predator strain with a patch-selection strategy $\beta = \{\beta_{it}\}$, so that in generation t a mutant predator selects patch i with probability β_{it} . Its reproductive success in generation t is then given by the arithmetic mean over the patches

$$F_t = \sum_{i=1}^n \beta_{it} \phi_{it}, \quad (\text{A1})$$

where ϕ_{it} denotes the per capita reproductive success of a predator in patch i in generation t . Assuming that the mutant is so rare that it does not influence within-patch processes, the latter is given by

$$\phi_{it} = \frac{\alpha_{it}^* N_t^* (1 - e^{-\beta_{it}^* P_t^*})}{\beta_{it}^* P_t^*}. \quad (\text{A2})$$

Population dynamics of the mutant is then linear and given by

$$P_{t+1} = P_t \sum_{i=1}^n \beta_{it} \phi_{it} \quad (\text{A3})$$

or, over an entire cycle,

$$P_T = P_1 \prod_{t=1}^T \sum_{i=1}^n \beta_{it} \phi_{it}. \quad (\text{A4})$$

Thus, the average per generation rate of increase is the geometric mean—over the cycle—of the arithmetic mean—over the patches—of reproductive success ϕ_{it} :

$$G(\beta, \Phi) = \sqrt[T]{\prod_{t=1}^T \sum_{i=1}^n \beta_{it} \phi_{it}}, \quad (\text{A5})$$

with $\beta = \{\beta_{it}\}$ and $\Phi = \{\phi_{it}\}$. This is the appropriate fitness measure: if G exceeds unity, the mutant invades; if it is less, it will go extinct. (A similar fitness measure can be derived for the prey; the only difference is in the expression for per capita reproductive success, $\phi_{it} = \lambda_i e^{-\beta_{it}^* P_t^*}$.)

Optimization of Rigid Strategies

If the predators are constrained to a rigid patch-selection strategy, their searching strategy will be independent of time, that is, $\beta_{it} = \beta_i$. Which $\beta = \{\beta_i\}$ (subject to the constraint $\sum \beta_i = 1$) should a mutant adopt to maximize its fitness? The maximum of G coincides with the maximum of

$$g(\beta, \Phi) = \ln G(\beta, \Phi) = \frac{1}{T} \sum_{t=1}^T \ln \sum_{i=1}^n \beta_i \phi_{it}. \quad (\text{A6})$$

Then,

$$dg = \sum_{i=1}^n \frac{\partial g}{\partial \beta_i} d\beta_i = \frac{1}{T} \sum_{t=1}^T \sum_{i=1}^n \frac{\phi_{it} d\beta_i}{\sum_{i=1}^n \beta_i \phi_{it}}. \quad (\text{A7})$$

Since we assume two types of patches, we can set $\beta_1 = \beta_H$ and $\beta_i = \beta_L = (1 - \beta_H)/(n - 1)$ for $i > 1$, leading to

$$\frac{dg}{d\beta_H} = \frac{1}{T} \sum_{t=1}^T \frac{\phi_{1t} - \frac{1}{n-1} \sum_{i=2}^n \phi_{it}}{\beta \phi_{1t} + \frac{1-\beta}{n-1} \sum_{i=2}^n \phi_{it}}. \quad (\text{A8})$$

Denoting $\phi_{1t} = \phi_{Ht}$ and $\phi_{it} = \phi_{Lt}$ ($i > 1$), we finally obtain

$$\frac{dg}{d\beta_H} = \frac{1}{T} \sum_{t=1}^T \frac{\phi_{Ht} - \phi_{Lt}}{\beta \phi_{Ht} + (1 - \beta) \phi_{Lt}}. \quad (\text{A9})$$

For a point attractor ($T = 1$) the sign of $dg/d\beta_H$ is given by $\phi_H - \phi_L$, independently of β_H . The optimal strategy for a mutant is then simply to select the patch with the highest per capita reproductive success. For attractors with larger periods, optimization becomes more complex, as the sign of $dg/d\beta_H$ is given by average difference in fitness between the patches, weighed by the average fitness of that generation.

Evolutionary stability requires that it does not pay to deviate from the resident strategy. Capturing the effect of the resident strategy on the environment in $\Phi(\beta_H^*)$, the first ESS condition thus becomes

$$\left. \frac{d}{d\beta_H} g(\beta, \Phi(\beta^*)) \right|_{\beta=\beta^*} = 0. \quad (\text{A10})$$

If $T = 1$, the problem amounts to finding a β_H^* such that $\phi_H = \phi_L$. This leads to equations (2). For $T > 1$, there is no easy solution.

Selection under a Limit Cycle

Suppose the resident predator strategy is a strategy that leads to an Ideal Free Distribution under equilibrium conditions, and suppose this equilibrium is unstable and gives way to a limit cycle. Then, we can consider ϕ_{Ht} and ϕ_{Lt} as stochastic variables that vary around a mean value of 1. Then, $dg/d\beta_H$ is equal to the expected value of the function

$$f(\phi_H, \phi_L) = \frac{\phi_H - \phi_L}{\beta \phi_H + (1 - \beta) \phi_L}. \quad (\text{A11})$$

If the amplitude of the limit cycle is not too large, application of the Taylor approximation leads to

$$E f(\underline{x}, \underline{y}) = f(\bar{x}, \bar{y}) + \frac{1}{2} f^{(xx)}(\bar{x}, \bar{y}) \text{Var}(\underline{x}) + f^{(xy)}(\bar{x}, \bar{y}) \text{Covar}(\underline{x}, \underline{y}) + \frac{1}{2} f^{(yy)}(\bar{x}, \bar{y}) \text{Var}(\underline{y}), \quad (\text{A12})$$

where $\bar{x} = E\underline{x}$, $\bar{y} = E\underline{y}$, and $f^{(xy)}$ denotes the partial derivative of f with respect to x and y . After some algebra, we obtain

$$\frac{dg}{d\beta_H} = f(\bar{\phi}_H, \bar{\phi}_L) + \frac{-\beta_H[\text{Var}(\underline{\phi}_H) - \text{Covar}(\underline{\phi}_H, \underline{\phi}_L)] + (1 - \beta_H)[\text{Var}(\underline{\phi}_L) - \text{Covar}(\underline{\phi}_H, \underline{\phi}_L)]}{[\beta_H \bar{\phi}_H + (1 - \beta_H) \bar{\phi}_L]^3}. \quad (\text{A13})$$

Note that if $\bar{\phi}_H = \bar{\phi}_L$, then $f(\bar{\phi}_H, \bar{\phi}_L) = 0$, and the sign of $dg/d\beta_H$ is completely determined by the sign of

$$-\beta_H[\text{Var}(\underline{\phi}_H) - \text{Covar}(\underline{\phi}_H, \underline{\phi}_L)] + (1 - \beta_H)[\text{Var}(\underline{\phi}_L) - \text{Covar}(\underline{\phi}_H, \underline{\phi}_L)].$$

This shows that if the expected fitness is equal in both types of patches, it will pay to decrease visits to the type of patch with the highest net variance in fitness.

Numerical simulations and evaluation using the approximation for $dg/d\beta_H$ suggest that the predators will spread themselves more evenly over the patches when populations fluctuate. This will reduce the set of parameter combinations leading to limit cycles. Evaluation of the selection differential on α (derived in a fashion similar to the derivation of $dg/d\beta_H$) suggests that also the prey will aggregate less. Taken together, evolution of rigid patch-selection strategies lead to more even distributions of prey and predators and to a reduced scope for coexistence.

Optimization of Flexible Strategies

If predators are flexible, a mutant predator is free to choose a strategy that varies over time, that is, a $\beta = \{\beta_{it}\}$ subject to the constraint $\sum_{i=1}^n \beta_{it} = 1$. Since the constraint implies $d\beta_{is}/d\beta_{it} = 0$ for $s \neq t$ (the choice of a patch-selection strategy in generation t does not constrain the patch-selection strategies for other generations), and since mutant fitness is proportional to a sum over generations,

$$g(\beta, \Phi) = \frac{1}{T} \sum_{t=1}^T \ln \sum_{i=1}^n \beta_{it} \phi_{it}, \quad (\text{A14})$$

optimization can be done for each generation separately. Thus the optimal patch-selection strategy for generation t is given by the maximum of

$$\ln \sum_{i=1}^n \beta_{it} \phi_{it}.$$

If the resident strategy does not lead to an Ideal Free Distribution in generation t , $\phi_{it} > \phi_{jt}$ for at least some i and j . Then the optimal patch-selection strategy for generation t is to select the patch with the highest per capita fitness ϕ_{it} , say patch k_t . Thus, there is an optimal path k_t through time and space. Since the mutant then has an advantage in at least some generations, it can invade, as

$$\ln \phi_{k_t} \geq \ln \sum_{i=1}^n \beta_{it}^* \phi_{it} \quad (\text{A15})$$

implies

$$g(\beta^{\text{opt}}, \Phi) \geq g(\beta^*, \Phi), \quad (\text{A16})$$

with $\beta_{ii}^{\text{opt}} = 1$ for $i = k$, and $\beta_{ii}^{\text{opt}} = 0$ for all other i and t .

Only when the resident predator population achieves an Ideal Free Distribution in each successive generation is there no such optimal path, and hence no mutant can invade. The ESS β^* should therefore satisfy

$$g(\beta, \Phi(\beta^*)) \leq g(\beta^*, \Phi(\beta^*)) \quad (\text{A17})$$

for all β , which implies

$$\sum_{j=1}^n \beta_{ji} \phi_{ji}(\beta^*) \leq \sum_{j=1}^n \beta_{ji}^* \phi_{ji}(\beta^*) \quad (\text{A18})$$

for all t . Hence, the ESS is characterized by

$$\begin{aligned} \phi_{ii}(\beta^*) &= \sum_{j=1}^n \beta_{ji}^* \phi_{ji}(\beta^*) & (\beta_{ii}^* > 0), \\ \phi_{ii}(\beta^*) &< \sum_{j=1}^n \beta_{ji}^* \phi_{ji}(\beta^*) & (\beta_{ii}^* = 0) \end{aligned} \quad (\text{A19})$$

for every generation t . This leads to expressions (11a) and (11b) in “Case 3: Flexible Prey and Flexible Predators.”

A More Formal Definition of “Rigid” and “Flexible” Patch Selection

The ESS β^* thus constitutes a sequence of searching strategies β_t^* . If the predators can genetically program this sequence, the ESS can be of the “rigid” type. However, so much genetic determinism is not required. If mutant predators can adopt a “flexible” searching strategy $\beta(N, P, \alpha, \beta^*)$ such that $\beta(N_t, P_t, \alpha_t, \beta_t^*)_{k_i} = 1$ (find the best patch for generation t , based on information on density and distribution of prey and predators in that generation), then it will invade (if the resident strategy does not lead to an Ideal Free Distribution in every generation).

APPENDIX B

Simultaneous Ideal Free Distributions

A recursive procedure can be used to find the set of visited patches. First rank the patches in order of prey fecundity,

$$\lambda_1 \geq \dots \geq \lambda_i \geq \dots \geq \lambda_n, \quad (\text{B1})$$

and then proceed as follows.

Step 1. Suppose that prey and predators are ideally and freely distributed over the k best patches.

Step 2. Calculate the average fitnesses K_k and L_k that would result for the Ideal Free Distributions over the k visited patches. After summing equations (11) over $i = 1, \dots, k$ we obtain

$$\begin{aligned} P &= \sum_{i=1}^k \ln \lambda_i - k \ln K_k, \\ N &= L_k \sum_{i=1}^k \frac{\lambda_i}{\lambda_i - K_k} (\ln \lambda_i - \ln K_k), \end{aligned} \quad (\text{B2})$$

from which K_k and L_k can be solved,

$$K_k = \exp\left[\frac{1}{k}\left(\sum_{i=1}^k \ln\lambda_i - P\right)\right]$$

$$L_k = N\left[\sum_{i=1}^k \frac{\lambda_i}{\lambda_i - K_k} (\ln\lambda_i - \ln K_k)\right]^{-1}. \quad (\text{B3})$$

Step 3. Check whether prey would be selected to move into the next best patch, which is the case if

$$\lambda_{k+1} > K_k. \quad (\text{B4})$$

If prey enter the next best patch, a proportion of the predators will follow, and thus both populations will settle on an Ideal Free Distribution over (at least) $k + 1$ patches. Hence if (B4) holds, increase k by one, and go to step 2 again, until (B4) no longer holds.

Literature Cited

- Abrams, P. A., and T. J. Kawecki. 1998. Adaptive host preference and the dynamics of host-parasitoid interactions. *Theoretical Population Biology* (in press).
- Abrams, P. A., and H. Matsuda. 1997. Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. *Evolutionary Ecology* 11:1–20.
- Abrams, P. A., and J. Roth. 1994. The responses of unstable food chains to enrichment. *Evolutionary Ecology* 8: 150–171.
- Armstrong, R., and R. McGehee. 1976. Coexistence of species competing for shared resources. *Theoretical Population Biology* 9:317–328.
- . 1980. Competitive exclusion. *American Naturalist* 115:151–170.
- Brown, J. S. 1998. Game theory and habitat selection. Pages 188–220 in L. A. Dugatkin and H. K. Reeve, eds. *Game theory and animal behavior*. Oxford University Press, New York.
- Chesson, P. L., and W. W. Murdoch. 1986. Aggregation of risk: relationships among host-parasitoid models. *American Naturalist* 127:696–715.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923–943.
- Comins, H. N., and M. P. Hassell. 1979. The dynamics of optimally foraging predators and parasitoids. *Journal of Animal Ecology* 48:335–351.
- Cook, R. M., and S. F. Hubbard. 1977. Adaptive searching strategies in insect parasites. *Journal of Animal Ecology* 46:115–125.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19:16–36.
- Fryxell, J. M., and P. Lundberg. 1993. Optimal patch use and metapopulation dynamics. *Evolutionary Ecology* 7: 379–393.
- . 1997. Individual behavior and community dynamics. Kluwer, Dordrecht.
- Godfray, H. C. J., and S. W. Pacala. 1992. Aggregation and the population dynamics of parasitoids and predators. *American Naturalist* 140:30–40.
- Godfray, H. C. J., L. M. Cook, and M. P. Hassell. 1992. Population dynamics, natural selection and chaos. Pages 55–86 in R. J. Berry, T. J. Crawford, and G. M. Hewitt, eds. *Genes in ecology*. Blackwell, Oxford.
- Hassell, M. P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, N.J.
- . 1984. Parasitism in patchy environments: inverse density dependence can be stabilizing. *IMA Journal of Mathematics Applied in Medicine and Biology* 1: 123–133.
- Hassell, M. P., and R. M. May. 1973. Stability in insect host-parasite models. *Journal of Animal Ecology* 42: 693–736.
- . 1974. Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43:567–594.
- Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structure and chaos in population dynamics. *Nature (London)* 353:255–258.
- Hastings, A., and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. *Science (Washington, D.C.)* 263:1133–1136.
- Hastings, A., C. L. Hom, S. Ellner, P. Turchin, and H. C. J. Godfray. 1993. Chaos in ecology: is mother nature a strange attractor? *Annual Review of Ecology and Systematics* 24:1–33.
- Hochberg, M. E., and R. D. Holt. 1995. Refuge evolution and the population dynamics of coupled host-parasitoid associations. *Evolutionary Ecology* 9:633–661.
- Hofbauer, J., and K. Sigmund. 1988. *The theory of evo-*

- lution and dynamical systems. Cambridge University Press, Cambridge.
- Holt, R. D. 1997. On the evolutionary stability of sink populations. *Evolutionary Ecology* 11:723–731.
- Holt, R. D., and M. P. Hassell. 1993. Environmental heterogeneity and the stability of host-parasitoid interactions. *Journal of Animal Ecology* 62:89–100.
- Holt, R. D., and M. A. McPeck. 1996. Chaotic population dynamics favors the evolution of dispersal. *American Naturalist* 148:709–718.
- Hubbard, S. F., and R. M. Cook. 1978. Optimal foraging by parasitoid wasps. *Journal of Animal Ecology* 47:593–604.
- Ives, A. R. 1992a. Continuous-time models of host-parasitoid models. *American Naturalist* 140:1–29.
- . 1992b. Density-dependent and density-independent parasitoid aggregation in model host-parasitoid systems. *American Naturalist* 140:912–937.
- Kacelnik, A., J. R. Krebs, and C. Bernstein. 1992. The Ideal Free Distribution and predator-prey populations. *Trends in Ecology & Evolution* 7:50–55.
- Křivan, V. 1997. Dynamic Ideal Free Distribution: effects of optimal patch choice on predator-prey dynamics. *American Naturalist* 149:164–178.
- May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology* 47:833–843.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. *Nature (London)* 246:15–18.
- McCann, K., and P. Yodzis. 1994. Nonlinear dynamics and population disappearances. *American Naturalist* 144:873–879.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- Metz, J. A. J. 1990. Chaos en populatie-biologie. Pages 320–344 in H. W. Broer and F. Verhulst, eds. *Dynamische Systemen en Chaos: een Revolutie vanuit de Wetenschap*. Epsilon, Utrecht.
- Murdoch, W. W., and A. Stewart-Oaten. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. *American Naturalist* 134:228–310.
- Pacala, S. W., M. P. Hassell, and R. M. May. 1990. Host-parasitoid associations in patchy environments. *Nature (London)* 344:150–153.
- Sih, A. 1998. Game theory and predator-prey response races. Pages 221–238 in L. A. Dugatkin and H. K. Reeve, eds. *Game theory and animal behavior*. Oxford University Press, New York.
- Sutherland, W. J. 1983. Aggregation and the “Ideal Free Distribution.” *Journal of Animal Ecology* 52:821–828.
- van Baalen, M., and M. W. Sabelis. 1993. Coevolution of patch selection strategies of predators and prey and the consequences for ecological stability. *American Naturalist* 142:646–670.

Associate Editor: Robert D. Holt