



UvA-DARE (Digital Academic Repository)

Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability

van Baalen, M.; Sabelis, M.W.

DOI

[10.1086/285562](https://doi.org/10.1086/285562)

Publication date

1993

Published in

American Naturalist

[Link to publication](#)

Citation for published version (APA):

van Baalen, M., & Sabelis, M. W. (1993). Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *American Naturalist*, 142, 646-670. <https://doi.org/10.1086/285562>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

COEVOLUTION OF PATCH SELECTION STRATEGIES OF
PREDATOR AND PREY AND THE CONSEQUENCES
FOR ECOLOGICAL STABILITY

MINUS VAN BAALEN AND MAURICE W. SABELIS

Department of Pure and Applied Ecology, University of Amsterdam, Kruislaan 320,
1098 SM Amsterdam, The Netherlands

Submitted December 26, 1991; Revised August 19, 1992; Accepted September 3, 1992

Abstract.—In a seminal publication Hassell and May demonstrated that sufficiently uneven spatial distributions can stabilize predator-prey systems. In this article we investigate whether such spatial distributions (of either predators or prey) can be caused by behavior that is favored by natural selection. If selection operates on predators only, evolutionarily stable patch selection strategies (ESSs) will lead to predator aggregation, provided the prey are unevenly distributed. However, to render the ecological equilibrium stable, prey aggregation needs to be very strong. If selection operates at both trophic levels, then simultaneous ESSs will exist for predator and prey. Where patches are of equal quality (as is implicitly assumed in Hassell and May's model), the distributions of both predators and prey will be homogeneous, and ecological stability will vanish. Where patches differ, for example, in prey reproduction or survival, aggregated distributions of prey and predators will result. A stable ecological equilibrium is then possible, but only if there are many patches of marginal quality. This article shows that the combination of both evolutionary and ecological stability criteria not only allows one to test whether ecological theories are compatible with the theory of natural selection but may also lead to new insights, such as *why* low-quality patches may constitute a partial refuge for the prey.

Hassell and May (1973) have shown that strong aggregation of predators in patches with high prey density confers stability to the otherwise unstable Nicholson-Bailey (1935) model for predator-prey dynamics. Because natural selection is expected to favor predators searching for profitable (e.g., high-prey-density) patches, foraging behavior that leads to predator aggregation is likely to be widespread. Thus, the aggregative response of predators to prey density may well be a general mechanism promoting persistence of predator-prey systems.

However, intuitive appeal needs scrutiny. First, one must consider what is optimal from the predator's point of view. Increasing numbers of predators in high-prey-density patches may intensify competition for prey. Competition may increase to such an extent that mutant predators foraging in low-density patches may be even more successful. Clearly, there are limits to the aggregative response that will evolve. Since Hassell and May (1973) have shown that, to be stabilizing, the degree of predator aggregation should be rather strong, one cannot assume *a priori* that the favored type of foraging behavior will promote ecological stability of the predator-prey interaction.

Second, natural selection operates on the prey as well. For an aggregative

response to have a stabilizing effect, there will have to be prey aggregations. Whether such prey aggregations are caused by adaptive behavior is an open question, however. Why would prey individuals aggregate if this increases their risk of being attacked by predators?

Although analysis of ecological stability can indicate the ecological consequences of different types of aggregative responses, it does not provide a clue as to which one is likely to occur. This problem can only be solved by assessing the *evolutionary* stability of this behavior—that is, by confirming that individuals with a different aggregative behavior cannot invade. Game theory (Maynard Smith and Price 1973; Maynard Smith 1982) can deal with this type of problem, since, as is the case for patch selection strategies, what is optimal for one individual depends on the strategies of others. It should be stressed that ecological stability (of populations) does not imply evolutionary stability (of behavioral strategies) or vice versa. Both properties must be determined separately.

The key question of this article is whether natural selection favors patch selection strategies (either of prey or of predators) that promote ecological stability. To what extent can we indeed *expect* predators or prey to distribute themselves in such a way that ecological stability is promoted?

OPTIMAL FORAGING

Many authors have recognized that aggregative behavior of predators may be explained by optimal foraging theory (Hassell and May 1973; Cook and Hubbard 1977; Free et al. 1977; Hubbard and Cook 1978; Stephens and Krebs 1986; Kacelnik 1989). 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. Comins and Hassell (1979) demonstrated that differential prey depletion (i.e., pseudointerference) (Free et al. 1977) may lead to an ideal free distribution that is sufficiently aggregated to promote ecological stability. Sutherland (1983) showed that the same holds for interference among the predators.

These earlier contributions have two limitations that warrant further study. First, by taking into account the details of searching behavior, Comins and Hassell's (1979) model is too complex to serve as a basis for studying coevolution. Second, both Comins and Hassell (1979) and Sutherland (1983) assume the ideal free distribution rather than model the underlying game itself.

Our approach differs from the previous analyses in that it is based on an explicit fitness-generating function (Vincent and Brown 1989)—that is, a function that expresses the fitness of a mutant when playing the field (Maynard Smith 1982). Our primary aim is to investigate whether Hassell and May's (1973) model can lead to different conclusions when ecological stability and evolutionary stability analyses are combined. Therefore, as done in Hassell and May's (1973) model, we will ignore underlying behavioral components, such as prey handling, between-patch traveling, or interference (Kacelnik et al. 1992), and define searching

strategies in terms of patch visitation probabilities only. In this way the model is kept tractable enough to study the consequences of coevolution on ecological stability.

COEVOLUTION OF PREDATORS AND PREY

Although much effort has gone into analyzing how natural selection shapes the aggregative response of predators, aggregations of the prey have usually been taken for granted. This is surprising, because when predation risk is a major component of prey fitness, optimal patch choice of the prey will strongly depend on the searching strategies prevailing in the predator population (Stewart-Oaten 1982; Sih 1984; Holt 1985, 1987).

In Hassell and May's (1973) model, simultaneous optimal patch selection by predators and prey will have profound consequences. Predators will always be selected to aggregate to some extent in patches with higher prey density. Thus, any difference in prey density will result in differential predation risk. Since in Hassell and May's (1973) model there are no other variable factors, prey will be selected to minimize predation risk and hence to avoid joining high-prey-density patches. As a consequence, the prey population distribution will become homogeneous, which leads to an unstable ecological equilibrium. This result suggests that, in a coevolved predator-prey system, predator aggregation is not expected to occur, let alone *stabilize* predator aggregation. Either we must conclude that, whenever uneven spatial distributions of the prey occur, they are caused by external factors and not by optimal prey behavior, or we must reexamine the assumptions on which Hassell and May's (1973) analysis is based.

In natural systems, patches will probably never be of equal quality. For example, there may be differences in food quality. Such differences also influence optimal patch selection strategies of the prey, and they might give prey individuals sufficient reason to aggregate despite the disadvantage of increased predation risk. As long as prey aggregate to some extent, some predator aggregation is always favored. The open question is whether such evolutionarily stable patch selection strategies will lead to ecological stability.

In the first part of this article, we take Hassell and May's (1973) model as a starting point and consider the evolution of patch selection strategies of the predators while the prey distribution is held fixed. Using game theory we specify ESS conditions and investigate the consequences for ecological stability.

In the second part we investigate the consequences of natural selection operating at both trophic levels. Now not only the predators but also the prey individuals are assumed to have a patch selection strategy. Then we seek an ESS for both trophic levels simultaneously—a pair of ESSs (Vincent and Brown 1989)—and perform an ecological stability analysis.

AGGREGATION AS A GAME BETWEEN PREDATORS

Hassell and May's (1973) model is based on Nicholson and Bailey's (1935) model for predator-prey interactions in discrete generations. Instead of a uniform

space, Hassell and May's model assumes a number of patches in which there is interaction between predator and prey. Every generation, the populations of predators and prey distribute themselves over these patches but not necessarily homogeneously: the fraction of the prey population that enters patch i is α_i , and the corresponding fraction of the predator population is β_i (where $i = 1, \dots, n$, and n is the number of patches). Since prey are vulnerable only to predators in the same patch, the following equations govern the dynamics of predator and prey:

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

and

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

where N_t and P_t denote the populations of prey and predators in generation t , λ denotes the per capita rate of increase of the prey population in the absence of predation, and a denotes the "attack rate" of the predators.

If the predators distribute themselves equally over the patches (i.e., all β_i are equal), the unstable dynamics of the Nicholson-Bailey model are recovered. However, Hassell and May (1973) found that, if the prey are unevenly distributed and the predators aggregate strongly in patches with high prey density, the ecological equilibrium of predator and prey may be stable.

Hassell and May (1973) chose to link the predator distribution to the prey distribution by an arbitrary "aggregation index." We will not make any such a priori assumptions but instead derive the predator distribution from an ESS analysis of predator searching strategies. Then the first question to be discussed is whether sufficiently strong predator aggregation will actually arise. Consider the case in which the prey population distribution $\{\alpha_i\}$ is fixed and set by external factors but the predators may choose where to forage. In Hassell and May (1973), β_i denoted the fraction of the predator population in patch i . However, β_i may also be interpreted as the probability that an individual predator will select patch i ; then $\{\beta_i\}$ represents the prevailing searching strategy of the predators in the population (the "population strategy"). We will denote this strategy by β .

If no mutant with searching strategy $\beta^m = \{\beta_i^m\}$ (with $\beta^m \neq \beta$) is able to invade the population, then $\beta = \{\beta_i\}$ is said to be an ESS and is denoted by $\beta^* = \{\beta_i^*\}$ (Maynard Smith and Price 1973; Maynard Smith 1982). This strategy specifies the degree of aggregation that is favored by natural selection, for a given prey distribution $\{\alpha_i\}$.

Predator Fitness

To find the ESS it is necessary to determine how the fitness of a predator depends on its searching strategy. More formally, it is necessary to quantify the expected fitness of a mutant adopting strategy β^m in a population of predators

adopting strategy β . Thus, a first step is to derive the predator "fitness-generating function" $F_P(\beta^m; N, P, \beta)$ (sensu Vincent and Brown 1989), where N and P denote the prevailing densities of prey and predators. To derive this function, we first determine the reproductive success of predators in the different patches, then weigh patch contributions by the mutant predator's probability of getting there.

Consider a predator in patch i . In this patch $\alpha_i N$ prey are available. A fraction $e^{-a\beta_i P}$ of these will survive, and hence a fraction of $1 - e^{-a\beta_i P}$ will be attacked by one of the $\beta_i P$ predators foraging in the patch. On the average, therefore, the i th patch yields

$$\frac{\alpha_i N(1 - e^{-a\beta_i P})}{\beta_i P} \quad (2)$$

attacked prey per predator. On the assumption that one attacked prey gives rise to one predator offspring (which is an assumption in Hassell and May's [1973] model), this expression gives the expected reproductive success of a predator in patch i .

Since a mutant predator with searching strategy β^m will end up in patch i with probability β_i^m , its expected fitness is then simply

$$F_P(\beta^m; N, P, \beta) = \sum_{i=1}^n \beta_i^m \frac{\alpha_i N(1 - e^{-a\beta_i P})}{\beta_i P}. \quad (3)$$

This approach ignores the mutant's influence on the risk of attack in patch i , which may be justified as long as the mutant predator does not represent a significant proportion of the predators present in a patch. (However, see App. A for an alternative derivation, which shows that this fitness function may also hold if the mutant does represent a significant proportion of the predators in a patch.)

Setting $\beta^m = \beta$ gives the fitness of a typical predator:

$$F_P(\beta; N, P, \beta) = \sum_{i=1}^n \frac{\alpha_i N(1 - e^{-a\beta_i P})}{P} = \frac{N \left[1 - \sum_{i=1}^n \alpha_i e^{-a\beta_i P} \right]}{P}. \quad (4)$$

This is indeed equal to the per capita fitness of predators in the Hassell and May (1973) model, which shows that fitness function (3) is fully consistent with this population dynamical model.

Evolutionarily Stable Strategy Conditions

Under ESS conditions (the population of predators has adopted the ESS patch selection strategy β^*), mutants with different searching strategies cannot do better, or, equivalently, no individual predator can gain by changing its searching strategy. From this it follows that reproductive success of the predators should be equal in all patches; otherwise there would be a patch with a higher associated fitness than others, and predators exclusively visiting this patch would do better than the rest. Hence, the ESS specifies an ideal free distribution (Fretwell and Lucas 1970). For the predators in the Hassell and May (1973) model, this means

that the ESS is characterized by β_i^* such that

$$\frac{\alpha_i \bar{N}(1 - e^{-a\beta_i^{\bar{P}}})}{\beta_i^* \bar{P}} = K \tag{5}$$

for all i , where K is a constant, and \bar{N} and \bar{P} are the equilibrium densities following from equations (1) with predator population distribution set to β^* . Note that K equals one under conditions of ecological equilibrium and that equilibrium densities will depend on the searching strategy adopted by the predator population.

Ecological Stability

What will be the consequences for ecological stability if the predators adopt the searching strategy β^* ? As Hassell and May (1973) point out, a straightforward stability analysis is impossible in the case of arbitrary population distributions. To simplify the problem, they introduce a system with only two types of patches. We will follow them in restricting the discussion of the consequences for ecological stability to this special case.

Consider a simple type of environment with just two types of patches: one high-prey-density patch with a fraction α of the prey and $n - 1$ patches with a fraction $(1 - \alpha)/(n - 1)$. The predator searching strategy is then given fully by one parameter β , the probability to search in the high-prey-density patch. The other patches are interchangeable (each harbors an identical fraction of the prey population), and hence the optimal probability to search in any one of them will be the same and equal to $(1 - \beta)/(n - 1)$.

Setting

$$\alpha_1 = \alpha, \alpha_i = \frac{1 - \alpha}{n - 1} (i > 1)$$

and (6)

$$\beta_1^* = \beta^*, \beta_i^* = \frac{1 - \beta^*}{n - 1} (i > 1),$$

equation (5) leads to the following equation that implicitly defines the evolutionarily stable searching strategy β^* :

$$\frac{\alpha \bar{N} [1 - e^{-a\beta^* \bar{P}}]}{\beta^* \bar{P}} = \frac{\frac{1 - \alpha}{n - 1} \bar{N} [1 - e^{-a(1 - \beta^*/(n - 1)) \bar{P}}]}{\frac{1 - \beta^*}{n - 1} \bar{P}} \tag{7}$$

Thus, ESS conditions are given by three equations (two defining the ecological equilibrium densities and one defining the ESS [eq. 7]) with three unknowns, the ecological equilibrium densities \bar{N} and \bar{P} and the ESS β^* . No explicit solutions could be found for this set of equations, but illustrative numerical solutions are given in figures 1 and 2.

Figure 1a shows the evolutionarily stable predator strategy β^* as a function of prey fecundity λ , for $n = 6$ patches. The ESS probability to search in the

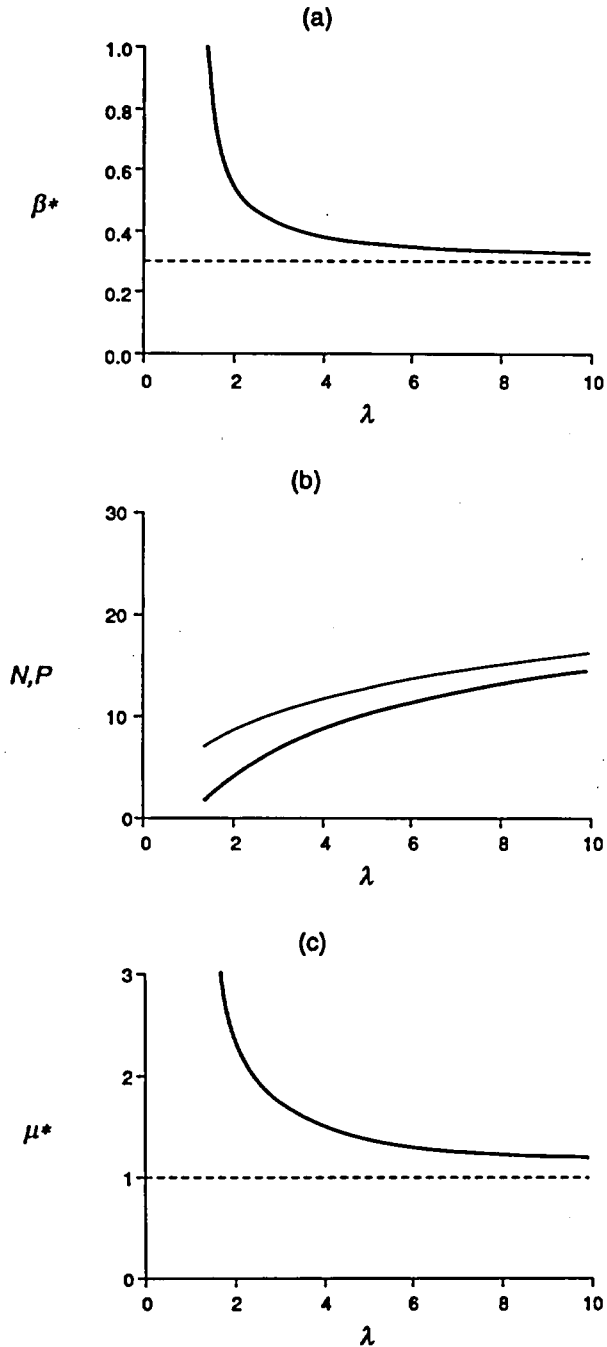


FIG. 1.—Evolutionarily stable predator patch selection strategies for a fixed prey distribution, for various values of prey fecundity λ , number of patches $n = 6$, and the fraction of prey in the high-density patch $\alpha = 0.3$. *a*, Evolutionarily stable predator searching strategy β^* (probability of searching in the high-prey-density patch) (solid line) and α (dashed line); *b*, equilibrium densities of predator P (thick line) and prey N (thin line); *c*, the value of aggregation index μ^* corresponding to β^* .

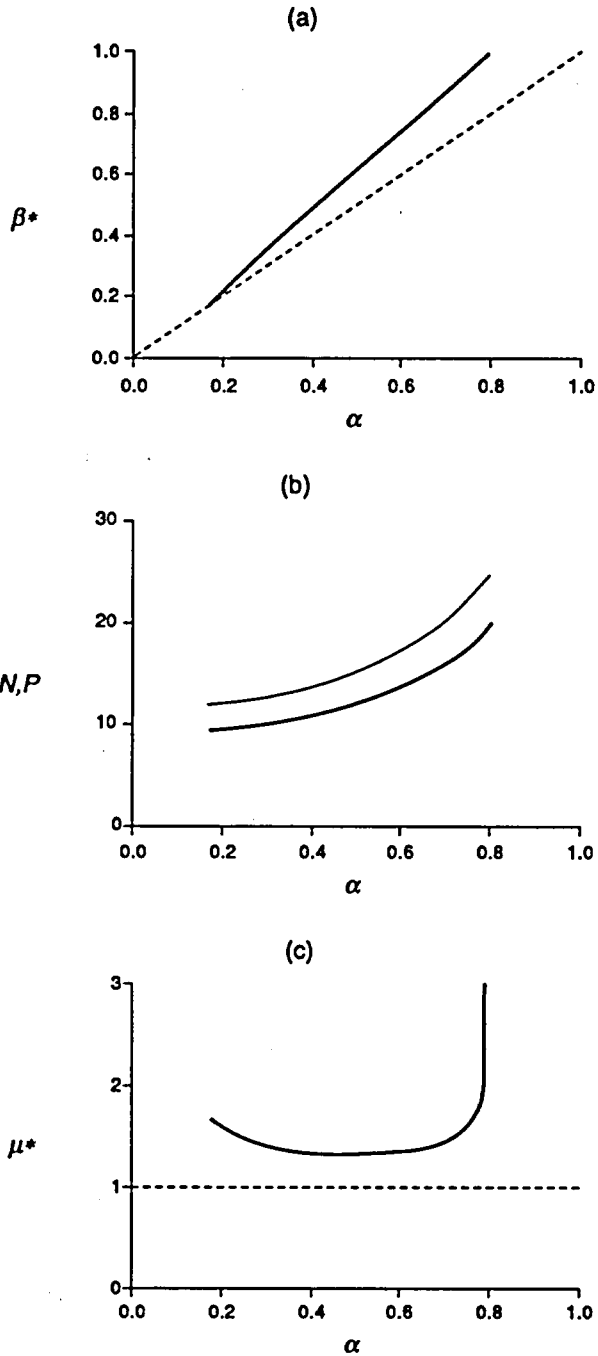


FIG. 2.—As in fig. 1, but now varying values of α (fraction of prey in the high-prey-density patch). Number of patches $n = 6$, prey fecundity $\lambda = 5$.

high-prey-density patch β^* decreases with increasing prey fecundity λ . This is explained by the fact that equilibrium densities of prey *and* predators increase with λ (fig. 1*b*). These higher densities imply intensified competition among the predators, which favors foraging in the low-prey-density patches.

Note that β^* is larger than α , which implies that predators should aggregate more strongly than the prey (figs. 1, 2). This follows from the conditions for the ideal free distribution; by rearranging equation (7) in the form

$$\frac{\alpha}{1 - \alpha} = \frac{\beta^*}{1 - \beta^*} Q, \quad (8)$$

it can be shown that, for $\alpha > (1 - \alpha)/(n - 1)$, Q is smaller than unity so that β^* must be larger than α .

To show how these results modify Hassell and May's (1973) conclusions, it is convenient to express the degree of predator aggregation in terms of an aggregation index μ , which is defined by

$$\beta_i = c \alpha_i^\mu, \quad (9)$$

where

$$c = \left(\sum_{i=1}^n \alpha_i^\mu \right)^{-1}$$

is a normalization factor to ensure that the β_i 's add up to unity. When, for the special case of one high-prey-density patch and multiple low-prey-density patches, all predators adopt the ESS β^* , the aggregation index μ^* is equal to

$$\mu^* = \frac{\ln \left[\frac{1}{\beta^*} \cdot \frac{1 - \beta^*}{n - 1} \right]}{\ln \left[\frac{1}{\alpha} \cdot \frac{1 - \alpha}{n - 1} \right]}, \quad (10)$$

which can be compared with the values of μ that are known to promote ecological stability. This comparison is shown in figure 3. In this figure, the parameter domain of ecological stability in the λ - μ plane is shown for the special case where $n = 6$ and $\alpha = 0.3$ (Hassell and May 1973). Superposed on this domain is the ESS μ^* . For smaller values of λ it can be seen that μ^* is well inside the stable domain, but for larger λ , where less aggregation is favored, it is not. Hence, if prey fecundity is too high, evolutionarily stable searching strategies of the predator population do not lead to ecological stability. It is important to note that for some values of λ , ecological stability is still possible in principle, but not under conditions of evolutionary stability.

If predator searching strategies evolve, the parameter μ is no longer a free parameter to be chosen at will but follows from the ESS. As can be seen in figure 3, this implies a new stability boundary. This boundary delimits the combinations of the remaining free parameters α , λ , and n that favor evolution of β^* (or μ^*),

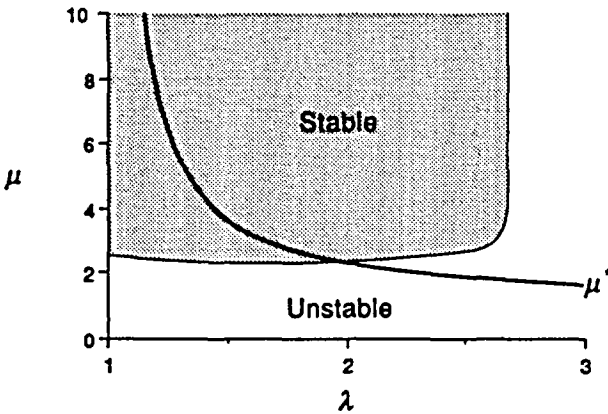


FIG. 3.—Stable domain for Hassell and May's (1973) model with $n = 6$ and $\alpha = 0.3$ (shaded area). Also shown is the aggregation index μ^* calculated from the evolutionarily stable predator searching strategy β^* (line).

which promotes ecological stability. Using the stability condition

$$\lambda a \bar{P} \left[\alpha \beta^* e^{-a\beta^*P} + (1 - \alpha) \frac{1 - \beta^*}{n - 1} e^{-a(1-\beta^*/n-1)P} \right] < \frac{\lambda - 1}{\lambda} \tag{11}$$

as given by Hassell and May (1973), the stable domain can be solved numerically. Some stable domains are shown in figure 4a and b, for $n = 6$ and $n = 11$ patches, respectively. From these figures it can be concluded that simultaneous ecological and evolutionary stability requires a prey distribution that is strongly skewed toward the high-prey-density patch. This skewness must be more pronounced if prey fecundity λ becomes large.

When prey fecundity is low, theory predicts that $\beta^* > 1$, which in fact means that all predators will aggregate in the high-prey-density patch ($\beta^* = 1$). This corresponds to a model with a partial prey refuge, which is always ecologically stable (Hassell and May 1973).

Within-Population Variability

The method for finding the ESS is based on backward reasoning: given that all predators have adopted the ESS, what then should it look like? This approach says nothing about whether all individuals of an evolving population of predators will eventually adopt it. Below we will briefly discuss this problem.

That evolution of patch selection strategies should give rise to an ideal free distribution makes intuitive sense. If predators visit a particular patch less frequently than expected, then mutants that visit this patch more often can increase. Their increase lowers the profitability of this patch, so evolutionary change will end when all patches offer equal reproductive success. However, this does not necessarily mean that the mutants will completely replace the original population.

When a population is distributed according to an ideal free distribution, no mutant searching strategy can be more successful than the population strategy.

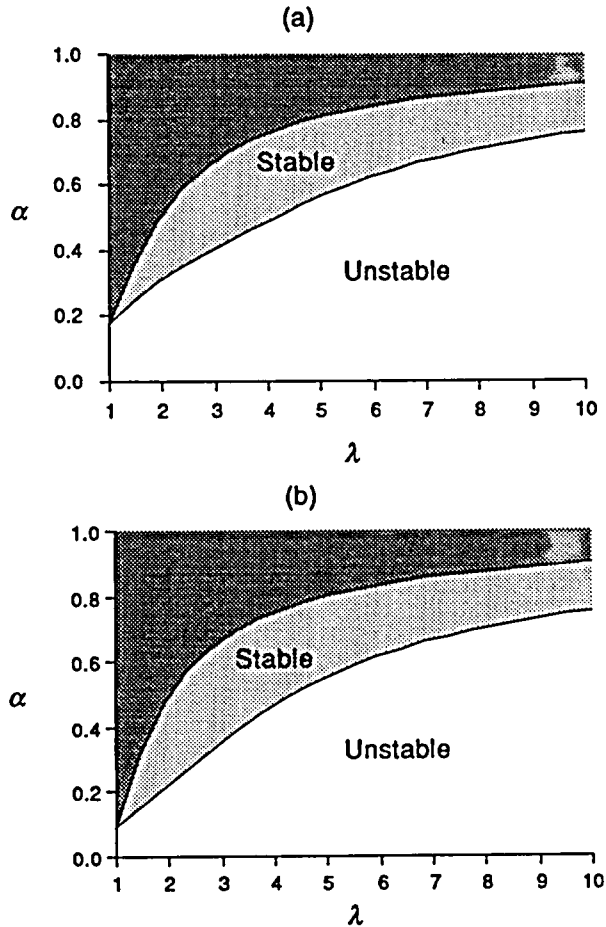


FIG. 4.—Part of the α - λ parameter space for which the ecological equilibrium is stable when all predators adopt the evolutionarily stable searching strategy. *Dark shading*: all predators aggregate in the high-prey-density patch ($\beta^* = 1$). Number of patches: *a*, $n = 6$; *b*, $n = 11$.

Thus, the first condition for evolutionary stability is met (Maynard Smith 1982; Parker and Hammerstein 1985). However, whereas under these circumstances no mutant strategy is selected *for*, no selection *against* mutant strategies takes place either. Because it has the same fitness as the population strategy, any mutant searching strategy could invade through random drift.

To prevent this, the second condition for evolutionary stability must be fulfilled as well (Maynard Smith 1982; Parker and Hammerstein 1985). This condition states that a mutant strategy that does as well as the population strategy should be selected against when its proportion in the population increases. We have no analytical proof that this condition is met, but in all numerical simulations we have done of system (1), with the predator population subdivided with respect to

searching strategy β , the distribution of the *total* predator population converged to the ESS searching strategy β^* . We take this to be sufficient to confirm our assumption that the ESS β^* is truly evolutionarily stable.

Whereas, in principle, ESS situations allow for variation in patch selection strategies in the population, the present analysis cannot predict the amount of variation that will remain in the long term (Parker 1984; Milinski 1988). This condition will depend on the presence and nature of disturbances and on the behavioral details of patch selection.

COEVOLUTION OF PREY AND PREDATORS

In the previous section, we have shown that natural selection may favor predator searching strategies that lead to stabilization of the ecological equilibrium, provided the prey population distribution is strongly clumped. As was pointed out above, such aggregated prey distributions are not likely to occur if the prey individuals are able to choose patches as well. Because high prey density is associated with increased predation risk, prey will be selected to choose low-prey-density patches, which leads to more evenly distributed prey populations.

Here, we will investigate the consequences of differential patch qualities, which may provide reasons for the prey individuals to aggregate, despite increased predation risk.

Prey and Predator Fitness

Differential patch qualities may arise for various reasons and may lead to differential predation-independent survival chances of the juvenile prey or to differential prey fecundities. For simplicity we will refer to the latter type of differences only, but the model applies equally well to the former. Let prey fecundity in patch i be given by λ_i , with $i = 1, \dots, n$, where the λ_i may differ in value. In addition, assume that all $\lambda_i > 1$, meaning that all patches allow for prey reproduction.

Incorporating predation risk, the expected reproductive success of a prey individual in patch i is $\lambda_i e^{-a\beta_i P}$. Therefore, a prey individual with a patch selection strategy $\alpha^m = \{\alpha_i^m\}$ has an expected fitness of

$$F_N(\alpha^m; N, P, \alpha, \beta) = \sum_{i=1}^n \alpha_i^m \lambda_i e^{-a\beta_i P}, \quad (12)$$

where $\alpha = \{\alpha_i\}$ and $\beta = \{\beta_i\}$ denote the patch selection strategies of the predator and prey population, respectively, and N and P denote their prevailing densities. Note that the fitness of a mutant prey individual is not directly dependent on the strategy of other prey in the population. This stems from the fact that prey fecundity is (assumed to be) independent of density. However, indirectly the fitness of a mutant prey individual does depend on the prey population strategy, through the response of the coevolving predator population.

With respect to the predators, nothing has changed except that the prey distri-

bution is no longer fixed. Thus, the predator fitness-generating function remains the same as in the first section, but it now also depends on the prevailing prey patch selection strategy α :

$$F_P(\beta^m; N, P, \alpha, \beta) = \sum_{i=1}^n \beta_i^m \frac{\alpha_i N (1 - e^{-\alpha \beta_i P})}{\beta_i P}. \quad (13)$$

Population Dynamics

When all prey individuals adopt strategy α and all predator individuals adopt strategy β , the population dynamics of this system are governed by

$$\begin{aligned} N_{t+1} &= N_t F_N(\alpha; N_t, P_t, \alpha, \beta) \\ &= N_t \sum_{i=1}^n \alpha_i \lambda_i e^{-\alpha \beta_i P_t} \end{aligned} \quad (14)$$

and

$$\begin{aligned} P_{t+1} &= P_t F_P(\beta; N_t, P_t, \alpha, \beta) \\ &= P_t \sum_{i=1}^n \beta_i \frac{\alpha_i N_t (1 - e^{-\alpha \beta_i P_t})}{\beta_i P_t}. \end{aligned}$$

The only difference between this model and Hassell and May's (1973) model is the assumption of different patch qualities; the latter is recovered if the λ_i 's are all equal. Because of the variability of the λ_i 's, ecological stability analysis (for arbitrary α and β) is even more complicated than in the case of Hassell and May's (1973) original model.

Coevolutionary Stability

It follows from the arguments given in the previous section that a pair of simultaneous ESSs $\alpha^* = \{\alpha_i^*\}$ and $\beta^* = \{\beta_i^*\}$ will be characterized by the simultaneous ideal free distribution of predators and prey. Hence, for a pair of coevolutionarily stable strategies α^* and β^* (by which we mean a pair of simultaneous ESSs—not to be confused with Roughgarden's [1979] definition of coevolutionarily stable strategies, which is not applicable here) it will hold that

$$\lambda_i e^{-\alpha \beta_i^* P} = K \quad (15)$$

and

$$\frac{\alpha_i^* \bar{N} (1 - e^{-\alpha \beta_i^* P})}{\beta_i^* \bar{P}} = L$$

for all i , where K and L are constants, and \bar{N} and \bar{P} are the ecological equilibrium densities associated with patch selection strategies α^* and β^* . These equilibrium densities are given by

$$N_{t+1} = N_t = \bar{N} \text{ and } P_{t+1} = P_t = \bar{P};$$

hence

$$\sum_{i=1}^n \alpha_i \lambda_i e^{-a\beta_i^* P} = 1$$

and (16)

$$\sum_{i=1}^n \beta_i \frac{\alpha_i^* \bar{N} (1 - e^{-a\beta_i^* P})}{\beta_i^* \bar{P}} = 1.$$

After substitution of conditions (15) for the coevolutionarily stable α and β into equations (16), it follows that under ESS conditions $K = L = 1$. Thus, the pair of coevolutionarily stable patch selection strategies is characterized by the fact that all patches provide an expected fitness of exactly one offspring to both prey and predators. Then, equations (15) lead to

$$\alpha_i^* \bar{N} = \frac{1}{a} \frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i$$

and (17)

$$\beta_i^* \bar{P} = \frac{1}{a} \ln \lambda_i,$$

from which, by summation over $i = 1, \dots, n$, the equilibrium densities

$$\bar{N} = \frac{1}{a} \sum_{i=1}^n \frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i$$

and (18)

$$\bar{P} = \frac{1}{a} \sum_{i=1}^n \ln \lambda_i$$

and the coevolutionarily stable searching strategies α^* and β^* can be calculated:

$$\alpha_i^* = \frac{\frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i}{\sum_{j=1}^n \frac{\lambda_j}{\lambda_j - 1} \ln \lambda_j}$$

and (19)

$$\beta_i^* = \frac{\ln \lambda_i}{\sum_{j=1}^n \ln \lambda_j}.$$

The spatial distributions of both prey and predators are entirely determined by the distribution of patch qualities. If the patch qualities are all equal, equations

(19) specify homogeneous distributions. Hence, only if (some of) the λ_i 's differ is the aggregation of both prey and predators coevolutionarily stable. This result confirms the verbal argument we gave in the introduction.

Equations (19) show that both α_i^* and β_i^* increase with patch quality λ_i . It can be inferred that equations (19) specify stronger aggregation of the predators than of the prey. Consider a system with a patch k with prey fecundity λ_k only slightly larger than one, which means that the patch is very marginal. Then, $\ln \lambda_k \approx \lambda_k - 1$, and we can write

$$\alpha_k^* \approx \frac{\lambda_k}{\lambda_k + \sum_{j \neq k}^n \frac{\lambda_j}{\lambda_j - 1} \ln \lambda_j}$$

and

$$\beta_k^* \approx \frac{\lambda_k - 1}{\lambda_k - 1 + \sum_{j \neq k}^n \ln \lambda_j}.$$

(20)

Where α_k^* is small but definite, β_k^* will approximate zero, because $\lambda_k - 1 \approx 0$. Because a smaller fraction of the predators than of the prey is found in low-quality patches, a larger fraction must be found in the high-quality patches. In other words, disproportionately more predators are found in the high-prey-density patches.

The coevolution of prey and predators can have profound consequences for optimal prey patch selection strategies. Consider the following illustrative example. Let there be $n = 5$ patches, one patch with a high prey fecundity of $\lambda_H = 5$, and four patches with a low prey fecundity of $\lambda_L = 1.05$ (fig. 5a). If there were no predators, the prey would aggregate all in the high-quality patch, because in that patch they would have the highest number of offspring. Nevertheless, the coevolutionary game with the predators drives them into the low-quality patches as well (fig. 5b). It is striking that patch-quality distribution is more conspicuously reflected in the ESS predator patch selection strategy than in the prey patch selection strategy.

Ecological Stability

Linearization around the ecological equilibrium shows that the ecological equilibrium of predators and prey is stable under ESS conditions if the following inequality holds:

$$\frac{\sum_{i=1}^n \frac{\lambda_i}{\lambda_i - 1} (\ln \lambda_i)^2}{\sum_{i=1}^n \frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i} + \frac{\sum_{i=1}^n \frac{1}{\lambda_i - 1} (\ln \lambda_i)^2}{\sum_{i=1}^n \ln \lambda_i} < 1 \quad (21)$$

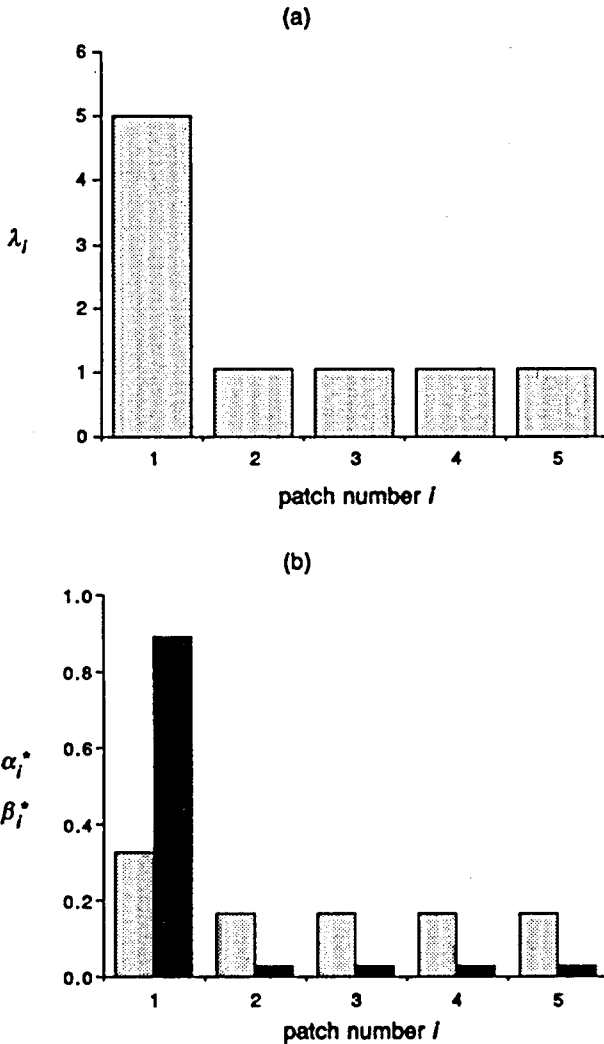


FIG. 5.—Coevolutionarily stable patch selection strategies of prey and predators. *a*, Distribution of patch qualities. Prey fecundity in high-quality patch $\lambda_H = 5$, and prey fecundity in the low-quality patches $\lambda_L = 1.05$. *b*, Coevolutionarily stable searching strategies: prey strategy α^* (light shading); predator strategy β^* (dark shading).

(the derivation of this inequality can be found in App. B). It is not immediately obvious whether this inequality can be satisfied and, if it can, under what conditions.

Yet, we can conclude the following. If the λ_i 's are all equal ($\lambda_1 = \dots = \lambda_n = \Lambda$), the left-hand side of inequality (21) becomes

$$\frac{\Lambda}{\Lambda - 1} \ln \Lambda, \tag{22}$$

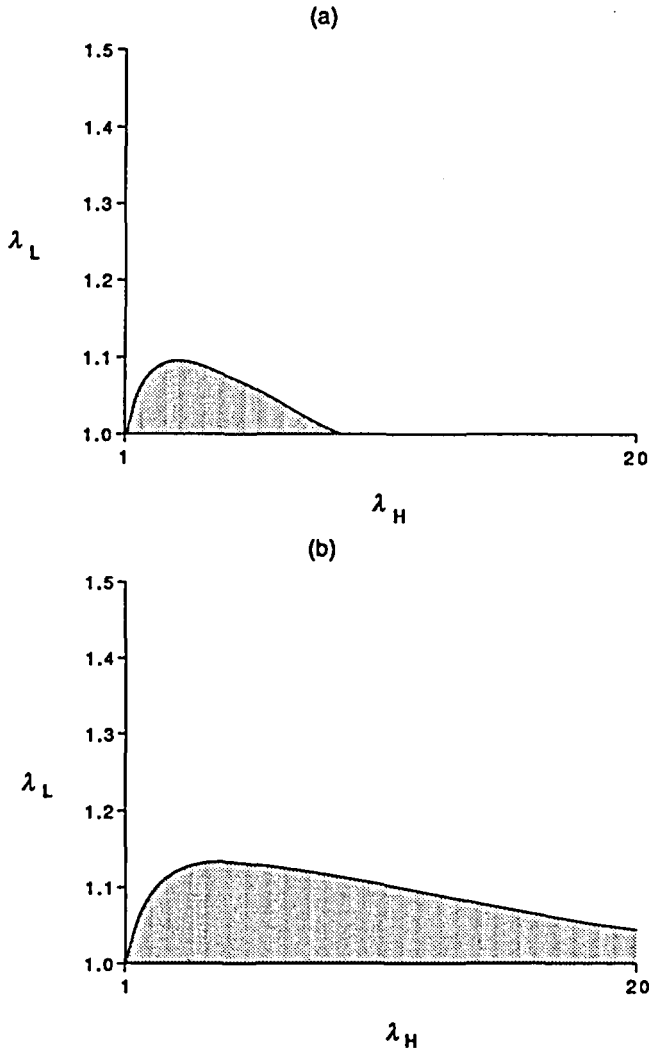


FIG. 6.—Domain of simultaneous ecological and coevolutionary stability, when one patch has high-quality λ_H and the others have low-quality λ_L . Note the differences in the scale of λ_H and λ_L . Number of patches: *a*, $n = 6$; *b*, $n = 11$.

which is larger than one ($\Lambda > 1$): no ecological stability follows under ESS conditions. (This is no surprise because under these circumstances the model is identical to the Nicholson-Bailey model.) Hence, if the inequality holds, it must be the case that at least some of the λ_i 's are different. However, they should not be too different. If inequality (21) holds for some combination of λ_i 's, it can be violated by increasing one of the λ_i 's, say λ_k , sufficiently. This follows from the fact that, where the numerators of both fractions on the left-hand side of inequality (21) depend on the square of $\ln \lambda_k$, their denominators depend only linearly on $\ln \lambda_k$.

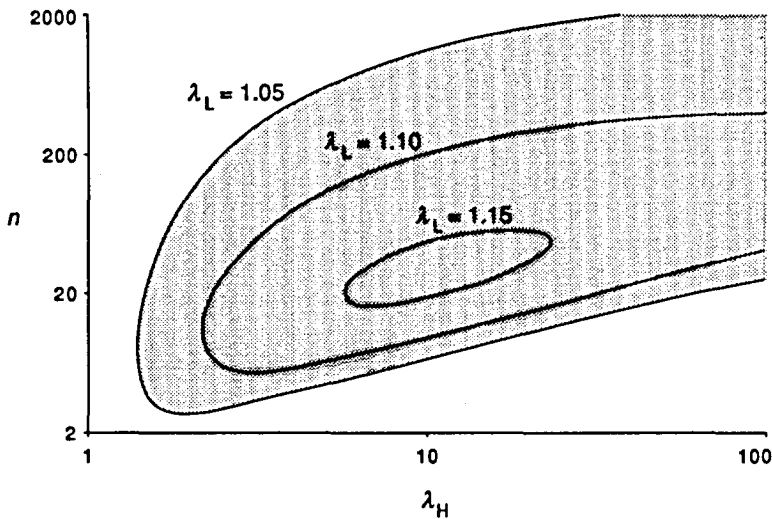


FIG. 7.—Domain of ecological and coevolutionary stability of the system with two patch qualities, in the λ_H - n plane for different values of λ_L . Both axes are on a log scale.

Consider a simple type of environment, with one high-quality patch with prey fecundity λ_H and $n - 1$ low-quality patches with prey fecundity λ_L ($\lambda_H > \lambda_L$). Then, for some combinations of λ_H and λ_L , the left-hand side of inequality (21) turns out to be less than unity. Hence, under certain circumstances the evolutionarily stable patch selection strategies stabilize the ecological equilibrium.

Examples of numerical solutions of the stable region are shown in figure 6 for $n = 6$ and $n = 11$ patches. From this figure it can be concluded that ecological stability only occurs under the distinctive condition that the low-quality patches are really marginal (i.e., characterized by a prey fecundity λ_L that is not much larger than unity, which barely allows for self-replacement). Figure 7 shows that for simultaneous evolutionary and ecological stability there should be many, but not too many, marginal patches.

DISCUSSION

Whereas analysis of ecological stability may delimit a broad set of parameter combinations for which predator-prey models have a stable equilibrium, the set of parameter values that comprises ESSs may be very different. What is more, there is no a priori reason why these sets should overlap. Thus, when not only ecological stability but also evolutionary stability is required, the resultant stability domain may be greatly reduced or may not exist at all.

Two cases have been considered here to illustrate how evolutionary and ecological stability combine to produce a new stability domain. First, the case of a fixed distribution of the prey was considered. For a given prey distribution, ESS conditions require that predators cannot gain by changing their searching strategy, which leads to the ideal free distribution of the predators (Fretwell and

Lucas 1970; Comins and Hassell 1979; Sutherland 1983). For an uneven prey distribution, the predator distribution will be of the aggregated type with more predators in the high-prey density patches. However, this predator aggregation is not necessarily strong enough to stabilize the equilibrium, as shown by the example in figure 3. For low values of λ the ESS values of μ are in the stability domain, whereas for high values of λ there is no ecological stability possible for any value of μ (whether under ESS conditions or not), and there is an intermediate range of λ for which ecological stability is possible in principle but not under conditions of evolutionary stability.

In the second case, the assumption of a fixed prey distribution was relaxed so that natural selection would operate on the patch selection strategies of both predator and prey. When patches are of equal quality (in terms of prey reproduction), predators and prey will distribute themselves equally over the patches. Only when patch quality varies, so that prey reproduction (λ) is higher in some patches than in others, do ESSs lead to the type of aggregated distributions that were assumed by Hassell and May (1973). Neither prey nor predator can gain by changing its patch selection strategy. Prey cannot gain because patch quality and predation risk counterbalance each other everywhere; predators cannot gain because high-prey density is counterbalanced by increased competition. As in the Hassell and May (1973) model, ecological stability is possible. However, only in a confined range of environmental conditions do evolutionary and ecological stability coincide: for any high-quality patch, there must be many low-quality patches, and these low-quality patches must be of marginal quality, so that they barely allow for prey reproduction.

Whereas in the absence of predators prey individuals would aggregate entirely in the high-quality patches, the evolutionary game with the predators forces them to select low-quality patches as well. The low-quality patches are then genuine refuges, in that they are good to escape from predator attack but not for much else. This condition is in contrast with the standard partial prey refuge model (Hassell 1978) in which residing in the refuge costs the prey nothing.

We have not tried to test our predictions, because our primary intention was to investigate the assumption of stabilizing predator aggregation with respect to its logical consistency. However, there have been some intriguing reports about spatial distribution and mortality factors of hosts in host-parasitoid systems. It has been noted that parasitism and other host mortality factors are often inversely related (Starks et al. 1972; Fritz and Nobel 1990). Recently, Valladares and Lawton (1991) investigated host mortality in relation to patch quality in holly leaf miners. They found that, although some patches (holly bushes) were of better quality than others and more heavily infested, leaf-miner performance was about equal in all types of patches. Because parasitism (higher in the high-quality patches) was density-dependent, they supposed that leaf miners were distributed according to an ideal free distribution. Valladares and Lawton did not attempt to explain the degree in density dependence in terms of simultaneous ideal free distributions of the parasitoids and their hosts, as in the analysis presented here.

In conclusion, natural selection may indeed favor predator aggregative behav-

ior that stabilizes the ecological equilibrium, if the prey distribution is fixed and also if the prey are allowed to select patches in response to the predator searching strategies. In the latter case, stabilizing spatial distributions occur only if spatial variation exists at another level, such as variation in patch quality. However, it should be stressed that our analysis applies exclusively to populations *in* ecological equilibrium. It remains to be investigated how ESS distributions affect the dynamics away from the equilibria.

Concluding Remarks

The results of this article highlight the notion of the ideal free distribution as a tool for understanding the interrelationship between population distributions and evolutionarily stable patch selection strategies. However, one can think of many reasons that such distributions may not be attained in nature. Individuals often have incomplete knowledge about their environment, may even need to guess at the profitability of the patch they currently inhabit, may need to base their decisions on ambiguous cues, need time to travel from patch to patch, must find mating partners, and may be unsure about the number, distribution, and behavior of their competitors. Furthermore, the weather or other abiotic factors may exert continuous or episodic disturbing influences on the population distribution. Indeed, it is observed that often spatial distributions of animals do not make sense (Lloyd 1967). If the ideal free distribution is a true ideal and never reality, then what can the present analysis teach us about real systems?

In the first place, whatever the current state of the environment, individuals will be selected to choose patches that offer the best prospects for reproduction under given circumstances and hence to balance fitness-related criteria as developed in this article. If competition is intense, it never pays to join a crowded patch. If food quality and predation risk are both important, then optimal choices take both aspects into account. In the second place, even if an ideal free distribution is never attained, it can be used to frame hypotheses about how population distributions will respond to external influences. For example, where external influences tend to cause aggregations, individuals could respond by increasing their dispersal rate, so as to avoid competition or high predation risk.

The approach developed in this article may be important for the understanding of aggregative behavior in systems other than predator-prey systems. Often, in ecological theory, aggregation of populations is simply assumed a priori, and conclusions are drawn without questioning *why* aggregation occurs. For example, aggregation has been modeled in a phenomenological way to explain the coexistence of competitors (Atkinson and Shorrocks 1984; Ives and May 1985; Ives 1988). In such models, coexistence is possible because aggregation of the individuals inevitably leaves room for others (individuals of either the same or other species). However, whether the behavior underlying this aggregation will be favored by natural selection is an open question. To solve such a problem we advocate that evolutionary stability analysis be used in addition to ecological stability analysis. In this way it may be possible to investigate critically the condi-

tions under which explanations for ecological phenomena are compatible with the theory of natural selection.

ACKNOWLEDGMENTS

We thank J. S. Brown, J. Bruin, R. Harmsen, and C. J. Nagelkerke for valuable comments and S. M. McNab for help with language and style.

APPENDIX A

ALTERNATIVE DERIVATION OF THE PREDATOR FITNESS GENERATING FUNCTION

Consider the more general case of Hassell and May's (1973) model, in which each attacked prey gives rise to γ predator offspring. This condition would lead to the following equation for the predator dynamics:

$$P_{t+1} = \gamma N_t \left(1 - \sum_{i=1}^n \alpha_i e^{-a\beta_i P_t} \right). \quad (A1)$$

Let the predators, once within a patch, search randomly for prey. If the search rate *within* the patch is a' and the number of predators in the patch is p , then the probability for a particular prey individual to escape from predator attack will equal $e^{-a'p}$. Now consider a particular mutant predator that ended up in a patch with R prey and k competitors. The expected fitness of this predator is given by

$$\Phi(R, k) = \frac{R(1 - e^{-a'(k+1)})}{k + 1}.$$

Note that the predation risk is determined by $k + 1$ predators: the presence of the mutant predator increases the predation risk.

Assume that the number of competitors \underline{k} is Poisson distributed with mean C . Then the expected fitness of the mutant is

$$\begin{aligned} E\Phi(R, \underline{k}) &= \sum_{k=0}^{\infty} \Pr(\underline{k} = k) \cdot \Phi(R, k) \\ &= \sum_{k=0}^{\infty} \frac{C^k}{k!} e^{-C} \frac{R[1 - e^{-a'(k+1)}]}{k + 1} \\ &= Re^{-C} \left[\sum_{k=0}^{\infty} \frac{C^k}{(k+1)!} - \sum_{k=0}^{\infty} \frac{C^k}{(k+1)!} e^{-a'(k+1)} \right] \\ &= Re^{-C} \left[\sum_{k=0}^{\infty} \frac{C^k}{(k+1)!} - e^{-a'} \sum_{k=0}^{\infty} \frac{(Ce^{-a'})^k}{(k+1)!} \right] \\ &= Re^{-C} \left\{ \frac{1}{C} \left[\sum_{k=0}^{\infty} \frac{C^k}{k!} - 1 \right] - \frac{1}{C} \left[\sum_{k=0}^{\infty} \frac{(Ce^{-a'})^k}{k!} - 1 \right] \right\} \\ &= \frac{Re^{-C}}{C} \left(e^C - e^{Ce^{-a'}} \right) \\ &= \frac{R(1 - e^{-(1-e^{-a'})C})}{C}. \end{aligned}$$

Now let $R = \alpha_i N$ be the density of prey in patch i and $C = a''\beta_i P$ be the expected number of arriving predators (a'' is the search rate for patches); then the expected fitness of a mutant in patch i is

$$E\Phi(\alpha_i N, k) = \frac{\alpha_i N [1 - e^{-(1-\epsilon^{-a'})a''\beta_i P}]}{a''\beta_i P},$$

and the expected fitness of a mutant with searching strategy β^m is

$$F_P(\beta^m; N, P, \beta) = \sum_{i=1}^n \beta_i^m \frac{\alpha_i N [1 - e^{-(1-\epsilon^{-a'})a''\beta_i P}]}{a''\beta_i P}.$$

If each attacked prey gives rise to γ' predators, the predator dynamics of a population adopting the searching strategy β are given by

$$\begin{aligned} P_{t+1} &= P_t \gamma' F_P(\beta, N_t, P_t, \beta) \\ &= \frac{\gamma'}{a''} N_t \left[1 - \sum_{i=1}^n \alpha_i e^{-(1-\epsilon^{-a'})a''\beta_i P} \right]. \end{aligned}$$

The predator equation (A1) is then obtained after setting

$$\gamma = \gamma' / a''$$

and

$$a = (1 - \epsilon^{-a'})a''.$$

It is assumed that the density of prey in a patch is not stochastic. If it is, the fitness-generating function becomes more complex, since a predator must take into account not only the average prey distribution but also the stochastic deviations. The correlation between the number of prey and the number of predators in a patch turns out to be an important statistic governing the ecological stability of the system (Chesson and Murdoch 1986).

APPENDIX B

THE ECOLOGICAL STABILITY CRITERION

The predator-prey system described by equations (14) can be written as

$$N_{t+1} = N_t f(P_t)$$

and

$$P_{t+1} = N_t [1 - g(P_t)],$$

with

$$f(P) = \sum_{i=1}^n \alpha_i \lambda_i e^{-a\beta_i P}$$

and

$$g(P) = \sum_{i=1}^n \alpha_i e^{-a\beta_i P}.$$

Note that both $f'(P) < 0$ and $g'(P) < 0$.

Substituting the ecological equilibrium conditions

$$f(\bar{P}) = 1$$

and

$$1 - g(\bar{P}) = \frac{\bar{P}}{\bar{N}}$$

into the Jacobian matrix, we obtain

$$\mathbf{J} = \begin{pmatrix} 1 & \bar{N}f'(\bar{P}) \\ \frac{\bar{P}}{\bar{N}} - \bar{N}g'(\bar{P}) & \end{pmatrix}.$$

The ecological equilibrium is asymptotically stable if the absolute values of both roots of the characteristic equation of \mathbf{J} are less than one. The characteristic equation is

$$\theta^2 - \theta \cdot \text{trace } \mathbf{J} + \det \mathbf{J} = 0$$

with

$$\text{trace } \mathbf{J} = 1 - \bar{N}g'(\bar{P})$$

and

$$\det \mathbf{J} = -\bar{N}g'(\bar{P}) - \bar{P}f'(\bar{P}).$$

The absolute values of both roots are less than one if and only if

$$|\text{trace } \mathbf{J}| - 1 < \det \mathbf{J} < 1.$$

Since $g'(\bar{P}) < 0$, $\text{trace } \mathbf{J} > 0$, which gives

$$-\bar{N}g'(\bar{P}) < -\bar{N}g'(\bar{P}) - \bar{P}f'(\bar{P}) < 1.$$

The first inequality holds because $f'(\bar{P}) < 0$, and therefore the stability characteristic of the ecological equilibrium is determined by

$$-\bar{N}g'(\bar{P}) - \bar{P}f'(\bar{P}) < 1. \quad (\text{B1})$$

Now

$$f'(P) = -a \sum_{i=1}^n \alpha_i \beta_i \lambda_i e^{-a\beta_i P}$$

and

$$g'(P) = -a \sum_{i=1}^n \alpha_i \beta_i e^{-a\beta_i P}. \quad (\text{B2})$$

According to equations (15), the following relation holds under ESS conditions:

$$\lambda_i e^{-a\beta_i \bar{P}} = 1$$

for all i . Substituting this into equations (B2) we have at equilibrium

$$f'(\bar{P}) = -a \sum_{i=1}^n \alpha_i^* \beta_i^*$$

and

$$g'(\bar{P}) = -a \sum_{i=1}^n \frac{\alpha_i^* \beta_i^*}{\lambda_i},$$

and thus condition (B1) becomes

$$\bar{N} a \sum_{i=1}^n \frac{\alpha_i^* \beta_i^*}{\lambda_i} + \bar{P} a \sum_{i=1}^n \alpha_i^* \beta_i^* < 1,$$

or

$$a \sum_{i=1}^n \left(\bar{P} + \frac{\bar{N}}{\lambda_i} \right) \alpha_i^* \beta_i^* < 1. \quad (\text{B3})$$

Since from equations (17) it follows that

$$\begin{aligned} \alpha_i^* \beta_i^* &= \left(\frac{1}{\bar{N}} \frac{\lambda_i}{\lambda_i - 1} \ln \lambda_i \right) \cdot \left(\frac{1}{\bar{P}} \ln \lambda_i \right) \\ &= \frac{1}{a^2} \frac{1}{\bar{N} \bar{P}} \frac{\lambda_i}{\lambda_i - 1} (\ln \lambda_i)^2, \end{aligned}$$

we get for condition (B3)

$$\frac{1}{a} \sum_{i=1}^n \left(\frac{\lambda_i}{\bar{N}} + \frac{1}{\bar{P}} \right) \frac{(\ln \lambda_i)^2}{\lambda_i - 1} < 1,$$

or

$$\frac{1}{a \bar{N}} \cdot \sum_{i=1}^n \frac{\lambda_i}{\lambda_i - 1} (\ln \lambda_i)^2 + \frac{1}{a \bar{P}} \cdot \sum_{i=1}^n \frac{1}{\lambda_i - 1} (\ln \lambda_i)^2 < 1,$$

or finally, after substitution of the equilibrium densities, inequality (21).

LITERATURE CITED

- Atkinson, W. D., and B. Shorrocks. 1984. Aggregation of larval Diptera over discrete and ephemeral breeding sites: the implications for coexistence. *American Naturalist* 124:336-351.
- Chesson, P. L., and W. W. Murdoch. 1986. Spatial distribution of risk: relationships among host-parasitoid models. *American Naturalist* 127:696-715.
- 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.
- Free, C. A., J. R. Beddington, and J. H. Lawton. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. *Journal of Animal Ecology* 46:543-554.
- 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.
- Fritz, R. S., and J. Nobel. 1990. Host plant variation in mortality of the leaf-folding sawfly on the arroyo willow. *Ecological Entomology* 15:25-35.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. *Monographs in Population Biology*. Vol. 13. Princeton University Press, Princeton, N.J.
- Hassell, M. P., and R. M. May. 1973. Stability in insect host-parasite models. *Journal of Animal Ecology* 42:693-736.
- Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of optimal habitat distribution. *Theoretical Population Biology* 28:181-208.
- . 1987. Prey communities in patchy environments. *Oikos* 50:276-290.
- Hubbard, S. F., and R. M. Cook. 1978. Optimal foraging by parasitoid wasps. *Journal of Animal Ecology* 47:593-604.
- Ives, A. R. 1988. Spatial distribution and the coexistence of competitors. *Annales Zoologici Fennici* 25:75-88.
- Ives, A. R., and R. M. May. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. *Journal of Theoretical Biology* 11:565-592.

- Kacelnik, A., J. R. Krebs, and C. Bernstein. 1992. The ideal free distribution and predator-prey interactions. *Trends in Ecology & Evolution* 7:50-55.
- Kareiva, P. 1989. Renewing the dialogue between theory and experiments in population ecology. Pages 68-88 *in* J. Roughgarden, R. M. May, and S. A. Levin, eds. *Perspectives in ecological theory*. Princeton University Press, Princeton, N.J.
- Lloyd, M. 1967. Species crowding. *Journal of Animal Ecology* 36:1-30.
- 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.
- Milinski, M. 1988. Games fish play: making decisions as a social forager. *Trends in Ecology & Evolution* 3:325-330.
- Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. I. *Proceedings of the Zoological Society of London* 3:551-598.
- Parker, G. A. 1984. Evolutionarily stable strategies. Pages 30-61 *in* J. R. Krebs and N. B. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific, Oxford.
- Parker, G. A., and P. Hammerstein. 1985. Game theory and animal behaviour. Pages 73-94 *in* P. J. Greenwood, P. H. Harvey, and M. Slatkin, eds. *Essays in honour of John Maynard Smith*. Cambridge University Press, Cambridge.
- Roughgarden, J. 1979. *Theory of population genetics and evolutionary ecology: an introduction*. Macmillan, New York.
- Sih, A. 1984. The behavioral response race between predator and prey. *American Naturalist* 123:143-150.
- Starks, K. J., R. Muniappan, and R. D. Eikenbary. 1972. Interaction between plant resistance and parasitism against the greenbug on barley and sorghum. *Annals of the Entomological Society of America* 65:650-655.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Monographs in Behavior and Ecology. Princeton University Press, Princeton, N.J.
- Stewart-Oaten, A. 1982. Minimax strategies for a predator-prey game. *Theoretical Population Biology* 22:410-424.
- Sutherland, W. J. 1983. Aggregation and the "ideal free distribution." *Journal of Animal Ecology* 52:821-828.
- Valladares, G., and J. H. Lawton. 1991. Host-plant selection in the holly leaf-miner: does the mother know best? *Journal of Animal Ecology* 60:227-240.
- Vincent, T. L., and J. S. Brown. 1989. The evolutionary response of systems to a changing environment. *Applied Mathematics and Computation* 32:185-206.

Associate Editor: Jon Seger