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Prey communities in patchy environments

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Individuals should exploit a spatially variable environment so as to increase their Darwinian fitness. Predators should aggregate in patches with relatively high densities of high-quality prey, and prey should in turn seek refuges providing protection from predators. This paper explores some of the consequences of such behavior for the coexistence of prey species in a patchy environment. It is argued that an aggregative predator response can lead to indirect interactions among otherwise non-interacting prey species co-occurring in a patch. In many circumstances, the interaction should be (–,–) (apparent competition), although in some situations other interactions may occur. If refuges are in short supply, then prey may compete for occupancy of refuges. Several models of such competition are presented. If predators act as density-independent mortality agents on prey outside refuges, it is shown for a simple model that two prey species cannot coexist when competing for a single refuge. Coexistence may be permitted if: (1) each prey has an exclusive refuge, (2) the dominant prey species experiences strong intraspecific interference, (3) there are trade-offs in competitive ability for refuges and for food resources, (4) the predator has a numerical response, and the prey that is subordinate in competition for refuge can better withstand predation (i.e., is superior in apparent competition). These models highlight the potential importance of spatial heterogeneity for understanding prey community structure.

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Introduction

A perennial problem in community ecology is to gauge the relative importance of competition and predation as factors structuring natural communities (e.g., Paine 1966, Lubchenco 1986). In some circumstances, the effects of predators are dramatic and seem to over-shadow the influence of competition for resources. In an early review of field studies, Connell (1975: 475) stated that "predation should be regarded as being of primary importance, either directly determining the species composition [of a community] or in preventing competitive exclusion." In a more recent review, Sih et al. (1985) critically examined 131 field studies of predation in which predator numbers were manipulated and prey responses monitored; 121 of these studies documented a large response by one or more prey species to a change in predator numbers. Strong et al. (1984) suggested that natural enemies, particularly parasitoids (see Lawton 1986), play a predominant role in determining the structure of phytophagous insect communities. In freshwater communities, predators seem to be conspicuously successful in preventing species invasions, thus limiting the species composition of local communities (Thorp 1986). Even the ungulate communities of East Africa, which are affected by resource limitation and partitioning, are also significantly influenced by predation (Sinclair 1985).

A large body of theory now exists which examines the joint effects of predation and competition on species coexistence (Slobodkin 1961, Cramer and May 1972, Van Valen 1974, Roughgarden and Feldman 1975, Comins and Hassell 1976, 1987, Yodzis 1976, 1978, 1986, Abrams 1977, Holt 1977, 1984, 1985b, Fujii 1977, Vance 1978, Armstrong 1979, Teramoto et al. 1979, Hanski 1981, Levin 1981, Noy-Meir 1981, Takeuchi and Adachi 1983). Most of this literature has been preoccupied with how predation modifies pre-existing competitive interactions, particularly in spatially homogeneous environments. The upshot of this work is that predation may either enhance or reduce the chances of coexistence for competing species; the exact outcome depends upon the interplay of a number of factors, including the degree to which predators are limited by their prey (Holt 1977, Noy-Meir 1981), the relation between predator preferences and prey competitive abilities (Lubchenco 1978), the predator's propensity for switching (Teramoto et al. 1979), and non-linearities in the competitive interaction (Abrams 1977, Holt 1985b). There is a growing appreciation that shared predation can have important and interesting consequences for prey community structure, even if there is little or no interspecific competition among prey for limiting resources. In particular, a numerical response by a predator population to its prey may generate a quasi-competitive interaction between alternative prey species, such that each prey suffers a reduction in abundance because the other prey is present. One prey may even by excluded indirectly by the other. Formal models exploring the implications of such apparent competition are presented in Holt (1977, 1984). Jeffries and Lawton (1984) review the idea and describe a number of field studies suggesting the influence of apparent competition, and Schmitt (in press) has recently provided an experimental demonstration of the predicted effect in a subtidal reef system. Moreover, the consequences of predation for species coexistence depend upon the spatial heterogeneity or patchiness of the environment. Theoretical analyses of the factors stabilizing the interaction between single predator and single prey populations often emphasize the singular importance of spatial dynamics. The causal mechanisms that have been examined theoretically include: the dispersion of predator and prey over many patches loosely coupled by passive dispersal (Crowley 1981); aggregative predator numerical responses (Hassell and May 1974); refuges from predation (Murdoch and Oaten 1975, McNair 1986); extinction-colonization dynamics (Hastings 1977, Caswell 1978); and spatial variation in population growth parameters (e.g., prey intrinsic growth rates) which with passive dispersal leads to a "source-sink" population structure (Holt 1984, 1985a). Given the mounting empirical evidence that spatial heterogeneity is important in determining the species richness of communities strongly structured by predation (see, e.g., Menge and Lubchenco 1981 for benthic marine communities), it seems desirable to examine theoretically how spatial heterogeneity and patchiness might modify the interaction between alternative prey mediated through their shared predator.

In a spatially heterogeneous, patchy environment, predators can increase the rate at which they accrue resources by seeking out areas with dense concentrations of prey relative to other areas; in the absence of direct interference amongst predators, this generates an aggregative numerical response. Prey, in turn, can lower their expected mortality rate by preferentially residing in refuges, areas with relatively few or no predators. In this paper, I examine how these behavioral strategies can influence the character of interactions between alternative prey species in spatially heterogeneous environments. Elsewhere (Holt 1984, Holt and Kotler, in press) I have argued that an aggregative numerical response by predators to the prey in a patch can generate (−,−) interactions among otherwise non-competing prey species. In the first part of the paper, I extend these ideas by explicitly incorporating the dynamics of prey recruitment and show that one prey type may exclude another from a patch because of an aggregative predator response. I examine two ends of a spectrum of possibilities: 1) prey dynamics in a single patch, when predators can forage over a large number of patches, 2) prey dynamics in two patches, between which predators can move as they forage. In these models, the interaction between alternative prey is mediated indirectly though changes in the behavior and spatial distribution of predators in a patchy environment.

When predators leave a patch because prey numbers there are too low, relative to other patches, the remaining prey enjoy a kind of implicit refuge from predation. From the prey's point of view, models with an aggregative predator response thus bear a family resemblance to models with absolute spatial refuges from predation. In the second part of the paper, I examine a series of simple models in which refuges from predation are available in limited supply to two co-occurring prey species. Given that prey selectively occupy refuges when space is available, this sets up a direct competitive interaction between prey. In contrast to more traditional kinds of competition (e.g., the competitive interactions modelled in the theoretical literature cited above), however, the fitness consequences of such competition depend entirely upon the action of predators, as measured by the increased mortality rate experienced by prey outside refuges. These models suggest that at times predation may increase competition by forcing prey to contend for access to refuges, a "resource" that would be unimportant in the absence of predators. A qualitative conclusion common to both parts of the paper is that if predation is intense, the sustained coexistence of alternative prey species may require that prey show habitat partitioning, with each prey in its own distinct patch type or refuge.

Predator aggregation and prey species coexistence

Prey dynamics in a single patch in a multi-patch environment

Predators should tend to aggregate in patches which have a high abundance of prey relative to other patches. While foraging in a single patch a predator should, through exploitation, lower prey availability there, thus gradually making that patch a less profitable place to forage for both itself and other predators. Considerable attention has been given to developing criteria for predicting when predators should abandon one patch and move on to greener pastures (Pyke 1984). According to the marginal value theorem of Charnov (1976), a patch should be left when the instantaneous rate of foraging yield in the patch, denoted here by Y, drops to an average rate of yield over all patches, $\hat{Y}$, including costs in time and energy of moving among patches. The foraging rule for predators in a patchy environment is quite simple: enter a given patch if $Y > \hat{Y}$, and leave it if $Y < \hat{Y}$. I will consider first the dynamics of two prey species in a single patch, given a predator that ranges over many patches. With enough patches, one can assume that for all practical purposes $\hat{Y}$ is a fixed constant; this allows us to explore within-patch interactions between alternative prey, given an invariant patch use criterion for the predator. Below, I examine the opposite extreme of predators moving between just two patches.

The instantaneous rate of yield from foraging in the patch is assumed to be a continuous function of the density of each prey, $Y(R_1, R_2)$. For most predator-prey systems, it is reasonable to assume that an increase in the abundance of either prey will increase the predator's rate of yield, i.e., $\partial Y/\partial R_i > 0$. However, in some circumstances, foraging yield may decline with an increase in the availability of one prey type (i.e., $\partial Y/\partial R_1 > 0$, but $\partial Y/\partial R_2 < 0$). This might occur, for instance, if the second prey is of low quality but is rare or absent in most patches in which the predator forages. The predator might then inadvertently (and suboptimally) include this item in its diet on those infrequent occasions when this prey type is encountered. The issue of when an increase in prey availability might decrease total predator foraging yield is discussed in detail in Holt (1983) and Holt and Kotler (in press).

Fig. 1 graphically depicts several ways the marginal value theorem for patch use can be applied to a patch containing two prey types. The curves $Y(R_1, R_2) = \hat{Y}$ separate those combinations of prey densities for which predators should be willing to enter and forage in the patch (i.e., $Y > \hat{Y}$) from those for which predators should leave the patch (i.e., $Y < \hat{Y}$). These curves are examples of isolegs (Rosenzweig 1981), for they represent switchpoints between qualitatively different predatory behaviors.

Exploitation will tend to depress prey abundances to values within or on an isoleg. To predict the consequences of this for prey coexistence, we allow prey recruitment and exploitation by predators to occur simultaneously:

$$dR_i/dt = G_i(R_i) - a_iP,$$

where R_i is the density of prey i; P is the predator density in the patch; a_i is the attack rate per prey, per predator; and G_i is the instantaneous growth rate of prey i (except for losses to predation). To simplify the following analysis, we will assume that attack coefficients are constants, and that $dG_i/dR_i < 0$. In other words, the predator has a linear functional response to

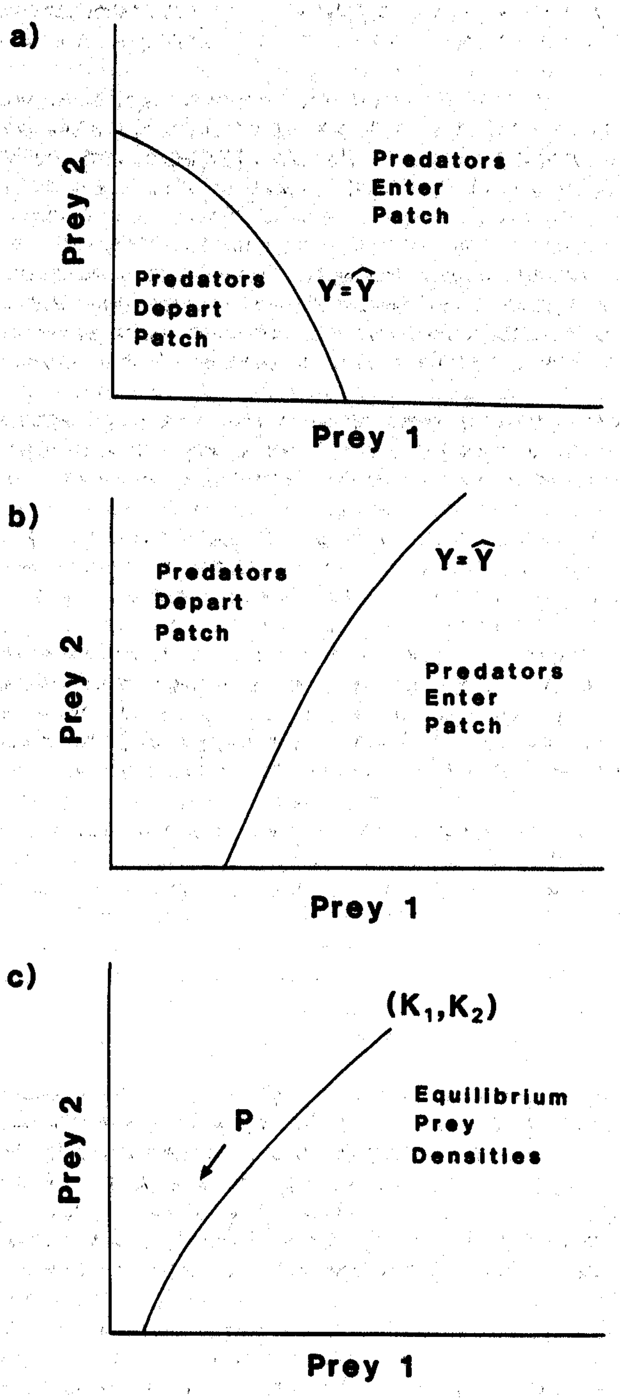

Fig. 1. Predator isolegs and the curve of prey equilibrium densities. (a) Predator isoleg: predator foraging rate increases with the density of each prey. The isoleg has a negative slope. At the isoleg, foraging yield just equals the average rate of yield over the entire habitat (including movement costs). The isoleg separates prey densities at which predators enter the patch from prey densities at which predators leave. (b) Predator isoleg: predator foraging rate decreases with increasing density of prey 2. The isoleg has a positive slope. (c) Curve of moving prey equilibria. Prey dynamics are assumed to be fast compared to predator dynamics. Prey densities decrease with increasing predator density, P, along a curve determined by prey recruitment (see text).

each prey type, and each prey experiences intraspecific negative density-dependence. There is no direct interspecific competition, but the two prey species may nonetheless interact because predators respond to the total number of prey in the patch in deciding whether to enter or leave. The prey's intrinsic growth rate will be denoted by r_i. We further assume that predators enter the patch when prey densities are to the right of the isoleg, and leave the patch to the left, at rates slow enough for prey densities to equilibrate (to a first-order approximation), tracking the slowly changing number of predators. Hence, $G_i(R_i^*) \cong a_i P$ (the asterisk denotes the moving equilibrium), and thus

$$G_1(R_1^*)/a_1 = G_2(R_2^*)/a_2.$$

The density of prey 2 can be expressed as a function of the density of prey 1:

$$R_2^* = f(R_1^*) = G_2^{-1}(a_2G_1(R_1^*)/a_1),$$

because G_i decreases monotonically with R_i, $dR_2^*/dR_1^* > 0$. In the (R_1, R_2) plane, this moving equilibrium is represented by a curve with positive slope (Fig. 1c). The curve pictorially depicts the prey densities realized at various predator densities. This curve has a terminus at (K_1, K_2) when $P = 0$. If $r_1/a_1 > r_2/a_2$, prey 2 is (just) driven to local extinction when $P = r_2/a_2$. At this density of predators, prey 1 equilibrates at a density determined from $G_1(R_1^*) = a_1P = a_1(r_2/a_2)$. The prey equilibrium curve intersects the R_1-axis at this value of R_1^*; if $r_1/a_1 < r_2/a_2$, the curve intersects the R_2-axis instead.

In Fig. 2 I put these ingredients together to predict how the final equilibrial abundance of each prey is influenced by the presence of the alternative prey, given that the predator's isoleg has a negative slope (i.e., the predator benefits from an increase in the density of either prey). The predator and its prey are in demographic equilibrium in the patch when the prey equilibrium curve intersects the predator isoleg. In Fig. 2a, we compare the final densities achieved by each prey when alone, to their joint densities when together. It can be seen that each prey suffers a reduction in its equilibrial population size due to the presence of the alternative prey. The essential reason for this is that with two prey types present, rather than just one, more predators must enter the patch, or predators must stay longer, before foraging yield can be depressed to the threshold departure level. This increase in the number of predators or the length of their foraging bouts within a patch reduces the density of each prey below the density it exhibits when alone in the patch.

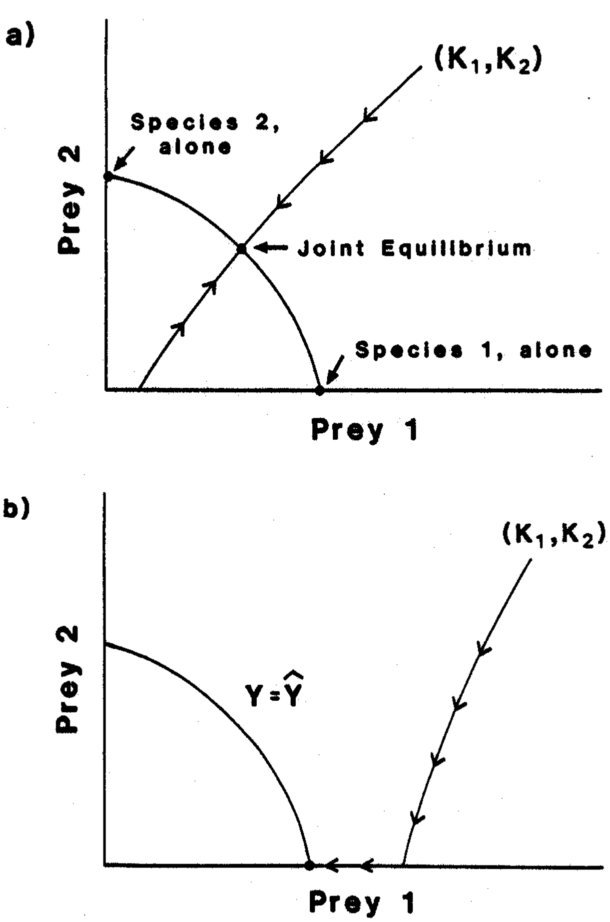

Fig. 2. Apparent competition due to an aggregative predator response. (a) The patch departure isoleg has a negative slope. The solid dots mark three possible equilibria: each prey alone, and together in a patch. At these states, neither predator densities nor prey densities are changing. Each prey species is depressed in abundance by the presence of an alternative prey. The arrows along the line with positive slope denote changes expected in prey densities as P changes; P increases to the right of the isoleg because predators enter the patch, and decreases to the left as predators leave the patch. (b) Exclusion due to within-patch apparent competition. Prey 1 attracts enough predators to the patch to exclude prey 2.

If prey grow logistically, i.e., $G_i = r_iR_i(1 - R_i/K_i)$, the equilibrium curve is a straight line intersecting the R_1-axis at $R_1 = K_1(1 - (r_2/a_2)/(r_1/a_1))$ (assuming that $r_1/a_1 > r_2/a_2$). If at this density of prey 1, $Y > \hat{Y}$, then prey 1 is able to attract enough predators to the patch to exclude prey 2; this alternative prey is less able to withstand predation than prey 1, either because of a lower intrinsic growth rate or a higher rate of mortality from predation. Prey 2 is more likely to be excluded from the patch at large values for K_1 and r_1. Hence, an increase in the productivity of prey 1 that increases either its intrinsic rate of increase or its carrying capacity will tend to reduce the equilibrial density of an alternative prey species, even to the point of local extinction. An example of such exclusion is shown in Fig. 2b.

Similar points were made in Holt (1977), with the difference that in the predator-prey systems considered there the predator population as a whole was assumed to be food-limited. The numerical response by the predator to each of its prey generated an indirect (−,−)

interaction between alternative prey. By contrast, in the present model the total population of predators may be rigidly limited by factors other than food availability. On a local, within-patch scale, however, alternative prey species may nevertheless experience a (−,−) interaction because of the tendency of predators to aggregate and stay longer in patches with a greater total density of prey.

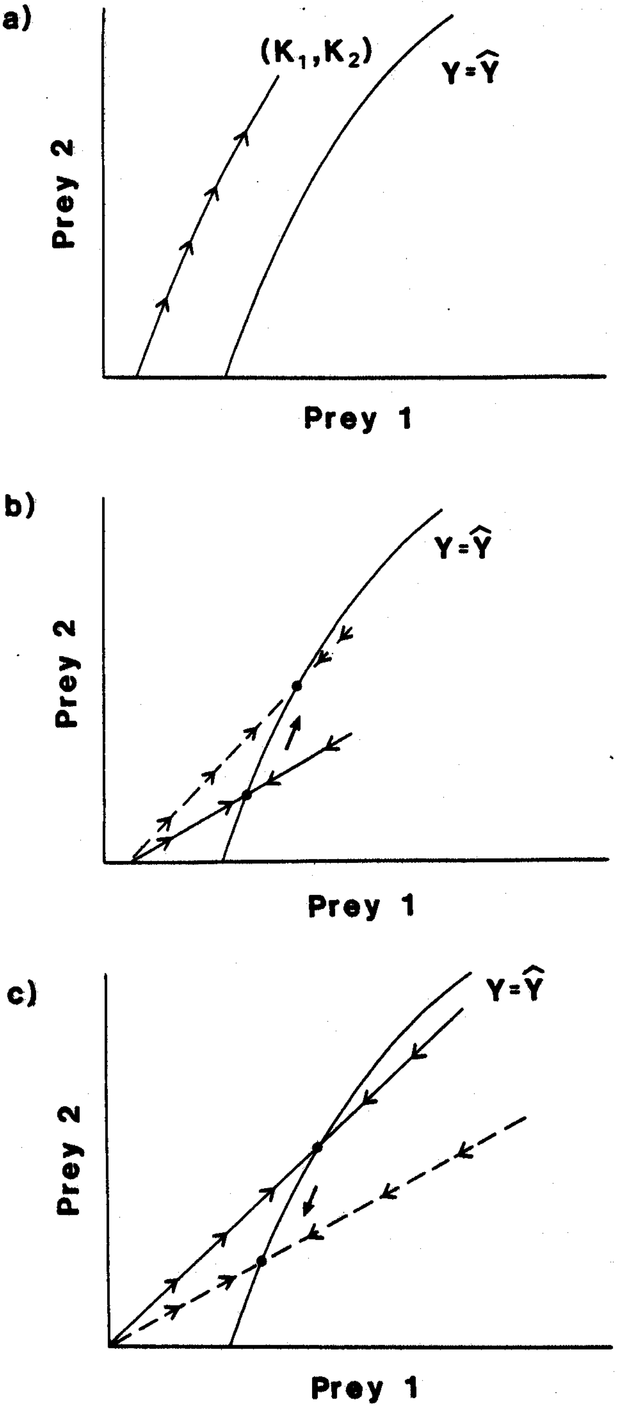

Fig. 3. Isolegs with positive slopes lead to a (+,−) interaction between alternative prey. (a) Prey 2 reduces patch quality below that required to attract predators to the patch (arrows denote changes in prey densities, tracking slow changes in P). (b) An increase in the carrying capacity of prey 2 increases equilibrial densities for both species. The prey equilibrium curve assumes that each prey follows a logistic growth law when alone. This implies that prey densities lie along a straight line. An increase in K_2 increases the slope of the equilibrium line. The solid dots denote equilibrial prey densities when predator numbers are stationary in a patch. The small arrows indicate how an increase in K_2 affects this equilibrium. (c) An increase in the carrying capacity of prey 1 decreases both prey species' densities. As in (3b), the prey grow logistically. An increase in K_1 decreases the slope of the line of prey densities.

These conclusons change when the predator isoleg has a positive slope, which is to say that the presence of one of the two prey types reduces overall foraging yields. In the cases shown in Fig. 3, prey 2 reduces the predator's foraging yield in the patch, and predators will entirely bypass the patch unless prey 1 is present and sufficiently abundant (Fig. 3a). The presence of the preferred prey tends to increase predation upon the less preferred prey. However, the preferred prey species benefits from the presence of a less preferred prey. An increase in the carrying capacity of prey 2 decreases patch quality and increases the equilibrial density of both prey species (Fig. 3b). By contrast, an increase in the carrying capacity of prey 1 decreases the equilibrial density of both species (Fig. 3c). In short, these alternative prey exhibit a (+,−) interaction (much like a model-mimic system).

This model suggests that prey which are similar in quality should tend to suffer reciprocal reductions in local density when they overlap in a patchy environment. Each prey species should thus be selected to avoid patches already occupied by the other prey species. This can lead to the evolution of habitat partitioning among prey species (Holt and Kotler, in press). By contrast, if alternative prey are highly dissimilar in quality (or in the tactics required to capture them), foraging on the low-quality prey may reduce the predator's capacity to capture or utilize the other prey enough to reduce overall foraging yield. If so, a high quality prey may benefit from occupying patches already inhabited by a low quality prey. However, the low quality prey species does not enjoy a corresponding advantage and in fact is disadvantaged by the presence of the high quality prey species. The scenario leading to a (+,−) interaction requires the predator to have a suboptimal diet within the patch; a priori, it seems likely that this will be less common than situations in which the predator benefits from both prey. (Departure rules other than the marginal value rule can lead to (+,+) interactions (Holt and Kotler, in press).)

Prey dynamics in a two-patch environment

I have been assuming that in choosing to enter or leave a particular patch, predators compare instantaneous rates of yield from foraging to a constant benchmark value that represents the average fruits of foraging over many patches. This assumption is inappropriate if predators are moving among only a few patches. I now turn to the question of how optimal predator foraging in a two-patch environment influences prey coexistence. Let Y_i be the rate of yield when a predator forages in patch i. If predators can move to whichever of the two patches provides the greater yield, without incurring travelling costs or interference from other predators, they should aggregate in the patch with higher yield. If predators at equilibrium are found in both patches, their numbers should be distributed such $Y_1 = Y_2$ (Fretwell 1972, Rosenzweig 1985, Holt 1985a).

Given this criterion for an optimal distribution of predators, we can examine its consequences for the interaction between co-occurring prey species. We consider in turn two limiting cases: (1) a food-limited predator, and (2) a predator fixed in population size at a constant level by factors other than food availability.

The first case was explored in Holt (1984). There it was shown that optimal habitat selection by predators has the effect of decoupling the prey communities found in different habitat patches. The densities of alternative prey species within any patch are reciprocally reduced by apparent competition, but the equilibrial abundances of prey in one patch are independent of the availability or productivity of prey in other patches, essentially because the number of predators found in any given patch is adjusted to reflect just the productivity of that patch.

When the predator population is fixed in size, it is no longer true that prey communities in different patches are independent. Yet alternative prey within a patch may still experience apparent competition. Here, I first characterize the equilibrial distribution of the predator population and a single prey population found in each of two patches and then examine how these distributions are modified by the introduction of a second prey species into one of the patches.

The variables of the system are P_i, the number of the predators found in patch i, and R_{ij}, the number of prey i in patch j. The total number of predators is fixed at $P_1 + P_2 = P$. We assume that each prey species experiences intraspecific density-dependence within, but not between, patches. As before, for simplicity we assume that the predator has a linear functional response to each prey type, and that components of predator fitness other than foraging success are equal in the two patches. The growth rate of prey i in patch j is

$$dR_{ij}/dt = R_{ij}\,(g_{ij}\,(R_{ij}) - a_{ij}\,P_i) = R_{ij}\,(F_{ij}),$$

where g_{ij} is the inherent per capita growth rate of prey i in patch j in the absence of predators, a_{ij} is the rate of attack upon prey i in patch j, and F_{ij} is a net per capita growth rate. The predator's rate of yield from foraging in patch j is

$$Y_j = a_{1j}\,b_1\,R_{1j} + a_{2j}\,b_2\,R_{2j},$$

where b_i is the value to the predator of each captured item of type i.

Our first task is to describe the equilibrial distribution of the predator and one prey species, say prey 1. The above growth equation for prey i assumes that there is no prey movement between patches. Hence, for the total prey population to be in demographic equilibrium, its growth rate in each patch must be equal to zero: $F_{11} = F_{12} = 0$. What if prey were free to move between the two patches? Habitat selection theory (Rosenzweig 1985) predicts that at the evolutionarily stable state (ESS, Maynard Smith 1982) for the population, fitnesses are equal across habitats. Hence, at the ESS, $F_{11} = F_{12}$. Moreover, if the total prey population is to be in demographic equilibrium, its average growth rate must equal zero:

$$R_{11}F_{11} + R_{12}F_{12} = 0.$$

Hence, once again, at equilibrium $F_{11} = F_{12} = 0$. For the predator population to be at its ESS, foraging yields (a proxy for fitness) must likewise be equal across habitats, so $a_{11}b_1R_{11} = a_{12}b_1R_{12}$, or $(a_{11}/a_{12})R_{11} = R_{12}$. Substituting into $F_{12} = F_{11} = 0$ leads to

$$g_{12}((a_{11}/a_{12})R^*_{11}) + (a_{12}/a_{11})g_{11}(R^*_{11}) = a_{12}P.$$

This can in principle be solved for R^*_{11}, which can then be substituted into $F_{11} = 0$ to find $P^*_1 = g_{11}(R^*_{11})/a_{11}$ and $P^*_2 = P - P^*_1$. (The asterisk denotes equilibrium). Because g_{ij} decreases monotonically with increasing R_{ij}, equilibrial prey density in both patches declines with increasing total predator numbers, as it should.

At equilibrium, the proportion of the prey population that is in habitat 1 is

$$R^*_{11}/(R^*_{11} + R^*_{12}) = a_{12}/(a_{11} + a_{12}) \equiv q.$$

The observed distribution of prey 1 thus reflects only its relative vulnerabilities to attack in the two patches and is independent of spatial variation in other growth parameters (e.g., r or K in a logistic model). Such variation instead leads to spatial variation in predator numbers. When $a_{12} = a_{11}$, $R^*_{11} = R^*_{12}$, and the fraction of the predator population in patch 1 is $g_{11}/(g_{11} + g_{12})$. Predator numbers tend to be biased toward the patch in which the prey population is most productive.

We now introduce a second prey, restricted to patch 2. The predator ESS requires $Y_1 = Y_2$, or

$$a_{11}b_1R_{11} = a_{12}b_1R_{12} + a_{22}b_2R_{22}.$$

The equilibrial proportion of prey 1 in habitat 1 is

$$a_{12}/(a_{12} + a_{11} - a_{22}b_2R^*_{22}/b_1R^*_{11}) > q \text{ (if } R^*_{22} > 0).$$

Thus, adding a second prey species to patch 2 reduces the equilibrial proportion of the population of prey 1 found in that patch. Were the second prey to be removed, the equilibrial proportion of the first prey's population in patch 2 would increase back to q. Hence, shared predation in a two-patch environment may lead to ecological compression and release for otherwise non-interacting, alternative prey species, even if the predator population as a whole does not show a numerical response to its prey. These effects should be observed both for relatively immobile prey (i.e., prey with low dispersal rates between patches) and for prey which can exhibit optimal habitat selection equalizing fitnesses across patches.

For the second prey to persist, it must be able to increase when rare. With just prey 1 present, the number of predators in patch 2 is $P_2^* = g_{12}(R_{12}^*)/a_{12}$. When prey 2 is rare and restricted to patch 2, its per capita rate of increase is $r_{22} - a_{22}P_2^*$. If this quantity is positive, prey 2 invades, increases in density, and enriches patch 2 relative to patch 1. Predators should then leave patch 1 and enter patch 2 until foraging yields are once again equal across patches. This relaxes predation on prey 1 in patch 1, but increases predation on individuals of prey 1 in patch 2. Thus, by attracting predators, the second prey has an indirect competitive effect on alternative prey with which it co-occurs, while simultaneously exerting an indirect mutualistic effect on alternative prey found in the other patch. The net effect on total prey numbers over both patches combined of adding a second prey may be either to reduce or to increase the population of the original prey (Holt, unpubl.). The basic conclusion from these models is that in most circumstances, predators which utilize patches so as to maximize foraging rates impose (−,−) interactions upon alternative prey within a patch. If each prey type is relatively superior at withstanding predation in a patch, this apparent competition may select for habitat or patch partitioning between the prey species.

Competition for refuges

In the models presented above, prey within a single patch enjoy a kind of refuge because of optimal foraging behavior by predators: if the number of prey in one patch is too low relative to other patches, predators will switch their attention elsewhere. This density-dependent response by predators might make it advantageous for some prey individuals in a patch to reduce their risk of mortality by excluding other prey, thereby making the patch unprofitable for predator foraging. In other words, predation may generate a kind of direct competition among prey for occupancy of refuges from predation. Moreover, as will be shown below, any model which assumes that a constant number of prey individuals can escape predation in spatial refuges generates a kind of direct competition for space among prey.

In this section I develop a series of interrelated models which explore the consequences of such competition for refuges. To see how the structure of these models links in a natural way to the models of predator foraging in a patchy environment considered above, consider again a single prey species in one patch within a system of many patches. Let the threshold density of prey at which predators leave the patch be $\hat{R}$ (corresponding to $\hat{Y}$). If $R_1 < \hat{R}$, then no prey is attacked; if $R_1 > \hat{R}$, all prey are attacked at the rate a_1P. In predator-prey models that incorporate constant-number absolute refuges from predation (see, e.g., Murdoch and Oaten 1975, McNair 1986), the relation between prey density and predator attack is as follows: if $R_1 < \hat{R}$, no prey is attacked; if $R_1 > \hat{R}$, the excess of prey outside the refuge, $R_1 - \hat{R}$, is exposed to attack. The "refuge" implicit in the models of predator foraging in a patchy environment presented above is all-or-nothing, for when predators are present all prey are vulnerable to attack; with absolute refuges, by contrast, the prey population is internally heterogeneous, with some prey individuals enjoying immunity from attack even at high total prey densities. Incorporating absolute refuges in this manner in effect introduces an element of direct competition between prey into predator-prey systems. This point can be illustrated with the following simple model. Let the prey population grow exponentially at rate r_1 without predation, and let prey outside the refuge incur an additional constant rate of mortality m_1. If the mortality outside the refuge comes from predation, assuming that mortality is constant implies that the predator shows a linear total response (numerical × functional response) to an increased availability of its prey (e.g., constant attack rate without a numerical response). This assumption will be relaxed below. The model is

$$\frac{dR_1}{dt} = r_1R_1, \text{ if } R_1 \leqq \hat{R};$$

$$\frac{dR_1}{dt} = r_1R_1 - (R_1 - \hat{R})m_1, \text{ if } R_1 > \hat{R}. \tag{A1}$$

The prey population equilibrates at a size

$$R_1^* = \hat{R}\left(\frac{m_1}{m_1 - r_1}\right) \equiv K_1,$$

given that $m_1 > r_1$. But this condition implies that the population would be driven to extinction were it not for the refuge. The population can be stationary in size because it is divided into two sub-populations: one part is inside the refuge growing at rate r_1, the other part is outside the refuge, declining at a rate $r_1 - m_1$, but persisting because of continual replenishment from the refuge.

This model implicitly incorporates intraspecific competition for access to the refuge, as can be seen from the form of the per capita growth rate for $R_1 > \hat{R}$:

$$\frac{1}{R_1}\frac{dR_1}{dt} = (r_1 - m_1) + \frac{\hat{R}m_1}{R_1} \tag{A2}$$

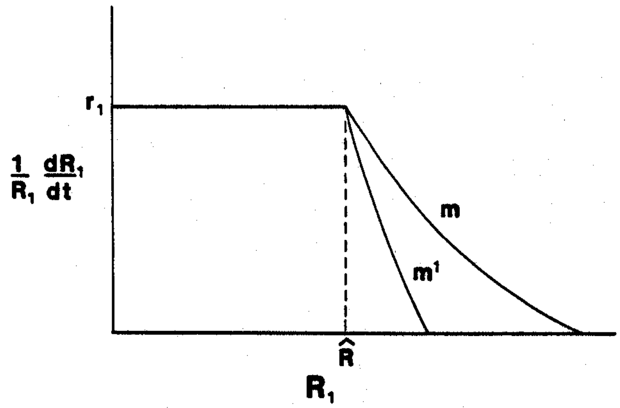

Fig. 4. Intraspecific density-dependence in a refuge model. There is a threshold change from exponential growth to negative density-dependence when population size exceeds the refuge size $\hat{R}$ (the figure assumes that $m' > m > r$).

This describes a hyperbolic growth model (see Fig. 4).

If there exists intraspecific competition over access to a refuge, we might also expect similar prey species to compete for refuges. The above model can be generalized in a natural way to two prey types as follows. If prey species 1 is alone, a randomly chosen individual is expected to be in the refuge with probability $\hat{R}/R_1$ when $R_1 > \hat{R}$. If the two prey species have equal competitive abilities, and there are R_2 individuals of species 2, the probability of occupation of the refuge by an individual of species 1 should be reduced to $\hat{R}/(R_1 + R_2)$, given that $R_1 + R_2 > \hat{R}$. The simplest way to incorporate unequal competitive abilities between species is to assume that the *relative* probability for an individual of one species to be in the refuge is constant, relative to an individual of another species, if the total number of prey individuals exceeds the size of the refuge. This occurs if the fraction of the population of prey 1 in the refuge is $\hat{R}/(R_1 + \beta R_2)$, and the fraction of the population of prey 2 found in the refuge is $\beta\hat{R}/(R_1 + \beta R_2)$. If N_i is the number of prey i found in the refuge, then

$$\frac{N_2}{N_1} = \beta \left(\frac{R_2}{R_1}\right) .$$

The parameter β measures the ability of species 2 to compete for access to the refuge, relative to species 1.

The two-species generalization of model (A2) is

$$\frac{1}{R_1}\frac{dR_1}{dt} = (r_1 - m_1) + \frac{\hat{R}m_1}{R_1 + \beta R_2}, \qquad (A3)$$

$$\frac{1}{R_2}\frac{dR_2}{dt} = (r_2 - m_2) + \frac{\beta\hat{R}m_2}{R_1 + \beta R_2}. \qquad (A4)$$

In this model, which can be interpreted as a case of competition for a single resource (see below), coexistence is impossible. Setting each equation equal to zero, one finds that there is no non-trivial solution of the above model with both species present, except in the unlikely event that $K_1 = \beta K_2$ (where $K_i = \hat{R}m_i/(m_i - r_i)$). At equilibrium, this model leads to parallel linear isoclines. If species 1 is present at equilibrium and species 2 invades, the initial growth rate of species 2 is $r_2 - m_2 + \hat{R}m_2/K_1$. After substitution, we find that species 2 is excluded if

$$\beta < \frac{K_1}{K_2}$$

This inequality also ensures that species 1 can invade when species 2 is resident at its equilibrium density. If the inequality is reversed, species 1 is excluded by species 2.

Direct competitive dominance is not sufficient to win the interaction. Even if $\beta > 1$ (i.e., individuals of species 2 are relatively dominant), species 1 may win if it has the higher value of r_i/m_i, which measures its ability to withstand predation outside the refuge. Hence, a prey species may emerge triumphant in competition for refuges because of its superiority in directly contending for the refuge, or its higher intrinsic growth rate, or its better ability at excluding the predator outside the refuge.

When prey densities are high enough to fill the refuge, this model of competition for refuges is structurally identical to Schoener's (1973, 1974, 1975, 1976) models for exploitative competition. He explicitly derives his population models from models of individual feeding; competition occurs because a fixed quantity of energy is partitioned among the members of one of more energy-limited populations. In Schoener's models, an amount $\hat{I}_1$ of energy is available for competition, is entirely consumed by the population(s), and instantly renews. Since the resource is divided equitably among the N_1 individuals within consumer population 1 when it is alone, the per capita growth rate scales like $\hat{I}_1/N_1 - C_1$, where C_1 denotes the density-independent maintenance and replacement costs for an individual of species 1. If there is a second consumer population present subsisting on the same resource base, whose relative propensity at grabbing the resource is measured by β', the growth equation for species 1 will have the form

$$\frac{1}{N_1}\frac{dN_1}{dt} = Q\left(\frac{\hat{I}}{N_1 + \beta' N_2} - C_1\right) . \qquad (A5)$$

where Q converts energy into numbers (Schoener uses the symbol R_1 instead of Q). Eq. (A5) is structurally identical to (A3) when $R_1 > \hat{R}$. As noted in Schoener (1973, 1975), hyperbolic (concave) growth curves are commonly observed in laboratory population growth experiments. This model for exploitative competition provides a simple mechanistic interpretation of such phenomena. Schoener's interpretation of competitive coexistence and exclusive is cast entirely in terms of resource overlap, relative efficiencies of resource use, and direct interference between competing consumers. The above models for absolute refuges from mortality start from a very different mechanistic assumption – that what is important in population regulation is to escape mortality factors, as in (A1) – and arrive at equations whose structure is the same as Schoener's models for exploitative competition. The reason is that in both situations, individuals in a population are conceived to divide a constant amount of something, be it refuges or food, among themselves.

There are two differences between the classes of models worth pointing out. First, their parameters can be related as follows (comparing Eq. (A3) with (A5)): $\hat{I} <=> \hat{R}m_i$, and $C_i <=> m_i - r_i$. The two independent input and output parameters of model (A5) are intrinsically coupled in the refuge competition model. The "input" term $\hat{R}m_i$ is the number of deaths that did *not* occur in population i because the $\hat{R}$ individuals in the refuge were not subject to the mortality factor acting at rate m_i. Secondly, in model (A5) the per capita growth rate uniformly decreases in a hyperbolic fashion at all population densities and is unbounded as $N_i \rightarrow 0$ (this assumption is modified in Schoener 1978); in the refuge model there is a sharp transition at $R_i = \hat{R}$ between exponential growth and damped population growth.

Once we have made this identification between the two systems it is straightforward to construct analogues of Schoener's models in which there is a mixture of exploitative and interference competition for prey populations experiencing competition over refuges. I here briefly outline several such models. Models 1, 2, and 3 correspond to models analyzed by Schoener; models 4 and 5 are new, although one can readily devise parallel equations for exploitative competition.

MODEL 1: Exclusive and overlapping refuges

Prey species may overlap only partially in the refuges they can exploit. When species i is rare, let us assume it preferentially occupies and exclusive refuge ($\hat{R}_i$), with the excess $R'_i = R_i - \hat{R}$ competing with the other species for access to the shared refuge $\hat{O}$. Interspecific competition for the shared refuge is described by (A3) and (A4). The growth equation for prey 1 is

$$\frac{dR_1}{dt} = r_1\hat{R}_1 + R'_1 m_1 \frac{\hat{O}}{R'_1 + \beta R'_2} + R'_1 (r_1 - m_1),$$

$$(R_i > \hat{R}_i, i = 1{,}2),$$

with an analogous equation for prey 2.

Interspecific competition occurs among those individuals outside the exclusive refuges over access to the shared refuge. For a single species, the model reduces to (A1) with $\hat{R} = \hat{R}_1 + \hat{O}$; without exclusive refuges, the model reduces to (A3) and (A4). It is clear that coexistence is assured if each species has an exclusive refuge. It is straightforward to show that at high mortality levels, the species subordinate in direct competition for the refuge (e.g., species 1 if $\beta < 1$) is restricted to its exclusive refuge. If species 2 is dominant in direct competition for the shared refuge, but has no exclusive refuge, it can be excluded by species 1 if

$$m_2\hat{O}\beta/(m_2-r_2) < \hat{R}'_1, \text{ where } \hat{R}'_1 = (r_1\hat{R}_1+m_1\hat{O})/(m_1-r_1).$$

Possession of an exclusive refuge may thus permit an intrinsically weaker competitor for a shared refuge to oust the other species, reversing the outcome of competition for refuges.

MODEL 2: Lotka-Volterra competition with exclusive refuges from mortality

A number of authors (Abrams 1977, Yodzis 1978, Holt 1985b) have discussed the effect of constant rates of density-independent mortality on coexistence in the Lotka-Volterra competition model. When two species have the same intrinsic growth rate r_i, and density-independent mortality hits them uniformly, changes in the level of mortality do not alter the conditions for coexistence (i.e., $K_i > \alpha_{ij}K_j$, $i,j = 1{,}2$, $1 \neq j$). What is the effect of intraspecific and interspecific competition for refuges from mortality on coexistence in this model? As a partial answer to this question, let each species have its own exclusive refuge. The growth equation for species 1 is

$$\frac{1}{R_1}\frac{dR_1}{dt} = r_1 (1 - \frac{1}{K_1} - \frac{\alpha_{12}}{K_1} R_2) - m_1 + \frac{\hat{R}_1 m_1}{R_1}, \; R_1 > \hat{R},$$

$$\frac{1}{R_1}\frac{dR_1}{dt} = r_1 (1 - \frac{R_1}{K_1} - \frac{\alpha_{12}}{K_1} R_2), \; R_1 \leqq \hat{R},$$

and similarly for species 2. In the absence of species 2, $R^*_1 = K_1$ if $\hat{R}_1 \geqq K_1$, and

$$R^*_1 = \frac{K_1}{2}\left[\left(1 - \frac{m_1}{r_1}\right) + \left(\left(1 - \frac{m_1}{r_1}\right)^2 + \right.\right.$$
$$\left.\left. + 4 \left(\frac{\hat{R}_1}{K_1}\frac{m_1}{r_1}\right)\right)^{1/2}\right]$$

if $\hat{R}_1 < K_1$. Species 2 may invade if $K_2 > \alpha_{21}R^*_1$, which is less stringent than the condition for invasion in the absence of the mortality factor, ($K_2 > \alpha_{21}K_1 \geqq \alpha_{21}R^*_1$).

As we uniformly increase the severity of the mortality factor, R_i^* approaches $\hat{R}_i$. The maximum relaxation of the competitive constraints on coexistence is reached at $K_2 > \alpha_{21}\hat{R}_1$, $K_1 > \alpha_{12}\hat{R}_2$. For a given m, the equilibrial prey population size increases with $\hat{R}_i$. Consequently, we will see a greater relaxation of competitive constraints with increasing mortality if exclusive refuges are scarce relative to the carrying capacities of the species, than if refuges are common. Were we to measure the intensity of predation, we might observe increasing niche overlap along axes other than those responsible for the division of refuges as the intensity of predation increases.

MODEL 3: Completely overlapping refuges, intraspecific interference

If each prey interacts aggressively within its own species such that per capita growth rates decline linearly with R_i even in the absence of predation, two prey can overlap completely in the refuges they utilize yet still coexist. Adding a term for direct interference to (A2) and (A4) leads to the following model:

$$\frac{1}{R_1}\frac{dR_1}{dt} = \frac{\hat{R}m_1}{R_1 + \beta R_2} - \hat{\imath}_1 R_1 + (r_1 - m_1)$$

and (B1)

$$\frac{1}{R_2}\frac{dR_2}{dt} = \frac{\beta\hat{R}m_2}{R_1 + \beta R_2} - \hat{\imath}_2 R_2 + (r_2 - m_2)$$

The parameter $\hat{\imath}_i$ measures the severity of intraspecific interference. For simplicity, consider the case where $r_1 = r_2 \equiv r$, $m_1 = m_2 \equiv m$, $\hat{\imath}_1 = \hat{\imath} \equiv i$, and $\beta < 1$. Without the interference term, species 1 excludes species 2. With interference and in the absence of species 2,

$$R_1^* = \frac{r - m}{2\hat{\imath}} + \left[\left(\frac{r - m}{2\hat{\imath}}\right)^2 + \frac{\hat{R}m^{1/2}}{\hat{\imath}}\right].$$

Species 1 can always invade. Species 2 invades if

$$(r - m) + \frac{\beta\hat{R}m}{R_1^*} > 0, \text{ or } \frac{r}{m} > 1 - \frac{\beta\hat{R}}{R_1^*}.$$

R_1^* monotonically decreases with increasing $\hat{\imath}$. This implies that the two species can coexist if self-interference in species 1 is great enough. Manipulating this expression shows that an increase in the availability of the refuge ($\hat{R}$) or the intrinsic rate of growth (r) makes invasion more likely; an increase in m decreases the chances of coexistence and restricts the range in β compatible with coexistence.

MODEL 4: Completely overlapping resources and refuges

Two similar species that contend for refuges may also at the same time compete for other resources. In certain systems competition may be represented best by models like the Lotka-Volterra (for example, if resources grow according to the logistic equation and consumers have a linear functional response (MacArthur 1970)). In others, such as consumer-detritus systems, Schoener's model (A5) is more appropriate. We now ask whether two competitors which completely share *both* refuges and food resources can coexist. In (A3) and (A4) we replace r_i by the energetic input term of (A5). With uniform mortality, the per capita rates of growth of the two prey species are described by

$$\frac{1}{R_1}\frac{dR_1}{dt} = \frac{I}{R_1 + \beta' R_2} + \frac{\hat{R}m}{R_1 + \beta R_2} - m,$$

(B2)

$$\frac{1}{R_2}\frac{dR_2}{dt} = \frac{\beta' I}{R_1 + \beta' R_2} + \frac{\beta\hat{R}m}{R_1 + \beta R_2} - m.$$

These equations assume that the joint densities are high enough both to completely fill the refuge, and to allow consumer satiation on the resource to be ignored. Each prey when alone achieves the equilibrial density $R^* = I/m + \hat{R}$. Each species can increase when rare provided

$$\frac{1}{\beta'}\frac{I}{m} + \frac{1}{\beta}\hat{R} > \frac{I}{m} + \hat{R} \qquad \text{(species 1)}$$

and (B3)

$$\beta'\frac{I}{m} + \beta\hat{R} > \frac{I}{m} + \hat{R} \qquad \text{(species 2).}$$

A necessary condition for these two inequalities to be jointly satisfied is that either $\beta' > 1$ and $\beta < 1$, or $\beta < 1$ and $\beta' > 1$: one species must be better at contending for the shared resource, the other at acquiring access to the refuge. Moreover, coexistence is more likely if both refuges and resources are roughly equal in importance. As $m \rightarrow \infty$, the inequalities (B3) approach $1/\beta > 1$ and $\beta > 1$, i.e. dominance in the refuge becomes all-important. Similarly, as I increases, competition for resources predominates; as $\hat{R}$ increases, competition for refuges determines which species persists. This appears slightly counter-intuitive, since it says that competition for the resource with the more rapid renewal rate determines the outcome of competition. This result depends upon the assumption of continuous population growth in (B2), which combines the effects of resources (via births) and refuges (via deaths forgone) additively to give the net population growth. Had we used a difference equation model of population growth, one that incorporated competition for food resources during one season, and competition to hide from mortality factors during another, the requisite with the slowest renewal rate could have been found to be most critical in determining overall competitive success.

MODEL 5: Completely overlapping refuges, food-limited predator

So far, we have considered the outcome of competition for refuges only in environments where the intensity of predation (m_i) on individuals outside refuges is determined independently of the number of exposed prey. If the predator has a non-linear total response to its prey (a numerical response or a non-linear functional response), the intensity of predation should be a dependent variable in the system. The consequences of competition for refuges then becomes considerably more complex. The expected decrease in the per capita growth rate of a prey population caused by predation is given by the probability that an individual will be exposed to predation – an increasing function of prey density – times the rate of mortality, given that the individual is outside the refuge – an increasing function of predator density. But predator density, in turn, should depend on the cumulative number of prey individuals that have become available for consumption outside refuges. The net effect of one prey species upon another thus depends upon the joint effect of direct competition for shared refuges, and apparent competition due to shared predation. A simple model for analyzing this mixture of direct and indirect competitive interactions is for each prey to grow independently according to a logistic equation in the absence of predation, to compete for a refuge in accord with Eqs (A3) and (A4), and to be fed on by a predator whose rate of growth increases linearly with the density of prey outside refuges. This model is:

$$\frac{1}{R_1}\frac{dR_1}{dt} = r_1\left(1-\frac{R_1}{K_1}\right) 1- a_1P\left(1-\frac{\hat{R}}{R_1+\beta R_2}\right)$$

$$\frac{1}{R_2}\frac{dR_2}{dt} = r_2\left(1-\frac{R_2}{K_2}\right) 1- a_2P\left(1-\frac{\beta\hat{R}}{R_1+\beta R_2}\right)$$

$$\tag{B4}$$

$$\frac{1}{P}\frac{dP}{dt} = b_1a_1\left(1-\frac{\hat{R}}{R_1+\beta R_2}\right)R_1 + b_2a_2\left(1-\frac{\beta\hat{R}}{R_1+\beta R_2}\right)R_2 - C$$

We assume that the total prey density is high enough to fill the refuge.

This model is related to the models discussed above as follows. If P is fixed, the model reduces to (B1) above, with $a_iP = m_i$. The logistic term represents intraspecific density-dependence (e.g., interference), which, as we have seen, tends to promote prey species coexistence. However, because the maintenance of the predator population depends upon the availability of prey outside the refuge, the predator is vulnerable to extinction at low prey carrying capacities. The condition for predator persistence is found by substituting $K_i = R_i$ into the above equation for (dP/dt)/P. I assume that this expression is positive, thus ensuring that the predator can increase when rare and the prey are at their respective carrying capacities. Predator persistence is ensured if the K_i are sufficiently large. I will further assume that each prey can support the predator when alone.

In the model with fixed mortality rates and no intraspecific interference presented above, prey coexistence was shown to be impossible. Therefore, it is of particular interest to examine the effect of variable mortality rates (induced by the predator's numerical response) in the limit $K_i \to \infty$. The two prey species will coexist if each can increase when rare. Let P_i^* denote the predator's equilibrial density when only prey i is present. If prey species j ≠ i is absent, the predator and prey i equilibrate at the following stable point equilibrium:

$$R_i^* = \hat{R} + \frac{C}{a_ib_i},\ P_i^* = \frac{r_i}{a_i}\left(\frac{\hat{R} + C/a_ib_i}{C/a_ib_i}\right)\left(1-\frac{C/a_ib_i}{K_i}\right)$$

Several authors have noted that in the one-prey one-predator version of (B4), where $K_1 \to \infty$, absolute refuges always stabilize the predator-prey interaction (Murdoch and Oaten 1975, Maynard Smith 1974). Allowing K_i to be finite just enhances local stability. Prey species 2 will increase when rare provided

$$r_2 - a_2P_1^*\left(1-\frac{\beta\hat{R}}{R_1^*}\right) > 0,$$

and species 1 will increase when rare if

$$r_1 - a_1P_2^*\left(1-\frac{\hat{R}}{\beta R_2^*}\right) > 0.$$

Looking at the latter expression, we see that prey 2 when resident reduces the growth rate of invading prey 1 in two distinct ways: by forcing a fraction $(1 - \hat{R}/\beta R_1^*)$ of prey 1 to reside outside the refuge (i.e., direct competition), and through supporting a density P_2^* of the predator outside the refuge which can attack these exposed individuals of prey 1 (i.e., apparent competition). An increase in the productivity of prey 2 (through an increase in either r_2 or K_2), through its effect on P_2^* makes invasion by prey 1 more difficult. It is convenient to define the following quantities:

$f_i \equiv \dfrac{R_i^* - \hat{R}}{R_i^*}$ = the fraction of population i found outside the refuge, when alone and at equilibrium;

$A_1 \equiv 1 - \dfrac{\hat{R}}{\beta R_2^*}$

$A_2 \equiv 1 - \dfrac{\beta \hat{R}}{R_1^*}$ = the fraction of population i found outside the refuge when rare, and the other prey is at equilibrium;

$\Delta_i \equiv \left(1 - \dfrac{R_i^*}{K_i}\right)$ = the fractional reduction of prey i below its carrying capacity K_i.

The conditions for coexistence are:

$$\text{(2 invades)} \Leftrightarrow \frac{f_1}{A_2\Delta_1} > \frac{r_1/a_1}{r_2/a_2} > \frac{A_1\Delta_2}{f_2} \Leftrightarrow \text{(1 invades)} \tag{B5}$$

This expression can be manipulated to examine coexistence and exclusion for several interesting special cases:

12) *No refuges:* $A_i = 1$ and $f_i = 1$. B5 reduces to the condition for coexistence between two prey species discussed in Holt (1977, 1984). Prey coexistence requires sufficiently strong negative density-dependence in the prey with higher r_i/a_i. In the limit $K_i \rightarrow \infty$, the prey species with higher r_i/a_i (which in the limit is the number of predators that can be sustained by this prey) can exclude the alternative prey.

2) *Equal competitive abilities:* $\hat{R} > 0$, but $\beta = 1$. The refuge is divided equitably between the two prey. $A_i/f_i = 1$, and B5 becomes identical to the condition for coexistence in the absence of refuges. The availability of refuges thus affects coexistence under apparent competition only if one prey is superior at seizing the refuge, i.e. $\beta \neq 1$.

3) *Fine-grained predation upon available prey,* $K_i \rightarrow \infty$: Let $a_1 = a_2 \equiv a$, $b_1 = b_2$, and $K_1 = K_2 \rightarrow \infty$. With such even-handed predation, $f_1 = f_2 \equiv f$. With these symmetry assumptions, f is the fraction of the total number of prey outside the refuge when the system is at equilibrium. It is thus a measure of the intensity of predation outside the refuge; at low f, most prey are restricted to the refuge. The two prey would grow exponentially were the predator to be removed from the system. The two prey coexist if

$$\frac{f}{1 - \beta(1 - f)} > \frac{r_1}{r_2} > \frac{1 - (1 - f)/\beta}{f} \tag{B6}$$

If $\beta = 1$, coexistence is impossible for $r_1 \neq r_2$; the prey with higher r_i dominates. By convention, we let prey 1 be dominant in competing for the refuge ($0 \leq \beta < 1$).

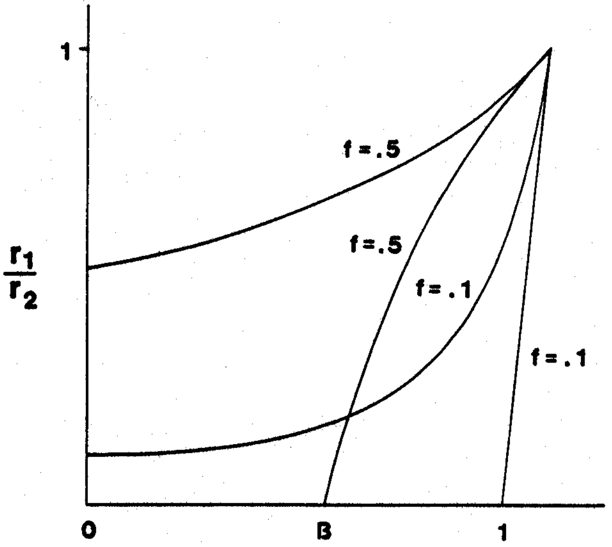

Fig. 5. Parameter combinations permitting coexistence in the model of competition for a single refuge with a food-limited predator. The quantity f is a measure of the intensity of predation; low f corresponds to few prey outside the refuge. The quantity β is a measure of the competitive ability of prey species 2, relative to prey 1. Each pair of lines marked by equal f-values demarcates a zone of parameter space allowing mutual invasibility.

As $f \rightarrow 1$, the two sides of (B6) converge on unity, and it becomes more difficult for prey with unequal r_i to coexist. A sufficient condition for prey 1 to invade is $\beta + f < 1$. If prey 2 is to increase when rare, it is necessary that $r_2 > r_1$, and sufficient that $r_2 > r_1/f$. Hence, for any given intensity of predation (measured by f), we can find a range of the parameters r_1, r_2, and β allowing prey coexistence. Fig. 5 illustrates how the parameter region allowing prey species coexistence varies with f. Coexistence occurs only if the competitive dominant has the lower intrinsic growth rate. Moreover, coexistence is easier to achieve if there is a strong trade-off between competitive ability (β) and intrinsic growth rate (r_i) (the region near the origin in Fig. 5).

In the absence of refuges and with uniform rates of predation the prey species with the higher r_i would exclude the alternative prey in the limit $K_i \rightarrow \infty$. In the model (A3, A4) of competition for refuges in the face of fixed levels of density-independent mortality, I showed that coexistence was impossible. I have now demonstrated that with a structurally similar model, by letting the mortality term vary in accordance with prey abundance because of the predator's numerical response, coexistence *is* possible. The reason is essentially that the simultaneous operation of direct competition (over refuges) and apparent competition (through the predator's numerical response) provides two limiting factors instead of just one. A prey species with low r will support few predators, which allows another prey with higher r to invade. If the low r prey is dominant in competing for available refuges, it can invade regardless of the number of predators sustained by the prey with higher r. Thus, coexistence is possible if the prey that can support the higher density of predators is subordinate in direct competition for the refuge.

Discussion

Recent years have seen an explosion of theory and experimentation concerned with understanding foraging behavior by consumers (see review in Pyke 1984) and escape behavior by prey (e.g., Sih 1979, Abrams 1986). That branch of behavioral ecology known as optimal foraging theory is designed to predict the influence of natural selection on feeding behaviors, given certain assumption about the relation between foraging rates and fitness, on the one hand, and constraints on phenotypic variation, on the other (Pyke 1984). Some authors have begun to develop the elements of a parallel optimal escape theory, although this line of research has not yet proliferated to match the current extent of optimal foraging theory.

If optimal foraging models adequately predict the behavior of predators, and optimal escape models the behavior of prey, such models can be used to build more realistic models of predator-prey population dynamics and, more broadly, the structure of interactions in food webs. Because the effectiveness of predator foraging strategies and prey escape strategies are interdependent, such population dynamic models may eventually need to incorporate game theoretic reasoning (Parker 1985). Hassell and May (1985) and Schoener (1986) survey recent work linking models of individual predator behavior to population dynamics and stress the dependence of models of population dynamics and community structure on assumptions made about individual behavior.

In this paper, I have used some simple ideas from behavioral ecology to generate predictions about how prey species may interact in a heterogenous environment. I have argued that mobile predators foraging on immobile prey tend to impose $(-,-)$ interactions on prey species found within a patch (with some exceptions, see above and Holt and Kotler, in press). The models presented here suggest that the expected $(-,-)$ interaction between alternative prey species within a patch may be observed whether predators are drawn from numerous patches, or shuttle between just two patches. This indirect interaction arises because generalist predators should respond to spatial variation in the total availability of suitable prey, rather than to variation in each prey species separately. All else being equal, this should promote the global coexistence of those prey species which utilize different patches in a variegated environment. This result is buttressed by the work of Hanski (1981) and Comins and Hassell (1987), who show in more detailed models that predator aggregation enhances the likelihood of coexistence for competing prey in a patchy environment, when the two prey are not tightly correlated in their spatial distribution. By contrast, non-aggregative predators which forage randomly across patches can be de-stabilizing.

Mobile prey should seek refuges from predation. I have argued that if refuges can be "filled up", predation can lead to a kind of competition as prey scramble to occupy the refuge or interfere with other prey to prevent them from entering. There has been considerable debate over the relative importance of competition and predation in natural communities (e.g., Connell 1975, Sih et al. 1985; see Lubchenco 1986 for a nice example of how to disentangle the effects of predation and competition). However, any attempt to separate the effects of competition and predation may be confounded by the existence of competitive interactions that exist solely because of predation, such as competition for refuges. The models of this phenomenon presented above point to several conclusions which are likely to hold in a broader class of models. First, if one prey species persists at a stable equilibrium only because of the existence of a refuge from a constant high level of predation (e.g., due to a general predator supported by alternative foodstuffs), it cannot coexist with a second prey species similarly dependent for its persistence on the same refuge. Coexistence may be allowed by any of several mechanisms: (1) each prey species may have an exclusive refuge from predation; (2) the dominant competitor for access to the refuge may experience strong intraspecific competition; (3) competition for resources may occur at the same time as competition for refuges, and the prey species that is better able to exploit the resource is less effective in competing for the refuge. Second, if the predator is itself limited by prey availability, coexistence may occur because the prey that is superior in apparent competition (mediated through a numerical response by the predator population) is inferior at directly competing for the refuge. The models presented here suggest that future work on the effects of predation on prey communities should pay close attention to predator movement strategies, the pattern of availability of species-specific refuges for prey, and the possible occurrence of direct competition among prey for access to refuges. These models highlight the potential importance of spatial heterogeneity and patchiness for maintaining the species richness of prey communities.

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References

Abrams, P. A. 1977. Density-independent mortality and interspecific competition: a test of Pianka's niche-overlap hypthesis. – Am. Nat. 111: 539–552.

– 1982. Functional responses of optimal foragers. – Am. Nat. 120: 382–390.

– 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. – Evolution 40: 1229–1247.

Armstrong, R. A. 1979. Prey species replacement along or gradient of nutrient enrichment: a graphical approach. – Ecology 60: 76–84.

Caswell, H. 1978. Predator-mediated coexistence: a nonequilibrium model. – Am. Nat. 112: 127–154.

Charnov, E. L. 1976. Optimal foraging; the marginal value theorem. – Theor. Popul. Biol. 9: 124–136.

Comins, H. N. and Hassell, M. P. 1976. Predation in multi-prey communities. – J. Theoret. Biol. 62: 93–114.

– and Hassell, M. P. 1987. The dynamics of predation and competition in patchy environments. – Theor. Pop. Biol. 31: 393–421.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities. – In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Harvard Univ. Press, Cambridge, MA, pp. 460–490.

Cramer, N. F. and May, R. M. 1972. Interspecific competition, predation, and species diversity: a comment. – J. Theor. Biol. 34: 289–293.

Crowley, P. H. 1981. Dispersal and the stability of predator-prey interactions. – Am. Nat. 118: 673–701.

Fretwell, S. D. 1972. Populations in a seasonal environment. – Princeton Univ. Press, Princeton, NJ.

Fuji, R. 1977. Complexity-stability relationship of two-prey-one-predator species system model: local and global stability. – J. Theor. Biol. 69: 613–623.

Hanski, I. 1981. Coexistence of competitors in patchy environment with and without predation. – Oikos 37: 306–312.

Hassell, M. P. and May, R. M. 1974. Aggregation in predators and insect parasites and its effect on stability. – J. Anim. Ecol. 43: 567–594.

– and May, R. M. 1985. From individual behaviour to population dynamics. – In: Sibly, R. M. and Smith, R. H. (eds), Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell, Oxford, pp. 3–32.

Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. – Theor. Popul. Biol. 12: 37–48.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – Theor. Pop. Biol. 12: 197–229.

– 1983. Optimal foraging and the form of the predator isocline. – Am. Nat. 122: 521–541.

– 1984. Spatial heterogeneity, indirect interactions and the coexistence of prey species. – Am. Nat. 124: 377–406.

– 1985a. Population dynamics in two-patch environments: Some anomalous consequence of an optimal habitat distribution. – Theor. Popul. Biol. 28: 181–208.

– 1985b. Density-independent mortality, non-linear competitive interactions, and species coexistence. – J. Theor. Biol. 116: 479–494.

– and Kotler, B. In press. Short-term apparent competition. – Am. Nat.

Jeffries, M. J. and Lawton, J. H. 1984. Enemy free space and the structure of ecological communities. – Biol. J. Linn. Soc. 23: 269–286.

Lawton, J. H. 1986. – In: Waage, J. and Greathead, D. (eds), The effect of parasitoids on phytophagous insect communities. 13th R. Ent. Soc. London Symp. Insect parasitoids, Academic Press, London, pp. 265–287.

Levin, S. A. 1981. Mechanisms for the generation and maintenance of diversity in ecological communities. – In: Hiorns, R. W. and Cooke, D. (eds), The mathematical theory of the dynamics of biological populations. II. Academic Press, London, pp. 173–194.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive abilities. – Am. Nat. 112: 23–39.

– 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 537–555.

MacArthur, R. H. 1970. Species packing and competitive equilibrium among many species. – Theor. Popul. Biol. 1: 1–11.

Maynard-Smith, J. 1974. Models in ecology. – Cambridge Univ. Press, Cambridge.

– 1982. Evolution and the theory of games. – Cambridge Univ. Press, Cambridge.

McNair, J. N. 1986. The effects of refuges on predator-prey interactions: A reconsideration. – Theor. Popul. Biol. 29: 38–63.

Menge, B. A. and Lubchenco, J. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradient. – Ecol. Monogr. 51: 429–450.

Murdoch, W. W. and Oaten, A. 1975. Predation and population stability. – Adv. Ecol. Res. 9: 1–131.

Noy-Meir, I. 1981. Theoretical dynamics of competitors under predation. – Oecologia (Berl.) 50: 277–284.

Paine, R. T. 1966. Food web complexity and species diversity. – Am. Nat. 100: 65–75.

Parker, G. A. 1985. Population consequences of evolutionarily stable strategies. – In: Sibly, R. M. and Smith, R. H. (eds), Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell, Oxford, pp. 33–58.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. – Ann. Rev. Ecol. Syst. 15: 523–576.

Rosenzweig, M. L. 1981. A theory of habitat selection. – Ecology 62: 327–335.

– 1985. Some theoretical aspects of habitat selection. – In: Cody, M. (ed.), Habitat selection in birds. Academic Press, New York, pp. 517–540.

Roughgarden, J. and Feldman, M. 1975. Species packing and predation pressure. – Ecology 56: 489–492.

Schmitt, R. J. in press. Indirect interactions between prey: Apparent competition, predator aggregation, and habitat segregation. – Ecology.

Schoener, T. W. 1973. Population growth regulated by intraspecific competition for energy or time: some simple representations. – Theor. Popul. Biol. 4: 56–84.

– 1974. Resource partitioning in ecological communities. – Science 185: 27–39.

– 1975. Competition and the form of habitat shift. – Theor. Popul. Biol. 5: 265–307.

– 1976. Alternatives to Lotka-Volterra competition: models of intermediate complexity. – Theor. Popul. Biol. 10: 309–333.

– 1978. Effect of density-restricted food encounter on some single-level competition models. – Theor. Popul. Biol. 13: 365–381.

– 1986. Mechanistic approaches to community ecology: A new reductionism? – Am. Zool. 26: 81–106.

Sibly, R. M. and Smith, R. H. (eds), 1985. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell, Oxford.

Sih, A. 1979. Stability and prey behavioural responses to predator density. – J. Anim. Ecol. 48: 79–89.

– et al. 1985. Predation, competition, and prey communities: a review of field experiments. – Ann. Rev. Ecol. Syst. 16: 269–312.

Sinclair, A. R. E. 1985. Does interspecific competition or predation shape the African ungulate community? – J. Anim. Ecol. 54: 899–918.

Slobodkin, L. B. 1961. Growth and regulation of animal populations. – Holt, Rinhart and Winston, New York.

Strong, D. R., Lawton, J. H. and Southwood, T. R. E. 1984. Insects on plants: Community patterns and mechanisms. – Harvard Univ. Press, Cambridge, MA.

Takeuchi, Y. and Adachi, N. 1983. Existence and bifurcation of stable equilibrium in two-prey, one-predator communities. – Bull. Math. Biol. 45: 877–900.

Teramoto, E., Kiawasahi, K. and Shigesada, N. 1979. Switching effect of predation on competitive prey species. – J. Theor. Biol. 79: 303–315.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. – Oikos 47: 75–82.

Vance, R. R. 1978. Predation and resource partitioning in one-predator, two-prey model communities. – Am. Nat. 112: 797–813.

Van Valen, L. 1974. Predation and species diversity. – J. Theor. Biol. 44: 19–21.

Yodzis, P. 1976. The effects of harvesting on competitive systems. – Bull. Math. Biol. 38: 97–109.

– 1978. Competition for space and the structure of ecological communities. – Springer, Berlin.

– 1986. Competition, mortality, and community structure. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 480–491.