

SPATIAL HETEROGENEITY, INDIRECT INTERACTIONS, AND THE COEXISTENCE OF PREY SPECIES

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The study of ecological communities has long been dominated by an emphasis on competition for limiting resources, and by the assumption that resource partitioning is the *sine qua non* of species coexistence (e.g., MacArthur 1972; Cody 1974; Diamond 1978; Tilman 1982). In recent years, ecologists have begun to reevaluate the central role of competition in ecological theory (e.g., Connell 1980; Strong 1983; Wiens 1983). In many communities, the effects of predation seem to outweigh those of resource competition (Paine 1966; Connell 1975; Zaret 1980). After surveying a number of field studies, Connell (1975, p. 475) concluded that "predation should be regarded as being of primary importance, either directly determining the species composition [of a community] or in preventing competitive exclusion." Even if this proves to be too sweeping a claim for the importance of predation (Schoener 1983), it is clear that any general theory of ecological communities must incorporate predation as an important determinant of community structure.

There is some evidence that the relative significance of predation and competition may vary predictably as a function of trophic level and environmental stability (Menge and Sutherland 1976; Schoener 1982, 1983). Even within trophic levels, however, the distinction between the effects of predation and competition blurs upon close inspection. On the one hand, the outcome of interference and exploitative competition may hinge on the relative abilities of competitors to withstand mortality factors (Slobodkin 1961; Abrams 1977; Whittaker 1979). Furthermore, the intensity of predation may influence the degree of overlap and intensity of competition between competing species (Roughgarden and Feldman 1975; Glasser 1979, 1982). On the other hand, community patterns exhibited by noncompeting prey species may closely mimic patterns generated by competition. This may occur if predators have a strong numerical response to their prey (Holt 1977, and below) or impose apostatic selection through their functional response (Ricklefs and O'Rourke 1975; Levin and Segel 1982). Instead of considering competition and predation to be alternative, incommensurable mechanisms for community structure, we may more broadly view these interactions as complementary components in a unified theory of the ecological niche. Interspecific

differences in strategies either of resource use or of predator avoidance may permit species coexistence (Levin 1970; Vance 1978). Predators may provide axes for niche differentiation among prey, just as prey, as resources, constitute niche dimensions for predators (MacArthur 1965; Lawton 1978; Jeffries and Lawton, in press; Kotler 1984).

In empirical studies of communities it is commonly observed that species segregate along one or more habitat dimensions (Schoener 1974*b*). Such patterns are usually interpreted in the light of competition theory. Here I show that, in principle, predation leads to patterns of habitat partitioning among prey similar to those resulting from resource competition. It is not my purpose to denigrate the role of competition in communities, but rather to demonstrate a certain symmetry in the consequences of predation and competition for the spatial structure of communities.

To place the theory developed below into a broader context, I first classify mechanisms through which a single predator species may structure assemblages of prey species that are not competing for resources. By assuming that prey are not directly competing, I hope to highlight the idea that shared predation, in and of itself, has interesting consequences for the structure of communities (see also Jeffries and Lawton, in press). Before exploring the potential role of spatial heterogeneity in prey coexistence, we need to have a clear understanding of how predation influences coexistence in spatially homogeneous environments. Hence, in section 2, I derive simple criteria for the coexistence of prey when their shared predator feeds upon them in a fine-grained fashion, and I argue that coexistence is unlikely at high intensities of predation. In section 3, the heart of the paper, I develop models for two species of immobile prey segregated into two habitats coupled by predator movement. The results to be presented suggest that habitat partitioning could be an important mechanism allowing alternative prey species to coexist. Section 4 examines the evolutionary stability of such habitat partitioning between prey. The paper concludes with a discussion of several suggestive empirical examples.

1. SHARED PREDATION AND MECHANISMS OF INTERACTION AMONG ALTERNATIVE PREY

That predation usually enhances diversity by relaxing interspecific competition was long part of the folk wisdom of ecology. It is now clear, on both theoretical and empirical grounds that this is not a universal effect of predation. Models of a predator interacting with a pair of prey populations can display a rich variety of dynamical outcomes (Holt 1977; Vance 1978; Gilpin 1979; Noy-Meir 1981). In the absence of switching behavior (Murdoch 1969) or reduced overlap in resource use among prey with increasing predation intensity (Glasser 1979), predation modifies the criteria for species coexistence without necessarily making coexistence more likely (Comins and Hassell 1976; Abrams 1977; May 1977; Vance 1978). Many field studies from a wide range of habitats have demonstrated that predators stably exclude prey species from natural communities (e.g., Brooks and Dodson 1965; Bergerud 1967, 1983; Goeden and Louda 1976; Macan 1977; Blakley and Dingle 1978; Zaret 1980; Hay 1981; Parker and Root 1981; Zaret 1980; Louda

1982; Luecke and O'Brien 1983; Jeffries and Lawton, in press). These examples suggest that predation may frequently restrict the number of co-occurring prey species, even though there are circumstances in which predation also permits competitively incompatible species to coexist (Lubchenco and Gaines 1981).

Shared predation poses a problem for the coexistence of species parallel to the familiar problem presented by the shared exploitation of a limiting resource. In figure 1A, two consumers and their common resource have been abstracted from a food web. All else being equal, in a constant environment we expect one consumer to tend to exclude the other by reducing the availability of the shared resource. Given examples that seem to resemble this figure, the usual field protocol is to attempt to identify mechanisms that might mitigate this tendency to exclusion (additional resources, strong intraspecific interference, etc.). In figure 1B, two prey populations share a common predator. A numerical response by the predator sets up an indirect interaction between these prey, a mirror image of exploitative competition. Because each prey tends to increase predator density, each may suffer a greater intensity of predation from the presence of the alternative prey. If one prey is sufficiently productive, the predator may be maintained at a density high enough to exclude the other prey from the community.

Elsewhere, I have shown this indirect $(-, -)$ interaction between prey to be a generic property of most predator-prey models in which the predator is food-limited (Holt 1977; but see Holt 1983, and section 3 below for possible exceptions). I referred to this indirect interaction as "apparent competition" to distinguish it from the more familiar $(-, -)$ interactions of exploitative and interference competition. One may find allusions to the existence of apparent competition in some of the classic writings of ecologists (e.g., Andrewartha and Birch 1954; Williamson 1957; MacArthur 1965; Janzen 1970). Unlike exploitative competition, however, mechanistic models of this interaction have received little attention. Analogues of many of the factors used to explain the coexistence of species competing for resources may also explain the coexistence of prey which share predators. The one explored here is habitat partitioning.

This indirect interaction between prey is called "apparent" competition for the simple reason that competition is usually defined in terms of the common exploitation of a limiting resource. Yet many of the population-level phenomena predicted from competition for resources—reciprocal reductions in abundance, exclusion of species from communities, and so forth—are also to be expected when species have nonoverlapping resource requirements but share predators with a strong numerical response. Observational and experimental studies that document the existence of these phenomena thus provide incomplete evidence for competition in the usual sense of the word. To discriminate between alternative mechanisms for observed $(-, -)$ interactions, such studies must be supplemented by analyses of resource utilization patterns, resource dynamics, and the effects of predators on the dynamics of the interacting populations. If one defines competition to be all $(-, -)$ interactions, regardless of the underlying mechanism, phrases such as "predator-mediated competition" or "competition for enemy-free space" could be used as synonyms for "apparent competition."

Apparent competition is only one of a number of mechanisms through which

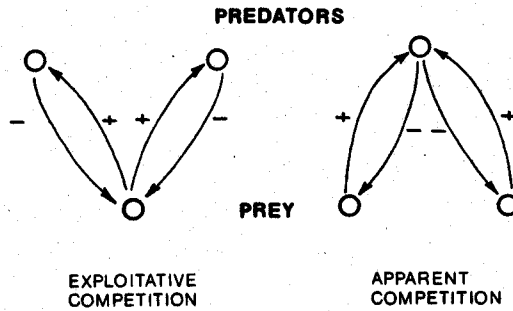


FIG. 1.—Apparent competition is a mirror image of exploitative competition.

prey may potentially interact by means of shared predation. Several others, listed in table 1, can be summarized in telegraphic form as follows: Within an isolated habitat patch, predator numbers can be nearly constant over short time periods, or may be fixed by factors other than food availability. Alternative prey may nevertheless interact through the predator's functional response. This can lead to (+, +) interactions between prey (Holt 1977; Noy-Meir 1981). Prey may also compete directly for access to refuges from predation. If the predator is food-limited, over longer time scales its reproductive numerical response leads to apparent competition.

Predator dispersal provides several additional avenues for indirect interactions between prey. Co-occurring prey may experience (-, -) interactions because of predator aggregation (see Discussion). Dispersing predators can also couple the dynamics of spatially separated populations. All else being equal, an influx of predators into a habitat should reduce prey density; the rate of influx may be influenced by the productivity of prey in the source habitat. Some predator-prey interactions are believed to persist because of a regional balance between local extinctions (resulting from overexploitation by the predator) and colonization of empty habitats (Huffaker 1958; Vandermeer 1973; Hilborn 1975; Hastings 1977; Caswell 1978; Crowley 1981). Even if alternative prey never co-occur, they may indirectly interact at a regional scale, for the simple reason that predators leaving a population of one prey species can potentially colonize populations of other prey species. Over evolutionary time, sharing predators may also lead to changes in the suite of antipredator adaptations characterizing a prey community, such as an increase in its "aspect diversity" (Ricklefs and O'Rourke 1975; Levin and Segel 1982). In practice, these conceptually distinct modes of interaction may intertwine in various ways with each other, and with resource competition as well.

2. COEXISTENCE UNDER FINE-GRAINED PREDATION

As a prelude to analyzing the consequences of spatial heterogeneity for prey coexistence, it is useful to consider briefly the requirements for coexistence in spatially homogeneous environments. We will do this using MacArthur's resource-consumer model (MacArthur 1970, 1972), which has received much atten-

TABLE 1
MECHANISMS OF INTERACTION POTENTIALLY ARISING FROM SHARED PREDATION

Mode of Interaction	Spatial Scale	Temporal Scale
Competition for refuges Coupled attack rates (e.g., predator satiation) Aggregative numerical response by predator (in patchy environment) Reproductive numerical response by predator	Within-patch	Short (ecological time)
Predator dispersal among patches Extinction-colonization dynamics	Among patch	
Evolutionary responses (e.g., character displacement in "escape space")	Within or among patches	Long (evolutionary time)

tion as a tractable caricature of exploitative competition for self-renewing resources (Schoener 1974a; Case and Casten 1979; Hsu and Hubbell 1979; Abrams 1980). The model is the following system of coupled differential equations for a single predator species feeding on n prey species:

$$\text{predator} \quad \frac{dP}{dt} = P \left(\sum_{i=1}^n a_i b_i R_i' - C \right),$$

and

$$\text{prey } k \quad \frac{dR_k'}{dt} = R_k' r_k \left(1 - \frac{R_k'}{K_k} \right) - a_k R_k' P, \quad k = 1, \dots, n. \quad (1)$$

Without predation, each prey grows logistically, with no direct interspecific competition. Without prey, the predator population declines exponentially. A linear functional response, scaled by a_k , describes the rate at which individual predators capture prey of type k . The quantity b_i converts prey captures into predator births. The ratio of two prey types in the diet is proportional to their actual relative abundances; the predator feeds in a "fine-grained" fashion.

Model (1) satisfies the qualitative stability criteria outlined by Jeffries (1974), so a feasible equilibrium (Roberts 1974; i.e., $P > 0$ and all $R_k > 0$) is necessarily locally stable. Elsewhere I (Holt 1977) have used this model to explore some implications of apparent competition, and I showed that a feasible equilibrium exists if and only if each species can increase when rare. The consequences of shared predation for community structure can be expressed compactly if we measure prey numbers by the effect each prey has on the predator's growth rate: $R_i \equiv a_i b_i R_i'$, and $K_i \equiv a_i b_i K_i'$. With this convention, model (1) becomes $dP/dt = P(\sum R_i - C)$ and $dR_k/dt = R_k r_k [1 - R_k/K_k - P(a_k/r_k)]$. (Summations are from $i = 1$ to n , unless otherwise indicated.) The quantity K_k^{-1} gauges the sensitivity of the

growth of prey k to an increase in its own density, and, in like manner, a_k/r_k measures its sensitivity to predation. At equilibrium (denoted by an asterisk), prey k is reduced below its carrying capacity by an amount determined by its sensitivity to predation:

$$R_k^* = K_k \left(1 - \frac{a_k}{r_k} P^* \right).$$

Let $K_T = \sum K_i$ (total prey numbers at equilibrium without predation) and $R_T^* = \sum R_i^*$ (total prey numbers with predation). The predator reduces prey numbers by the fractional amount

$$\Delta \equiv 1 - \frac{R_T^*}{K_T},$$

a measure of the intensity of predation on the prey community. The intensity of predation on prey species k is defined to be

$$\Delta_k = 1 - \frac{R_k^*}{K_k}.$$

Before predation, the average sensitivity to predation is

$$\overline{a/r} = \sum \left(\frac{K_i}{K_T} \right) \frac{a_i}{r_i}.$$

With these definitions, the expressions of table 2 can be derived.

Although this model has many simplifying assumptions, it does nicely illustrate several qualitative features of prey communities under shared predation, features also found in more complex, realistic models. First, if predation limits total prey abundance, alternative prey should experience apparent competition. In the model, predation reduces total prey numbers from K_T to $R_T^* = C$ (assuming that $K_T > C$, a requirement for predator persistence). With n prey species, the average equilibrium abundance per species is C/n , which decreases with increasing n , an expression of apparent competition. Secondly, predation changes the relative abundances of prey that are differentially sensitive to predation (expressions iii and iv in table 2). If prey k is more sensitive to predation than the community average ($a_k/r_k > \overline{a/r}$), its relative abundance decreases with increasing Δ . Thirdly, predation upon some prey may be so intense that they are excluded entirely from the community. For prey k to persist, its intrinsic rate of growth must at least balance predation, or $r_k \geq a_k P^*$. The abundance of a food-limited, generalist predator is ultimately controlled by the availability and productivity of all its prey. The intensity of predation upon prey k is thus governed indirectly by properties of alternative prey in the predator's diet. In this model, $P^* = \Delta/\overline{a/r}$, so prey k persists (i.e., $R_k^* > 0$) if

$$\frac{\overline{a/r}}{\Delta} > a_k/r_k. \quad (2)$$

At first glance this seems to insufficiently characterize persistence, for $\overline{a/r}$ and Δ are defined for the community with species k . If we use a prime to denote these

TABLE 2
 PROPERTIES OF THE PREY COMMUNITY PREDICTED BY MODEL I

i. Definitions

Average sensitivity to predation (measured without predation)

$$\text{(with prey } k) \quad \bar{a}/r = \sum_i \left(\frac{K_i}{K_T} \right) \left(\frac{a_i}{r_i} \right)$$

$$\left(K_T = \sum_i K_i \right)$$

$$\text{(without prey } k) \quad \bar{a}/r' = \sum_{i \neq k} \left(\frac{K_i}{K_T} \right) \frac{a_i}{r_i}$$

$$\left(K_T = \sum_{i \neq k} K_i \right)$$

Intensity of predation on prey K

$$\Delta_k = 1 - R_k^*/K_k$$

Intensity of predation on prey community

$$\text{(with prey } k) \quad \Delta = 1 - R_T^*/K_T = 1 - C/K_T$$

$$\left(R_T^* = \sum_i R_i^* = C \right)$$

$$\text{(without prey } k) \quad \Delta' = 1 - C/K_T$$

ii. Equilibrium densities

$$\text{Predator} \quad P^* = \left(\sum_i K_i - C \right) / \sum_i K_i a_i / r_i = \frac{\Delta}{a/r}$$

$$\text{Prey } k \quad R_k^* = K_k \left(1 - \frac{a_k}{r_k} P^* \right)$$

iii. Intensity of predation

$$\text{on prey } k \quad \Delta_k = \frac{a_k/r_k}{a/r} \Delta$$

on prey k , relative to prey m

$$\frac{\Delta_k}{\Delta_m} = \frac{a_k/r_k}{a_m/r_m}$$

iv. Relative abundance of prey k , compared to its relative abundance

without predation (K_k/K_T)

$$\frac{R_k^*}{R_T^*} = \frac{K_k}{K_T} \left[\frac{1 - \Delta \frac{a_k/r_k}{a/r}}{1 - \Delta} \right]$$

v. Average sensitivity to predation, at equilibrium with predator

$$\sum_i \left(\frac{R_i^*}{R_T^*} \right) \frac{a_i}{r_i} = \bar{a}/r \left[1 - \frac{\Delta(cv)^2}{1 - \Delta} \right]$$

$(cv = \left[\sum_i (K_i/K_T)(a_i/r_i - \bar{a}/r)^2 \right]^{1/2} / (\bar{a}/r))$, the coefficient of variation in a_i/r_i before predation).

NOTE. Prey abundances are scaled so that $R_i = a_i b_i R_i'$, $K_i = a_i b_i K_i'$.

same quantities defined over the community without species k , after a few lines of algebra we find inequality (2) to be equivalent to

$$\frac{\overline{a/r'}}{\Delta'} > a_k/r_k.$$

Given an initial assemblage of prey species, by manipulating this inequality we can determine which subset can coexist under shared predation. If all prey have the same a_i and K_i , condition (2) takes the simple form $r_k > r_H \Delta$, where r_H is the harmonic mean of intrinsic growth rates in the community.

High prey diversity is permitted if (1) alternative prey have similar sensitivities to predation ($\overline{a/r} \cong a_k/r_k$ for all k); or (2) prey with low sensitivities to predation also have low carrying capacities; or (3) the intensity of predation is low (permitting substantial variation in a/r). To see (2), it is useful to define

$$\text{Ave } (a/r) = \frac{1}{n} \sum \frac{a_i}{r_i}$$

(an average a_i/r_i across species) and to let $\text{cov}(K, a/r)$ be the covariance of K_i and a_i/r_i across species. Because

$$\overline{a/r} = n \text{cov}(K, a/r)/K_T + \text{Ave } (a/r),$$

a positive correlation between K_i and a_i/r_i increases $\overline{a/r}$ and makes (2) easier to satisfy. The intensity of predation is

$$\Delta = 1 - \frac{C}{K_T}.$$

The average carrying capacity per prey species is $\hat{K} = K_T/n$, hence

$$\Delta = 1 - \frac{C}{n\hat{K}}.$$

A low Δ is compatible with a high n if the average carrying capacity is low compared to the predator's resource requirements. Conversely, if \hat{K} is large compared to C , $\Delta \rightarrow 1$ and (from [2]) coexistence requires $\overline{a/r} \cong a_k/r_k$. Prey species should usually differ somewhat in parameters such as a_i and r_i . If so, their sustained coexistence is unlikely at high intensities of predation.

With two prey species, prey 1, when alone, experiences an intensity of predation

$$\Delta_1 = 1 - \frac{C}{K_1},$$

and similarly prey 2 by itself experiences an intensity of predation

$$\Delta_2 = 1 - \frac{C}{K_2}.$$

The condition for coexistence is

$$\frac{1}{\Delta_2} > \frac{a_1/r_1}{a_2/r_2} > \Delta_1. \quad (3)$$

As predation becomes more intense (i.e., $\Delta_i \rightarrow 1$), coexistence requires an increasingly delicate balance between attack rates and intrinsic growth rates.

A high diversity of prey thus seems incompatible with a high intensity of predation. Yet some species-rich communities (e.g., phytophagous insect assemblages [Lawton and Strong 1981]) seem to be structured by intense predation and thus appear to contradict a principal conclusion of the fine-grained predation model. There are a number of ways we could make model (1) more realistic (see e.g., Holt 1977; Vance 1978; Noy-Meir 1981). Many reasonable modifications, such as incorporating nonlogistic growth, direct interspecific competition, or predator satiation, do not alter the fundamental conclusion that prey coexistence is unlikely at high intensities of predation. One change that does is spatially segregating prey.

3. HABITAT PARTITIONING AND PREY COEXISTENCE

The spatial scale perceived by a predator need not match that experienced by its prey. Even spatially segregated prey may indirectly interact if their shared predator is highly mobile. To explore the potential role of habitat partitioning as a mechanism allowing prey coexistence, we will imagine that two prey species have mutually exclusive habitat distributions, with prey i just in habitat i . The two habitats occur as single large patches, closely enough juxtaposed so that at any instant most predators are in one or the other of the two patches, with a negligible number in transit.

The basic model is a generalization of model (1). Without the predator, prey species i grows at the per capita rate $\Phi_i(R_i)$. A predator in patch i captures prey at rate $a_i R_i$, has a corresponding rate of foraging yield $a_i b_i R_i$, and experiences a rate of mortality C_i . The density of predators in patch i is P_i . Let I_i and e_i , respectively, be rates of predator immigration and emigration for patch i . We will assume zero mortality during transit. The model is

(predator in patch i)

$$\frac{dP_i}{dt} = P_i(a_i b_i R_i - C_i) + I_i - e_i, \quad (4)$$

(prey i in patch i)

$$\frac{dR_i}{dt} = R_i \Phi_i(R_i) - a_i P_i R_i, \quad i = 1, 2.$$

The quantities I_i and e_i could be complicated functions of predator and prey densities. If ρ is the fraction of the total area contained in patch 1, the average predator density is $P = \rho P_1 + (1 - \rho)P_2$. A fraction $t_1 = \rho P_1/P$ of the predator population is in patch 1, and the remaining fraction $t_2 = (1 - \rho)P_2/P$ is in patch 2. The growth rate of the predator population is

$$\frac{dP}{dt} = P(t_1 a_1 b_1 R_1 + t_2 a_2 b_2 R_2 - \bar{C}), \quad (5)$$

where $\bar{C} = t_1 C_1 + t_2 C_2$. This representation of predator growth will prove useful below.

We first transform model (4) into a graphical model that allows us to compare the consequences of optimal habitat selection by the predator with the effects of rapid, random movement. We then return to (4) and derive coexistence conditions for the special case of random predator movement and exponential prey growth.

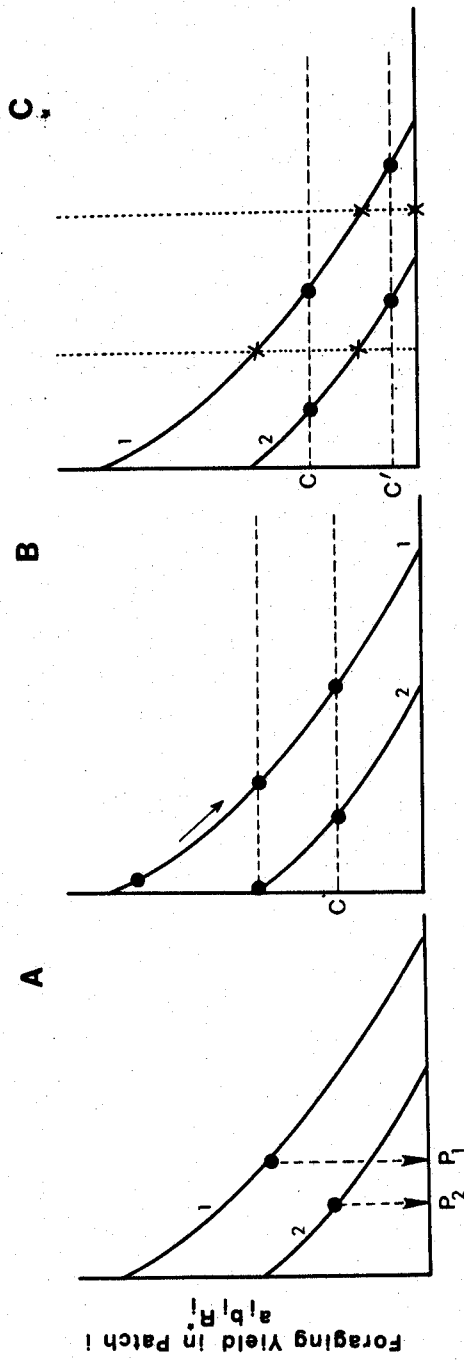
A. A Graphical Representation of the Two-Patch Model

A standard tool in analyses of multispecies models is to reduce dimensionality by assuming that populations with relatively fast response times are at or near equilibrium, conditional on the densities of those populations with slower response times. (This procedure is the "ecological abstraction" of Schaffer [1981].) MacArthur (1970, 1972), for instance, linked the traditional Lotka-Volterra model of competition to the resource-consumer model (eqq. [1]) discussed earlier by allowing resources to equilibrate rapidly compared with changes in consumer densities. By this device, the parameters r , K , and α of the traditional model become invested with a mechanistic interpretation incorporating individual foraging rates and resource dynamics. In this spirit, let us assume that both prey populations respond quickly to changes in predator density and experience negative density-dependence at all densities (i.e., $d\Phi_i/dR_i < 0$). In patch i , prey productivity should just match the rate of predation, or $\Phi_i(R_i^*) \cong a_i P_i$. The growth function Φ_i has a unique inverse, so $R_i^* = \Psi_i(P_i)$. The function Ψ_i describes how prey densities change with predator density in patch i . With our assumptions about Φ_i , prey i declines monotonically as P_i increases. In a phase plane with axes R_i and P_i , the graph of Ψ_i is the prey isocline (Rosenzweig and MacArthur 1963).

Given rapid prey equilibration, in patch i an individual predator feeds at rate $a_i b_i R_i^* = a_i b_i \Psi_i(P_i)$, which decreases with increasing P_i . Foraging yield for a predator in a given patch, as a function of predator density in that patch, is thus a simple transformation of the prey isocline. In figure 2A, we plot the foraging yields of both patches as a function of patch-specific predator densities. When predator density in both patches is near zero, each prey is at its carrying capacity, and a predator in patch i forages at a rate $a_i b_i K_i$. With increasing predator densities, prey densities decline, with a corresponding reduction in foraging yield. A density of predators of r_i/a_i in patch i can depredate to extinction prey i . The negative slope of the yield curve is an expression of exploitative competition among predators. The shape of the yield curves is determined by the form of Φ_i . For example, with logistic prey growth the yield curve is the straight line $a_i b_i R_i^* = a_i b_i K_i - (a_i^2 b_i K_i / r_i) P_i$. If both prey are encountered and utilized at the same rate ($a_1 = a_2$, $b_1 = b_2$), the yield lines intersect if the prey with lower K_i has a higher r_i . Intersection also occurs if prey differ just in a_i ; at low P , the prey species (patch) with higher a_i provides the higher yield, but the reverse is true at high P . For simplicity, we will assume that predator mortality is spatially uniform (i.e., $C_1 = C_2 \equiv C$). With this graphical machinery, we can now contrast different patterns of predator movement.

B. Optimal Foraging in a Coarse-Grained Environment

Optimal habitat and patch selection has been the subject of much theoretical research in recent years (Schoener 1971; Fretwell 1972; Charnov 1976; Comins



Predator Density in Patch i , P_i

FIG. 2.—A, With P_1 predators in patch i , there are R_1 prey in patch i , and the foraging yield is $a_1 b_1 R_1$. The intersection of this yield curve with the abscissa is $a_1 b_1 K_1$, and with the ordinate is r_1/a_1 . B, Optimal habitat selection (modified from Fretwell 1972). At low predator numbers, all predators should reside in patch 1. As predator numbers rise, the density of prey 1 falls until it becomes advantageous for some predators to forage in patch 2. As predator numbers continue to rise in the two patches, the densities of both prey should decline. The equilibration of foraging yields expected under optimal habitat selection is represented by the horizontal dashed lines. At equilibrium, $a_1 b_1 R_1^* = C$ in both patches. (C is the predator's density-independent rate of mortality.) C, A comparison of fine-grained foraging and optimal habitat selection. With rapid indiscriminate predator movement, $P_1 = P_2$. This is shown by the dotted vertical lines. With equal patch area, the average rate of yield is halfway between the two yield curves. At equilibrium, the average rate of yield equals C . The fine-grained forager underexploits prey 1 and overexploits prey 2. At a lower rate of mortality, C' , predator numbers rise until the average yield equals C' . There are now enough predators moving through patch 2, supported by the production of prey in patch 1, such that prey 2 becomes extinct and the yield in patch 2 is zero.

and Hassell 1979; Slatkin 1979; Rosenzweig 1981). These authors are in broad agreement about the expected outcome of optimal habitat selection. Let us assume that predators encounter prey in a "coarse-grained" manner and forage selectively so as to maximize rates of foraging. If there is no cost to moving, and predators do not directly interfere with each other, all predators should be found in whichever patch has the higher foraging yield. If predators continue to forage in both patches, the yield of the two patches should therefore be equal. The distribution of predators that equalizes foraging yields is the "ideal free distribution" proposed by Fretwell (1972). The prediction that foraging yields at equilibrium should be spatially uniform is a special case of a general evolutionary principle elucidated by Slatkin (1979): given frequency-dependent fitnesses, and two alternative phenotypic classes, selection tends to distribute the relative frequencies of the two phenotypes until they have equal fitness. In the model under discussion, foraging yield is a proxy for fitness.

The equalization of yields expected in optimal habitat selection has important consequences for prey coexistence. The ideal free distribution of predators is represented graphically by a horizontal line in figure 2B. If the optimally foraging predator consumes both prey, it must be true that $a_1 b_1 R_1^* = a_2 b_2 R_2^*$. It immediately follows that at equilibrium, the predator cannot continue to subsist on one prey (say, prey 1, $R_1^* > 0$) while having eaten the other to extinction ($R_2^* = 0$); exclusion because of apparent competition cannot occur. From equation (5), at equilibrium $t_1^* a_1 b_1 R_1^* + t_2^* a_2 b_2 R_2^* = C$. Because the predator is selecting patches optimally, we can substitute $a_1 b_1 R_1^*$ for $a_2 b_2 R_2^*$, and we find that $R_1^* = C/a_1 b_1$. (Recall that $t_1 + t_2 = 1$.) This is exactly the equilibrium prey density that would be expected were the other prey species absent, and the predator foraged exclusively on prey 1 in patch 1. Similarly, $R_2^* = C/a_2 b_2$. This result readily generalizes to n prey species distributed among n distinct patches. If alternative prey are spatially segregated and appear coarse-grained to a predator, and the predator forages optimally without movement costs or interference, there is no apparent competition at equilibrium.

Why does this prediction contradict my earlier assertion (Holt 1977 and above) that alternative prey in the diet of a food-limited predator should display apparent competition? My argument required the predator isocline in the R_1, R_2 plane to have a negative slope. An optimally foraging predator that switches abruptly between habitats as relative prey abundances change, however, can be shown to have a rectangular isocline (Holt 1983).

Habitat partitioning among prey, coupled with optimal habitat selection by the predator, may thus greatly enhance the likelihood of prey coexistence. Consider a predator initially specialized on prey 1 in patch 1. This predator should broaden its diet to include prey 2 only if $a_2 b_2 K_2 > a_1 b_1 R_1^*$. At equilibrium, $a_1 b_1 R_1^* = C$, so $a_2 b_2 K_2 - C > 0$ is the criterion for species 2 to be added to the diet. This inequality also must be satisfied in order for a predator population specialized on just prey 2 to persist. Thus, each prey type contained in the equilibrium diet of an optimally foraging, coarse-grained predator, by itself can support a predator population. By contrast, in the fine-grained model (eq. [1]), any prey for which $b_i > 0$ can be profitably included in the diet. Diet generalization is thus less likely if

prey are coarse-grained than fine-grained, and some prey may be able to escape predation entirely. Moreover, at equilibrium there are $P_i^* = \Phi_i(R_i^*)/a_i$ predators in patch i . This is the density expected when the predator is restricted to patch i . At equilibrium, the spatial pattern in abundance of both the optimally foraging predator and its prey is exactly that predicted were there no movement of predators among patches at all. Optimal patch selection by the predator may provide, therefore, refuge for prey species with relatively high sensitivities to predation (e.g., high a_i/r_i), if such prey are spatially segregated from alternative prey.

I should caution that these results characterize a stable equilibrium, given that one exists. To examine stability requires specification of the movement rules in model (6). Numerical studies of model (6) with a variety of dispersal functions approximating optimal foraging suggest that stability is usually observed.

C. Fine-Grained Predation: A Graphical Approach

If the assumptions of the optimal habitat selection model do not hold, alternative prey may experience apparent competition despite habitat partitioning. In particular, the fine-grained predation assumed in model (1) may occur if predators cannot discriminate between habitat patches occupied by different prey and move rapidly among patches. With two prey in two patches, because ρ is the proportion of the total area contained in patch 1, a fine-grained forager will spend a fraction ρ of its foraging time in habitat 1, and a fraction $1 - \rho$ in patch 2. Predator densities in the two patches are equal under rapid dispersal ($P_1 = P_2 = P$), and the predator population should thus grow at a rate $dP/dt = P[\rho a_1 b_1 R_1 + (1 - \rho) a_2 b_2 R_2 - C]$.

The influence of predator density upon habitat-specific foraging yields may now be represented graphically by a vertical line (fig. 2C). The change from a horizontal line (fig. 2B) to a vertical line (fig. 2C) reflects a change in the quantity assumed equal across habitats. Optimal foraging ensures equalization of yields and implies spatial variation in predator densities; random foraging with rapid rates of movement leads to equal predator densities and unequal rates of yield in the two patches. Assume that the patches are equal in area (i.e., $\rho = 1/2$). The per capita growth rate of the predator is $1/2(a_1 b_1 R_1 + a_2 b_2 R_2) - C$. Equilibrium is reached when the average rate of yield equals C . Graphically, the average rate of yield at a given P is along the vertical line halfway between the two yield curves (fig. 2C). With this figure, we can demonstrate the existence of apparent competition and predict the exclusion of prey species. With prey i alone, equilibrium occurs at $a_i b_i R_i^* = 2C$, whereas with both prey, $a_1 b_1 R_1^* + a_2 b_2 R_2^* = 2C$. Each prey necessarily suffers a reduction in density if the alternative prey is present. At low enough C , the prey population providing the higher yield may maintain a density of predators great enough to drive the second prey to extinction (see fig. 2C). This graphical model portrays predator "spillover": randomly foraging predators, supported by a productive prey in one patch, can move through a second patch and overexploit prey there to the point of extinction.

Interference between predators can also lead to indirect interactions between spatially segregated prey. If interference is more intense in the more productive

habitat, predators will tend to be displaced from there into the less productive habitat. The influx of predators into low-productivity habitats should increase the intensity of predation upon resident prey. The consequences of predator interference for prey coexistence should be bracketed by the effects of optimal habitat selection without interference (no apparent competition at equilibrium) and those of rapid, random dispersal (potential extinction of prey with high a_i/r_i).

D. Random Predator Movement: Analytical Model

The graphical fine-grained model is a limiting case of the following model in which predators move randomly and symmetrically between patches, but not so rapidly as to homogenize predator densities. Let us assume the two patches to be equal in area. With random dispersal, model (4) becomes

$$\frac{dP_i}{dt} = P_i(a_i b_i R_i - C_i) - EP_i + EP_j, \quad i, j = 1, 2, \quad i \neq j, \quad (6)$$

and

$$\frac{dR_i}{dt} = R_i \Phi_i(R_i) - a_i P_i R_i, \quad i = 1, 2. \quad (7)$$

The dispersal parameter E scales the rate of predator movement. If prey equilibrate rapidly, then as before we can approximate R_i^* by some function $\Psi_i(P_i)$ and replace R_i with $\Psi_i(P_i)$ in (6). This approximation transforms the model into a model for population dynamics in two patches that has been studied by Freedman and Waltman (1977) and Holt (1984). Assume that at $E = 0$, $P_1^* > P_2^*$. Freedman and Waltman show that at small E , increases in E decrease P_1^* and increase P_2^* . (A graphical analysis of this model is in Holt [1984].) The implication for the prey is that random predator movement reduces predator density in the more productive patch and increases it in the less productive patch. Because of the inverse relation within a patch between predator density and prey density, the less productive prey is always reduced in density by random predator movement. As E becomes sufficiently large, P_1^* and P_2^* converge to a common value, P^* , and this model reduces to the fine-grained model discussed above.

With exponential prey growth ($\Phi_i = r_i$), the condition for prey coexistence takes a particularly simple form. The assumption of exponential prey growth amounts to an assumption of intense predation within each patch ($R_i \ll K_i$). Without dispersal ($E = 0$), the system is a pair of neutrally stable Lotka-Volterra predator-prey equations. First consider the special case of $R_2 = 0$. Patch 2 is a "sink" where predators are maintained solely by immigration. The equilibrium densities are $P_1^* = r_1/a_1$, $P_2^* = P_1^*[E/(C_2 + E)]$, and $R_1^* = [C_1 + E - E^2/(C_2 + E)]/a_1 b_1$. Predator dispersal into the sink increases both the total number of predators and the abundance of prey 1. In the Appendix it is shown that this equilibrium is locally stable for all finite $E > 0$. These effects hold quite generally in predator-prey models with a "source-sink" structure (Holt 1984).

With prey 1 and the predator at equilibrium, can the second prey invade? It can if $r_2 - a_2 P_1^* > 0$, or

$$\frac{r_2/a_2}{r_1/a_1} > \frac{E}{C_2 + E}.$$

Similarly, if prey 2 is at present at equilibrium with the predator, prey 1 invades if $r_1 - a_1 P_2^* > 0$ or

$$\frac{r_1/a_1}{r_2/a_2} > \frac{E}{C_1 + E}.$$

The condition for mutual invasibility can be written as

$$\left(\frac{E}{C_1 + E}\right)^{-1} > \frac{a_1/r_1}{a_2/r_2} > \frac{E}{C_2 + E}. \quad (8)$$

With exponential prey growth, from equations (6) and (7), at equilibrium

$$P_1^* = r_1/a_1, P_2^* = r_2/a_2, \quad R_1^* = \left[C_1 + E - E \left(\frac{a_1/r_2}{a_2/r_2} \right) \right] / a_1 b_1,$$

and

$$R_2^* = \left[C_2 + E - E \left(\frac{a_2/r_2}{a_1/r_1} \right) \right] / a_2 b_2.$$

Given that both prey are present at the equilibrium, the spatial pattern of predator densities tracks the local productivity of prey and is independent of the rate of predator movement. For R_1^* and R_2^* to be positive, condition (8) must hold. The positivity of the joint equilibrium therefore implies mutual invasibility. Random predator movement increases the density of the prey with lower a_i/r_i and decreases the density of the alternative prey. If this equilibrium exists, it is stable provided $r_1 a_1 b_1 R_1^* \neq r_2 a_2 b_2 R_2^*$ (see Appendix). This inequality is guaranteed to hold for almost any parametric combination that incorporates spatial heterogeneity (e.g., $r_1 \neq r_2$, with all other parameters spatially uniform). In the Appendix, I discuss why random dispersal in a heterogeneous environment stabilizes the neutrally stable Lotka-Volterra model.

Habitat partitioning facilitates the coexistence of prey, but within limits set by the rate of predator movement. If the two patches are weakly coupled by predator dispersal (e.g., $E \cong 0$), spatial segregation will allow most species pairs to persist. By contrast, at high rates of dispersal the two patches effectively merge into a single large patch within which predators encounter prey in a fine-grained fashion; the two sides of inequality (8) converge on unity, and only prey with similar sensitivities to predation can coexist.

This two-patch model can be generalized in many ways to n prey species segregated among n patches, depending upon how the predator is assumed to

move among patches. For instance, if predators leave each patch at a per capita rate E , and then disperse uniformly to the other $n - 1$ patches, we have

$$\frac{dP_i}{dt} = P_i(a_i b_i R_i - C_i) + \frac{E}{n-1} \sum_{j \neq i} P_j - EP_i, \quad i = 1, \dots, n,$$

and

$$\frac{dR_i}{dt} = R_i(r_i - a_i P_i).$$

At equilibrium, if prey are present in each patch, $P_i^* = r_i/a_i$, hence

$$R_i^* = \left[C_i + E - \left(\frac{E}{n-1} \right) \sum_{j \neq i} \frac{r_j/a_j}{r_i/a_i} \right] / a_i b_i.$$

Thus, $R_i^* > 0$ only if

$$r_i/a_i > \left(\frac{E}{C_i + E} \right) (\widehat{r/a}),$$

where

$$(\widehat{r/a}) = \frac{1}{n-1} \sum_{i \neq j} r_j/a_j$$

is the average r/a of species in the community other than species i . If prey i has a relatively low r_i/a_i , it is vulnerable to exclusion, particularly if E is high or C_i is low. The question of stability in this n -species model is still open.

To summarize the results of this section, if a predator can choose where to forage without interference from other predators, (at least) as many species of prey can coexist in the predator's diet as there are distinct patches discriminated by the predator. Even with random predator movement, habitat partitioning may permit the coexistence of multiple prey species at high intensities of predation, although this becomes less likely if the predator moves rapidly among patches or experiences a low rate of mortality. For these results to be robust, however, such patterns of habitat partitioning must themselves be stable over time.

4. THE EVOLUTIONARY STABILITY OF HABITAT PARTITIONING BETWEEN PREY

Predation can generate a stable pattern of habitat partitioning, even if in the absence of predation, alternative prey overlap in habitat use. (For instance, the resources required by prey i might not be restricted to patch i .) The essential idea I develop here is that if each prey is superior at withstanding predation in its own patch, each may locally exclude the other because of shared predation; this leads to stable segregation. To examine this idea, we need some additional formalism. Let R_{ij} be the density of prey i in patch j , and F_{ij} its corresponding per capita growth rate. In patch j the intrinsic growth rate of prey i is r_{ij} , and $a_{ij}P_j$ is the rate of capture by predators. We assume that within each patch the predator forages in a fine-grained manner.

Without the predator, prey i should be found wherever $r_{ij} > 0$. We assume that each prey could occupy both patches were there no predation. With the predator, in the models discussed above the segregated prey settle into an equilibrium with $F_{11} = 0$, $F_{22} = 0$, and P_j^* predators in patch j . For this to be stable against cross-patch invasion, it must be the case that $F_{12} < 0$ and $F_{21} < 0$, or $F_{ij} = r_{ij} - a_{ij}P_j^* < 0$, $i \neq j$. Otherwise, an individual of prey i dispersing into patch j would experience a positive growth rate, and the habitat partitioning would break down.

Prey i is excluded from patch j if $r_{ij}/a_{ij} < P_j^*$. P_j^* is in turn influenced by the properties of prey j . In the model of random predator dispersal with exponential prey growth analyzed above, given that $R_j^* > 0$, at equilibrium $P_j^* = r_{ij}/a_{ij}$. Sharp patch specialization thus requires:

(prey 1 excluded from patch 2)

$$a_{12}/r_{12} > a_{22}/r_{22},$$

(prey 2 excluded from patch 1)

$$a_{21}/r_{21} > a_{11}/r_{11}.$$

If, say, the first inequality does not hold, prey 1 can invade. When it does, predator density in patch 2 re-equilibrates at r_{12}/a_{12} and prey 2 becomes extinct. Hence, these inequalities, together with condition (8) (replacing a_{ij}/r_i by a_{ij}/r_{ij}), summarize the requirements for the long-term coexistence of a pair of prey species, stably segregated in space yet indirectly coupled by random predator movement: Each species must in turn have the lower sensitivity to predation in its own patch, and these sensitivities can differ only up to a limit set by the rates of predator dispersal and mortality.

Introducing negative density dependence in the prey (e.g., logistic growth), by lowering prey productivity, decreases equilibrium predator density. This makes it less likely that predation alone can maintain a stable pattern of habitat partitioning.

In the optimal patch selection model, at equilibrium there are $P_i^* = \Phi_i(R_{ii}^*)/a_{ii}$ predators in patch i , where R_{ii}^* is the density of prey i in patch i when it alone supports the predator. Since species j cannot invade if $r_{ij}/a_{ji} < P_i^*$, we again see that habitat partitioning between prey is stable if each prey is excluded by apparent competition from the other's patch. The crucial distinction between the model with random dispersal and the optimal patch selection model is that in the former, a between-patch criterion must be met for prey coexistence (inequality [8]), whereas in the latter, each species must merely be superior at withstanding predation in its own patch.

Habitat partitioning may therefore promote the coexistence of prey by relaxing apparent competition between them, but itself may be stable only because of apparent competition operating separately within each patch.

The circumstances in which habitat partitioning is ecologically stable should also lead to evolutionary stability. It is selectively disadvantageous for an individual of prey to reside in patch j if $F_{ij} < F_{ii}$. Given habitat partitioning, at equilibrium $F_{ii} = 0$, hence patch i should be avoided by prey j if $F_{ii} < 0$, or $r_{ij}/a_{ij} < P_i^*$. The evolution of optimal patch selection by prey thus leads to the same pattern of

habitat specialization as predicted from the invasibility criterion. Levin and Segel (1982) have recently developed a general model for analyzing the evolution of aspect diversity under the influence of predator switching. Their approach promises to illuminate, for a broader range of conditions than considered here, the circumstances in which shared predation can lead to evolutionarily stable habitat partitioning among prey.

5. DISCUSSION

These results suggest that, at high intensities of predation, the coexistence of alternative prey is unlikely within patches of homogeneous habitat, defined as such by patterns of predator movement. Habitat partitioning can permit coexistence even when predation is intense, essentially because it allows the number of predators exploiting a given prey to be determined independently of the availability and productivity of alternative prey. We have seen that this can happen in two distinct ways. First, slow rates of random predator movement may partially decouple the dynamics of predator subpopulations, leaving each largely supported by a single prey species. Secondly, optimal habitat selection by predators may produce a pattern of predator densities across patches such that each prey population is subject to no more predation than would occur were it alone in the predator's diet. The spatial structure of the environment thus can permit a single predator species to provide multiple, partially independent limiting factors (Levin 1970) for the prey community. This is similar to having each prey population attacked by specialized natural enemies, distinct from the enemies attacking other prey, which also allows the maintenance of high prey diversity (Janzen 1970). Here, too, habitat partitioning among prey may be an important aspect of species coexistence. If two prey segregate by habitat, natural enemies specialized to them will also be segregated. If predators specialize by foraging in a particular patch, and attack whichever prey are encountered there, the habitat partitioning may persist because each prey is excluded by predation from the other's patch. Unlike a guild of specialized predators, however, it is possible for "spillover" of general predators to occur between patches so that some prey are excluded from the community despite habitat partitioning.

The potential importance of spatial heterogeneity as a stabilizing factor in interactions between predators and single prey species is widely recognized by ecologists (e.g., Huffaker 1958; Murdoch and Oaten 1975; Levin 1976; McMurtrie 1978; Hastings 1977; May 1978; Hassell 1980; Crowley 1981). Beddington et al. (1978) suggest that spatial heterogeneity, in one guise or another, is the most plausible source of stability at the high intensities of predation documented in many insect host-parasitoid systems. Previous work on prey coexistence in spatially heterogeneous environments has concentrated on predation's effect in preventing competitive exclusion when prey compete for resources (the colonization-extinction models of Caswell [1978], Hastings [1978*b*], and Crowley [1979]), or on the potential for predator switching, which can change a destabilizing functional response to a stabilizing functional response (Murdoch 1977). The models developed here suggest that spatial heterogeneity may also provide axes for niche

diversification among prey even if there is no competition for resources (see also Jeffries and Lawton, in press).

Our results show that spatial variation in either a_i or r_i could be significant in prey community structure. There may be spatial variation in the pattern of predator attacks even if prey resources are uniformly distributed. For instance, slow-moving prey typically rely upon crypsis against their background to escape attacks by predators that hunt visually (Edmunds 1974; Endler 1978). A mosaic of visually distinct backgrounds may provide niche axes for prey diversification if the prey phenotype that best matches one background is vulnerable against other backgrounds (for possible examples, see Ricklefs and O'Rourke 1975; Otte and Joern 1977; Cates et al. 1978). What counts as a "distinct" background is determined by the predator's movement behavior and its ability to discriminate among backgrounds occupied by different prey. Switching behavior may account for the build-up of "aspect diversity" in some communities (Ricklefs and O'Rourke 1975; Levin and Segel 1982), but randomly foraging predators may be responsible for similar patterns in other communities. Given a particular background mosaic, to understand the diversity of the prey community, we must (1) ascertain what limits the number of prey species co-occurring within a given background class; and (2) determine how, if at all, prey in different backgrounds interact with each other via their shared predator. Apparent competition may restrict the number of prey species per background class.

If alternative prey utilize different resources, they are likely to show discordant spatial variation in r , with each species reaching its maximum r at different points across a landscape. If predation is intense and uniform on all species, each prey will be restricted to those areas in which it has the highest relative r . The ability of a prey population to withstand predation is determined both by its direct ability to escape predation (measured by a_i) and by its capacity for replenishing its numbers (measured by r_i). In some cases, habitat partitioning may be closely associated with interspecific differences in resource use, yet exist because of shared predation rather than because of exploitative competition for resources.

Throughout this paper it has been assumed that the indirect interaction between prey is driven by changes in predator population size. I have suggested that optimal patch selection by a food-limited predator meliorates the lot of prey with low productivity if they occupy patches distinct from those occupied by highly productive prey. Even if the total size of the predator's population is fixed independently of the productivity of its prey, however, optimal patch selection by predators can produce (-, -) interactions between alternative prey found in the same patch. Consider a single patch embedded in a very large number of patches, among which predators freely move. The total number of predators is fixed. Initially there is just prey 1 in the patch. A predator in patch 1 feeds at an instantaneous rate $a_1 b_1 R_1$. According to the marginal value theorem (Charnov 1976), predators should enter and remain in this patch until the rate of yield is reduced to the average rate of yield, C' , over all patches; prey availability should be reduced until $a_1 b_1 R_1 = C'$. Now add prey 2 to the patch. The aggregative numerical response of the predators, and their willingness to stay longer in more productive patches, should decrease the total rate of yield in the patch until it is

again reduced to $a_1b_1R_1 + a_2b_2R_2 = C'$; if the second prey is present, the first prey must show a reduction in density as compared with its density when alone. (C' does not change because we are comparing this patch to an average over many patches.) Since the effect is reciprocal, we see that an aggregative numerical response in a spatially heterogeneous environment can produce what amounts to apparent competition between prey within a patch, even if the predator population is not food limited. (W. Mitchell [personal communication] observed a phenomenon similar to this in a study of hummingbird foraging and independently arrived at this prediction of apparent competition based on an application of the marginal value theorem.) Something like this may account for the near extermination of the blue whale by man. Fin whales, which have a higher carrying capacity and intrinsic growth rate than blue whales and overlap with them in space, allow whaling on blue whales to remain profitable even when blue whales are extremely rare (Clark 1976). At an abstract level, exploitative competition, apparent competition resulting from a change in the total number of predators, and apparent competition deriving from an aggregative response, all share one unifying feature: a constraint is placed on the total density of a species assemblage (e.g., $\sum_i a_i b_i R_i^* = C$ in model [1]), and the equilibrium density of a particular species is carved out of this.

What evidence exists to support the validity of these models and, more broadly, the existence of apparent competition? No detailed test of these models has yet been made. Jeffries and Lawton (in press) point out that many field examples match in a general way the expectation that shared predation leads to apparent competition between prey. We might suspect the existence of apparent competition wherever resident predators stably exclude a particular prey species from a community, for the simple reason that a predator population should not be able to persist without sustenance from some prey. This alternative prey should be more resistant to predation than is the excluded prey or it, too, should have been excluded by predation from the community!

Controlled field experiments, an increasingly popular tool in community ecology (Connell 1975, 1983; Schoener 1983), may permit discrimination of the effects of shared predation from those of resource competition. Ideally, such experiments should use a nested experimental design in which the densities of both the predator and its alternative prey are simultaneously varied (Connell 1983). Even if it is impracticable to manipulate predators directly, one can attempt to monitor changes in predator abundance or activity while experimentally altering densities. Munger and Brown (1981) suggest that tracking variation in the abundance of a third prey type, known to not compete with the species pair being manipulated, may allow one to infer changes in the overall level of predation. Interpreting the results of field experiments, however, is not a trivial matter. Short-term manipulations can document the existence of direct interactions between individuals, but may not always display the community-level consequences of such interactions. For instance, predator satiation or switching behavior may produce (+, +) interactions between prey over short time scales, even though the predator's numerical response leads to an indirect (-, -) interaction over longer time scales (Holt 1977). This problem is compounded by the fact that competition for re-

sources and apparent competition are not mutually exclusive hypotheses; species may at once share predators and resources. Moreover, these factors may interact in complex ways not built into the standard models of community theory. An increase in predation may intensify exploitative competition if, for instance, prey hide from predators by crowding into spatially restricted refuges. Like strong competition, strong predator-prey interactions tend to self-destruct, leaving for our study mainly weak ones. A given prey species that is sharply restricted in habitat by shared predation may be rare or even absent in the predator's diet most of the time. If predation intensity is high, over evolutionary time this habitat specialization could become genetically fixed. Experimental manipulations would then show little change in prey distribution following predator removal.

There are serious methodological difficulties in invoking past competition to explain the absence of competition today (Connell 1980). Similar difficulties face any attempt to test evolutionary hypotheses based upon past shared predation. All these caveats aside, manipulative experiments hold great promise for the study of the community-level consequences of shared predation.

Several examples from natural communities strongly suggest that apparent competition does occur and leads to habitat partitioning between prey.

Gilbert (1984) suggests that rare *Heliconius* butterflies are confined to a restricted range of larval host plants, species not used by more common *Heliconius* species, so as to escape parasitoids supported by these more common prey. The parapatric distributions of the arctic hare (*Lepus arcticus*, tundra) and the snowshoe hare (*L. americanus*, forests) in Newfoundland appear to result from shared lynx predation (Bergerud 1967, 1983; see Holt 1977 for further discussion). Kotler (1984) presents evidence that microhabitat use and niche separation in desert rodents are influenced by predation. Parker and Root (1981) have experimentally demonstrated that herbivory by the acridid grasshopper *Hesperotettix viridis* produces a pattern of spatial segregation between the composition *Gutierrezia sarothrae* (arid grasslands) and *Machaeranthera canescens* (roadsides). In two examples the predator population in one patch is maintained by one resistant prey (lynx on snowshoe hare; *H. viridis* on *G. sarothrae*) and is therefore able to consume to the point of local extinction an alternative prey.

The classic accounts by Dodd (1940, 1959) of the moth *Cactoblastis cactorum* laying waste the introduced cactus *Opuntia* in Australia include natural history anecdotes suggestive of the phenomena modeled here. *Cactoblastis* appears to limit the abundance of *Opuntia*, and is in turn limited by the availability of its food (Monro 1967, 1975; Birch 1971). At its height, the cactus infestation included 12 species of *Opuntia*. Dodd suggests that the efficacy of control by *Cactoblastis* was at times determined by the availability of alternative host plants. For example, the tree cactus *O. streptacantha* was largely resistant to herbivory when adult (providing a partial refuge from herbivory), but new joints and young individuals were attacked. The presence of stands of this species led to more effective control of other *Opuntia* species because the moth could be stably maintained at higher densities. Variation in growth form in two species, *O. inermis* and *O. stricta*, provides another good example. One variety, known as "yellow pear" for its yellowish-green appearance, is stunted, grows slowly, and is nitrogen-deficient in

comparison with the typical form. It occurs on poor soils, particularly on stony ridges, whereas the typical green form occupies richer soils. Dodd notes that, when yellow pear was found in patches embedded in much more extensive stands of the ordinary succulent form, it was efficiently destroyed by an overflow of *Cactoblastis* from surrounding stands of the typical form. In New South Wales, however, yellow pear was predominant and the succulent form patchy in distribution. Here *Cactoblastis* was much less effective at controlling populations of both the yellow and typical form. Dodd experimentally demonstrated that increasing the nitrogen content of the soil transformed yellow pear into green pear and produced a buildup in the *Cactoblastis* population. Not only did the moth better control the treated area, but a spillover of moths led to a reduction in *Opuntia* densities in neighboring, untreated, yellow pear areas; the enriched populations of *Opuntia* indirectly reduced the densities of other, spatially separated populations. Hence, local "hot spots" with high prey productivity can depress prey densities in adjacent areas with low productivity if there is a net outflow of predators from the high productivity area. As discussed above, a net outflow is assured if predators passively disperse or if social interactions in productive patches force some individuals to emigrate. In the *Cactoblastis-Opuntia* system, spillover may have occurred for an additional reason: as moths overexploited one population of *Opuntia*, it may have become advantageous for them to disperse into adjacent areas, in which case the observed overflow might be a transient phenomenon of the initial dynamics of the system.

I have concentrated here on the influence of mobile predators on immobile prey. To fully characterize the requirements for prey coexistence or exclusion, one may often need to consider the effects of prey movement as well. Two examples illustrate this point. In the vineyards of the San Joaquin Valley, Flaherty (1969) observed that the Willamette mite, *Eotetranychus willametti*, occurred in lower densities on grapevines surrounded by Johnson grass than it did on vines kept clear of the grass. Yet its principal predator, the spider mite *Metaseiulus occidentalis*, occurred in both vine habitats. The grass supported a second species, the two-spotted mite *Tetranychus urticae*, which moved onto grape leaves in response to deteriorating food quality. The spider mite was restricted to grape leaves but seemed to prefer the two-spotted mite, when available. Flaherty reasoned that the influx of a preferred prey species allowed the predatory mite to depress the Willamette mite to lower densities than otherwise possible. Patterns of host mobility may similarly influence the outcome of indirect interactions arising from shared parasitism. Embree (1979) suggests that white-tailed deer indirectly limit the geographical range of caribou and the local habitat distribution and abundance of moose by supporting populations of a nematode parasite, relatively benign when infecting deer but fatal in both caribou and moose. He argues that differences in movement patterns account for the difference in the spatial consequences of this indirect interaction. Caribou herds wander over wide areas and are likely to come into contact with parasitized populations of the intermediate host (terrestrial gastropods, consumed incidentally during browsing) maintained by infected deer populations. By contrast, moose are solitary and

rather sedentary and thus may persist, uninfected, in isolated patches of habitat unsuitable for deer (typically, woods with a deep winter blanket of snow). These examples suggest that one must consider the movement patterns of prey, as well as of predators, to understand the full implications of spatial heterogeneity for prey community structure.

SUMMARY

Predation may generate patterns in the structure of communities similar to those produced by competition. The potential role of spatial heterogeneity in promoting the coexistence of prey species is explored with both analytical and graphical models. In these models, prey interact indirectly through their effect on predator numbers: an interaction that leads to "apparent competition" and a problem in species coexistence. A model of prey coexistence in a homogeneous habitat is explored. If prey grow logistically, prey abundance is measured by the effect prey have on predator growth, and the predator consumes prey in a fine-grained manner, the criterion for species k to remain in the community takes a simple form: its sensitivity to predation (a_k/r_k) cannot exceed the average sensitivity to predation of the entire community, (\bar{a}/\bar{r}) , divided by a measure of the intensity of predation on the community (Δ). At high Δ , species must have very similar values for a_i/r_i to coexist. This suggests that in spatially homogeneous environments, prey coexistence is difficult to achieve at high intensities of predation.

There are two distinct ways in which spatial segregation may promote prey coexistence. First, habitat selection by the predator may provide each prey with an implicit refuge in the presence of the alternative prey, because predators will tend to leave a habitat in which their foraging yields are relatively low. If predators can select their habitats optimally without cost, and without interference from other predators, it is shown that at equilibrium no prey suffers a reduction in density because other prey are present in the diet. Nonoptimal habitat selection or interference between predators makes prey that have either low intrinsic growth rates (r_i) or high rates of predator attack (a_i) vulnerable to density reductions or extinction, as a result of predator "spillover" between patches.

Second, if prey are spatially segregated, the predator population may be broken into two, partially independent subpopulations coupled by random predator movement. If each prey grows exponentially in the absence of predation, the permissible difference in their sensitivities to predation (a_i/r_i) is bounded by a measure of spatial coupling; the more tightly the two patches are linked by predator movement, the more similar the values for a_i/r_i must be if the prey are to continue to coexist. This model also provides a simple illustration of how spatial heterogeneity may stabilize an otherwise unstable predator-prey system.

The evolutionary stability of segregation between prey is briefly discussed. Even if habitat partitioning relaxes apparent competition between prey occupying separate patches, the segregational pattern itself may persist because of apparent competition within each patch.

Several examples from field studies suggest that habitat partitioning and the movement behavior of both predators and prey are important factors affecting coexistence in prey communities.

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APPENDIX

1. LOCAL STABILITY

We will analyze the local stability properties of the following model, which is more general than the one discussed in the text in that it allows asymmetrical patterns in predator dispersal as well as in the other parameters of the model:

$$\begin{aligned} dP_i/dt &= P_i(a_i b_i R_i - C_i) - E_{ii} P_i + E_{ij} P_j, & i, j = 1, 2, & i \neq j \\ dR_i/dt &= R_i(r_i - a_i P_i). \end{aligned} \quad (A1)$$

We assume that $E_{11} \geq E_{21}$ and $E_{22} \geq E_{12}$, which is to say that either dispersal is conservative or predators die during dispersal. Consider first the case with $R_2 = 0$ (a "source-sink" model). The equilibrium population densities are $P_1^* = r_1/a_1$, $P_2^* = P_1^* E_{21}/(C_2 + E_{22})$, and $R_1^* = [C_1 + E_{11} - E_{12} E_{21}/(C_2 + E_{22})]/a_1 b_1$.

The Jacobian is

$$J = \begin{bmatrix} a_1 b_1 R_1^* - C_1 - E_{11} & E_{12} & a_1 b_1 P_1^* & - E_{12} E_{21}/(C_2 + E_{22}) & E_{12} & r_1 b_1 \\ E_{21} & -C_2 - E_{22} & 0 & E_{21} & -C_2 - E_{22} & 0 \\ -a_1 R_1^* & 0 & r_1 - a_1 P_1^* & -a_1 R_1^* & 0 & 0 \end{bmatrix}$$

The characteristic equation is $\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0$, where $a_1 = E_{12} E_{21}/(C_2 + E_{22}) + C_2 + E_{22}$, $a_2 = r_1 b_1 a_1 R_1^*$, and $a_3 = (r_1 b_1 a_1 R_1^*)(C_2 + E_{22})$, and λ is an eigenvalue of J . For each of the three eigenvalues to have negative real part, by the Routh-Hurwitz criterion (May 1975) it must be true that $a_1 > 0$, $a_3 > 0$, and $a_1 a_2 > a_3$. By inspection, the first two inequalities hold, and the third reduces to $E_{12} E_{21}/(C_2 + E_{22}) > 0$, which is true for all $E_{12} E_{21} > 0$, and E_{22} and $C_2 < \infty$. Hence the equilibrium is locally stable for all possible patterns of density-independent dispersal, except when the predator moves so rapidly that the two patches merge into one, or the rate of mortality in the sink is so great that no predators are maintained there at equilibrium, or there is no back migration ($E_{21} = 0$).

The Jacobian of the full four-dimensional model with $R_1^* > 0$ and $R_2^* > 0$ is

$$\begin{bmatrix} a_1 b_1 R_1^* - C_1 - E_{11} & E_{12} & a_1 b_1 P_1^* & 0 & -E_{12} \mu & E_{12} & b_1 r_1 & 0 \\ E_{21} & a_2 b_2 R_2^* - C_2 - E_{22} & 0 & a_2 b_2 P_2^* & = & E_{21} & -E_{21} \mu^{-1} & 0 & b_2 r_2 \\ -a_1 R_1^* & 0 & r_1 - a_1 P_1^* & 0 & -a_1 R_1^* & 0 & 0 & 0 \\ 0 & -a_2 R_2^* & 0 & r_2 - a_2 P_2^* & 0 & a_2 R_2^* & 0 & 0 \end{bmatrix}$$

where $\mu = (a_1/r_1)/(a_2/r_2)$ is a measure of the relative sensitivities of the two prey to predation. $R_1^* = (C_1 + E_{11} - E_{12}\mu)/a_1 b_1$ and $R_2^* = (C_2 + E_{22} - E_{21}\mu^{-1})/a_2 b_2$. The characteristic equation is $\lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 = 0$, in which $a_1 = E_{12}\mu + E_{21}\mu^{-1}$, $a_2 = b_1 r_1 a_1 R_1^* + b_2 r_2 a_2 R_2^*$, $a_3 = E_{21}\mu^{-1} b_1 r_1 a_1 R_1^* + E_{12}\mu b_2 r_2 a_2 R_2^*$, and $a_4 = (b_1 r_1 a_1 R_1^*)(b_2 r_2 a_2 R_2^*)$. The first three Routh-Hurwitz stability criteria, $a_1 > 0$, $a_3 > 0$, and $a_4 > 0$, are satisfied if $R_1^*, R_2^*, E_{12} > 0$, and $E_{21} > 0$. The fourth criterion is $a_1 a_2 a_3 > a_3^2 + a_1^2 a_4$. After some manipulation, this reduces to $(b_1 r_1 a_1 R_1^* - b_2 r_2 a_2 R_2^*)^2 > 0$, which is the condition cited in the text. This is true provided $r_1(C_1 + E_{11} - E_{12}\mu) \neq r_2(C_2 + E_{22} - E_{21}\mu^{-1})$. This inequality holds if all parameters in turn are spatially homogeneous except for (1) $C_1 \neq C_2$; (2) $a_1 \neq a_2$; (3) $r_1 \neq r_2$; (4) $E_{11} - E_{12} \neq E_{22} - E_{21}$ (e.g., asymmetrical dispersal, $E_{11} = E_{21} \neq E_{12} = E_{22}$); (4) $\mu \neq 1$, $r_1 \neq r_2$, and $r_1/r_2 \neq (1 - Q\mu^{-1})/(1 - Q\mu)$, where $Q = E/(C + E)$ ($E = E_{11} = E_{12} = E_{21} = E_{22}$). Spatial heterogeneity in prey productivity, rates of attack, predator death rates, or predator dispersal rates may stabilize the interaction.

2. THE STABILIZING INFLUENCE OF DISPERSAL IN A HETEROGENEOUS ENVIRONMENT

Model (A1) could also describe two populations of a single prey species. There is an enormous literature on the stability of one-predator, one-prey interactions. Space may facilitate the persistence of predator-prey interactions in several distinct ways. Levin (1976) usefully distinguishes between phase differences and local uniqueness.

A. *Phase differences.*—If dispersal rates are sufficiently low, the sheer size of a system may permit spatial variation in population densities to arise and be maintained by chance events in colonization, extinction, and population growth. This effect has been extensively explored in discrete state, extinction-colonization models (Maynard Smith 1974; Hilborn 1975; Hastings 1977, 1978b; Zeigler 1977; Caswell 1978; Gurney and Nisbet 1978; Crowley 1979). In these models, the prey is a fugitive species, able to coexist with a predator regionally, despite local extinctions, because of colonization of new patches. Crowley (1981) shows that in a sufficiently large system of numerous identical cells, phase differences in oscillations may lead to nearly constant, spatially averaged densities, although no single cell is stable. However, it is well known that in a homogeneous environment, random dispersal does not by itself stabilize (in the sense of local stability) the neutrally stable Lotka-Volterra model (Chewning 1975; Hastings 1978a; McMurtrie 1978; Crowley 1981).

B. *Local uniqueness.*—It is well known that in a spatially heterogeneous environment, nonrandom behavior by either predator or prey can be stabilizing. Nonrandom predator search for clumped prey tends to stabilize both host-parasitoid models (Hassell and May 1974; May 1978) and predator-prey models (Murdoch and Oaten 1975; Murdoch 1977). Optimal patch use by predators in effect provides a relative refuge for prey in low density patches (Comins and Hassell 1979; Hassell 1980). Nonrandom escape behavior by the prey may also stabilize the interaction (Sih 1980). For instance, if a fixed number of prey hide in refuges, and the remainder are exposed to predation, the Lotka-Volterra model becomes stable (Murdoch and Oaten 1975).

It seems to be less well known that random dispersal in a spatially heterogeneous environment can also produce a stable interaction. Our analysis of the two-patch Lotka-Volterra model (eqq. [A1]) demonstrates that almost any combination of anisotropic dispersal and inhomogeneous growth parameters leads to a locally stable equilibrium. The stabilizing effect of asymmetrical dispersal in a homogeneous environment has been previ-

ously noted by Comins and Blatt (1974). Chewning (1975) showed that small amounts of migration in a heterogeneous environment are stabilizing. Kawasaki and Teramoto (1979) constructed a Lyapunov function for a chain of patches, each described by the Lotka-Volterra model and linked to adjacent patches by passive, symmetrical dispersal. Their result shows that model (A1) (which describes a chain of two patches) is globally as well as locally stable if $E_{11} = E_{22} = E_{12} = E_{21}$ and the other parameters are spatially heterogeneous. To hone our intuition as to why spatial heterogeneity is stabilizing in this model, consider what happens when patch 2 is coupled to an external "bath" (Levin 1976; Crowley 1981), rather than to patch 1. The model is $dP_2/dt = P_2(a_2b_2R_2 - C_2) + I$ and $dR_2/dt = R_2(r_2 - a_2P_2)$, which is stable for all $I > 0$. Even if no prey are present ($R_1 = 0$), the predator is stably maintained by immigration at $P_2^* = I/C_2$. In the special case of model (A1) when $R_2^* = 0$ because of predator overflow from patch 1, $dP_2/dt = P_2(-C_2 - E_{22}) + E_{21}P_1$. Were P_1 constant, patch 1 would be a "bath" stabilizing the dynamics of patch 2. But of course P_1 may vary through time. The equation for dP_2/dt is a linear differential equation, which can be formally solved to give

$$P_2(t) = P_2(0)e^{-(C_2 + E_{22})t} + E_{21} \int_0^t P_1(t')e^{-(C_2 + E_{22})(t' - t)} dt'.$$

For simplicity, set $P_2(0) = 0$, and substitute into dP_1/dt :

$$dP_1/dt = P_1(a_1b_1R_1 - C_1 - E_{11}) + E_{12}E_{21} \int_0^t P_1(t')e^{-(C_2 + E_{22})(t' - t)} dt'.$$

The sink habitat thus has two distinct effects on the dynamics of P_1 : it increases the effective rate of mortality, from C_1 to $C_1 + E_{11}$; and it provides a source of time-lagged recruitment, comparable in effect to coupling with a "bath." Hastings (1983) has recently observed that time lags in recruitments can stabilize predator-prey systems. There appears to be a correspondence between the stabilizing influence of such recruitment and the effect of a predator sink, and between both of these and coupling with an external "bath." If $a_1/r_1 < a_2/r_2$, with passive dispersal patch 1 is a "source," and patch 2, a "sink," even if $R_2^* > 0$. This suggests that a source-sink phenomenon accounts in part for the stability of this two-patch system.

Now consider the case of $a_1/r_1 = a_2/r_2$. Because the two prey populations are equally sensitive to predation, $R_1^* = C_1/a_1b_1$. Neither predator population is a source or sink for the other: $P_1^* = P_2^*$. Let us assume $b_1 = b_2$, $r_1 = \alpha r_2$, $a_1 = \alpha a_2$, and $C_1 = \alpha C_2$, where $\alpha > 1$. This implies $R_1^* = R_2^*$. The stability condition is $r_1a_1b_1R_1^* \neq r_2a_2b_2R_2^*$, which reduces to $r_1C_1 \neq r_2C_2$. This is true for all $\alpha > 1$. We therefore have constructed a class of examples in which both the predator and prey have spatially uniform densities, yet their interaction is stable nonetheless. This suggests that the source-sink explanation of stability in this model is not the full story.

Recall that if patch i is isolated, it exhibits neutrally stable oscillations around the center (R_i^* , P_i^*) with a period approximately proportional to $\sqrt{r_iC_i}$. If $r_1C_1 \neq r_2C_2$, dispersal couples patches that, in isolation, oscillate with different periods. The stability of the system appears to be related to this spatial variation in period.

We can conclude that spatially heterogeneity allows random dispersal to be stabilizing for two distinct reasons. First, parametric variation may lead to spatial variation in abundances. Random dispersal sets up a system of sources and sinks, and the time lag provided by dispersal into and out of the sinks tends to buffer fluctuations in the source populations. This stabilizing effect of sink habitats is quite general (Holt 1984). Secondly, even if there is no spatial variation in abundance, there may be spatial variation in the natural periodicity of local systems. In this model, coupling patches with different periods by random dispersal leads to a stable system. However, coupled oscillators may exhibit quite complex behaviors (for a general review, see Winfree 1980), so this effect may not be a general property of predator-prey systems in spatially heterogeneous environments.

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