



Short-Term Apparent Competition

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SHORT-TERM APPARENT COMPETITION

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When MacArthur and Pianka (1966) first formulated the basic concepts of optimal foraging theory, they aimed at constructing a theory of community structure based on the economics of consumer choice (MacArthur 1972). In subsequent years, optimal foraging models have typically focused more narrowly on aspects of individual ecology. Ecologists have recently begun to reconsider the implications of this body of ideas for population dynamics and interspecific interactions (see, e.g., Rosenzweig 1981, 1985; Pimm and Rosenzweig 1981; Abrams 1984, in press; Belovsky 1984; Sih 1984; Hassell and May 1985; Schoener 1986). An understanding of the foraging behavior of predators is essential for, among other things, predicting the influence of predators on the coexistence of prey species. The importance of predation in determining the species composition of communities is now widely recognized (see, e.g., Connell 1975; Menge and Lubchenco 1981; Jeffries and Lawton 1984; Kotler 1984). Field experiments in a wide variety of communities have demonstrated that predators can greatly reduce the density of prey populations and shift competitive dominance among prey species (Sih et al. 1985). If two prey species compete for a limited resource, optimal foraging by a shared predator can in some circumstances enhance their chances for sustained coexistence (Gleeson and Wilson 1986).

Shared predation can also generate indirect interactions among otherwise noninteracting, potentially coexisting prey. A positive numerical response by a food-limited predator to each prey type in its diet leads to a $-,-$ relationship between the equilibrium densities of alternative prey (see Holt 1977 for a formal argument). This indirect interaction between prey is labeled "apparent competition" to distinguish it from either direct interference or exploitative competition. Many of the community patterns traditionally explained by resource competition may also be caused by shared predation. For instance, in a spatially heterogeneous environment, shared predation can lead to habitat partitioning among prey species even in the absence of direct competitive interactions (Holt 1984). Considerable evidence from a number of communities suggests that natural enemies do in fact influence patterns of habitat segregation among prey (e.g., desert rodents, Kotler 1984; *Heliconius* butterflies, Gilbert 1984; phytophagous insect com-

munities in general, Lawton 1986; grasshoppers, A. Joern, pers. comm.). However, it seems unlikely that numerical responses by entire predator populations of the sort envisaged earlier (Holt 1977; see also 1984) can always account for the observed segregational patterns. Predators are often considerably larger in body size than their prey and have correspondingly longer generations (Peters 1984). This means that on the time scale governing prey dynamics, predator numbers should vary relatively little. This might seem to imply that apparent competition should not be predicted for any prey whose predators show only a slow demographic response to changes in prey numbers.

Yet, alternative prey types may interact indirectly through their effects on the feeding behavior of individual predators, as well as through the numerical response of entire predator populations. In this paper, we examine the influence of predator foraging behavior in a patchy environment on the character of the indirect interaction between alternative prey species within a single patch. Simply stated, if predators are mobile, they may show an aggregative numerical response to an increase in the density of prey within a given patch. This local numerical response can occur quite rapidly, compared with the predator's generation length. As briefly noted earlier (Holt 1984), even if total predator numbers are fixed, an aggregative response to total prey numbers in a patch can lead to apparent competition between alternative prey species within that patch. We elaborate on this argument below and suggest that the effect is most likely if predators forage in accord with a simple optimality criterion (the marginal-value theorem; Charnov 1976) for deciding when to enter or leave a patch. Alternative foraging rules can lead to interactions in which just one prey species benefits from the presence of another prey species in its patch (a +, - interaction) or in which each benefits from the other (a +, + interaction). The qualitative nature of the interaction between alternative prey species in a patchy environment is thus strongly influenced by the rules guiding individual predator behavior.

THE MODEL

The theory developed here is cast in a graphical form that allows the consequences of different foraging rules to be contrasted easily. We focus on how the presence of one prey species in a patch influences the cumulative mortality experienced by a second prey species in the same patch. Incorporating these effects into a population-dynamics model with prey recruitment is discussed elsewhere (Holt, in press).

Consider a patchy environment made up of numerous discrete patches among which predators move during foraging. Two prey species are present. Both prey types can potentially be found together in any patch. Coexistence is ensured if each prey type can increase when rare. When one of the prey species (say species 2) is rare, it should be found in just one or a few of the patches available for predator foraging. We concentrate on prey population dynamics in these few patches (out of the many over which predators forage) in order to elucidate the influence of shared predation on the chances of persistence of a rare prey species or of a rebound attempt by a typically common species from a transient phase of

low numbers. The rate of increase of a rare prey species depends in part on the rate of predation it experiences. To what degree is this rate of predation augmented or diminished by the presence of alternative prey in patches occupied by the rarer prey? To answer this question, we must consider how the presence of an alternative prey influences two components of predator foraging behavior: the functional response, including handling-time effects and predator selectivity (selectivity may change as the patch is depleted); and patch choice and exploitation.

Diet Choice and Patch Depletion

We assume that if the predator includes prey species i in its diet, the instantaneous rate of consumption of prey i by an individual predator within a patch (C_i) is adequately described by the widely used "disc" equation (Holling 1965; for discussion of the two-species case, see Lawton et al. 1974; Murdoch and Oaten 1975):

$$C_i = \frac{a_i R_i}{1 + \sum_{j=1}^2 a_j h_j R_j}, \quad (1)$$

where a_j is the instantaneous rate of capture of prey j during search (if the predator does not incorporate prey j in its diet, $a_j = 0$); h_j , the per-item handling time; and R_j , the density of prey j .

Equation (1) describes a type-2 functional response by the predator to each of its prey (given that the prey type is included in the diet). That is, the total rate of consumption of prey i increases monotonically with its density, but the rate of mortality per unit of prey is inversely density-dependent. We can use this model to describe how exploitation depresses prey numbers within a patch (Charnov et al. 1976) and to examine diet selectivity. If there are $P(t)$ predators in the patch at time t , the rate of depletion of prey numbers because of consumption is

$$\frac{dR_i}{dt} = \frac{-a_i R_i P(t)}{1 + \sum_{j=1}^2 a_j h_j R_j}, \quad i = 1, 2. \quad (2)$$

For illustrative purposes, we further assume that a given bout of patch depletion is short enough in duration that prey recruitment and nonpredatory mortality can be ignored. This in effect means that relative to prey recruitment, the number of predators changes rapidly as a result of movement into or out of the patch. Equation (2) then completely describes the rate of decline of the population of prey i in a patch.

Both prey species decrease in number if the predator is nonselective ($a_i > 0$, $i = 1, 2$). From equation (2),

$$(dR_1/dt)/(dR_2/dt) = dR_1/dR_2 = a_1 R_1/a_2 R_2. \quad (3)$$

With an initial density $R_i(0)$ of prey i , solving equation (3) yields

$$R_2(t) = R_2(0) [R_1(t)/R_1(0)]^{a_2/a_1}. \quad (4)$$

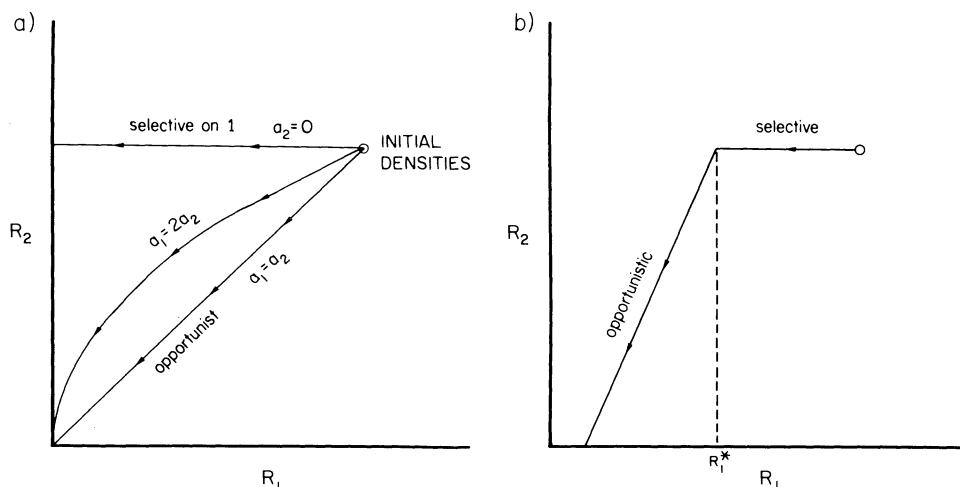


FIG. 1.—Patch-depletion trajectories for two prey species, without recruitment, from equation (2) in text. R_i , density of prey i ; a_i , attack rate per predator, per prey, during search; open circles, initial densities. *a*, Patch depletion by predators selective on prey 1 and by two opportunistic foragers (the curved trajectory is for a predator better able to capture prey 1). *b*, Patch depletion by a predator that feeds selectively on prey 1 for $R_1 > R_1^*$ and broadens its diet to include prey 2 for $R_1 < R_1^*$; when feeding opportunistically, the predator feeds evenly on both prey ($a_1 = a_2$).

Equation (4) describes patch-depletion trajectories in a phase plane with axes (R_1, R_2). Some examples are shown in figure 1*a*. If $a_1 = a_2$, the trajectory of prey numbers during patch depletion is a straight line connecting the initial densities to the origin. If $a_1 > a_2 > 0$, prey numbers follow a curved trajectory as the patch is depleted. For a selective predator, the patch-depletion trajectories are either horizontal lines (selection of prey 1 only) or vertical lines (selection of prey 2 only). The trajectories are independent of temporal variation in both handling times and predator density; although these quantities do influence the rate at which prey populations move along the trajectory from a given set of initial densities, they do not change the shape of the trajectory itself.

If foraging rates influence predator fitness (Schoener 1971), predators may be labile in choosing prey within patches. When overall prey numbers are high, predators might select only high-quality prey. As prey numbers decline as a result of exploitation, initially selective predators might become less discriminating. Figure 1*b* shows a patch-depletion trajectory for a predator switching from a selective to an opportunistic diet at a threshold density R_1^* of prey 1. At R_1^* , the trajectory has a discontinuous change in slope.

Standard optimal-diet models (reviewed in Pyke 1984) assume that prey abundances are constant during foraging. These models thus cannot be applied straightforwardly to diet choice within patches that are depleted during exploitation. In the Appendix, we argue that if multiple predators aggregate and forage within a patch, the evolutionarily stable foraging strategy is the one that maximizes the instantaneous rate of foraging yield. This leads to a simple criterion for

diet selectivity (expression 7, below). If only a single predator forages within a patch, however, this criterion does not hold (Heller 1980; W. Mitchell and J. Brown, pers. comm.; see the Appendix). We therefore assume in the remainder of the paper that more than one predator forages in the patch. As discussed more thoroughly below, relaxing the assumption that predators maximize their instantaneous rate of yield throughout their foraging bouts does not affect the salient qualitative conclusions of the present model.

If alternative prey are substitutable resources (in the sense of Tilman 1982), each captured individual of prey species i is worth a net amount b_i to the predator (measured in a common currency such as joules). Further, if equation (1) describes the rate of capture of prey i , then the instantaneous rate of foraging yield for an opportunistic predator is

$$Y_g = (b_1 a_1 R_1 + b_2 a_2 R_2) / (1 + a_1 h_1 R_1 + a_2 h_2 R_2). \quad (5)$$

The instantaneous rate of foraging yield for a predator selecting just prey 1 is

$$Y_s = b_1 a_1 R_1 / (1 + a_1 h_1 R_1). \quad (6)$$

Expression (6) assumes that the predator can instantaneously distinguish the two prey types (see Hughes 1979; Holt 1983). If the predator maximizes its instantaneous rate of yield, the predator should selectively feed on prey 1 if and only if $Y_s > Y_g$, which implies that

$$b_2 / h_2 < b_1 a_1 R_1 / (1 + a_1 h_1 R_1). \quad (7)$$

We assume that $b_1 / h_1 > b_2 / h_2$; hence, at sufficiently high R_1 , the predator selects only prey 1. But if inequality (7) is reversed, the predator should include prey 2 in its diet. Criterion (7) determines a threshold density of the better-quality prey; below this density, the predator expands its diet to include the lower-quality prey. This simple diet model has been derived and discussed by many authors (for review, see Pyke 1984). For a variety of reasons, predators may in some circumstances appear to have a suboptimal choice of diet, as gauged by this model, because of constraints not incorporated into it. For instance, if substantial time must be invested in discriminating between prey types, foragers should be more opportunistic than the threshold criterion (7) predicts (Hughes 1979; Holt 1983). Below, when we say that a predator shows "suboptimal" foraging behavior, we mean only that the predator does not forage in accordance with the canonical predictions of simple diet-choice and patch-use models, not that the predator's behavior is maladaptive in any ultimate sense.

Patch Use

The structure of the foraging models discussed above suggests that a rare prey species benefits from co-occurring in patches with a more common prey species (particularly if the rarer prey is less preferred). If a predator is an opportunistic forager, it is clear from expression (2) that the alternative prey experience short-term mutualism:

$$(\partial / \partial R_j) \{ (dR_i / dt) / R_i \} > 0, \quad i \neq j.$$

Consumption of individuals of one prey species reduces the time available to the predator for encountering and capturing the alternative prey (for further discussion, see Holt 1977; Abrams, in press). Moreover, predator selectivity may provide an implicit refuge for a low-quality prey, if the preferred prey is sufficiently abundant. Considerations of the form of the functional response and diet selectivity thus suggest that alternative prey within a patch should enjoy a form of indirect mutualism.

However, the total rate of mortality experienced by prey also depends on the amount of time predators spend foraging in a patch and the number of predators attracted to the patch. The time a predator remains in a patch should reflect a variety of factors, including the rate of return from that patch, expected rates of yield in other patches, and the cost of moving among patches. The marginal-value theorem (Charnov 1976) provides a simple optimality criterion to determine when a predator should leave a given patch: the predator should depart when its instantaneous rate of foraging in the patch, $Y(R_1, R_2)$, declines to the average rate of yield, \hat{Y} , over the entire habitat in which the predator is foraging (\hat{Y} includes the cost of moving from one patch to another). Conversely, if $Y(R_1, R_2) > \hat{Y}$, predators should aggregate in the patch and remain until prey densities are reduced to the point at which $Y(R_1, R_2) = \hat{Y}$. Considerable evidence (summarized in Krebs et al. 1983) shows that the marginal-value theorem is qualitatively correct.

Recall that we are examining prey dynamics in a single patch out of the many patches over which predators can forage. If a large pool of predators is distributed over these patches and most predators are foraging elsewhere as a single patch is depleted, then it is reasonable to assume that \hat{Y} is a constant. This allows the patch-use rules to be displayed graphically (fig. 2). The instantaneous rates of return from foraging, $Y(R_1, R_2)$, can be plotted as families of curves: $Y(R_1, R_2) = k$, where k is a constant, in a phase plane with axes R_1 and R_2 . We call these curves "constant-yield isoclines"; for the combinations of prey densities along a given isocline, the predator's instantaneous rate of return from foraging is a constant value. We call the particular isocline described by $Y(R_1, R_2) = \hat{Y}$ the "giving-up isocline." Figure 2 shows three possible shapes for the giving-up isocline. These curves are examples of isolegs (Rosenzweig 1981), which are graphical depictions of the relationship between individual behavior (in the present case, patch use) and system variables (prey densities). By assuming that predators are drawn from a large pool and enter or leave the patch rapidly, as compared with prey recruitment, we ensure that the predator depresses prey abundances to values near or within the giving-up isocline.

To examine in more detail the circumstances giving rise to these isocline shapes, we assume that equations (5) and (6) describe the rates of return for opportunistic and selective foragers, respectively. A selective forager leaves a patch when $Y_s = \hat{Y}$. The quantity Y_s is a function of R_1 only, and hence this corresponds to a vertical isocline (fig. 2*b*). If it is optimal for the predator to be selective at the time it leaves the patch (when densities of the preferred prey are lowest during the foraging bout), obviously it is optimal for the predator to be selective during the entire time it is in the patch. This implies that neither prey has an effect on the other through shared predation. Moreover, a vertical giving-up

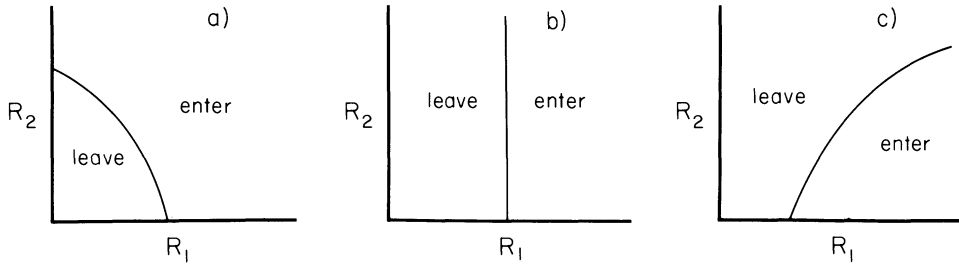


FIG. 2.—Giving-up isoclines. The lines are such that $Y(R_1, R_2) = \hat{Y}$, where R_i is the density of prey i (i.e., the rate of foraging for a predator in a patch just matches the average rate of foraging over the entire constellation of patches among which predators move). To the right of each line, prey densities are high enough for predators to be willing to enter and remain in the patch. To the left, it pays predators to leave the patch. Predators tend to depress prey abundances until they lie along the giving-up isocline. *a*, The isocline has a negative slope; sufficiently high densities of each prey species can make the patch attractive to predators. *b*, The predator is indifferent to the presence of prey 2. *c*, The predator feeds suboptimally on prey 2; an increase in the abundance of prey 2 reduces the quality of the patch. This leads to a giving-up isocline with a positive slope.

isocline implies that there is no density of prey 2 for which it pays a predator to enter a patch containing prey 2 alone.

An opportunistic forager abandons the patch when $Y_g = \hat{Y}$. These constant-yield isoclines are straight lines with either negative or positive slopes: the opportunist giving-up isocline has a negative slope if it is optimal to be a generalist at the moment of patch departure as gauged by criterion (7); if, by contrast, opportunistic foraging is suboptimal, the opportunist isocline has a positive slope (for more details, see Holt 1983). Just before a predator leaves a patch, the optimal-diet strategy should be to maximize the instantaneous rate of return from foraging, regardless of the criterion used in expanding the diet as the patch is depleted. Hence, an opportunistic predator with an optimal diet at the time of departure has a giving-up isocline with a negative slope; by contrast, an opportunistic predator with a suboptimal diet at the time of departure has a giving-up isocline with a positive slope.

Within-Patch Interactions between Prey

We now examine three models that combine in various ways optimal and suboptimal diet and patch use by the predator. In the first model, the optimal-diet model is joined with the marginal-value theorem (fig. 3). For prey densities to the right of the heavy vertical line denoted R_1^* in figure 3, the predator should be a specialist; to the left of the line, it should be a generalist. Several patch-depletion trajectories are shown. In a rich environment (dashed line), $\hat{Y} > R_1^*$, and the predators remain selective on prey 1 throughout the foraging bout, ignoring prey 2 entirely. In a poor environment, $\hat{Y} < R_1^*$, and the predator feeds opportunistically by the time it leaves the patch. The consequences of this for prey abundances are shown in figure 4. The open circles show three combinations of initial prey densities— $[R_1(0), 0]$, $[0, R_2(0)]$, and $[R_1(0), R_2(0)]$ —all assumed to be within the

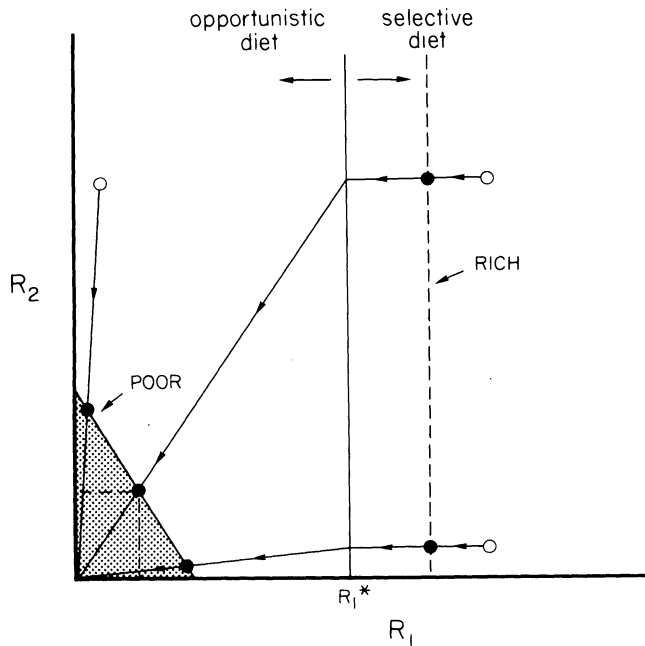


FIG. 3.—Giving-up isoclines and patch-depletion trajectories: within-patch optimal diet and optimal-patch departure by predator. $a_1 = a_2$; $b_1/h_1 = 1$; $b_2/h_2 < 1$. In a rich environment, the predator specializes on prey 1 throughout its foraging bout and leaves when prey 1 (the preferred prey) is depressed to the dashed line. In a poor environment, the predator switches from a selective to an opportunistic diet when $R_1 = R_1^*$ and leaves when prey densities are depressed to the solid line. *Open circles*, initial densities; *solid circles*, final densities. The lines with arrows connect initial densities to final densities.

region wherein it is optimal for predators to feed opportunistically. If $a_1 = a_2$, the patch-depletion trajectories are straight lines through the origin. Predators leave the patch when $Y_g = \hat{Y}$. Because the giving-up isocline has a negative slope, each prey is reduced in its final density because of the presence of the alternative prey. With evenhanded predation ($a_1 = a_2$) and negligible handling times ($h_1 = h_2 \approx 0$), the density of prey 2 at the moment the predator leaves the patch is reduced below the density that would occur if it were alone (i.e., \hat{Y}/a_2b_2) by the fractional amount $b_2R_2(0)/[b_1R_1(0) + b_2R_2(0)]$. The density of low-quality prey can thus be substantially reduced by the presence of a higher-quality alternative prey.

The presence of an alternative prey permits opportunistic predators to remain longer in a patch before foraging rates decline to the threshold departure level, thus increasing the time over which a given prey species can be captured. This implies that alternative prey species experience a short-term $-,-$ interaction. That is, increasing the initial density of one prey leads to a decrease in the final density of the other prey. We call this $-,-$ interaction resulting from predator foraging behavior "short-term apparent competition." Prey recruitment has been incorporated elsewhere (Holt, in press) into a population model, and it has been

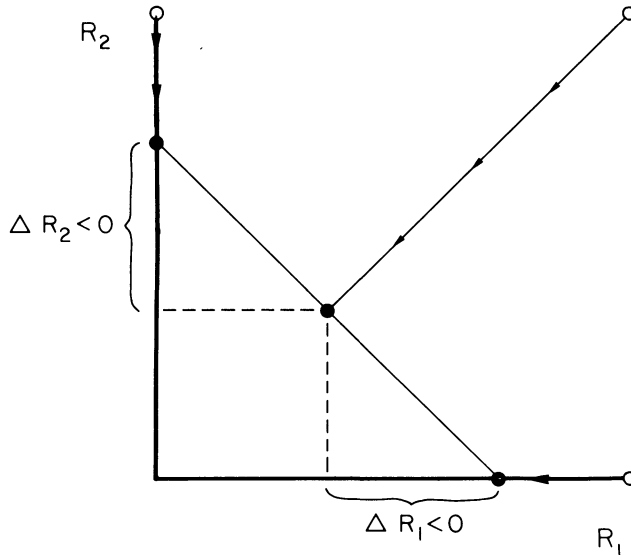


FIG. 4.—Apparent competition because of predator patch use when both patch use and diet are optimal. Patch-depletion trajectories are shown for different initial densities. *Open circles*, initial densities; *solid circles*, final densities. The lines with arrows connect initial to final densities. The dashed lines show the depression in final abundance for each prey caused by the presence of the alternative prey. The line with negative slope is the giving-up isocline.

shown that one prey species may be able to exclude another prey species from a patch because of a shared predator's aggregative response.

As noted above, in a rich environment, when the predator leaves the patch while still selective, the giving-up isocline is vertical, and there is no interaction between the prey. Suboptimal predator behavior may lead to other kinds of interactions between prey. As noted earlier, our labeling a predator's behavior "suboptimal" does not imply that the behavior is maladaptive but merely that the predator's behavior differs from that predicted by simple optimality models, either because of constraints not incorporated into these models (e.g., the need for recognition time) or because of the importance for fitness of factors other than foraging rates (e.g., mortality risks).

Here, we consider two of the many possible kinds of such suboptimality. First, a predator may at all prey densities be an indiscriminate opportunist within patches but leave patches when it should in accord with the marginal-value theorem. For example, the shore crab *Carcinus maenas* apparently cannot discriminate between dogwhelks (*Nucella lapillus*) differing in prey value, and thus it attacks all dogwhelks encountered (Hughes 1979). This lack of discrimination forces this predator to have a suboptimal diet by criterion (7) whenever its preferred prey is abundant. However, the predator might still be expected to leave patches of prey that are unusually low in average foraging return compared with

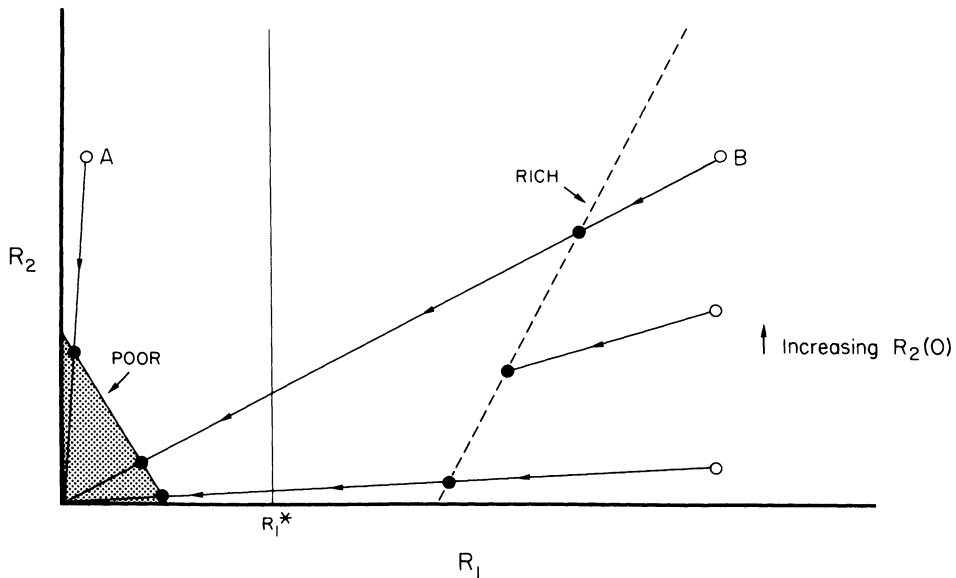


FIG. 5.—Giving-up isoclines and patch-depletion trajectories when patch use is optimal but diet is suboptimal (i.e., predator opportunistic at all prey densities). Symbols are as in figure 4. For prey densities to the right of the vertical line (i.e., $R_1 > R_1^*$, determined from eq. 7), constant-yield isoclines $Y(R_1, R_2) = k$ have a positive slope; to the left, they have a negative slope (see Holt 1983, p. 525). In a rich environment, predators leave when prey densities are on or to the left of the dashed line. An increase in $R_2(0)$ increases the final density of prey 1. By contrast, an increase in $R_1(0)$ decreases the final density of prey 2 (e.g., at point A, the predator does not enter the patch at all, whereas at point B, the predator enters the patch and depresses the numbers of both prey species). In a poor environment, by contrast, each prey reduces the final density of the alternative prey.

other patches; thus, shore crabs might approximate the prediction of the marginal-value theorem in leaving and entering patches. At high densities of the preferred prey, the constant-yield isoclines have positive slopes. In a rich environment, predators should tend to leave patches at high threshold rates. If the preferred prey is sufficiently abundant in a patch, the predator leaves when prey densities are reduced to values along a giving-up isocline of positive slope. This implies that the high-quality prey species incurs less cumulative predation when in a patch with the other prey, but that the low-quality prey suffers more predation because the high-quality prey is present. Increasing the initial density of prey 2 decreases patch quality and therefore reduces the cumulative mortality experienced by prey 1 (fig. 5). By contrast, an increase in the initial density of prey 1 enhances patch quality and makes it more likely that predators are attracted to the patch. Hence, these prey experience a short-term +, - relationship. In a poor environment, however, the yield isocline at the point of departure has a negative slope, and the -, - relationship reappears (fig. 4).

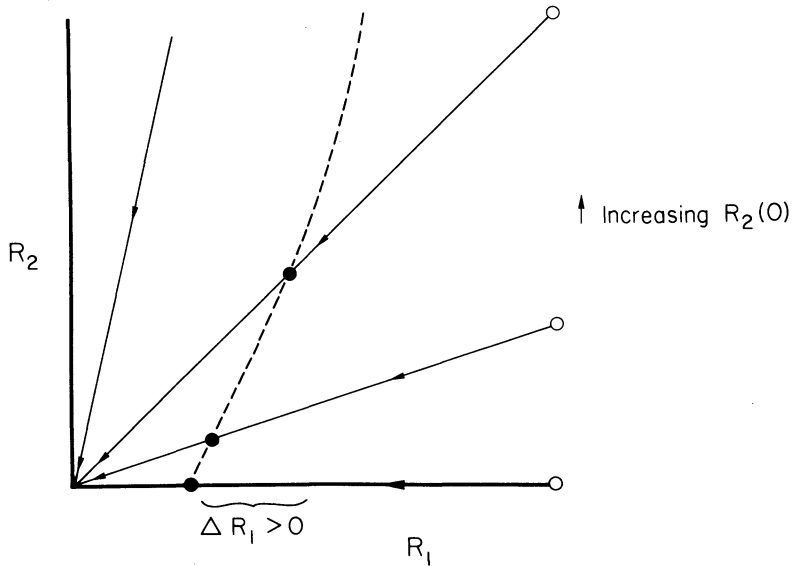


FIG. 6.—Patch-depletion trajectories and fixed-number patch-departure rule when both diet and patch use are suboptimal. Predator leaves patch when it has caught a given summed quantity of prey. An increase in $R_2(0)$ decreases predation on prey 1.

A predator may also be suboptimal in its use of patches. If predators enter and leave patches at a rate that is independent of patch quality, there is no aggregative numerical response, and alternative prey interact only through the predator's functional response. For predators that leave a patch after capturing a fixed number of prey, captures of one prey type directly reduce the number of the other prey caught (see fig. 6). Similarly, if predators forage for a fixed period of time or leave for reasons uncorrelated with prey densities, the time spent handling one prey reduces the time available for capturing the other. These effects are reciprocal and may imply a +, + relationship between alternative prey, regardless of habitat richness.

In short, if predators utilize a patchy environment optimally (i.e., in accord with the marginal-value theorem in Charnov 1976) and select an optimal diet within each patch (i.e., in accord with criterion 7 at the time of patch departure), coexisting prey within a patch should experience a -, - interaction in a poor environment and a 0,0 interaction in a rich one. This effect occurs because of shared predation and is independent of any direct competitive interaction between the prey. If predators enter and leave patches independently of prey density, alternative prey within a patch may show a +, + interaction. And, if the predator leaves patches when it is optimal to do so but does not discriminate between prey differing in quality within a patch, the interaction between prey is +, - in a rich environment and -, - in a poor environment.

DISCUSSION

Alternative prey within a patch may thus interact indirectly in qualitatively different ways, depending on whether their shared predator follows standard optimal foraging rules in choosing which prey types to consume and when to utilize or abandon patches. The theory presented above can be generalized in several ways. First, if handling times vary as a function of prey density and predator numbers vary over time, the rate of depletion of prey i is

$$dR_i/dt = -P(t)a_iR_i/[1 + a_1h_1(R_1,R_2)R_1 + a_2h_2(R_1,R_2)R_2].$$

Forming dR_1/dR_2 , we see that the denominators and $P(t)$ cancel, and equation (4) follows. Therefore, the shape of the patch-depletion trajectories is independent of variable handling times and predator numbers. If attack rates during search are a function of prey densities, that is, if $a_i = a_i(R_1, R_2)$, the equation for the trajectories becomes more complex than equation (4). However, we know from the fundamental properties of ordinary differential equations that if the attack functions $a_i(R_1, R_2)$ and their derivatives are continuous, the solution trajectories must pass uniquely through any point that is not an equilibrium. Because we have assumed no prey renewal (i.e., birthrates are slow relative to the length of foraging bouts), $dR_i/dt < 0$; hence, dR_1/dR_2 has a positive sign (i.e., the trajectories between the origin and the initial densities have a positive slope, even though they may bend in various complicated ways). Incorporating variable handling times or attack rates can also affect the shape of the isoclines. However, so long as the giving-up isocline has a negative slope (see Holt 1983), the predicted effect of apparent competition resulting from predator patch-use behavior will continue to be observed. Were we to increase the initial density of one prey, the patch-depletion trajectory would necessarily pass through the giving-up isocline at a point where the alternative prey is at a reduced density. The graphical theory presented here is thus robust and can incorporate a wide range of more detailed foraging models.

As noted earlier (Holt 1984, p. 396), W. Mitchell (University of Arizona) independently arrived at the prediction of apparent competition based on application of the marginal-value theorem in a patchy environment. He and Joel Brown (pers. comm.) recently explored the generality of this idea in several directions and in particular incorporated nonforaging activities into the predator's fitness function. Not surprisingly, if resources are abundant, factors other than foraging loom large in determining predator fitness, and predators do not necessarily impose $-$, $-$ interactions on alternative prey. Mitchell and Brown are testing these ideas in hummingbird and desert rodent systems.

The model presented here has several implications for the assembly of prey communities. In the case in which a prey species invades a community containing an established prey species, a sufficiently rare invader is found in only a few patches. The higher the growth rate of an invading species, the more likely it is to become established in the community. Our model suggests that the relation between spatial overlap among alternative prey and the chance for successful

invasion may depend critically on whether the predator forages optimally, both within and among patches.

If it is optimal for a predator to forage opportunistically by the time it leaves a patch and if patch departure matches the marginal-value criterion, prey co-occurring within a patch exhibit a $-$, $-$ interaction. If there exist patches suitable for prey 2 but not containing prey 1 (but that are otherwise equivalent with respect to resources, etc., for prey 2), individuals within such patches incur less mortality and enjoy a higher per capita growth rate than their counterparts in patches with species 1. Selection within prey 2 should favor avoidance of patches occupied by the alternative prey species and thus accentuate pre-existing differences in the range of patches accepted by the two species. Hence, an aggregative response by predators may select for habitat partitioning in prey communities.

A recent experimental study in subtidal hard-substrate communities (Schmitt, in press) showed that shared predators (a lobster, octopus, and whelk) can impose apparent competition on alternative prey classes (gastropods and bivalves) that do not compete for resources. In this study, the increase in local predator numbers because of local prey enrichment clearly resulted from predator aggregation. This system provides an experimental demonstration of the theoretical effect explored above. Schmitt suggested that shared predation and apparent competition may explain the pattern of habitat segregation observed in these prey groups.

Predator learning may also select for habitat partitioning between prey species. A predator learns to recognize only those prey it encounters during the course of its movements and concentrates its sampling in those patch types that have in earlier foraging forays harbored sufficient prey. If an unfamiliar prey type occurs in a patch with a familiar prey, the predator, during the course of foraging bouts there, has an opportunity to sample the new prey and add it to its diet. By contrast, if an unfamiliar, rare prey type occurs in patch types not occupied by the familiar prey, the predator may perceive those patches as bereft of acceptable food and not forage in them. A rare prey type may therefore find a refuge from predation if it avoids patches in the predator's foraging area that are already occupied by more-common prey. Gilbert (1984) suggested that a mechanism like this may account for habitat or host-plant specialization in rare *Heliconius* butterflies.

We have examined how alternative prey may interact within a patch when many patches are available to the predator for foraging. Clearly, the assessed character of an interaction between species depends on the spatial and temporal scales under consideration. If we were to increase the overall abundance of a common, resident prey species across all patches and there were no corresponding numerical response by the predator population, a rare or invading prey species might benefit: because the environment as a whole is enriched, predators should have higher threshold foraging rates at which they are willing to leave any single patch. When the second prey is sufficiently common, the first prey likewise benefits. Therefore, we have the mildly surprising result that two prey may be globally mutualistic, in that an increase in the average density of one reduces the average rate of predation experienced by the other, but both prey may exhibit apparent

competition on a local, within-patch scale because of an aggregative numerical response by predators.

If predators move only between two patches, enrichment of one patch should lead to a decrease in predation pressure in the other patch because predators tend to abandon the patch that provides the lower foraging rate. Hence, two prey species occupying different patches may exhibit short-term mutualism, even though the same two species, when occupying the same patch, experience short-term apparent competition.

A complete theory of prey coexistence obviously must consider other important components of the system, such as prey behavior, recruitment, and direct competitive interactions. Some of these effects are explored elsewhere (Holt, *in press*; Abrams, *in press*). Nonetheless, shared predation tends to foster habitat partitioning between alternative prey in a patchy environment, given that the predator forages so as to maximize its rate of harvesting. This conclusion complements the suggestion put forth earlier (Holt 1984) that habitat partitioning promotes prey-species coexistence when predators show a strong numerical response to their prey. This result also accords with theoretical findings (Hanski 1981; Comins and Hassell 1987) that patchiness enhances the coexistence of competing prey species.

In what types of communities is within-patch apparent competition driven by an aggregative response likely? The patches containing the community must be "open" to the predators. Predators should be mobile and able to disperse actively rather than passively. If predators are relatively sedentary and hence have low dispersal rates, the number of predators found in a patch largely reflects *in situ* dynamics. Alternative prey in a patch may still interact in the short term through the predator's functional response or through the long-term numerical response by the predator population. However, apparent competition will not be observed if the predator is strongly limited by factors other than prey availability (Holt 1977). If predators disperse rapidly but do so for reasons unrelated to local food availability (e.g., because predator movement is driven by physical transport processes), there is no reason to expect predators to forage differentially in patches with high densities of prey. Predator movement may still be important since it allows the "spillover" of predators from productive to less productive habitats (Holt 1984), but such predators are unlikely to impose within-patch apparent competition on their prey.

Territoriality or other forms of spacing behavior may place a low ceiling on the number of predators that aggregate to a patch. This complicates the analysis of how alternative prey interact through their shared predator. For simplicity, assume that there is never more than a single predator in a patch. The presence of an alternative prey in a patch increases the likelihood that a predator will set up a territory on that patch. Hence, co-occurrence with a second prey type makes the first prey type more vulnerable to some predators. However, for those patches with an established predator territory, an increase in the density of either prey should decrease the predation experienced by the other prey (e.g., because of predator satiation). The average within-patch effect of one prey on the other thus depends on the degree to which the patchy environment is saturated with preda-

tors. The prey communities that are most likely to experience apparent competition driven by predator aggregation are those in which predators are highly mobile (on a spatial scale encompassing several distinct prey patches) and only weakly territorial.

To end on a broader note, optimality and game-theoretic models can be used to construct models of species interactions. One virtue of this approach to community ecology is that the components of such models can at times be directly tested in the field and, in any case, have a more transparent biological meaning than do the parameters of traditional models. Moreover, the difference between optimal and suboptimal foraging behavior by a predator may lead to qualitative differences in how its prey interact. We believe that a fruitful direction for the development of sounder ecological theories is the judicious use of models of individual behavior to construct models of population dynamics and community structure.

SUMMARY

Interspecific interactions reflect the cumulative consequences of individual behavioral acts. The foraging decisions made by predators influence the way in which predation shapes the structure of prey communities. Alternative prey species co-occurring in a patch embedded in a matrix of many similar patches may interact through a shared mobile predator in two distinct ways. First, the functional response by an individual predator foraging in the patch to one prey species may be affected by the density of a second prey species in the patch (e.g., any time spent handling one prey reduces the time available for capturing other prey). Second, the presence of a second prey species may alter the propensity of predators to aggregate or remain in a given patch. We argue that this aggregative numerical response can in many circumstances generate $-$, $-$ interactions (apparent competition) between prey species that otherwise would not interact. This is most likely if predators use a simple optimality criterion for prey selectivity within patches and the marginal-value theorem for deciding when to enter and leave patches. By contrast, if predators have suboptimal diets within patches but leave in accord with the marginal-value theorem, alternative prey may experience a $+$, $-$ interaction; and, if predators use patches independently of prey availability, a $+$, $+$ interaction between alternative prey can occur. Hence, the qualitative character of the interaction between alternative prey in a patchy environment depends on the degree to which predators do, or do not, match the canonical predictions of optimal foraging theory.

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APPENDIX

AN EVOLUTIONARILY STABLE FORAGING STRATEGY

It is tempting to apply criterion (7) for diet selectivity directly to situations in which exploitation depresses prey abundance. If this were appropriate, as numbers of the preferred prey were depleted below the threshold density determined from criterion (7), the predator should switch from a selective to an opportunistic diet.

A simulation study (Heller 1980), however, suggests that this criterion for dietary generalization is not always valid. Heller proposed that when predators forage singly in patches, the optimal foraging strategy might sometimes be to begin feeding selectively on the more profitable prey and then expand the diet to include less profitable prey when the better prey is reduced to some critical abundance (an "expanding specialist" strategy). This qualitatively matches the criterion (7) derived from maximizing instantaneous rates of yield. However, the actual switch point may differ from that given by criterion (7). Moreover, if a predator remains in a patch long enough to deplete most of the prey, Heller found that the optimal strategy may be to forage opportunistically throughout the foraging bout. A predator that passes up a less preferred prey early on will have to hunt for it again, thus increasing the total amount of searching time invested for the same cumulative energy gain. This suggests that criterion (7) cannot be the criterion for selective foraging by a solitary forager in a depletable patch.

Heller (1980) briefly noted that when several predators were simultaneously foraging in a patch in his simulations, the expanding-specialist strategy appeared to be optimal. We here expand on this observation and argue that maximizing the instantaneous rate of yield is the evolutionarily stable foraging strategy (ESFS; Maynard Smith 1982), when multiple predators aggregate in a patch and interact only through their joint exploitation of prey (i.e., no direct interference). Consider two phenotypic classes of predators, α and β , that are identical except for their criterion for switching from selective to opportunistic foraging during patch depletion. This implies that both kinds of predators experience the same densities of prey and garner the same benefit from a given captured prey item. We assume that at time 0, a number of predators enter the patch, and all leave at time T , by which time both strategies are opportunistic. The α predators feed in accord with criterion (7), thus ignoring prey 2 if $Y_s > Y_g$ and feeding opportunistically if $Y_s < Y_g$. The switch point occurs at time τ . The β predators, by contrast, become opportunistic at an earlier time, τ' , $0 \leq \tau' < \tau$. The foraging bout during the time $0 \leq t \leq T$ consists of three distinct phases: (a) $0 < t < \tau'$, both predator types selectively feed on prey 1; (b) $\tau' < t < \tau$, α predators are selective, β predators are opportunistic; and (c) $\tau < t < T$, both predator types are opportunistic.

Average rates of yield for the two predator types over the foraging bout are

$$\bar{Y}_\alpha = \left(\int_0^{\tau'} Y_s dt + \int_{\tau'}^{\tau} Y_s dt + \int_{\tau}^T Y_g dt \right) / T$$

$$\bar{Y}_\beta = \left(\int_0^{\tau'} Y_s dt + \int_{\tau'}^{\tau} Y_g dt + \int_{\tau}^T Y_g dt \right) / T,$$

for the α and β predators, respectively. The α predators feed at the greater average rate if $\int_{\tau'}^{\tau} Y_s dt > \int_{\tau'}^{\tau} Y_g dt$. But during the period $\tau' < t < \tau$, by assumption, $Y_s > Y_g$. Hence, α predators feed at the greater average rate when sharing a patch with β predators. This is true regardless of the total number of predators or the relative frequencies of the two

alternative foraging strategies in the patch. A similar argument holds if $\tau' > \tau$. If there is a monotonic relationship between foraging rate and fitness, α predators (the instantaneous-foraging-rate maximizers) always have a higher fitness gain than do β predators in a patch shared by both.

This does not suffice to show that the prevalent feeding behavior of the predator population is that which maximizes instantaneous foraging rates. A phenotype is an evolutionarily stable strategy (ESS) only if it can exclude any feasible, rare, alternative phenotype (Maynard Smith 1982). The appropriate measure of fitness in an ESS analysis is an average over all the environments in which each alternative phenotype occurs. If β predators are rare and randomly distributed among patches, most individuals with this phenotype occur as single individuals with α predators. By contrast, most α predators occur in patches exclusively with other α predators. The relevant fitness comparison for predicting that α is an ESS is to examine the fitness of a single β (in a patch otherwise occupied by α 's) with the average fitness of an α in patches exclusively occupied by α 's. Symbolically, foraging strategy α is an ESS if $W_{\beta}[(N-1)\alpha, 1\beta] < W_{\alpha}(N\alpha, 0\beta)$, where N is the number of predators in the patch.

The following argument suggests that if the number of predators aggregating in a patch is large, the ESFS is to maximize instantaneous foraging rates. With a large number of predators in a patch, changing the foraging strategy of a single predator from β to α should change only slightly the time trajectory of declining prey numbers. Because foraging rates and hence predator fitnesses are a function only of prey densities, the average fitness of α predators in a patch containing a single β predator (denoted by $W_{\alpha}[(N-1)\alpha, 1\beta]$) should nearly equal the average fitness of α predators in patches with only α predators (denoted by $W_{\alpha}[N\alpha, 0\beta]$). Together with the previous argument, this implies that for large N ,

$$W_{\beta}[(N-1)\alpha, 1\beta] < W_{\alpha}[(N-1)\alpha, 1\beta] \approx W_{\alpha}(N\alpha, 0\beta).$$

This is just the condition for the α phenotype to be an ESS. This argument shows that the foraging strategy that maximizes the instantaneous rate of return from foraging is an ESS, given that the number of predators within a patch is large enough that exploitation is dominated by the more common phenotype.

This leaves open the questions of what strategy is optimal when only a few predators occur in a patch and of how many predators must be present for the above argument to hold. W. Mitchell and J. Brown (pers. comm.) recently showed that when a predator has exclusive use of a patch, it may do best when it is completely opportunistic, when it is completely selective, or when it possesses partial preference, depending on the initial densities of prey and the amount of time the forager spends in the patch. However, a predator is always opportunistic if criterion (7) is violated. Hence, a solitary forager should be more generalized, but never more specialized, than would be predicted by instantaneous-rate maximization. A mixed strategy may be the appropriate ESFS when there are only a few predators in a patch. If some patches contain only one predator and other patches two (or many) (a likely scenario), predators may show interpatch variability in the time elapsed before they switch from selective to opportunistic foraging during patch depletion.

This result can be understood intuitively as follows. A single forager in a patch can "manage" that patch to maximize its overall rate of return from foraging, averaged over its entire foraging bout. This long-term maximization need not imply instantaneous maximization. By contrast, if multiple foragers in the patch are locked into a scramble competition for a declining pot of resources, no individual has the luxury of forgoing feeding on high-quality prey early in a foraging bout (as a result of the consumption and handling of low-quality prey) because these prey are likely to be consumed by another individual instead.

LITERATURE CITED

- Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. *Am. Nat.* 124:80-96.
 ———. In press. Indirect interactions between species that share a predator: varieties of indirect

- effects. *In* A. Sih and C. Kerfoot, eds. Indirect interactions in aquatic ecosystems. University Press of New England, Hanover, N.H.
- Belovsky, G. E. 1984. Snowshoe hare optimal foraging and its implications for population dynamics. *Theor. Popul. Biol.* 25:235–264.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* 9:129–136.
- Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. *Am. Nat.* 110:247–259.
- Comins, H. N., and M. P. Hassell. 1987. The dynamics of predation and competition in patchy environments. *Theor. Popul. Biol.* 31:393–421.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities. Pages 460–490 *in* M. L. Cody and J. M. Diamond, eds. Ecology and evolution of communities. Harvard University Press, Cambridge, Mass.
- Gilbert, L. E. 1984. The biology of butterflies. *Symp. R. Entomol. Soc. Lond.* 11:41–54.
- Gleeson, S. K., and D. S. Wilson. 1986. Equilibrium diet: optimal foraging and prey coexistence. *Oikos* 46:139–144.
- Hanski, I. 1981. Coexistence of competitors in patchy environment within and without predation. *Oikos* 37:306–312.
- Hassell, M. P., and R. M. May. 1985. From individual behavior to population dynamics. Pages 3–32 *in* R. M. Sibly and R. H. Smith, eds. Behavioural ecology. Blackwell, Oxford.
- Heller, R. 1980. On optimal diet in a patchy environment. *Theor. Popul. Biol.* 17:201–214.
- Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45:1–60.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. 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.
- . *In press.* Prey communities in patchy environments. *Oikos*.
- Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *Am. Nat.* 113:209–221.
- Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.* 23:269–286.
- Kotler, B. 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.
- Krebs, J. R., D. W. Stephens, and W. J. Sutherland. 1983. Perspectives in optimal foraging. Pages 165–221 *in* G. A. Clark and A. H. Brush, eds. Perspectives in ornithology. Cambridge University Press, Cambridge.
- Lawton, J. H. 1986. The effect of parasitoids on phytophagous insect communities. *Symp. R. Entomol. Soc. Lond.* 13:265–287.
- Lawton, J. H., J. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 141–158 *in* M. B. Usher and M. H. Williamson, eds. Ecological stability. Chapman & Hall, London.
- MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York.
- MacArthur, R. H., and E. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603–609.
- Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.
- Menge, B., and J. Lubchenco. 1981. Community organization in temperate and tropical intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51:429–450.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Adv. Ecol. Res.* 9:1–131.
- Peters, R. 1984. The ecological implications of body size. Cambridge University Press, Cambridge.
- Pimm, S. L., and M. L. Rosenzweig. 1981. Competitors and habitat use. *Oikos* 37:1–6.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* 15:523–575.
- Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology* 62:1051–1069.
- . 1985. Some theoretical aspects of habitat selection. Pages 517–540 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, New York.

- Schmitt, R. J. In press. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. *Ecology*.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369–404.
- . 1976. The compression hypothesis and temporal resource partitioning. *Proc. Natl. Acad. Sci. USA* 72:4169–4172.
- . 1986. Mechanistic approaches to community ecology: a new reductionism? *Am. Zool.* 26:81–106.
- Sih, A. 1984. Optimal behavior and density-dependent predation. *Am. Nat.* 123:314–326.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16:269–312.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, N.J.