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OPTIMAL FORAGING AND THE FORM OF THE PREDATOR ISOCLINE

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The principal goal of optimal foraging theory is to predict how natural selection shapes foraging behavior (Pyke et al. 1977; Krebs 1978). This burgeoning body of theory, if successful, can in turn provide tools for constructing models of ecological communities, and in particular models of predator-prey systems (Pulliam 1976; Glasser 1979; Abrams 1982). The coevolution of a single predator with a single prey in the context of population dynamic models has received considerable theoretical attention (Rosenzweig 1973; Gilpin 1975; Levin and Udovic 1977; Schaffer and Rosenzweig 1978; Slatkin and Maynard Smith 1979). Yet strict monophagy is relatively rare (Williamson 1972). A general coevolutionary theory for predators feeding on multiple prey does not now exist. As one small step toward such a theory, I discuss here how optimal foraging may constrain isocline shape for a predator feeding on a pair of prey species. Isocline analysis is a useful technique in the study of competition (Slobodkin 1961; Rosenzweig 1981; Nunney 1980), predation (Rosenzweig 1977), and mutualism (May 1981). Although it does not fully capture the often complex dynamics of interacting populations, particularly among three or more populations (May and Leonard 1975; Gilpin 1979), isocline analysis does provide insight into the qualitative properties of interactive systems. The shapes of isoclines of predators consuming two species of prey have figured prominently in discussions of exploitative competition (Tilman 1980) and prey coexistence (Holt 1977).

My purpose here is not to argue that predators should always appear to forage optimally. Whether or not they do so depends on, among other factors, the realism of the constraints built into particular optimality models; the fitness costs of deviations away from a predicted optimum (Sih 1982); and the costs of perception and discrimination required for optimal behavior (Schoener 1971). Instead, for two foraging models (a model of the type 2 functional response, and a model of predator switching) I demonstrate that the isoclines of optimally foraging predators differ qualitatively from those of nonoptimal predators. This demonstration suggests that several models of switching that have been proposed in the ecological literature portray predators that forage suboptimally. The consequences of

optimal foraging for isocline shape are examined in the context of a continuous-time, deterministic model of predator-prey dynamics:

$$\begin{aligned}\frac{dP}{dt} &= PF_p(P, R_1, R_2), \\ \frac{dR_i}{dt} &= R_i\Phi_i(R_1, R_2) - m_i(R_1, R_2, P), \quad i = 1, 2.\end{aligned}\tag{1}$$

P is predator density and R_i is the density of prey i . F_p is the per capita growth rate (or absolute fitness) of the predator. Φ_i is the per capita growth rate of prey population i , excluding mortality from predation, and m_i is the total rate of predation suffered by prey i . For simplicity I will focus on the isoclines of food-limited predators (noninteractive predators *sensu* Caughley and Lawton [1981]). For such predators, we can write $F_p = F_p(R_1, R_2)$ and $m_i = N_i(R_1, R_2)P$, where N_i is the instantaneous functional response to prey i . Let $a_i(R_1, R_2) = N_i/R_i$ denote the rate of attack per prey item, per predator. Since a_i depends on current densities, any lag in the predator's response to changes in prey abundance (e.g., the time required for training effects) is assumed to be short compared to the time scale of the population dynamics.

Isoclines are determined from the equation $F_p(R_1, R_2) = k$, where k is an arbitrary constant. Figure 1 catalogs a number of isocline shapes, ranked from A to F in order of the decreasing profitability of mixed diets. These isoclines fall into two groups: those with nonpositive slopes at all prey densities (A – D), and those with at least some isocline segments of positive slope (E and F). I will argue that isoclines such as E and F indicate that the foraging behavior of the predator is to some degree suboptimal. Yet isoclines like E and F are implied by several current predator-prey models (see fig. 4 and below), and apparent examples of such isoclines have been observed in both laboratory and natural populations (Maly 1975; Downing 1981). The frequent occurrence of such populations could restrict the explanatory scope of several areas of community theory (see *Discussion*). It thus seems useful to examine the relation between foraging behavior and isocline shape so that we might predict the occurrence of these aberrant isoclines.

To construct isoclines of a food-limited predator we must know two things: (1) the quantity of each prey captured as a function of prey densities, the functional response; and (2) the prey-specific effect of consumption upon predator fitness. If either nonlinearly depends on prey density, the isocline may be nonlinear. I assume, in accordance with most optimal diet models (Krebs 1978; but see Rapport 1980), that all prey are valued in a common currency (e.g., net calories or nutrients gained per item), and that per-item values are independent of prey density. Each item of prey i , when captured, is worth a net positive amount b_i . The total rate of resource acquisition or foraging yield is:

$$Y(R_1, R_2, \dots) = \sum_i b_i N_i = \sum_i b_i a_i R_i.$$

Assume that the per capita growth rate of a food-limited predator is a function solely of Y , i.e., $F_p = F_p(Y)$, and that $\partial F_p / \partial Y > 0$. For two prey, an isocline $F_p[Y(R_1, R_2)] = k$ corresponds directly to a curve of constant yield, $Y(R_1, R_2) = k'$.

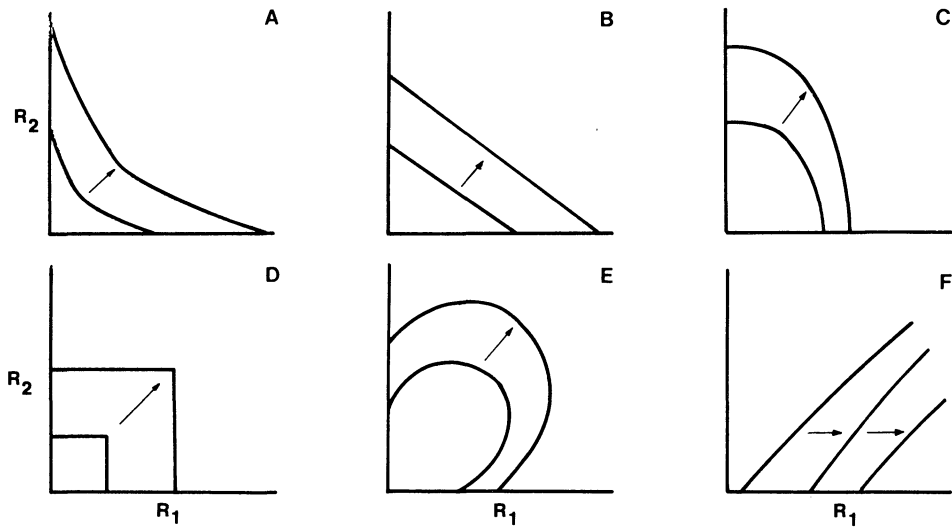


FIG. 1.—Possible isocline shapes, $F_p(R_1, R_2) = k$. In each case, the line farthest to the right corresponds to the greatest yield. *A*, Prey are complementary resources. *B*, Prey are substitutable resources. The prey are partially or completely inhibitory in *C–F*. Isoclines *A–D* correspond to resource classes *C–F* in the resource classification suggested by Tilman (1980; summarized in his fig. 1). Here I contrast these 4 isocline classes as a group to isocline classes *E* and *F*, which are not represented in Tilman's classification.

With these assumptions, we can characterize the two isocline groups of figure 1 by considering the properties of constant yield curves. At a point (R_1, R_2) the slope of the isocline $Y = k'$ is $-(\partial Y/\partial R_1)/(\partial Y/\partial R_2)$. This is positive if and only if $\partial Y/\partial R_1$ and $\partial Y/\partial R_2$ differ in sign. In other words, a positive slope requires that total foraging yield decline with the increasing abundance of one prey. Since

$$\frac{\partial Y}{\partial R_j} = b_j a_j + \sum_i b_i R_i \frac{\partial a_i}{\partial R_j} \quad (2)$$

and each $b_i > 0$, one or more $\partial a_i/\partial R_j$ must be negative and of sufficient magnitude in order to make $\partial Y/\partial R_j$ negative. The next two sections of this paper explore two kinds of models in which this can occur. In the first, time spent handling one prey diminishes the rate of attack upon others by reducing the predator's available search time. In the second, handling times are assumed to be negligible, yet because of predator switching behavior an increase in the density of one prey type decreases the attacks experienced by the alternative prey.

THE ISOCLINES OF NONSWITCHING PREDATORS

The usual multispecies generalization of Holling's "disc" equation (Holling 1965) is

$$N_u = \frac{a'_u R_u}{1 + \sum_{i=1}^n a'_i h_i R_i} \quad (3)$$

(Lawton et al. 1974; Murdoch 1977; Hassell 1978), where a'_i is a constant capture rate per item of i during search, h_i is a per-item handling time, and n is the number of prey types in the diet. This model describes a type 2 functional response to prey u when all other prey types have fixed densities. Per-item attack rates are inversely density dependent ($\partial a_i / \partial R_j < 0$), and from equation (2) we see that isoclines of positive slope are therefore possible.

The total rate of foraging yield is

$$Y = \sum_{i=1}^n b_i N_i = \frac{\sum_i a'_i b_i R_i}{1 + \sum_i a'_i h_i R_i}. \quad (4)$$

Expressions similar in structure to equation (4) are found in many optimal diet models of predators that hunt in fine-grained environments and capture prey one at a time (Schoener 1974; Maynard Smith 1974; Werner and Hall 1974; Charnov 1976; Krebs et al. 1977). As in standard optimal diet models (e.g., Pyke et al. 1977), I first assume that prey recognition is instantaneous. If a predator attacks an item of prey u , its average rate of yield during the time required for attack and handling is b_u/h_u . If a predator does not attack prey u at all, its expected rate of yield is given by expression (4), with the summations taken over all $i \neq u$. Since an optimal forager should maximize its rate of yield, the optimality criterion for inclusion of u in the diet is simply

$$\frac{b_u}{h_u} > \frac{\sum_{i \neq u} a'_i b_i R_i}{1 + \sum_{i \neq u} a'_i h_i R_i}. \quad (5)$$

The implications of this criterion for optimal diet structure are discussed in detail in the papers cited above. The character of the isosurface $Y(R_1, R_2, \dots) = k'$ may be determined by differentiating expression (4) with respect to each R_i . By doing so, it may be seen that $\partial Y / \partial R_u > 0$ if and only if

$$\frac{b_u}{h_u} > \frac{\sum_i a'_i b_i R_i}{1 + \sum_i a'_i h_i R_i}. \quad (6)$$

At first glance, inequality (6) seems to differ from inequality (5): The right-hand side of (5) is the total rate of yield of a diet without type u , and the right-hand side of (6) is the rate of yield with type u . The two inequalities are actually the same, however, since multiplying both sides of (6) by $h_u(1 + \sum_i a'_i h_i R_i)$, subtracting $a'_u b_u h_u R_u$ from both sides, and rearranging leads to inequality (5), while similar manipulations on (5) lead back to (6). Thus inequalities (5) and (6) are formally equivalent assertions about the diet. Given that a predator feeds optimally, its foraging yield, and hence its growth rate, should increase with the density of each prey type in its diet. If a predator feeds suboptimally, its per capita growth rate declines with an increase in the density of one or more prey.

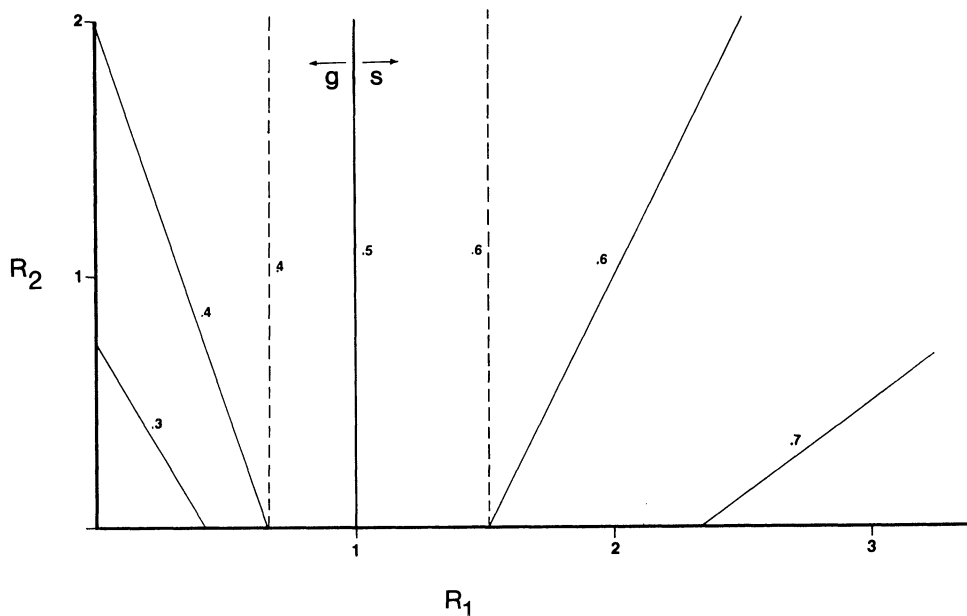


FIG. 2.—Constant yield isoclines for a nonswitching predator feeding in accord with eq. (4). Prey 1 is more valuable than prey 2 ($b_1/h_1 > b_2/h_2$). Solid lines = isoclines of a generalist feeding on both prey; dashed lines = isoclines of a specialist on prey 1. It is optimal to be a generalist at densities left of the vertical solid line (g), and to be a specialist at densities to the right (s). This threshold occurs when $Y_g = b_2/h_2$. The value of R_1 at the vertical line is $b_2(a_1b_1h_2 - a_1b_2h_1)^{-1}$. In this example, $a_1 = a_2 = 1$, $h_1 = h_2 = 1$, and $b_1 = 2$, $b_2 = 1$. Numbers beside each isocline are corresponding values for Y .

With just two prey types, equation (4) defines a family of linear isoclines. Let $b_1/h_1 > b_2/h_2 > 0$. From condition (5), prey 1 should always be in the diet, and so from (6) $\partial Y_1/\partial R_1 > 0$. If it is optimal to be a generalist, $\partial Y/\partial R_2$ is also positive and the isocline has a negative slope. By contrast, a suboptimal generalist reduces its total rate of yield by consuming prey 2; the greater the abundance of this low quality prey, the lower is total yield, because an increasing fraction of foraging time is spent handling low quality rather than high quality prey. To maintain a constant rate of yield, the abundance of the preferred prey must be increased; this produces an isocline with a positive slope. Figure 2 illustrates this relation between isocline slope and foraging strategy, and shows that the switch from generalist to specialist optimal strategies corresponds to a change in the sign of the slope of generalist isoclines. (Gleeson [1980; personal communication] has independently observed this correspondence between isocline slope and optimality in a model of optimal diet choice.)

Contrary to one prediction that can be made from inequality (5), in several studies predators have consumed low quality prey even though better prey were sufficiently available to make specialization advantageous (e.g., shore crab, Elner and Hughes 1978; brown trout, Rigler 1979). Hughes (1979) has pointed out that this might be expected if predators must invest time handling a prey item before

they can ascertain its quality; even in predators that attempt to maximize foraging yield, perceptual limitations may preclude instantaneous recognition (see also Houston et al. 1980). It is useful for several reasons to examine an optimal diet model that incorporates recognition time. First, in this model, unlike the previous one, there is not an isomorphism between optimality and nonpositive isocline slopes; the model provides a plausible explanation for isoclines with positive slopes. Second, in keeping with the general theme of this paper, I argue that although in this model such isoclines are possible in an optimizing predator, selection to maximize foraging yield should still reduce the acuteness of the rightward slope of the isocline.

Following Hughes (1979), let total handling time consist of τ , the time required for recognition, and h'_i , a residual handling time: $h_i = \tau + h'_i$. Expression (4) becomes:

$$Y = \frac{\sum_i a'_i b_i R_i}{1 + \sum_i a'_i h_i R_i + \tau \sum_e a'_e R_e}. \quad (7)$$

The summations over i are for items actually consumed, and the additional term in the denominator comes from time wasted on items not consumed, once recognized.

With two prey species, the rate of yield of a generalist is

$$Y_g = \frac{\sum_{i=1}^2 a'_i b_i R_i}{1 + \sum_{i=1}^2 a'_i h_i R_i}, \quad (8)$$

and that of a specialist on 1 is

$$Y_s = \frac{a'_1 b_1 R_1}{1 + a'_1 h_1 R_1 + \tau a'_2 R_2}. \quad (9)$$

As before, I assume that $b_1/h_1 > b_2/h_2 > 0$. The generalist is favored if $Y_g > Y_s$. After manipulating expressions (8) and (9) it can be seen that this criterion for being a generalist reduces to $b_2/h'_2 > Y_s$, or

$$\frac{b_2}{h'_2} > \frac{a'_1 b_1 R_1}{1 + a'_1 h_1 R_1 + \tau a'_2 R_2}. \quad (10)$$

Hughes (1979) discusses the ways in which the optimal diets predicted from this criterion differ from those predicted from (5).

Both strategies lead to straight isoclines. At a particular point $\bar{R} = (R_1, R_2)$ generalist and specialist isoclines have respective slopes

$$\frac{a'_1 (b_1 - Y_g h_1)}{a'_2 (Y_g h_2 - b_2)} \quad \text{and} \quad \frac{a'_1 (b_1 - Y_s h_1)}{a'_2 \tau}. \quad (11)$$

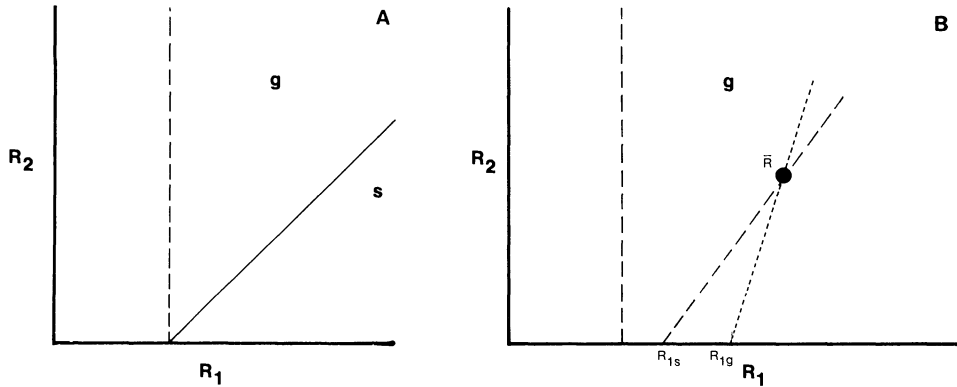


FIG. 3.—Isoclines for predators with nonzero recognition times. A, The parameters used are the same as in fig. 2, except that $\tau = 1$, $h'_1 = 0$, and $h'_2 = 1$. Solid line separates prey densities at which the predator should specialize on prey 1 (area *s*) from densities where being a generalist is favored (*g*). Dashed line = corresponding line for a predator with instantaneous recognition, and is the same as the solid vertical line of figure 2. Refer to text for meanings of \bar{R} , R_{1g} , and R_{1s} in B. Dashed line passing through \bar{R} = isocline of a specialist; dotted line = isocline of a generalist.

Since $b_1/h_1 > Y_g$ and $b_1/h_1 > Y_s$, the slope of a generalist is negative if $Y_g < b_2/h_2$ and positive if $Y_g > b_2/h_2$. A specialist isocline always has positive slope. In figure 3A, left of the vertical dashed line the optimal diet (generalist) has an isocline with a negative slope, while to the right both strategies have positive slopes. The solid line separates generalized from specialized optimal diets.

Thus, optimal predators with poor discriminatory abilities may have isoclines with positive slopes if preferred prey are at high densities. Nevertheless, even in this circumstance optimal diet choice ameliorates the acuteness of the rightward slope. Consider the combination of prey densities at \bar{R} in figure 3B. At \bar{R} both strategies have positive isocline slopes. Since Y_s and Y_g are families of straight lines, radiating from \bar{R} there is a single specialist isocline, $Y_s = k_s$, and a single generalist isocline, $Y_g = k_g$, which intercept the R_1 -axis at the densities R_{1s} and R_{1g} , respectively. On the R_1 -axis, Y_g and Y_s are identical functions of R_1 . In the figure, $R_{1g} > R_{1s}$, so it must be the case that $k_g > k_s$. This implies that at \bar{R} , $Y_g > Y_s$ and the predator should be a generalist. By inspection of the figure, the generalist has a less pronouncedly rightward isocline slope than does the specialist. If the isoclines are relabeled so that $R_{1s} > R_{1g}$, then $Y_s > Y_g$ and once again optimal diet choice leads to the isocline that is more upright.

The above arguments assume that predators attempt to maximize rates of yield given fixed attack rates (a_i) and handling times (h'_i , τ). Natural selection should also act upon any heritable variation in the predator that influences these parameters. What is the effect of such selection upon isocline slope? Selection should increase a parameter α if $\partial Y/\partial \alpha > 0$, and decrease it if $\partial Y/\partial \alpha < 0$ (Levins 1975). In the simplest case, selection will act independently upon each parameter. At a given \bar{R} , by differentiating expressions (8) and (9) with respect to each parameter

it can be shown that selection should increase the capture rate of the more profitable prey, minimize all handling times, and reduce the rate of capture of the less profitable prey if the isocline has a positive slope (i.e., $\partial Y/\partial a_2' < 0$ if $Y > b_2/h_2$). Manipulation of expressions (8), (9), and (11) reveals that for a particular \bar{R} , increasing a_1' and decreasing h_1' pivots the isocline further to the right. This seems to contradict my previous assertion about the influence of selection upon isocline slope. The contradiction holds only if the predator has no influence over prey numbers. Given a food-limited predator, as in model (1), an increase in capture rates eventually reduces prey densities. If a predator has a positive per capita growth rate whenever its foraging yield exceeds a constant, C (the cost of maintaining and replacing an individual predator), and a negative growth rate below C , then the predator population is in demographic equilibrium only when $Y(R_1, R_2) = C$. Selection on foraging parameters changes the prey densities at which this equilibrium is reached. At equilibrium, the slope of the zero-growth isocline of the generalist is $a_1'(b_1 - Ch_1)/a_2'(Ch_2 - b_2)$. Given that the slope is positive ($b_2/h_2 < C < b_1/h_1$), even if prey 2 is very abundant it alone cannot support the predator. From (10) we see that at equilibrium in a food-limited predator population, the criterion for including prey 2 in the diet is simply $b_2/h_2' > C$, which does not depend on prey abundance. The slope becomes steeper as a_1 increases or a_2 , h_1 , and h_2 decrease; thus selection diminishes the rightward tilt of the zero-growth isocline. A similar result holds for the specialist.

The relationship to be expected between isocline slope and prey density in a predator that maximizes food intake depends on the constraints facing the predator. If a predator requires little time to discriminate among prey of unequal quality, as long as it is optimal to be a generalist its isoclines should have negative slope. If a predator is unable to discriminate rapidly, when valuable prey are sufficiently abundant we expect to observe isoclines of positive slope. Yet even here natural selection acts on food-limited predators to diminish the degree of rightward slope of the zero-growth isocline.

SWITCHING AND ISOCLINE SHAPE

Switching is part of the behavioral repertoire of many predators (Cornell 1976), although not all general predators switch (e.g., coccinellids, Murdoch and Marks 1973; cyclops, Jamieson 1980; mites, Santos 1976). Switching may stabilize prey dynamics (Murdoch and Oaten 1975); result in frequency-dependent selection that can maintain genetic polymorphisms (Ayala and Campbell 1974); and enable competing prey species to coexist (Roughgarden and Feldman 1975; May 1977). The potential importance of switching as an ecological factor has prompted a number of theoretical studies of predator-prey dynamics which incorporate explicit models of predator switching (Comins and Hassell 1976; Jacobs 1977; Murdoch and Oaten 1975; Murdoch 1977; Steele 1974; Tansky 1978; Teramoto et al. 1979; Vance 1978). In this section I first discuss the isocline shapes implied by these models and then develop an optimality model of switching. This analysis will suggest that these models depict nonoptimal predators.

These switching models are listed in table 1. In the cited papers, models 1

through 4 were components of standard differential equation models of predator-prey dynamics equivalent in structure to equations (1) (Jacobs 1977 did not explicitly model the predator population.) Model 7 was embedded in a discrete-generation host-parasitoid model. These models were used to explore the effect of switching on prey coexistence. By contrast, Murdoch and Oaten developed models 5 and 6 to examine the influence of the functional response on a prey population's stability and were not directly concerned with the predator's dynamics or species coexistence.

In these switching models alternative prey reciprocally reduce each others' risk of predation during predator search. Several (*viz.*, models 4, 5, and 6) also include handling time. As the relation between handling time and isocline slope was discussed above, in this section handling times are assumed to be zero. For most of the models, with this simplification $\partial a_i / \partial R_i > 0$ and $\partial a_i / \partial R_j < 0$, $i \neq j$. (In submodels (b) and (c) of model 6, these inequalities hold for $i = 1$, but are replaced by equalities for $i = 2$. For model 4 these inequalities are true if $-.5 < \log[R_1/R_2] < .5$.) Some authors (e.g., Teramoto et al. 1979) have assumed that these inequalities are tantamount to switching. This is not quite true. The most widely cited definition of switching is that of Murdoch (1969). Given R_1, R_2 , let the ratio of N_1/N_2 to R_1/R_2 define c , a measure of predator preference (Cock 1978). The preference measure c may be written $a_1(R_1, R_2)/a_2(R_1, R_2)$. A predator is said to switch if c increases with relative prey abundance $R_1/R_2 = Z$. The models of table 1 (except for submodels [b] and [c] of model 5) can be written as functions of Z when handling times are zero, and it can be shown that c increases with Z . But consider the model $a_i(R_1, R_2) = f(R_i + \epsilon R_j)$, $i = 1, 2$, $i \neq j$, $0 \leq \epsilon < 1$, where f increases with its argument. Given fixed total densities $R = R_1 + R_2$, as Z goes from 0 to ∞ , c increases from $f(\epsilon R)/f(R)$ to $f(R)/f(\epsilon R)$. In this model the predator switches *sensu* Murdoch yet $\partial a_i / \partial R_j > 0$.

Many behavioral mechanisms for switching, however, do imply that $\partial a_i / \partial R_j < 0$, $i \neq j$. These include (Murdoch et al. 1975; Lawton et al. 1974): (a) variable encounter rates caused by shifts in perception (e.g., the development of a "search image," Dawkins 1971; Rausher 1978); (b) movement among foraging patches (Murdoch et al. 1975); (c) variable rejection rates (Murdoch 1969; Cornell and Pimentel 1978); (d) variable use of alternate search modes or capture tactics, coupled with specialized prey escape tactics (Lawton et al. 1974; Akre and Johnson 1979).

Each of these mechanisms requires behavioral plasticity. As relative prey frequency varies, the predator changes its locale, sensory responses, or foraging tactics, such that as attacks upon one prey increase there is a concomitant decrease in attacks upon the alternative prey. Of the models in table 1, model 5 was derived from a mechanistic model of predator training, and model 6 was intended to represent the consequences of movement among foraging patches. The other models were not based upon any particular mechanism for switching. Nonetheless, one or more may prove to provide reasonable descriptions of switching behavior. For instance, the preference measure c predicted from model 1 is similar in form to an empirical model of variable preference that is known to fit some feeding data (Fullick and Greenwood 1979; Greenwood and Elton 1979).

TABLE 1
 MODELS FOR PREDATOR SWITCHING*

MODEL 1	$\frac{a_1 R_1^n}{R_1^n + R_2^n}, \quad n > 0$	Tansky 1978 Teramoto et al. 1979
MODEL 2	$a_1 \left(\frac{R_1}{R_1 + R_2} \right)^n, \quad n > 0$	Vance 1978
MODEL 3	$a_1 \left(\frac{R_1}{R_1 + c_1 R_2} \right), \quad c_1 > 0$	Jacobs 1977
MODEL 4	$0 \quad \text{if } \log(R_1/R_2) < -.5$ $\frac{a_1}{1 + h_1 R_1} [\log(R_1/R_2) + .5]$ $\quad \text{if } -.5 \leq \log(R_1/R_2) \leq +.5$ $\frac{a_1}{1 + h_1 R_1} \quad \text{if } \log(R_1/R_2) > +.5$	Steele 1974
MODEL 5	$\frac{\lambda p_{21}(p_{11}R_1 + p_{12}R_2)}{p_{21}R_1 + p_{12}R_2 + \lambda(p_{11}p_{21}h_1R_1^2 + p_{12}p_{21}(h_1 + h_2)R_1R_2 + p_{12}p_{22}h_2R_2^2)}$	Murdoch and Oaten 1975 Oaten and Murdoch 1975
MODEL 6	$\frac{a_1 \phi_1}{1 + \sum_i a_i \phi_i h_i R_i}, \quad \text{where } \phi_1 + \phi_2 = 1$	Murdoch 1977
Submodels for ϕ_1 include (from Murdoch and Oaten 1975; Murdoch 1977)		
(a)	$\phi_1 = \frac{R_1}{R_1 + R_2},$	
(b)†	$\phi_1 = c + dR_1, \quad c < \phi_1 < 1 - c, \quad d > 0$	
(c)†	$\phi_1 = c + (1 - 2c)[1 - \exp(-dR_1)],$	
(d)	$\phi_1 = c + (1 - 2c) \frac{R_1^n}{R_1^n + R_2^n}, \quad n \geq 1$	

TABLE 1 (Continued)

MODEL 7	Hassell and Comins 1976
$a_1 \left(1 + s \frac{R_1 - R_2}{R_1 + R_2} \right)$	

* The per-item rates of capture of prey 1, $a_1(R_1, R_2)$, are tabulated. To get $a_2(R_1, R_2)$, interchange 2 for 1 in models 1 through 5 and 7. In model 6, substitute ϕ_2 for ϕ_1 in the basic model, and retain (a) through (d) for ϕ_1 . In model 5, λ is the maximal rate of attack on both 1 and 2, and p_{ij} is the probability that an encountered individual of species j will be captured, given that the last individual caught was of species i . Switching occurs if $p_{11} > p_{21}$ and $p_{22} > p_{12}$.

† Since submodels (b) and (c) are functions of just R_1 , switching depends entirely on variation in R_1 .

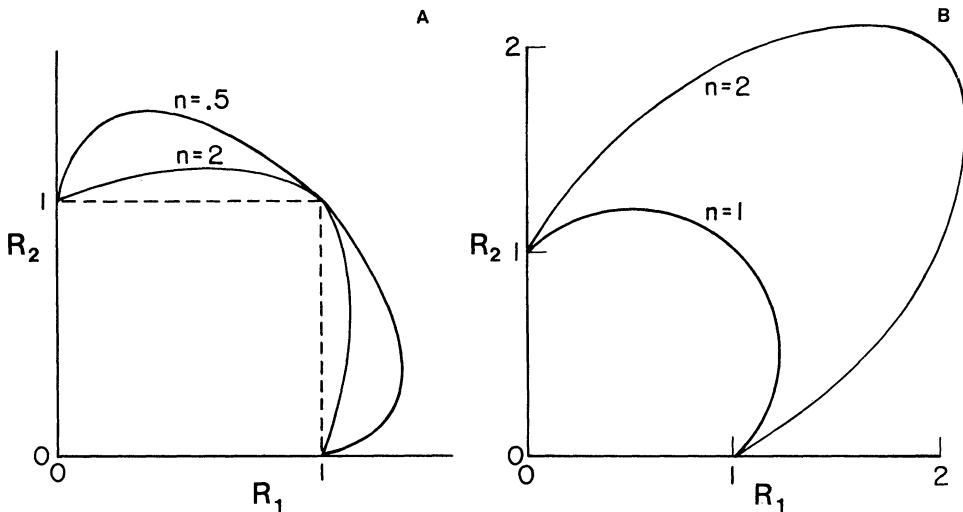


FIG. 4.—Constant yield isoclines for the switching models of A (Tansky 1978) and B (Vance 1978). Parameter values are $a_1' = a_2' = 1$, $b_1 = b_2 = 1$.

From expression (2) it is clear that for the attack functions of table 1 we could pick disparate values of b_1 and b_2 so that for some prey densities $\partial Y/\partial R_i < 0$ and isoclines would have locally positive slopes. Even if $a_1' = a_2'$, and $b_1 = b_2$, all the models in table 1 can produce bulbous isoclines like that of figure 1E. It is straightforward, but tedious, to demonstrate this assertion by directly evaluating $\partial Y/\partial R_i$ for each model in the table. In figures 4A and 4B several isoclines for models 1 and 2 are shown; these typify the isoclines implied by the switching models of table 1.

Table 2 and figure 5 delineate those parameter values of the models in table 1 that produce strongly bowed isoclines similar to those of figure 4. Several models always lead to such isoclines; others do so only for particular ranges of parameters or prey densities. In general, with these models an increase in density of the rarer

TABLE 2

PARAMETER VALUES FOR WHICH THE PREDATOR ISOCLINE HAS AN ENTIRELY NEGATIVE SLOPE*

Model	1	none
	2	none
	3	none
	4	none
	5	$\frac{P_{21}}{P_{11}} > \frac{1}{2}$ and $\frac{P_{12}}{P_{22}} > \frac{1}{2}$
	6	(a) none
		(b) $R_2 < \frac{c}{d}$
		(c) $R_2 < \frac{c}{d(1 - 2c)}$
		(d) See fig. 5.
	7	$s < \frac{1}{3}$

* It is assumed that $b_1 = b_2$ and $h_1 = h_2 = 0$.

prey produces a disproportionate decrease in attacks upon the more common prey, and hence a decline in total foraging yield; this leads to isoclines with locally positive slopes.

Surely a predator should not switch unless by so doing it increases, or at least does not decrease, its foraging yield. This simple observation suggests that the models in table 1 portray predators with nonoptimal foraging behaviors. To sharpen this suggestion, I now develop an optimality model of switching and use it to predict the isocline shape of an optimally switching predator. As noted above, for several switching mechanisms it is reasonable to expect that an increase in the rate of attack upon one prey will necessarily decrease attacks upon the other. The simplest way to express this reciprocal reduction in attack rates is to assume that a_1 and a_2 are functionally related by $a_2 = f(a_1)$ and that $\partial a_2 / \partial a_1 < 0$. Such a function provides a constraint that can govern diet optimization.

Figure 6 shows several possible forms for this constraint. Lawlor and Maynard Smith (1976) have discussed a model for the evolution of attack rates that relies on constraints between attack rates reminiscent of these forms (see their fig. 1). The constraints they consider, however, are quite different from those envisaged here. In their model, an individual predator is characterized by a pair of constant per-item attack rates (there is no switching), and a constraint between a'_1 and a'_2 describes the between-individual variation in the a'_i available for natural selection. By contrast, the constraints under consideration here are experienced by individual predators attempting to maximize foraging yield as relative prey abundances change. The attribute fashioned by selection is, in a sense, a behavioral "rule" prescribing how a predator shifts its attack rates in accord with the constraint $f(a_1)$ as prey numbers vary. Isocline shape is determined by this within-individual variation in foraging. Many empirical tests of optimal foraging theory actually depend on such within-individual, rather than between-individual, variation in foraging behavior.

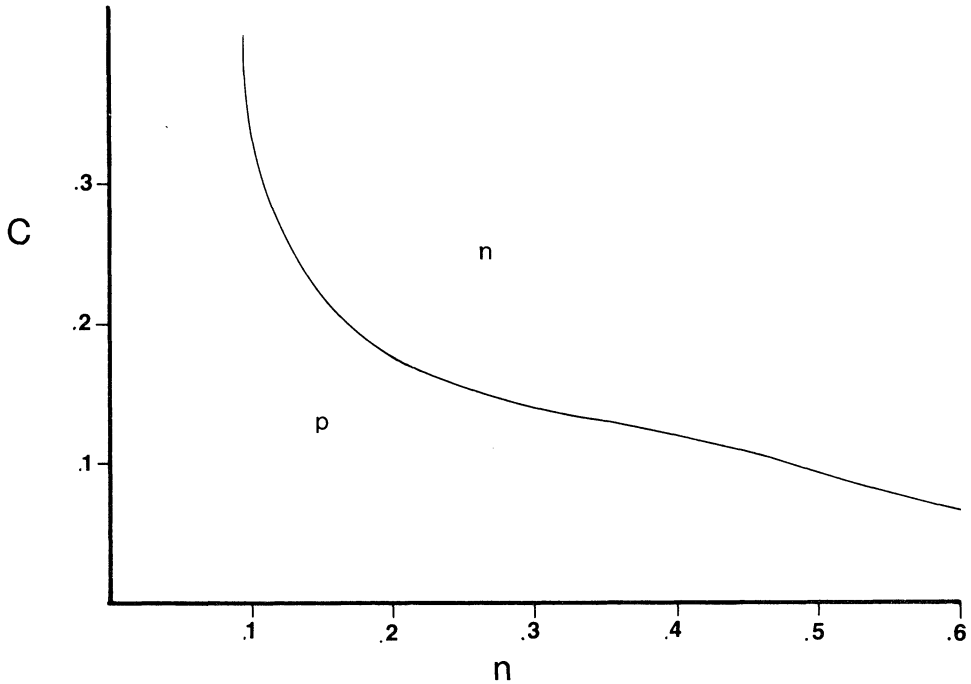


FIG. 5.—Combinations of parameters leading to isoclines with partially positive slope for submodel (4) of model 7. $a'_1 = a'_2$, $b_1 = b_2$, $h_1 = h_2 = 0$. Region p produces isoclines resembling those in fig. 4. In region n , isoclines have negative slopes.

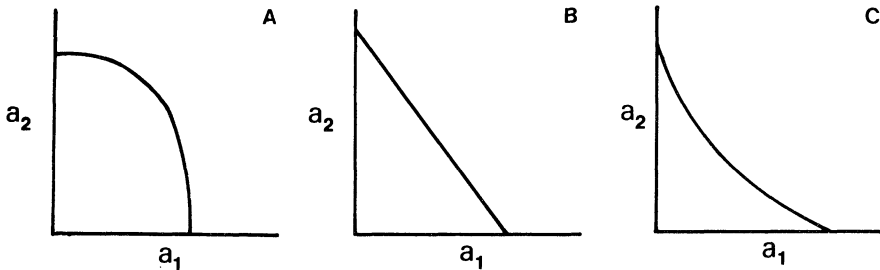


FIG. 6.—Possible trade-offs between a_1 and a_2 , $a_2 = f(a_1)$. A, convex constraint; B, linear constraint; C, concave constraint.

One possible biological realization of these constraints might be for the two prey to be spatially segregated: prey 1 occurs only in patch 1, and prey 2 just in patch 2. Of the predator's total search time, a fraction ϕ_i is spent in patch i , and T in transit between the two patches. Model 6 was in fact developed by Murdoch (1977) with this scenario in mind. Optimal switching behavior in this case is an expression of optimal patch selection. Given that a predator is in patch i , its instantaneous per-item capture rate is a'_i . Hence $a_1 = a'_1\phi_1$, and $a_2 = a'_2\phi_2$. Three

different assumptions about the a_i' and T correspond to the three trade-offs pictured in figure 6. (1) Constant a_i' , $T = 0$. Since $\phi_2 = 1 - \phi_1$, this produces a linear constraint. (2) Constant a_i' , $T > 0$ if a predator feeds on both prey. If a predator divides its search time between both patches it wastes time in transit, while if it concentrates on either one, no time is lost; this generates concave constraints. (3) Variable a_i' , $T = 0$. If prey actively avoid predation by hiding in refuges or becoming immobile when a predator is present, we might expect a_i' to decline with increasing ϕ_i ("submergent behavior," Maiorana 1976; "depression," Charnov et al. 1976). This makes the trade-off convex.

The predator's rate of yield is $Y = a_1 b_1 R_1 + a_2 b_2 R_2$. If the predator is free to shift its attack rates within the constraint $f(a_1)$, it should redistribute a_1 and a_2 until Y is at a local maximum

$$\partial Y / \partial a_1 = b_1 R_1 + b_2 R_2 \partial a_2 / \partial a_1 = 0,$$

or

$$\frac{\partial a_2}{\partial a_1} = -\left(\frac{b_1 R_1}{b_2 R_2}\right). \quad (13)$$

Following a standard microeconomic argument we can superimpose on the (a_1, a_2) plane of figure 6 a family of constant yield lines, each with slope $-b_1 R_1 / b_2 R_2$. The optimal set of attack rates is that point on $f(a_1)$ that is on the line of highest yield. At an interior optimal point (each $a_i > 0$), this line is tangent to $f(a_1)$. With linear or concave constraints, yield is usually maximized by specialization on a single prey, and as relative prey densities change the predator should abruptly and completely switch from one prey to the other. This produces rectilinear isoclines. If the constraint is convex, it may be optimal for the predator to feed on both prey simultaneously. (Even here, if R_1/R_2 deviates greatly from 1, it may pay to specialize.) Assume that the predator consumes both prey, i.e., $a_1 > 0$ and $a_2 > 0$. As prey densities change, the predator concordantly varies a_1 and a_2 along $f(a_1)$ to maximize its yield. Then

$$\frac{\partial Y}{\partial R_2} = b_1 R_1 \frac{\partial a_1}{\partial R_2} + b_2 a_2 + b_2 R_2 \frac{\partial a_2}{\partial R_2},$$

where the derivatives on the right-hand side reflect the way the predator alters its attack rates as R_2 increases. Since

$$\frac{\partial a_2}{\partial R_2} = -\left(\frac{\partial a_2}{\partial a_1}\right)\left(\frac{\partial a_1}{\partial R_2}\right),$$

we can substitute from (13). Thus, $\partial Y / \partial R_2 = b_2 a_2 > 0$. In like manner,

$$\partial Y / \partial R_1 = b_1 a_1 > 0.$$

Since $c = a_1/a_2$ is the predator's preference for prey 1, the isocline slope is

$$-\left(\frac{\partial Y / \partial R_2}{\partial Y / \partial R_1}\right) = -\frac{b_2 a_2}{b_1 a_1} = -\frac{(b_2/b_1)}{c} < 0,$$

TABLE 3

SHAPE OF CONSTRAINTS ON ATTACK FUNCTIONS IMPLICIT IN THE SWITCHING MODELS OF TABLE 1 WHEN $h_i = 0$ FOR $i = 1, 2$

1	linear
2	$n < 1$, convex
	$n = 1$, linear
	$n > 1$, concave
3	$c_1 c_2 < 1$, convex
	$c_1 c_2 = 1$, linear
	$c_1 c_2 > 1$, concave
4	linear for values of z such that both a_1 and $a_2 > 0$
5	linear
6	linear
7	linear

where the preference c depends on relative prey numbers. If the predator switches optimally yet continues to consume both prey, its isoclines should have negative slopes.

Selection on the predator's switching response should produce gently bowed isoclines (convex constraints; fig. 1C) or rectangular isoclines (linear or concave constraints; fig. 1D), but not strongly bowed isoclines (fig. 1E). If a switching predator has an isocline with partially positive slopes, it would appear to be foraging nonoptimally.

What about the attack models of table 1? Since we are assuming that handling times are zero, all the attack rates can be written as a function of single variables Z , $a_1 = a'_1 g_1(Z)$, and $a_2 = a'_2 g_2(Z)$, where $Z = R_1/R_2$ (most models) or $Z = R_1$ (submodels [b], [c] of model 5). Since g_1 and g_2 have monotonic (but opposite) responses to increases in Z , for each model we can write Z as a function of a_1 , $Z = g_1^{-1}(a_1/a'_1)$. Hence

$$a_2 = a'_2 g_2 \left[g_1^{-1} \left(\frac{a_1}{a'_1} \right) \right] = \Psi(a_1)$$

and $\partial \Psi / \partial a_1 < 0$, since $\partial g_2 / \partial Z < 0$ and $\partial g_1^{-1} / \partial a_1 > 0$. Each attack model in table 1 seems to embody an implicit constraint that governs how an increase in the rate of attack on one prey decreases the rate of attack on the other. The attack models themselves specify how, as Z changes, the predator adjusts its attack rates in accord with this implicit constraint. Table 3 outlines the geometric properties of these constraints. Model 6 was purposely designed to represent a trade-off, the allocation of foraging time between patches, each with a single prey species. For the other models the constraints do not explicitly represent any particular mechanistic trade-off in the predation process. Most of the attack models of table 1 appear to follow linear constraints yet require predators to have mixed diets whenever both prey are present. These attack models thus seem to depict predators that to some degree are suboptimal.

I should emphasize that the force of the basic idea motivating the original use of these models—that switching can stabilize prey dynamics and permit the coexis-

tence of competitors—depends only on qualitative features of switching as experienced by alternative prey (Roughgarden and Feldman 1975; May 1977) and not on the exact form of particular switching models. In detailed studies of predator-prey dynamics, however, the use of a switching model that appears to portray maladapted predators should be avoided unless this feature of the model can be explicitly justified. Such justification may require the specification of additional constraints on predator foraging behavior within mechanistic models of switching, such as the predator training model developed by Oaten and Murdoch (1975) and McNair (1981). Moreover, some predators may prove to be imperfectly optimal by the canons of simple optimality models; for such predators, the switching models of table 1 might be adequate representations of switching behavior.

DISCUSSION

Much predator-prey and resource-consumer theory assumes without argument that predator isoclines have negative slopes (e.g., Tilman 1980). The exceptions are models that incorporate handling times or switching. I have shown that the tendency for isoclines of positive slope to occur in these models is mitigated or eliminated if predators forage optimally. If one accepts my argument that isoclines with positive slopes suggest the existence of suboptimal foraging behavior, it is perturbing to note that several examples of such isoclines are known. Maly (1975) found that a laboratory population of the rotifer *Asplanchna brightwelli* had an isocline with positive slope when consuming two alternative prey (*Paramecium aurelia* and *Euglena gracilis*). Downing (1981) has demonstrated that the growth rates of two natural populations of Cladocera are inhibited by increases in the density of one or more food types. Several of the isoclines depicted in his paper are reminiscent of *E* and *F* in figure 1. The mechanisms responsible for these unusual isoclines are not well understood, and the frequency of such isoclines in natural populations is not known.

I have already discussed how isoclines with positive slopes might be observed if recognition times are large and preferred prey are relatively common. Some other possible circumstances should be mentioned briefly. All of these hinge upon the existence of constraints on foraging behavior not built into the optimality models discussed above. (1) In temporally varying environments, the techniques of deterministic optimization and isocline analysis used here may not provide a suitable framework for interpreting predator-prey interactions (Oaten 1977); the approach to stochastic model-building outlined by Chesson (1978) could be more profitable. Moreover, the direction of selection may be set by those environmental states which occur in greatest frequency. If two prey show marked negative correlations in abundance over time and are rarely encountered in near-equal abundance, selection may favor specialized attack tactics at the expense of generalist abilities. This could produce strongly convex isoclines. (2) Isocline shape could reflect the counteradaptations of prey against predation. For instance, model-mimic systems should usually lead to predator isoclines with positive slope, as an increase in abundance of the model should tend to decrease predator fitness. As another possible example, if a herbivore switches by changing the sensory cues it uses to

find its host plants, reciprocal "associational resistance" (Atsatt and O'Dowd 1976) among plants may sufficiently reduce the herbivore's attack rates in mixed-species stands to lead to strongly bowed isoclines. (3) In all the foraging models discussed above, foraging yield rises with total prey density, given a fixed array of relative densities. In a number of studies, however, foraging yields have been observed to decrease with density at high prey densities: the type 4 response of Holling (1962). In some cases, these domelike functional responses result from prey group formation (e.g., jacks feeding upon Hawaiian anchovies, Major 1978; Taylor 1981), and in others from interference (e.g., the mite *Phytoseiulus persimilis* consuming *Tetranychus articae*, Mori and Chant 1966). Whatever the underlying mechanism might be, such a functional response dramatically alters the character of the predator isocline and the predator's response to spatial variation in prey density. At high prey densities the arrows of figure 1 are reversed, and isoclines can have positive slopes. Predators will tend to leave patches with very high prey densities and aggregate in lower density patches (e.g., Heller and Milinski 1979); this effect could compound the dynamic instability noted by Taylor (1981). (4) Finally, I have assumed throughout that selection should maximize the rate of foraging yield. If foraging rates do not strongly affect fitness, we might expect predators to forage suboptimally (Sih 1982); this could lead to isoclines with positive slope. However, the decoupling of foraging rates from fitness seems unlikely in a food-limited predator.

Several central ideas and models of community theory require predator isoclines to have negative slopes. For example, the building blocks of qualitative models of community structure are the signs of intra- and interspecific interactions (May 1975; Levins 1975, 1977; Jeffries 1974; Finerty 1980). But how can one determine the sign of an interaction without direct experimental manipulation? May (1975, p. 70) suggests that "The sign of the community matrix elements [interaction terms] can often be found by inspecting the food web diagram, even in the total absence of any quantitative data." But given isoclines like *E* and *F* in figure 1 or domed functional responses, this suggestion will not work; the effect of an increase in prey density upon predator growth might be either + or -. Ambiguity in the assignment of signs to interactions vitiates the predictive power of qualitative community models (Levins 1975).

As a second example, consider the relationship between resource overlap and competition. Overlap in resource utilization between a pair of consumers is necessary but not sufficient for the existence of exploitative competition. A second necessary condition is that each consumer should suffer a reduction in fitness because of reduced resource availability. A predator with a positively sloping isocline caused by, say, prey *i*, benefits if another predator reduces the abundance of prey *i*. Were such isoclines common, one obviously could not infer competition from overlap.

Finally, I have argued elsewhere (Holt 1977) that the alternative prey of a polyphagous, food-limited predator should show reciprocal density reductions indirectly mediated through the numerical response of the predator: Prey should appear to compete even if they do not directly compete at all. My argument requires that the isocline of a food-limited predator have a negative slope. If it

does, the sharing of predators poses a problem for prey species coexistence, a mirror image of the coexistence problem faced by species sharing resources in exploitative competition. By contrast, if the predator isocline has a wholly or partially positive slope, some prey species may indirectly benefit because others are present in the predator's diet.

I have shown that in two foraging models optimal foragers should not have isoclines with positive slopes. I have also demonstrated, however, that the addition of constraints to optimal foraging models, such as being unable to recognize poor quality prey without first handling them, may lead to isoclines of positive slope, even in optimizing predators. This suggests that examples of such isoclines in natural populations may correspond to situations in which simple optimal foraging models fail, possibly because of constraints on foraging not built into the models. I suspect that such isoclines are uncommon in natural populations. What is now needed are further empirical studies of isocline shape, with particular focus on the *raison d'être* of positive isocline slopes.

SUMMARY

I explore the relation between optimal foraging and the geometrical character of the predator isocline. Two basic models are discussed. The first is a multispecies generalization of Holling's "disc" equation. If a predator can rapidly discriminate among prey types, it is argued that its isoclines should not have positive slopes. Isoclines with positive slopes may occur if the predator must invest time discriminating between prey of unequal value, and there is a high absolute abundance of the better quality prey species. For a food-limited predator, however, selection should moderate the degree of rightward slope. In the second model, encounter and capture rates vary directly with relative prey abundance because of switching behavior. A number of published switching models are shown to produce isoclines with partially positive slopes. If the attack rates on each of two prey species are functionally related, it is argued that an optimally foraging predator will either have rectangular isoclines or isoclines with negative slope. This suggests that existing switching models are not completely satisfactory representations of switching behavior. A few examples of predators with isoclines of positive slope have been observed. Some possible mechanisms for generating such isoclines are discussed briefly. Several central ideas in community theory would founder were predators often to have isoclines with positive slopes.

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