

SIMPLE RULES FOR INTERSPECIFIC DOMINANCE IN SYSTEMS WITH EXPLOITATIVE AND APPARENT COMPETITION

ROBERT D. HOLT,*† JAMES GROVER,‡ AND DAVID TILMAN§

*Museum of Natural History, Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045; †Natural Environment Research Council Centre for Population Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, United Kingdom; §Department of Ecology, Evolution, and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, Minnesota 55108

Submitted December 22, 1992; Revised January 11, 1994; Accepted January 24, 1994

Abstract.—Because mechanistic models of interspecific interactions are often complex, one should deliberately seek simple unifying principles that transcend system-specific details. Earlier work on resource competition has led to the “ R^* rule,” which states that a dominant competitor suppresses resources to a lower level than any other competing species. This rule describes the outcome of even ornate models of competition. Here we show that analogous simple rules can characterize systems with predation. We first demonstrate, for a simple two-prey, one-predator model without resource competition but with a predator numerical response leading to apparent competition, that the winning prey supports (and withstands) the higher predator density; that is, the outcome is described by a “ P^* rule.” We then develop a general model in which predation is inflicted evenhandedly on two prey species competing for a single resource and show that the R^* and P^* rules hold: the winning prey both depresses resources to the lowest level and sustains the higher predator density. We next examine a more complex model with differential predation. Assuming a closed system (i.e., a fixed nutrient pool), we portray the four-dimensional system dynamics in a two-dimensional graphical model, and we assess the domain of applicability of simple dominance rules in more complex systems. We address the generality of our conclusions and end by examining the implications of different, reasonable biological constraints for community structure.

In ecology, the search for simple, unifying principles often clashes with the observed idiosyncracies of ecological systems. This problem has led to the realization that each simple theory has limited bounds within which it applies. MacArthur (1972; see Schoener 1986a) may have been the first to articulate this insight when he called for the development of contingent ecological theory.

The study of interspecific interactions is particularly illustrative of the intellectual currents leading toward contingent theory. During the 1960s and early 1970s, a large, general body of Lotka-Volterra competition theory and related niche overlap theory developed, followed by a period of sharp criticism, introspection, and the inclusion of numerous modifications tailored to the specific attributes of particular systems. The search for a general theory of competition seemed, at times, to be lost in a sea of special cases.

† To whom correspondence should be addressed; E-mail: predator@kuhub.cc.ukans.edu.

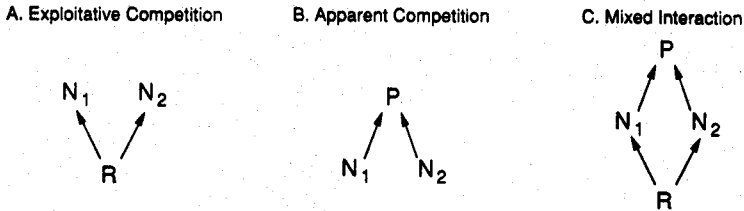


FIG. 1.—Community modules. A, Exploitative competition between a pair of consumer species for a shared resource (Tilman 1982); B, a mirror image of exploitative competition—apparent competition between a pair of prey species via a shared predator (Holt 1977); C, mixed exploitative and apparent competition.

In recent years, researchers have recognized the need to develop explicit models of the mechanisms of competition rather than phenomenological models, whose parameters must be fit afresh in each novel environment (Tilman 1977, 1987; Armstrong and McGehee 1980; Schoener 1986*b*). Mechanistic models for interspecific exploitative competition (see, e.g., Tilman 1982) incorporate three separate submodels, one for each of the components shown in the simple food web module of figure 1A. For each consumer species, an equation describes its population growth rate as a function of the abundance of the limiting resource. Another equation portrays the dynamics of the resource as a joint function of resource renewal (e.g., soil nutrient mineralization rates) and consumption. Mechanistic models of exploitative competition have several advantages over more traditional phenomenological models (Tilman 1977, 1982): they highlight the need to monitor resources as well as consumers in studies of interspecific competition; they permit direct links to ecosystem-level processes that influence resource levels (DeAngelis 1992); they make explicit the role of various biological factors (e.g., resource conservation and uptake, resistance to agents of mortality) in determining competitive ability; and they allow *a priori* predictions about the dynamics and eventual outcome of interspecific competition, based on single-species studies. None of these are possible in more traditional competition theory.

However, mechanistic models can become quite complex as additional mechanistic details are added, which raises the specter that the study of resource competition may once again become a compilation of special cases. Some have argued (Tilman 1990) that this is not the case, because the outcome of resource competition can often be predicted by a simple rule of thumb: the winner in exploitative competition (fig. 1A) is the species that depresses equilibrium resource abundance (denoted R^*) to the lowest level consistent with its own maintenance, relative to the levels required by competing species. The R^* for a given consumer is defined as the resource level at which that consumer's birth rate just matches its death rate. Even quite complex models of interspecific competition for a single limiting resource, with numerous parameters, can be characterized by the R^* rule (Tilman 1990). The details of the models cannot, of course, be entirely ignored, for they govern the nonequilibrium behavior of a system (see, e.g., Grover 1990, 1991) and moreover provide the mechanistic basis for predicting the value of a given species' R^* . Nonetheless, the R^* rule clearly highlights an abstract conceptual unity among potentially disparate competitive systems.

This rule for competitive dominance raises the question of whether other interspecific interactions can be similarly characterized by simple rules of thumb. The interaction that, after competition, has received the most attention from community ecologists is predation. It has been shown both theoretically (Holt 1977, 1984; Holt and Lawton 1993) and empirically (Schmitt 1987; Reader 1992) that shared predation (i.e., a generalist predator that attacks two or more prey species, as in fig. 1B) can readily mimic the effects of exploitative competition, such as the indirect exclusion of one prey species by another, reciprocal reductions in abundance in sympatry compared to allopatry, and habitat shifts. This effect, called *apparent competition*, rests on a particular mechanism, namely a numerical response by a predator to its prey. The predator's numerical response can either be a behavioral response over short timescales (e.g., predator aggregation to a particular patch in a heterogeneous environment; see Holt and Kotler 1987; Schmitt 1987) or a demographic response that leads to an increased predator population over longer timescales (due to predator birth rates increasing, and/or death rates decreasing, in response to increased prey availability).

At a broad level, there is a symmetry between exploitative competition—which depends on the ability of a consumer population to decrease resource levels—and apparent competition—which depends on the capacity of a prey population to increase predator levels (Holt 1984). Given this symmetry, can one characterize the action of apparent competition with a simple rule of thumb, analogous to the R^* rule (Tilman 1982, 1990)? In this article, we first show that in some simple models one can indeed define a P^* rule to characterize the outcome of apparent competition (see also Holt and Lawton 1993). We then examine the consequences of mixing exploitative and apparent competition (as in fig. 1C) to determine whether either or both of these rules remain useful as guides to the net outcome of the interspecific interactions in this more complex community module. Previous workers who have examined mixed competition-predation systems have largely emphasized how predation can permit the coexistence of otherwise competitively incompatible species (see, e.g., Roughgarden and Feldman 1975; Abrams 1977; Armstrong 1979; Comins and Hassell 1987; Leibold 1989; Yodzis 1989; Oksanen 1992). Our concern is not mainly with this issue (though our results help clarify the requirements for coexistence) but rather with the domains of applicability of simple rules for dominance in circumstances with potentially complex interactions between species.

We will approach this goal by considering two models with both exploitative and apparent competition whose assumptions bracket a wide range of systems. The first model incorporates rather general resource dynamics and nonlinear functional responses but makes the simplifying assumption that the predator feeds on the two prey types in an evenhanded manner. In our second model, we relax the latter assumption, but at the cost of assuming for simplicity linear functional responses at all trophic levels and a simple form of resource renewal, pertinent to a closed system.

In Appendixes A and C, we show that the conclusions drawn from these two simple but biologically transparent models characterize more general families of multispecies models. A follow-up manuscript (J. Grover, D. Tilman, and R. D.

Holt, unpublished manuscript) explores the utility of simple rules of thumb for dominance in a model, appropriate for zooplankton feeding on competing phytoplankton, that incorporates nonlinear functional responses, asymmetrical predation, and a variety of resource renewal dynamics. It is our experience that the conceptual insights gleaned from the simple models analyzed below help sharpen one's intuition about phenomena in such more complex food web models, suggest general features of interspecific interactions, and illuminate the limits of applicability of conclusions drawn from simple models of interspecific interactions.

AN EXAMPLE OF THE P* RULE

We start with a simple model showing that the dominant species in apparent competition is the prey species that maintains the highest density of the shared predator, relative to other prey species.

Food web models (e.g., for the community modules in fig. 1) require a source of stabilizing, density-dependent feedback that prevents either extinction or unbounded, exponential growth. Three basic mechanisms allow stability in a one-predator, two-prey food web: direct density dependence in the prey or predator populations, a stabilizing functional response by the predator to these prey (e.g., switching; Murdoch and Oaten 1975), and spatial coupling between a local ensemble and other communities (Holt 1984, 1993; Nisbet et al. 1993).

Direct density dependence most often arises from the limited availability of resources (e.g., nest sites for predators, food for prey). Because we wish first to focus on shared predation, not resource competition, we assume that there is no resource limitation, either explicit or implicit, in the prey population. Though stabilizing functional responses do occur, they do not seem to be the norm in strong predator-prey interactions (Murdoch and Bence 1987). Our initial model assumes a type 1 functional response, which is neither directly stabilizing nor destabilizing.

We instead use a simple kind of spatial dynamic to stabilize the predator-prey interaction. Imagine that a mobile predator consumes relatively immobile prey. The system as a whole can be stabilized because of the spatial coupling of the local predator population to a much larger "bath" of propagules (*sensu* Levin 1976) whose dynamics are ignored. The equations for the predator and the two prey species are as follows:

$$\frac{dP}{dt} = P \left(\sum_{i=1}^2 a_i b_i N_i - c \right) + I - eP \quad (1)$$

and

$$\frac{dN_i}{dt} = N_i(r_i - a_i P), \quad i = 1, 2. \quad (2)$$

The local dynamics fit the same assumptions as in the classical Lotka-Volterra predator-prey model. We assume that the predator has a linear functional response to each prey, scaled by an attack rate a_i (per predator, per prey rate of

attack). Each captured prey leads on the average to b_i predator births. Predators experience a density-independent death rate of c . The intrinsic rate of growth for prey i is r_i .

The model differs from the usual predator-prey model because the predator population is open, coupled by dispersal to a larger ensemble of local predator populations whose dynamics are not being explicitly modeled. There is a constant rate of immigration (I) of predators from that ensemble, and predators emigrate at per capita rate e . The immigration term is strongly stabilizing, for it provides a kind of induced density dependence (the contribution of constant immigration on a per capita basis to local population growth is I/P , which is strongly density-dependent at low P ; Holt 1993). This model structurally parallels a model for resource competition in which resource renewal is described by a constant input of resources, a model that has been thoroughly explored elsewhere (Tilman 1980, 1982).

Consider the community comprised of just the predator and prey species 1. There are two possible equilibria. If

$$\frac{r_1}{a_1} < \frac{I}{c + e}, \quad (3)$$

then $N_1^* = 0$, and $P^* = I/(c + e)$ (the asterisks denote equilibrium). The number of predators maintained by the balance of immigration with local predator deaths and emigration suffices to exclude prey 1.

If inequality (3) is reversed, prey 1 can increase when rare, given that the predator is at its immigration-maintained equilibrium. In this case, the equilibrial abundances of both species are as follows:

$$P_1^* = r_1/a_1, \quad N_1^* = \frac{c + e - \frac{I}{r_1/a_1}}{a_1 b_1}. \quad (4)$$

The index on P_i^* indicates the equilibrial abundance of the predator when just prey i is present. It is easy to show that the Jacobian matrix defining the local stability properties of this equilibrium has the sign structure

$$\begin{bmatrix} 0 & - \\ + & - \end{bmatrix},$$

which is qualitatively stable (Jeffries 1976).

Can prey species 2 invade? When species 2 is rare and prey species 1 and the predator are at their respective equilibria, the growth rate of the invading prey is

$$\frac{dN_2}{dt} = N_2(r_2 - a_2 P_1^*). \quad (5)$$

The growth rate is positive if $r_2/a_2 > P_1^*$. Now note that $r_2/a_2 = P_2^*$, where P_2^* is the equilibrial density of predators, were the predator interacting with just prey 2. Thus, one can compactly write the condition for invasion by prey 2 as $P_1^* <$

P_2^* . In like manner, if $P_1^* > P_2^*$, prey 2 is excluded. If prey 2 can invade, it reaches equilibrium when the predator density has increased to P_2^* . But this density of predators exceeds the level that prey 1 can withstand. Hence, if $P_2^* > P_1^*$, prey 2 displaces prey 1 via indirect competition mediated through the predator's numerical response—apparent competition (sensu Holt 1984). Reversing the inequality switches the outcome. The prey species with the higher P_i^* sustains so many predators that consumption by these predators overwhelms the intrinsic growth rate of the alternative prey.

This suggests a simple rule of thumb for the outcome of apparent competition: the prey species that dominates is the one that withstands (and indeed maintains) the highest density of the shared predator. Using shorthand to describe this situation, one may refer to a " P^* rule." It has been shown (Holt and Lawton 1993) that a similar rule characterizes indirect host dominance in multiple host species–parasitoid systems. In Appendix A, we show that a P^* rule applies in a wider range of predator–prey systems than just equations (1) and (2).

A GRAPHICAL MODEL OF MIXED EXPLOITATIVE AND APPARENT COMPETITION

Two limiting features of the above model are that the prey species do not experience resource limitation and that the predator has a simple, linear functional response. We now consider a more general model for the diamond-shaped food web module of figure 1C that to a degree relaxes both these assumptions. The model is as follows:

$$\frac{dP}{dt} = PF(N_1, N_2),$$

$$\frac{dN_1}{dt} = N_1[g_1(R) - Ph_1(N_1, N_2)],$$

$$\frac{dN_2}{dt} = N_2[g_2(R) - Ph_2(N_1, N_2)], \quad (6)$$

and

$$\frac{dR}{dt} = f(R) - \Phi_1(R)N_1 - \Phi_2(R)N_2.$$

The function $F(N_1, N_2)$ is the per capita growth rate of the predator. By expressing predator growth as solely a function of prey densities, we are assuming that the predator is strictly food limited. We further assume that F increases with both N_1 and N_2 (for conditions in which this might not hold, see Holt 1983) and that there is a connected set of low prey densities for which $F < 0$. This implies that in a phase space with prey densities as axes, a zero-growth isocline of negative slope describes those combinations of prey densities for which the predator has a zero growth rate; for prey densities between this isocline and the origin, the predator population declines, whereas outside the isocline, predator density increases (fig. 2A).

The h_i functions describe the rate of prey capture per predator for each prey species; in general, these attack rates are density-dependent. The quantities $\Phi_i(R)$

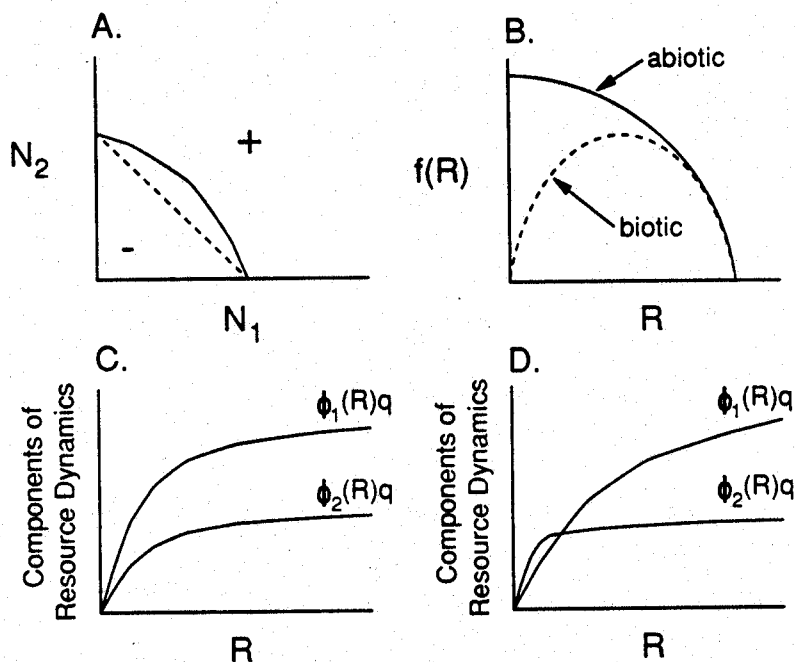


FIG. 2.—Components of graphical model. A, Predator zero-growth isoclines—combinations of prey densities for which the predator has a zero growth rate. In general, predator isoclines are curvilinear with negative slope (Tilman 1982; Holt 1983), but with equivalent prey the predator isocline is a straight line of slope = -1 . B, Resource recruitment ($f(R)$) as a function of R , resource abundance. Nonliving resources may recruit maximally at low R ; living resources usually have humped recruitment curves. C and D, Total resource uptake rates by two consumer species, each respectively fixed at density q ; $\Phi_i(R)$ is per capita resource uptake for consumer i . In C, species 1 is always superior. In D, the rank order of uptake rates varies with R .

describe the rate at which individual prey of species i consume the resource, and the functions g_i indicate the growth rate of consumer i on this resource (implicitly accounting for any mortality in the system other than that imposed by the top predator). And, finally, the function $f(R)$ portrays resource dynamics, except for depletion due to consumption by the intermediate consumers.

We now introduce some simplifications. First, we assume that the underlying resource is abiotic with dynamics such that $f(0) > 0$ (i.e., there is always some resource renewal even at very low resource levels), that $df/dR < 0$ (i.e., resource renewal is self-damped), and that for some $R = R''$, $f(R'') = 0$ (i.e., there exists an equilibrational abundance of the resource in the absence of consumption (fig. 2B).

Second, we assume that the prey populations' per capita resource uptake rates and per capita growth rates are related simply by $g_i(R) = b' \Phi_i(R) - c'$. Here, b' is a constant converting resources consumed into prey births, and c' measures density-independent mortality. As written, this equation assumes that with respect to resource consumption, the two prey species may differ in their ability

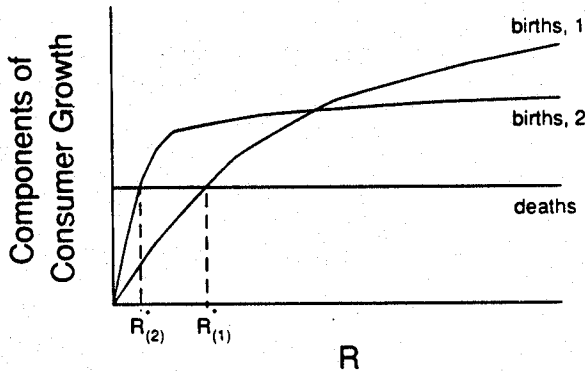


FIG. 3.—Consumer demographic components. Birth rates increase with R , whereas death rates are constant. Consumer species i equilibrates when resources are at $R_{(i)}^*$.

to capture the resource but not in their postcapture efficiency in use or capacity to withstand ambient sources of mortality in the environment. For simplicity, we consider in detail the case in which the relative rates of resource capture differ with resource availability, but with only a single switch point, as in figure 2D; other cases, such as that in which one prey is unilaterally superior at capturing the resource (fig. 2C), lead to similar conclusions about dominance rules.

Finally, and importantly, we assume that the prey are identical from the predator's point of view. Hence, $h_1(N_1, N_2) = h_2(N_1, N_2) = h(N_1 + N_2)$, and $F(N_1, N_2) = F(N_1 + N_2)$. The predator may have a nonlinear functional response (due to handling times, learning, etc.), but this response is to the summed availability of the two prey species rather than to each one separately. Moreover, the prey are captured at equal per capita rates, and when captured they make equal contributions to the predator's population growth. Below we will examine in some detail the consequences of relaxing these symmetry assumptions. Analyzing this simple model proves useful in interpreting more complex, nonsymmetrical situations. In what follows, we concentrate on systems that allow stable point equilibria and ignore limit cycles or more complex dynamics. Our general approach is to examine equilibria in which one prey species is present and determine whether the other prey species can invade.

Consider first the interaction between the two prey species in the absence of the top predator. Following a procedure described elsewhere (Tilman 1982), in figure 3 we simultaneously plot the per capita birth and death rates of the two prey species as a function of resource availability. The birth rates depicted are simply multiples of the resource uptake functions shown in figure 2D, and the death rate is a constant for both species at all resource levels. As drawn, we see that when species 1 is in demographic equilibrium, sufficient resource is present for species 2 to invade; conversely, when species 2 is present and in demographic equilibrium, species 1 necessarily declines toward extinction. This graphical model portrays the R^* rule: the species depressing resources to the lower level wins.

Now assume that the top predator is present. The predator population is at

equilibrium when $F(N_1^{**} + N_2^{**}) = 0$. (We use double asterisks to indicate equilibrium population abundances in systems experiencing limitation by both predation and resource exploitation.) Let $q = N_1 + N_2$ denote the total prey abundances at which the predator has a zero growth rate. We now examine equilibria for the other three components of the system, given that the predator population has depressed total prey abundance to q , so that the predator itself is in equilibrium. Prey i is in equilibrium when

$$\frac{1}{N_i} \frac{dN_i}{dt} = b' \Phi_i(R) - Ph(N_1 + N_2) - c' = 0. \quad (7)$$

Assume that prey i alone is present and at equilibrium with both the resource and the top predator. Let $R_{(i)}^{**}$ and $P_{(i)}^{**}$ denote the equilibrium densities of the bottom resource and top predator, evaluated when prey species i is the only prey species present. (The double asterisks indicate that both resource and predator limitation are present. Parentheses around the subscript i denote that the quantities R and P are being evaluated when prey species i is present.) Equation (7) implies that

$$\frac{b'}{h(q)} \Phi_i(R_{(i)}^{**}) = P_{(i)}^{**} + \frac{c'}{h(q)}. \quad (8)$$

Recall that q is the density of prey fixed by the predator (i.e., the prey density at which the predator itself is in equilibrium). Because this is a constant, so is $h(q)$. The above expression shows that the number of predators, at equilibrium, increases linearly with the per capita rate of resource uptake by prey i .

To complete the analysis, we must characterize the conditions for equilibrium in the resource base. The resource is in equilibrium with prey i , given that the predator is in equilibrium, when

$$\frac{dR}{dt} = f(R) - \Phi_i(R)N_i = f(R) - \Phi_i(R)q = 0. \quad (9)$$

The equilibrium supply of the resource when prey i and the predator are both at equilibrium is set by equating the resource supply rate to the total rate of resource uptake, or $f(R_{(i)}^{**}) = \Phi_i(R_{(i)}^{**})q$. The quantity $\Phi_i(R)q$ is simply an uptake function for prey species i , multiplied by a constant equal to the total prey abundance observed when the predator's dynamics are in equilibrium. The two components of resource dynamics (renewal and consumption; see fig. 2) can now be plotted simultaneously against resource availability for each prey species, when that prey is alone at the prey density maintained by the top predator (fig. 4). The equilibrium resource level is the intersection of these two component curves. The equilibrium prey level is q , and the equilibrium predator level can, finally, be found from equation (8).

The example illustrated in figure 4 can be read as follows. At the density q of prey determined by the predator (for which $F(q) = 0$), in the example depicted $R_{(1)}^{**} < R_{(2)}^{**}$, which is to say that prey 1 (when alone with the predator) is better able to suppress the limiting resource than is prey 2 (when it in turn is alone with

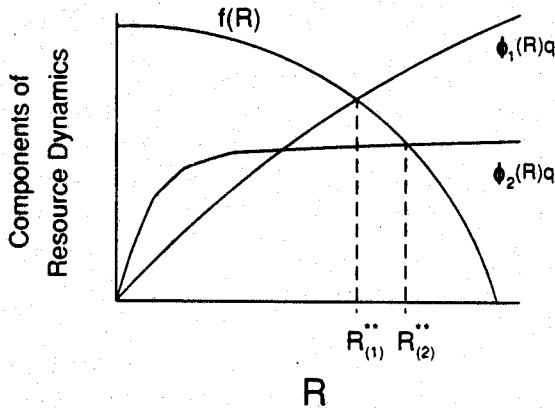


FIG. 4.—Determining equilibril resource levels as a balance between resource recruitment and consumption. The predator fixes abundance for prey i ($= 1, 2$) at q . These prey consume resources at total rate $\Phi_i(R)q$. The resource is in balance (at $R_{(i)}^{**}$) when consumption equals recruitment, $f(R)$. Prey 1 excludes prey 2.

the predator). Because the curves shown are simply the uptake rates times q , this implies that $\Phi_1(R_{(1)}^{**}) > \Phi_2(R_{(1)}^{**})$, so prey 1 also has the higher uptake rate on the resource at this resource level. This in turn implies (from eq. [8]) that the predator density (supported ultimately by this prey uptake) is also higher.

Consider an attempt at invasion by prey 2 when prey 1, the predator, and the resource are all in equilibrium. The invading propagule of prey 2 experiences the same rate of mortality as the resident prey but has a lower birth rate (because of its lower resource uptake rate). Because the resident prey's birth rate just matches its death rate, the invading prey clearly has a negative growth rate and will be excluded. Conversely, if prey 2 is present and at equilibrium with the other system components and prey 1 invades, its invasion will succeed—the invader experiences mortality equal to the resident but enjoys a higher birth rate.

To summarize: with symmetrical predation on two prey species that exploit a single limiting resource, the winning prey species is the one that maintains the lower resource density, and it is also the one that sustains the higher predator density. Our rules of thumb, here expanded to cases in which several species interact to determine R^{**} and P^{**} , give isomorphic predictions.

The underlying reason for this symmetry is that equilibril resource and predator levels are both dependent variables that respond in opposite directions to the same attribute, namely prey resource uptake. A prey population with a rapid resource uptake tends to depress resource levels. Productive prey populations (i.e., ones with efficient resource capture) also tend to support large predator populations. All else being equal, resource suppression and predator enhancement go hand in hand.

An intriguing prediction of this model is that the outcome of competition under shared predation may depend on resource productivity (see also Armstrong 1979). Figure 5 shows two ends of a gradient in resource renewal rates (reflected in the

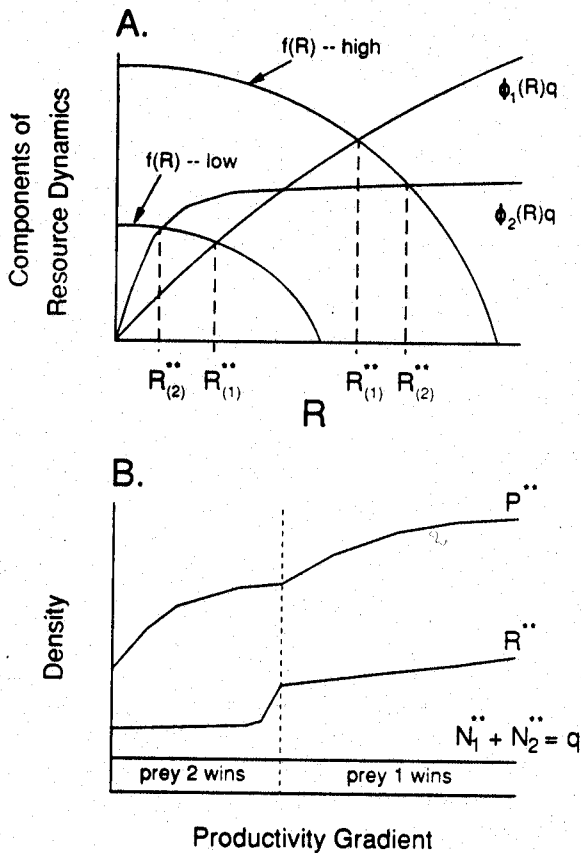


FIG. 5.—A, Effect of resource productivity on competitive dominance, given a predator fixing prey abundance at q . An increase in productivity shifts $f(R)$ away from the origin. If the $\Phi_i(R)$ curves cross at a single point (as depicted), dominance varies with R . B, Patterns in resource, prey, and predator densities along a productivity gradient.

position of $f(R)$). The species that is dominant shifts as one moves from low to high resource productivity. Along a gradient in resource renewal rates, one might observe a sharp transition from one prey species to another. In contrast, without predation the same species should dominate all along the gradient, regardless of resource renewal rates (as long as a single resource provides the sole limiting factor, and the rate of density-independent mortality is constant along the gradient; see Tilman 1982).

A SIMPLE MODEL WITH ASYMMETRICAL PREDATION

To further explore the possible applicability of simple R^* and P^* rules to more complex interactions, we now relax the assumption of symmetrical predation. To keep matters tractable, we assume that the system is completely closed and that R

is an abiotic resource such as an inorganic nutrient. The total amount of nutrient, summed over available (e.g., dissolved) forms and nutrient bound in organisms, is fixed at S . We also assume that the predator's functional response and the prey's nutrient uptake rates are linear. The system dynamics are given by

$$\frac{dP}{dt} = P(a_1 b_1 N_1 + a_2 b_2 N_2 - c),$$

$$\frac{dN_1}{dt} = N_1(a'_1 b'_1 R - c'_1 - a_1 P),$$

$$\frac{dN_2}{dt} = N_2(a'_2 b'_2 R - c'_2 - a_2 P),$$

and

$$\begin{aligned} \frac{dR}{dt} = & \frac{c'_1 N_1}{b'_1} + \frac{c'_2 N_2}{b'_2} + \frac{cP}{b_p} + a_1 N_1 P \left(\frac{1}{b'_1} - \frac{b_1}{b_p} \right) \\ & + a_2 N_2 P \left(\frac{1}{b'_2} - \frac{b_2}{b_p} \right) - a'_1 R N_1 - a'_2 R N_2. \end{aligned} \quad (10)$$

The predator's net per capita rate of increase is determined by a linear functional response (with attack rate a_i and birth efficiency b_i), minus density-independent losses at a rate c . The prey's net per capita rate of increase is determined by a linear uptake of nutrient (with affinities a'_i and yield coefficients b'_i), minus density-independent losses at rates c'_i and losses to predation. (Primed parameters denote prey dynamics, and unprimed parameters, the predator.)

The above equation for resource dynamics implicitly assumes that consumer death immediately frees nutrients bound in consumer bodies, so there is instantaneous recycling into the nutrient pool. We make this assumption to make the model mathematically tractable, but we note that it should be a reasonable approximation whenever the rate of decomposition is faster than the demographic processes in the system.

The b'_i parameters gauge the number of prey produced per unit of resource consumed by prey i ; the inverse of this quantity is the amount of resource produced per dead prey. In like manner, for predators the parameter b_p describes how many predators are produced per unit basal resource, and $1/b_p$, the amount of resource released per dead predator. Additional nutrient recycling may result from incomplete assimilation (see App. B). The equation for resource dynamics is not strictly necessary, because in this closed system a simple algebraic mass balance expression holds:

$$R = S - \frac{N_1}{b'_1} - \frac{N_2}{b'_2} - \frac{P}{b_p}.$$

The above set of equations can be solved to ascertain the effects of the model parameters on equilibrial abundances and thus the abilities of simple rules (such

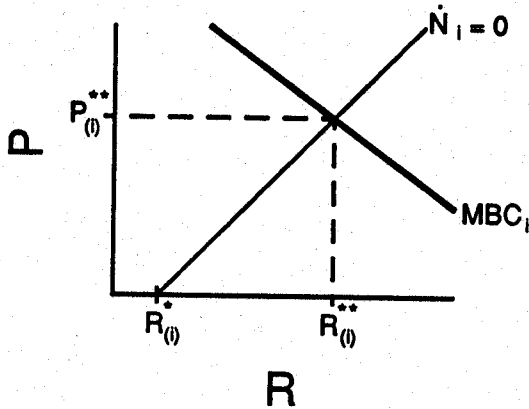


FIG. 6.—Prey isoclines and mass-balance constraints (MBCs) in the resource-predator (RP) phase plane. Without predation, prey i equilibrates at $R = R_{(i)}^*$. Increasing P increases the level of resource needed to sustain prey i . With the model assumptions in the text, the prey isocline is a straight line. With a fixed resource pool, and assuming the predator to be at equilibrium, all resources not in prey are either free or in predators, so the system is constrained to a line of negative slope—the MBC line.

as the R^* rule) to predict the outcome of interspecific interactions. This and other tedious but essential mathematical details (e.g., stability analyses) are banished to Appendix B.

Although the phase space of the full system is four-dimensional, the argument presented in Appendix B justifies an approach that permits our results to be portrayed in a graphical model in a two-dimensional plane defined by axes of resource and predator densities. Here we concentrate on this graphical model, because our interest is in sharpening our biological understanding of the factors determining dominance rather than in the mathematical details of the models per se. In Appendix C we briefly discuss how this approach generalizes to a broader family of models, and we sketch some general limitations in our approach.

Essentially, the method relies on using a mass-balance constraint (MBC) that is conditional on the predator's being at equilibrium. The key insight is that the predator is at equilibrium when it has reduced its prey to a given density, which in effect fixes the amount of nutrient locked in prey. Because the total nutrient pool is assumed to be constant, predator density and the amount of resource available for prey consumption are constrained to a particular set of the resource-predator (RP) plane whenever the predator is in dynamic equilibrium. For the subsystem of prey i and the predator, this set is a line (fig. 6; see also App. B), which we refer to as the "MBC line" for prey i (though it implicitly involves the dynamic constraint of predator equilibrium, as well as the MBC). Biologically, this line describes the possible partitioning of mass in the system between the predator and the resource, given that the predator constrains prey i , when alone, to a density of N_i^{**} . Differences among prey (e.g., in a_i) lead to a family of parallel MBC lines differing in their intercepts; differences in total nutrient supply (S) shift the intercept of the MBC lines for a given prey species (eq. [B4]).

When growing alone with the predator, the isocline for prey i in the RP plane is a line intersecting the R -axis at $R_{(i)}^*$, the amount of resource required for this prey to be in equilibrium in the absence of predation (fig. 6; eq. [B5]). To the left (above) the isocline of prey i , its net growth rate is negative; to the right (below) it is positive. The positive slope of the prey isocline expresses the increase in available resource prey i required to balance a given increase in predator density. The intersection of the MBC line for prey i with its isocline sets the equilibrium values of $R_{(i)}^{**}$ and $P_{(i)}^{**}$ (fig. 6; eq. [B6]).

When both prey species are present with the predator, equilibrium of the latter fixes a weighted sum of the two prey densities (eq. [B9]) but otherwise leaves them free to vary in relative abundance within these bounds. For the full system, the region of the RP plane consistent with both mass balance and predator equilibrium lies between the two MBC lines for each prey when growing alone with the predator. The assumption of linear functional responses implies that the prey have the same isoclines when together as when alone (eq. [B5]). Thus, we can superimpose these isoclines on the RP plane to study competitive dynamics and use invasibility analyses to determine the possible outcomes of the interaction.

Graphically, prey 1 increases when rare if its isocline lies above that of prey 2, given that R is fixed (at $R_{(2)}^{**}$) at the equilibrium of prey 2 (eq. [B11]). Similarly, prey 2 increases when rare if its isocline lies above that of prey 1, when R is fixed (at $R_{(1)}^{**}$) by the equilibrium of prey 1 (eq. [B11]). We first work through the formal possibilities of the model and evaluate the utility of various rules for diagnosing the outcomes. In the Discussion, we outline how the incorporation of reasonable biological constraints may make some outcomes more plausible than others.

Coincident MBCs

Consider first the special case when the two MBC lines are coincident (which requires $a_1 b_1 b_2' = a_2 b_2 b_1'$). The two prey may nevertheless differ in a_i' and c_i' , and so their isoclines may differ. If $a_1' > a_2'$ and $c_1' < c_2'$, the isocline for prey 1 is to the left of the isocline for prey 2 (fig. 7A). Recall that a given prey species has a positive growth rate to the right of its isocline and a negative growth rate to the left. By inspecting the figure, one can readily see that prey 1 increases when rare, if prey 2 is present and at equilibrium with the resource and predator; conversely, prey 2 is excluded when prey 1 is resident and at equilibrium. In this case, the species that wins under shared predation is the same species that wins given purely exploitative competition (i.e., it has the lower R^*).

At first glance, this situation seems to suggest that predation is unimportant in the exclusion of species 2. But by inspecting the figure one can see that were predation discounted at equilibrium, the growth rate of prey 2 on the ambient resource level would in fact be positive! Invasion is precluded because the resident prey supports sufficient predators that predation on the invader overwhelms its inherently positive growth rate on the resource level at this equilibrium. If the predator were selective just on species 1, species 2 could invade. Thus, any short-term, mechanistic explanation for the exclusion of species 2 must invoke

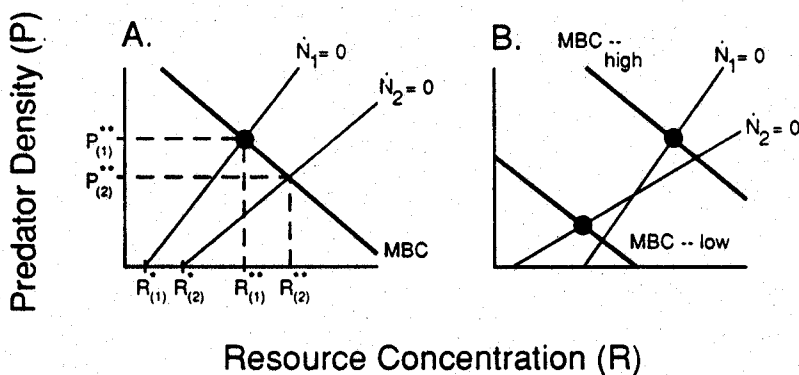


FIG. 7.—Species dominance with coincident MBCs. A, Nonintersecting prey isoclines. The same species (here prey 1) resists density-independent mortality factors more effectively (lower c') and better exploits the resource (higher a'). B, Intersecting prey isoclines. Prey 2 has lower c' , prey 1 the higher a' . The outcome depends on the position of the MBC line. At low resource pool sizes, prey 2 wins; at high pool sizes, prey 1 wins. In all cases the winner supports a higher predator density, on a lower ambient resource level, than does the loser. The filled circles denote noninvasible equilibria.

both enhanced predation and reduced resources caused by the presence of prey species 1.

It is immediately apparent from the figure that with nonintersecting isoclines and coincident MBCs, the winning prey is the one that, on its own, sustains the higher predator and lower resource levels, so both the P^{**} and R^{**} rules hold. This is also the case if the prey isoclines cross (fig. 7B), which can occur if the prey better able to acquire the resource is more sensitive to density-independent mortality factors (i.e., if $a'_1 > a'_2$ and $c'_1 > c'_2$). As drawn, without the predator prey 2 would competitively exclude prey 1. At low total resource supply (MBC near the origin) this is still true, but with sufficiently high resource supply competitive dominance switches to prey 1. Yet the R^{**} and P^{**} rules unvaryingly hold.

The reason for the switch in dominance is that with increasing resource levels, the predator becomes increasingly abundant; this diminishes the importance of other, density-independent mortality agents (measured by c_i) and sharpens the importance of resource accrual (governed by a'_i) to replace losses to predation. An increase in a'_i steepens the prey isocline and pushes it toward the origin (fig. 7A), without changing the MBC. This condition reduces the supply of free resource and enhances predator density. This is a particular realization of the influence of prey resource accrual rates on predator density noted earlier. Coincident MBCs are most likely if predation is symmetrical (i.e., $a_1 = a_2$, etc.), and indeed the above results match the conclusions from the earlier graphical model (eqq. 6; fig. 4).

Unilateral Dominance

If the prey isoclines do not cross, coexistence is impossible. The prey whose isocline is closer to the origin dominates unilaterally, regardless of its MBC (and

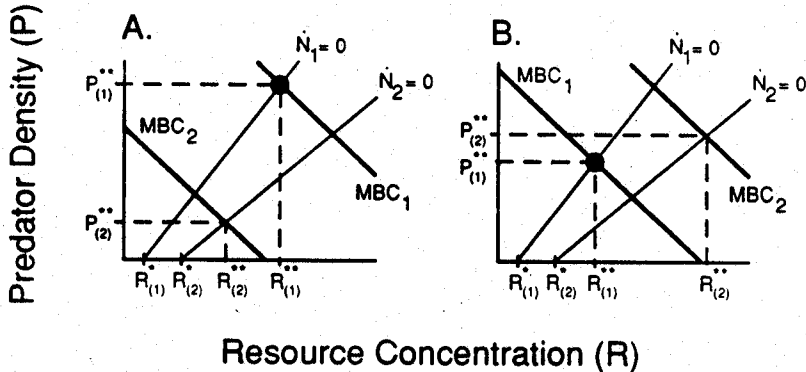


FIG. 8.—Species dominance with noncoincident MBC lines. A, The winning species has an MBC line farther from the origin; the dominant species sustains a higher P , but not a lower R than the loser. B, The winning species' MBC line is closer to the origin. As drawn, the winning species depresses resources to a lower level than the loser but does not sustain more predators.

hence of resource supply, nutritional value of prey to the predator, etc.). The conditions for this (assuming prey 1 dominates) are

$$\frac{a'_1 b'_1}{c'_1} > \frac{a'_2 b'_2}{c'_2}, \quad \frac{a_1 b_1}{a_1} > \frac{a_2 b_2}{a_2}.$$

These inequalities basically state that the species superior at resource exploitation is also superior at withstanding predation. The terms in the second inequality are the prey isocline slopes. A steeper isocline implies that fewer resources are required to offset a given increase in predator density. So the species with lower R^* (inequality [B7]) also wins under shared predation. Thus, the original R^* rule (Tilman 1982, 1990) holds, regardless of predation.

What happens to the R^{**} and P^{**} rules? This is determined by the positions of the MBC lines. The outermost MBC is for that prey species with a greater value of $a_i b_i b'_i$, a measure of the rate at which free resources are converted into predator biomass, via prey i . If the MBC line of prey 1 is farther from the origin than the line for prey 2 (fig. 8A), the winning prey sustains the higher predator density; it may, but need not, also depress resources to the lower level when experiencing this level of predation. One plausible scenario leading to the relative positions of the prey isoclines and MBC lines shown in figure 8A is for prey 1 to be more efficient than prey 2 at converting resource capture into new prey (higher b'_i) but for the two prey to be similar in other respects.

If the relative positions of the MBCs are reversed (fig. 8B; differential predator attack on the inferior exploitative competitor can lead to this), the winning prey may, in some cases, actually support fewer predators than would the losing prey. However, in this case the winning species always depresses the resource to a lower level than the other species.

Thus, either the R^{**} or the P^{**} rule applies, but not both at once; which works depends on species traits as reflected in the positions of the MBC lines.

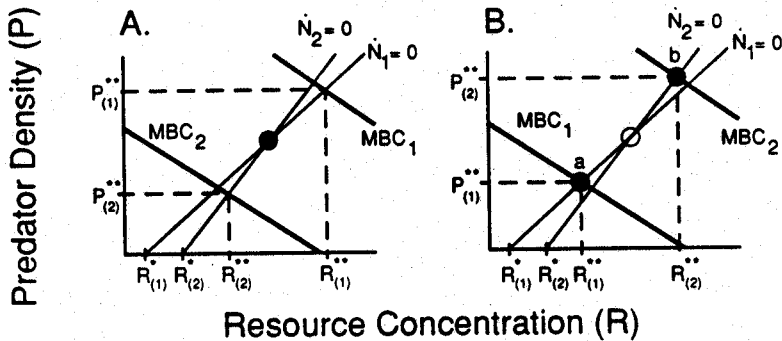


FIG. 9.—Crossing prey isoclines (trade-off between exploitative competition and escape from predation). A, Prey 1, superior at resource competition, has an MBC farther from the origin. Prey coexistence is feasible. B, Prey 1 has an MBC closer to the origin. The prey exhibit priority effects. (See text.)

Potential Coexistence and Priority Effects

The greatest range of possible outcomes is observed if the prey isoclines cross. The outcomes observed—which range from dominance, to coexistence, to priority effects (when either prey can exclude the other, contingent upon initial conditions)—vary with the absolute and relative positions of the MBCs (and hence on overall resource supply).

Consider first coexistence, which requires that each species be able to increase when rare. For mutual invasibility the invasion conditions for both prey species must be met (inequalities [B11] and [B12]); graphically, the prey isoclines must intersect for some R lying between $R_{(1)}^{**}$ and $R_{(2)}^{**}$ (e.g., fig. 9A). Crossing of the prey isoclines is necessary for coexistence, but it is not sufficient, for we must assure that predator equilibrium and overall mass-balance requirements are also met at the intersection. Suppose that prey 1 has the lower R^* . To satisfy the invasion conditions, the MBC line for prey 1's subsystem must then lie above that for prey 2's subsystem (see App. B). This also guarantees that the intersection of the isocline occurs in the feasible space between the MBC lines for the single-prey subsystems (as shown in fig. 9A). Coexistence thus requires that the prey superior at resource exploitation (lower R^*) has (1) a shallower isocline and also (2) a constraint line lying farther from the origin. One prey has a higher $P_{(i)}^{**}$, while the other has the lower $R_{(i)}^{**}$. Thus there is a trade-off, in some sense, between abilities to dominate in exploitative and apparent competition.

Requirement 1 for coexistence states that the prey that is superior at resource exploitation is also more vulnerable to predation. Requirement 2 states that the predator must equilibrate with less of the fixed nutrient pool locked up in this competitively dominant prey (which thereby permits an exploitatively inferior prey to enjoy a richer resource environment). Both must hold for coexistence to be feasible.

Competitive exclusion can occur in three ways, even though the isoclines cross somewhere in phase space. If the isocline intersection is not contained within the

two MBCs, the species with the isocline nearer the P -axis wins. If this is species 1, and this species also has its MBC farther from the origin (analogous to fig. 8A), the P^{**} rule always holds, but not necessarily the R^{**} rule. Conversely, if the winner has its MBC line closer to the origin, the R^{**} rule always works, but not necessarily the P^{**} rule (analogous to fig. 8B).

The final possibility is for the isoclines to cross within the MBC lines, but in such a way that either prey can potentially exclude the alternative prey (fig. 9B), with the identity of the winner determined by initial conditions. For this to occur, the superior resource competitor must (1) have a shallower isocline (i.e., be more sensitive to predation), and (2) its MBC line must lie closer to the origin. The two potential alternative stable states correspond to either the R^{**} rule (e.g., point a in fig. 9B) or the P^{**} rule (point b in fig. 9B), but both rules do not hold simultaneously.

In all cases, the closer the two MBC lines are, the more congruent the R^{**} and P^{**} rules are as predictors of dominance. The more effective the predator is at limiting all its prey (i.e., larger values for a_i, b_i), the closer the two MBC lines are. Thus, the simple rules for dominance work best when predation strongly suppresses both prey populations, well below the levels set by the resource supply. Such strong suppression usually implies exclusion of one prey via apparent competition (Holt 1984).

DISCUSSION

We have shown that there is a simple rule—which we call the P^* rule, similar to the R^* rule (Tilman 1990)—that can predict the outcome of apparent competition among two prey species that do not interact via resource competition but that do share a predator (see also Holt and Lawton 1993). When there is evenhanded predation in a simple food web that includes two consumer species competing for a single limiting resource and a single predator that feeds on these two species, analogous rules, which we call the R^{**} and P^{**} rules, work simultaneously. Both correctly predict the outcome of interspecific competition, in that the dominant prey species simultaneously depresses resources to the lowest level and enhances predator density to the highest level, relative to alternative prey. The models (Tilman 1977, 1982, 1990) that led to the R^* rule included density-independent mortality (which might include some predation) but not predators with a numerical response to their prey (which corresponds to delayed density dependence in the prey population). Incorporating a predator with a numerical response, as in equation (6), in effect makes the level of mortality a dependent variable of the system, dependent in particular on the prey's ability to exploit the limiting resource. In the case of symmetrical predation on multiple prey species, the winning prey is the one depressing resources to the lowest level, given that the predator is present (which may or may not correspond to the prey depressing resources to the lowest level in the absence of the predator). This same prey species also maintains the highest density of predators.

Our most complex food web model, which does not assume evenhanded predation, illustrates that no simple rule need apply universally. The patterns predicted

by the theoretical results are, in principle, testable: the necessary experiments consist of each prey species grown alone, both prey species grown together, and both prey together with the predator, all the while monitoring R , N_i , and P . Aside from the obvious technical challenge of such a protocol, based on our above theoretical results, researchers contemplating such a project might seem to face a bewildering array of possible outcomes. This difficulty may be more apparent than real, because the universe of possibilities may be circumscribed by constraints that govern the ability of organisms to acquire and use resources and to resist natural enemies. The cases presented in figures 7–9 represent all possible combinations in model (10) of parameters for consumers and predators. Some of these parameter combinations may be evolutionarily improbable or impossible because of unavoidable, allocation-based trade-offs that organisms face. Incorporating such trade-offs should provide deeper insights into the likely generality and limitations of each rule.

To sharpen our understanding of the implications of such constraints, it is useful to consider the outcome of competitive interactions among plants along a productivity gradient—that is, a gradient from habitats with low total resource (low S) to habitats with high total resource (fig. 10). Let us first assume that the species that is the best competitor in the absence of the predator (in this case, the herbivore) is also the most susceptible to predation (i.e., that the prey isoclines cross). The trade-off between prey competitive ability and susceptibility to predation could be caused by interspecific differentiation in the proportion of plant biomass allocated to competitive structures such as roots, stems, or leaves, versus structures or secondary compounds involved in herbivore defense. There are two possible cases.

Consider, first, the case in which the prey that is the superior resource competitor (lower R^* ; species 1 in fig. 10) also has the MBC farther from the origin. Habitat productivity increases with increasing S . There is a region (region a in fig. 10B) in which there is insufficient resource for the survival of either prey (and hence the predator too). At higher resource supply rates, region b , prey 1 is present but the predator is unable to survive. This is followed by region c in which prey 1 and the predator are present. At yet higher S , region d , both prey species and the predator are present. In region e , prey 2 alone persists with the predator. The densities of these species as the resource changes along the gradient are shown in figure 10B.

The original R^* rule (Tilman 1990) correctly predicts the dominance of prey 1 and the exclusion of prey 2 from regions b and c . However, the simple R^* rule (which ignores mortality caused by the predator) fails in regions d and e . Thus, the simple R^* rule of competition for a single limiting resource applies, even in the presence of predators, but only in less productive habitats. It fails once a habitat is sufficiently productive to support enough predators to allow predation-mediated coexistence.

The R^{**} and P^{**} rules also have limited domains. Neither rule applies in regions a and b because there is insufficient resource to sustain the predator. In region c , the prey that supports the higher predator density displaces the species that drives the resource to the lower level when alone with the predator. Thus,

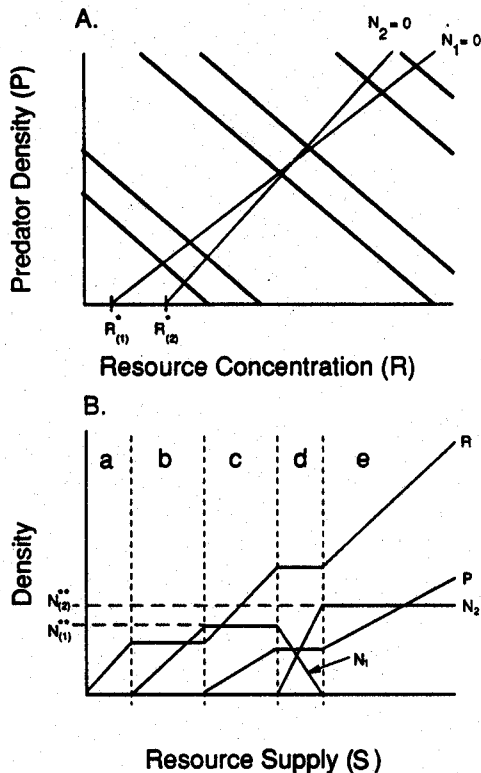


FIG. 10.—Species interactions along a gradient in resource supply, S . Increasing S shifts the MBC lines away from the origin without changing the difference between a given pair of species' MBC lines. A, The shaded areas indicate MBC lines for three points along a resource gradient. The text considers two alternative cases: (1) species 1 has the outer MBC; (2) species 2 has the outer MBC. B, Species densities along the gradient for case 1.

the P^{**} rule predicts the outcome in region c , but the R^{**} rule does not. Coexistence occurs in the region in which one species is superior at apparent competition and the other at resource competition. The R^{**} but not the P^{**} rule predicts the outcome in region e . It is surprising to us that when the system parameters are such that predator-mediated coexistence is possible, the P^{**} rule works in less productive habitats, and the R^{**} rule works in more productive habitats.

For the second case, the species that is the poorer resource competitor, in the absence of predation, has its MBC line farther from the origin. In this case (fig. 10A; note that fig. 10B does not apply), the species replacement pattern along a gradient of increasing total resource supply is as follows: region a , neither prey present; region b , prey 1 alone; region c , prey 1 present with the predator; region d , a zone in which the outcome depends on initial conditions; region e , prey 2 alone with the predator. The R^* rule correctly predicts the outcome in regions a , b , and c but not in regions d and e . The R^{**} and P^{**} rules do not apply until region c . The R^{**} rule correctly predicts the outcome in region c but not in any

other regions. The P^{**} rule works in region e . In region d , there are priority effects, and no rule ignoring initial conditions is reliable.

Thus, if consumer species have an interspecific trade-off in their competitive abilities versus their susceptibility to predation, none of the simple rules universally applies at all points along a resource gradient. The R^* rule only applies in less productive habitats in which predation on the consumer species is of relatively low intensity. The R^{**} and P^{**} rules apply at different productivity levels along the gradient.

It is possible, but seems less likely, for there to be no interspecific trade-off between competitive ability and susceptibility to predation—that is, for the isoclines of the consumer species not to cross (fig. 8A, B). For instance, a given prey species might be near the edge of its thermal tolerance limits (e.g., near a distributional limit along a climatic gradient). This could lead it to be less efficient at both resource acquisition and predator escape. In both the above cases, once the habitat is sufficiently productive for the species with the lower R^* to survive, this species displaces the other species at all higher regions on the productivity gradient. Thus, the R^* rule holds universally if there is no competition-predation trade-off. The R^{**} but not the P^{**} rule holds in some cases (fig. 8B), and the P^{**} but not the R^{**} rule holds in the other (fig. 8A).

There are also likely to be constraints on the predator. In particular, predator traits should tend to be those that lead to higher predator fitness. Consider for example a system in which prey are nitrogen-limited plants and the predator is a protein-limited herbivore. The herbivore should feed preferentially on plants with higher protein content. As a simple expression for such biased preference, let the attack rate of the herbivore on plant species i , a_i , be inversely related to the b'_i of the plant (i.e., $a_i = k/b'_i$, where k is a constant). If the herbivore is protein limited, its birth efficiency, b_i , should depend on the efficiency, e , with which it extracts protein from a plant. This would give $b_i = eb_p/b'_i$, which represents a simple conversion of plant protein into herbivore biomass. If these two relations ($a_i = k/b'_i$ and $b_i = eb_p/b'_i$) are substituted into the equations for the MBC, the MBC equation becomes $R = b_p(S - R - cb'_i/keb_p)$.

The MBCs of the two plant species differ only in b'_i . The species with the lower b'_i will have its MBC closer to the origin. Substitution of $a_i = k/b'_i$ into the equation for the plant isocline leads to the slope of the isocline being proportional to $b_i'^2$ and to R^* being proportional to $1/b'_i$. Thus, if all else were equal, a plant with lower protein content would be a superior competitor (lower R^* , proportional to $1/b'_i$), would have the more steeply sloped isocline (slope proportional to $b_i'^2$), and would have its MBC farther from the origin. This is the case illustrated in figure 8A. In this case the R^* rule always holds, as does the P^{**} rule. The R^{**} rule never holds.

These particular constraints also preclude the possibility of predator-mediated coexistence. Intuitively, this occurs because the same trait that permits a plant species to be superior in resource competition—its ability to grow with lower protein content—also makes it less desirable as a foodstuff for a herbivore. Predator-mediated coexistence is likely to be observed only when the traits that promote competitive superiority also enhance risk of predation. For instance, if prey

are mobile, higher mobility might permit both a higher rate of resource intake at low resource levels and greater exposure to predation.

CONCLUSIONS

We have shown that some simple rules of thumb can provide useful summaries of relatively complex interactions. However, these simple rules are not universally applicable. The R^* rule only universally applies in less productive habitats in which predator densities are low. The P^* rule works best when predation acts evenhandedly on both species or reduces both their densities well below their respective carrying capacities. The applicability of all the rules depends on the trade-offs exhibited by the consumer species and on the factors constraining predator foraging and predator numerical responses. All organisms face costs that constrain their traits to a subset of those traits that might be possible in the absence of constraints. Recognizing the specific character of these constraints and trade-offs can simplify theory and allow the development of more realistic theory—contingent theory that has a well-defined domain of applicability. Our purpose in developing the specific models used here was to illustrate this qualitative process, to demonstrate that rules that do not universally apply to all habitats and situations may still provide useful, unifying rules of thumb for ecological interactions, and to indicate how ascertaining the limits of such rules can point the way to a deeper understanding of multi-trophic-level interactions.

ACKNOWLEDGMENTS

We thank Imperial College at Silwood Park and the Natural Environment Research Council (NERC) Centre for Population Biology for their sustained support, hospitality, and encouragement. For useful comments we would like to thank C. Briggs, M. Hassell, J. Lawton, and in particular B. Ebenhöf, who generously provided a detailed, thoughtful review nudging us in the direction of the more general results contained in the appendixes. We are especially grateful to J. Lawton for freewheeling discussion about the importance of contingent theory in ecology. We also acknowledge financial support from the National Science Foundation, the University of Kansas General Research Fund, and the NERC.

APPENDIX A

A GENERALIZED P^* RULE

The specific model described in equations (1) and (2) can be generalized to a broader array of models, as follows:

$$\frac{dN_i}{dt} = r_i(P)N_i$$

and

$$\frac{dP}{dt} = g(N_1, N_2, \dots)P,$$

for $i = 1, \dots, n$ prey species. An alternative formulation for P is $P = G(N_1, \dots, N_n)$. The latter may describe systems in which one is monitoring rapid aggregation of mobile predators to and departures from a particular habitat patch. The predator density P is an example of a collective variable (B. Ebenhöf, personal communication), because it depends (either directly, expressed as an algebraic expression, or with a time lag, as in the above differential equation) on all the prey, whereas the per capita growth rate of each prey depends only on the same P (albeit in different ways).

Because we are considering predator-prey systems, it is reasonable to assume that $r_i(P)$ is monotonically decreasing in P . Now assume that the system has an equilibrium and that this equilibrium is locally stable. For each i , at equilibrium either $N_i = 0$, or $r_i(P^*) = 0$. In general, this is unlikely to be true simultaneously for two or more prey species. Let species 1 be the species that equilibrates at the highest value for P^* . Given that species 1 is at equilibrium, all other species experience a higher predator density than is consistent with their persistence. A comparable general result for multiple species host-parasitoid systems is discussed elsewhere (Holt and Lawton 1993).

The core of this result rests on the assumption that the expression for prey growth for species i cleaves into two factors, one containing a collective variable (here, the predator) and the other being the density of species i . This channeling of indirect interactions through a single intermediary variable in general constrains the opportunity for coexistence. In fact, it can be viewed as a special case of Levin's (1970) classic result that in equilibrial communities, coexistence among n species requires the number of independent limiting factors to equal or exceed n . See Appendix C for further discussion.

APPENDIX B

PROPERTIES OF MODEL 10

The formal properties of the asymmetrical three-species, predator-prey model are best seen as we compose it from its pieces. Suppose that only prey i is present. The system dynamics are given by

$$\frac{dN_i}{dt} = N_i(a'_i b'_i R - c'_i)$$

and

$$\frac{dR}{dt} = \frac{c'_i N_i}{b'_i} - a'_i R N_i.$$

The prey population is at equilibrium when the resource availability is $R_{(i)}^* = c'_i/a'_i b'_i$ (Tilman 1982); the total resource in the habitat, S , must exceed this equilibrium requirement for prey i to persist. Given that this condition is met, at equilibrium any nutrient in excess of $R_{(i)}^*$ is contained in prey at density $b'_i(S - R_{(i)}^*)$.

If the density of prey i is large enough, a predator population can be supported by it. The predator dynamics are

$$\frac{dP}{dt} = P(a_i b_i N_i - c),$$

and the predator population is in equilibrium when the density of prey i is $N_{(i)}^{**} = c/a_i b_i$. Hence, the predator can invade the system with prey i at equilibrium if $b'_i(S - R_{(i)}^*)$ exceeds $N_{(i)}^{**}$. Rearranging, the required total nutrient supply for predator persistence is

$$S > R_{(i)}^* + \frac{N_{(i)}^{**}}{b'_i}. \quad (\text{B1})$$

Assuming the predator can invade, the dynamics of the system are governed by

$$\begin{aligned}\frac{dP}{dt} &= P(a_i b_i N_i - c), \\ \frac{dN_i}{dt} &= N_i(a_i' b_i' R - c_i' - a_i P),\end{aligned}\tag{B2}$$

and

$$\frac{dR}{dt} = \frac{c_i' N_i}{b_i'} + \frac{cP}{b_p} + a_i N_i P \left(\frac{1}{b_i'} - \frac{b_i}{b_p} \right) - a_i' R N_i.$$

The parameter b_p (the yield coefficient for the predator) budgets the amount of nutrient recycled from dead predators. Incomplete assimilation during predator feeding may give additional nutrient recycling. The flux of nutrient associated with the consumption of prey i is $a_i N_i P / b_i'$, and the assimilated flux is $a_i b_i N_i P / b_p$; the flux of nutrient recycled is thus

$$a_i N_i P \left(\frac{1}{b_i'} - \frac{b_i}{b_p} \right).$$

Because only a nonnegative recycling flux is meaningful, we require that $b_p / b_i' > b_i$; that is, the ratio of the nutrient contents of prey to predator must exceed the predator's birth efficiency. Since these efficiencies are typically less than one for predators, this is not a stringent restriction.

By graphically analyzing this single-prey system with prey i , we determine the equilibrium values $R_{(i)}^{**}$ and $P_{(i)}^{**}$. Though the phase space of equation (B2) is three-dimensional (fig. B1A), we use a trick to represent the system in the two-dimensional phase plane with axes R and P . The conservation of total resource mass implies a mass-balance constraint

$$S = R + \frac{N_i}{b_i'} + \frac{P}{b_p}.\tag{B3}$$

This constraint confines the feasible phase space to a simplex, the triangle indicated in figure B1A. (The system is constrained to move along this plane.) The predator isocline is a plane, parallel to the RP plane, intersecting the N -axis at the value $N_i = N_{(i)}^{**}$ (fig. B1A). The intersection of the predator's isocline with the MBC simplex defines a line giving the set of all values of R and P consistent with both mass balance and the predator equilibrium. In figure B1A, we show this line projected onto the RP plane. In the main text, we refer to this projection as the "MBC line for prey i ." Its equation is

$$P = b_p \left(S - R - \frac{c/a_i b_i}{b_i'} \right),\tag{B4}$$

which has a slope of $-b_p$.

The isocline for prey i is

$$P = \frac{a_i' b_i'}{a_i} R - \frac{c_i'}{a_i}.\tag{B5}$$

In the RNP phase space, this defines a plane parallel to the N_r -axis, so we can represent the isocline in the RP plane by the line defined by equation (B5). The isocline's intersection with the R -axis is at $R_{(i)}^* = c_i' / a_i' b_i'$, which is the amount of resource required for this prey to be in equilibrium in the absence of predation. The isocline has a positive slope of $a_i' b_i' / a_i$.

The intersection of equations (B2) and (B3) (see fig. 6) determines the equilibrium values of $R_{(i)}^{**}$ and $P_{(i)}^{**}$.

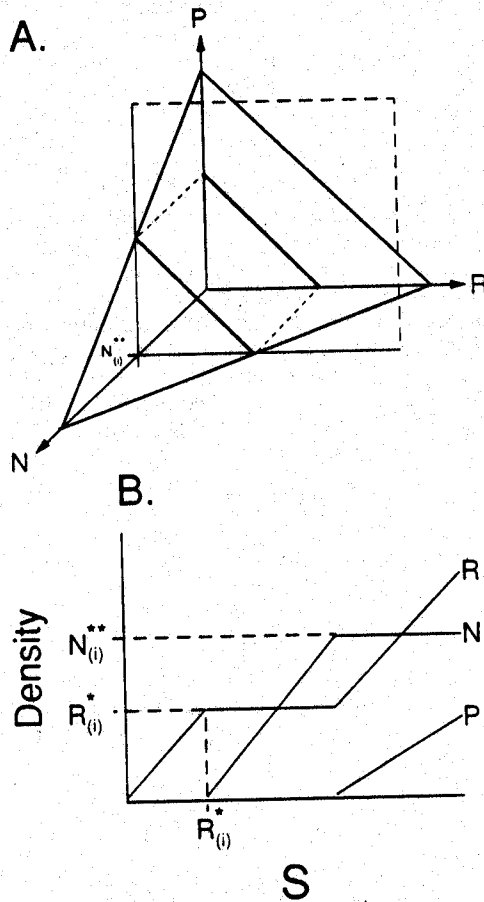


FIG. B1.—A, Resource-prey-predator (*RNP*) phase space. A mass-balance constraint can be represented by a triangular plane, intersecting each axis. The system dynamics is constrained to this plane. The predator has zero growth along a vertical plane intersecting the prey axis. The heavy line is the intersection of the predator's isoplane with the MBC plane. This intersection can be projected onto the *RP* plane; this is the MBC line described in the main text; it can be interpreted as the possible states of the system, given that the predator is in equilibrium and so has restricted prey to a given density. B, Abundances along a gradient in resource supply.

$$P_{(i)}^{**} = \frac{a'_i b'_i b_p}{a'_i b'_i + a_i b_p} \left(S - \frac{N_{(i)}^{**}}{b'_i} \right) - \frac{b_p c'_i}{a'_i b'_i + a_i b_p} \tag{B6}$$

and

$$R_{(i)}^{**} = S - \frac{N_{(i)}^{**}}{b'_i} - \frac{P_{(i)}^{**}}{b_p}.$$

The predator cannot persist if the MBC line cuts the *R*-axis below the *R* intercept of the prey isocline. The existence of an intersection between the MBC line and the prey isocline corresponds to condition (B1) for predator invisibility. Both $R_{(i)}^{**}$ and $P_{(i)}^{**}$ increase linearly

with S , though with $P_{(i)}^{**}$ increasing more rapidly, and the ratio $R_{(i)}^{**}/P_{(i)}^{**}$ approaches asymptotically $a_i/a_i' b_i'$.

For this model, as total nutrient supply increases from zero, prey i can persist once its requirement $R_{(i)}^*$ is met (i.e., $S > R_{(i)}^*$, as in figure B1B). As S continues to increase, R becomes fixed at $R_{(i)}^*$ by the prey; additional nutrient is all channeled into prey. Once prey density reaches the predator's minimal requirement, $N_{(i)}^{**}$, the predator can persist; at this point, prey density no longer increases with S . Additional nutrient is partitioned into increases in available nutrient and predator density (fig. B1B).

Allowing two prey species to exploit the resource together with the predator, we arrive at the full system (eq. [10]). The prey isoclines in this system have the same equations (B5) as in the single-prey subsystems, and so are hyperplanes orthogonal to the RP coordinate plane, parallel to the N_i -axes. The projections of these isoclines onto the RP plane are the same for the single-prey subsystems and the full system, so we can superimpose them for the purpose of the graphical analysis used in the main text. Since the prey isoclines are linear, an intersection corresponds to a unique equilibrium. The relative positions of the superimposed prey isoclines are controlled by two inequalities. The R intercept of prey 1's isocline is nearer to the origin than prey 2's if $R_{(1)}^* < R_{(2)}^*$, or

$$\frac{c_1'}{a_1' b_1'} < \frac{c_2'}{a_2' b_2'} \quad (\text{B7})$$

Prey 1's isocline has a shallower slope than prey 2's if

$$\frac{a_1' b_1'}{a_1} < \frac{a_2' b_2'}{a_2} \quad (\text{B8})$$

The MBC for the full system defines a three-dimensional simplex in the four-dimensional phase space, analogous to that pictured in figure B1A. As before, we assume that the values of N_1 and N_2 are constrained by requiring that the predator be at equilibrium, defined by the predator's isocline:

$$\frac{a_1 b_1}{c} N_1 + \frac{a_2 b_2}{c} N_2 = 1. \quad (\text{B9})$$

This is an isocline for a pair of linearly substitutable resources (Tilman 1982), and it states that the predator fixes a weighted sum of prey densities. The intercepts on the N_i -axes are simply the predator's requirements for each prey at equilibrium in the single-prey subsystems (i.e., the quantities $N_{(i)}^{**}$). The set of values of the N_i consistent with the predator's isocline can be intersected with the MBC simplex and then projected onto the RP plane, in a procedure analogous to that used to get a single prey's MBC line in figure B1A.

Doing so, we get a connected set in the RP plane consistent with both predator equilibrium and mass balance. This is exactly the set of points lying between the two (projected) MBC lines for the single-prey subsystems (which are parallel). A three-species equilibrium only occurs if the prey isoclines intersect in the region bounded by the MBC lines. The MBC line for prey 1 lies above that of prey 2 when

$$a_1 b_1 b_1' > a_2 b_2 b_2'. \quad (\text{B10})$$

Consider invasion by prey 1 when prey 2 is at equilibrium with the predator. Prey 1 increases when rare if

$$\frac{a_1' b_1'}{a_1} R_{(2)}^{**} - \frac{c_1'}{a_1} > \frac{a_2' b_2'}{a_2} R_{(2)}^{**} - \frac{c_2'}{a_2}. \quad (\text{B11})$$

Thus at $R = R_{(2)}^{**}$, prey 1's isocline must lie above prey 2's isocline. A similar condition for invasion of prey 2 when prey 1 is at equilibrium with the predator is

$$\frac{a'_2 b'_2}{a_2} R_{(i)}^{**} - \frac{c'_2}{a_2} > \frac{a'_1 b'_1}{a_1} R_{(i)}^{**} - \frac{c'_1}{a_1}; \tag{B12}$$

that is, when $R = R_{(i)}^{**}$, prey 2's isocline must lie above prey 1's.

We now consider briefly the stability of the model equilibria. When prey i is alone with the predator, the three-dimensional system of equation (B2) can be reduced by one dimension if R is substituted in the prey equation, using the mass balance relation (eq. [A3]). We then eliminate the equation for resource dynamics and calculate the partial derivatives composing the Jacobian matrix in the usual way. The result is

$$J = \begin{bmatrix} 0 & a_i b_i P_{(i)}^{**} \\ -\frac{c}{b_p} \left(\frac{a'_i b'_i + a_i b_p}{a_i b_i} \right) & -\frac{a'_i c}{a_i b_i} \end{bmatrix}.$$

There are two Routh-Hurwitz stability conditions (Nisbet and Gurney 1982). The first is $\det[J] > 0$; after rearrangement, this is equivalent to

$$S - \frac{N_{(i)}^{**}}{b'_i} - R_{(i)}^* > 0.$$

This is simply the invasion condition for the predator (inequality [B1]), which is always satisfied when the equilibrium of prey i and the predator is feasible. The second stability condition, $\text{tr}[J] < 0$, is unconditionally satisfied. This two-dimensional system satisfies the conditions of the Kolmogorov-Brauer theorem (Nisbet and Gurney 1982), so that local stability implies global stability.

For the three-species system with both prey and the predator, the four-dimensional system of equation (9) can be reduced one dimension, by substituting for R from the mass-balance relation (eq. [10]) and eliminating the equation for resource dynamics. Proceeding in the usual manner, the resulting Jacobian matrix is

$$J = \begin{bmatrix} 0 & a_1 b_1 P^{**} & a_2 b_2 P^{**} \\ -\frac{a'_1 b'_1}{b_p} N_1^{**} - a_1 N_1^{**} & -a'_1 N_1^{**} & -\frac{a'_1 b'_1}{b'_2} N_1^{**} \\ -\frac{a'_2 b'_2}{b_p} N_2^{**} - a_2 N_2^{**} & -\frac{a'_2 b'_2}{b'_1} N_2^{**} & -a'_2 N_2^{**} \end{bmatrix}.$$

(The absence of parentheses in the subscripts for the prey indicates that these are equilibria with all species present.) This is stable if three Routh-Hurwitz conditions (see, e.g., Nisbet and Gurney 1982) hold. Two of these are always satisfied: $\text{tr}[J]$ is always negative, and a second condition is equivalent to

$$\frac{N_1^{**}}{b'_1} \left(\frac{a'_1 b'_1}{b_p} + a_1 \right) + \frac{N_2^{**}}{b'_2} \left(\frac{a'_2 b'_2}{b_p} + a_2 \right) > 0,$$

which holds. The third stability criterion is equivalent to

$$(a_1 a'_2 b'_2 - a_2 a'_1 b'_1)(a_1 b_1 b'_1 - a_2 b_2 b'_2) > 0. \tag{B13}$$

The first factor in this expression controls whether the prey isoclines cross. If we label prey 1 as the one with lowest R^* , then the prey isoclines cross if the first factor is positive, which ensures that prey 1's isocline has a shallower slope than prey 2's (see inequality [B8]). Unless the first factor is positive, there can be no equilibrium at all. If there is an equilibrium, then stability requires that the second factor of inequality (B13) also be positive. When it is, the MBC line for prey 1 lies above that for prey 2. Given crossing isoclines,

a necessary and sufficient condition for local stability of a three-species equilibrium is thus that the prey with lowest R^* have the highest MBC line, exactly as shown in figure 9A. A mutually invisable system has a locally stable three-species equilibrium, whereas a mutually noninvasible system has an unstable three-species equilibrium.

Our three-species system satisfies the conditions of Hutson and Law's (1985) permanence theorem. This theorem makes invasibility of equilibria an especially robust indicator of coexistence, because the global repelling or attracting nature of the boundary is indicated by whether the boundary equilibria are repellents or attractors. Thus, no trajectory of the three-species system with coexistence asymptotically approaches any boundary. Together with the above invasibility and local stability analyses, this suggests that the graphic approach used in the main text suffices for us to understand all the potential outcomes of the system.

It is well known that adding a predator with linear functional responses to each of two prey, competing among themselves according to the Lotka-Volterra competition model, can lead to systems with stable limit cycles or chaotic dynamics (Vance 1978). Such complex dynamics are precluded in our mechanistic model of predation on two species experiencing exploitative competition for a limiting resource, given the reasonable constraint that the total nutrient base is a conserved quantity. This is an intriguing example of how ecosystem-level constraints can simplify the dynamics of interacting species.

APPENDIX C

GENERALIZED PREY ISOCLINES

A more general formulation of the model described by equation (10) is as follows:

$$\frac{dN_i}{dt} = r_i(R, P)N_i, \quad i = 1, \dots, n,$$

$$\frac{dR}{dt} = G_R(N_1, \dots, N_n, R, P),$$

and

$$\frac{dP}{dt} = G_P(N_1, \dots, N_n, R, P).$$

This formulation assumes that one can cleanly separate the two collective variables, R and P , from the prey densities in determining prey growth rates. If prey growth declines monotonically with increasing predator density and increases monotonically with increasing resource density, one can define prey zero-growth isoclines as curves in the RP phase plane, as shown for a four-prey system in figure C1 (a more general rendition of figs. 7-9). A given prey species increases in abundance for values of R and P to the right of its isocline and decreases for values to the left of its isocline. These zero-growth isoclines have positive slopes, because with increasing predation a given prey requires more resource to remain in demographic equilibrium. If prey growth rates saturate with increasing resource level, the isoclines should be concave downward, as shown.

The system equilibrates only if the magnitudes of P and R are such that no prey is increasing in abundance. This occurs only along the left boundary of the collective isoclines indicated in the figure. Because there are just two limiting factors (one predator and one resource population), in general at most two prey species can coexist, and when they do the equilibrium values for R and P are at the intersections of their respective isoclines.

However, coexistence is not guaranteed; a single prey species may dominate the system. To ascertain the actual outcome requires a portrayal of resource and predator dynamics. Following the procedure given in Appendix B, assume there is a mass-balance constraint because of nutrient conservation in a closed system, conditional on the predator being at

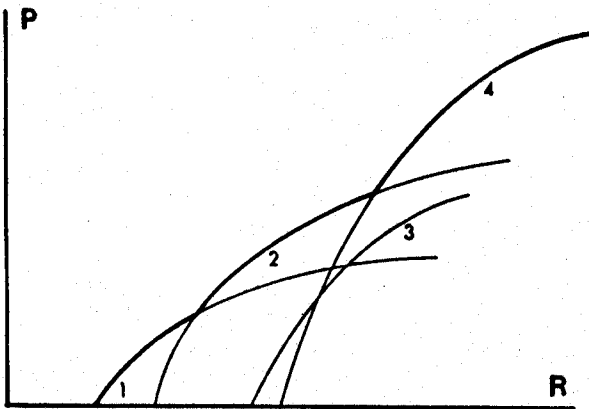


FIG. C1.—Prey isoclines in the resource-prey (RP) phase plane for general, separable models. The isoclines of four prey species are shown. (See text and fig. 6 for more detail.)

equilibrium with prey i alone at a particular value for R_i . One can in this case express the constraint for each prey species as a straight line of negative slope, analogous to equation (B4) in Appendix B. Given that there are a number of prey species present, the potential equilibria of the system are confined within a band between parallel lines, comparable to those portrayed in figures 7–10 (e.g., the gray zones in fig. 10A). If these constraints are nearly coincident, then in general one prey species will dominate the system. By placing trace lines on the figure, one can be easily convinced that this dominant prey is the one that simultaneously matches the R^* and P^* rules. If the constraints are not coincident, coexistence or priority effects become possible. The line of argument presented in the main text can be modified to ascertain which of these outcomes will obtain.

This approach does not require one to assume a closed conservative system. B. Ebenhöf (personal communication) points out that setting the predator and resource equations equal to zero, given that only prey species i is present, defines a curve in the RP plane; with n prey species, there are n such curves, which collectively circumscribe a band within which the equilibrium states of the system must be contained. By overlaying this band on the array of prey isoclines, one can determine whether unilateral dominance, coexistence, or priority effects are likely outcomes.

The main body of the text is concerned with ascertaining the limits of rules of dominance for systems that are in a sense radically simple (i.e., linear functional responses, no spatial or temporal heterogeneity, no intraspecific dominance, etc.). It is well known that incorporating nonlinear functional responses, environmental heterogeneity, and strong direct density dependence greatly increases the scope for species coexistence and makes analyses of dynamics more difficult. For instance, if the equilibrium is unstable, limit cycles or chaotic dynamics may permit competing species to coexist (Armstrong and McGehee 1980). The existence of temporal and spatial heterogeneity in effect opens up other niche dimensions, which can facilitate coexistence (though not always; see Holt 1993). Other complications may arise because one cannot cleanly separate the growth equations, for example, owing to strongly nonlinear functional responses or adaptive behaviors (Abrams 1987). In addition to increasing the scope of possibilities for coexistence, these factors doubtless change the rules that characterize species dominance relations when there is competitive exclusion and in particular make it unlikely that a given simple rule will apply widely across numerous scenarios.

Recognizing this range of possibilities seems at first glance to lead in the direction of nihilism, a turbulent conceptual sea in which all things are possible. But we have a cheerier disposition. To us, the simple, biologically transparent models we have examined provide

a conceptual anchor in this sea, starting points that, if clearly understood, help one ascertain the magnitude of any effects arising from more complex biological assumptions.

LITERATURE CITED

- Abrams, P. A. 1977. Density-independent mortality and interspecific competition: a test of Pianka's niche-overlap hypothesis. *American Naturalist* 11:539-552.
- . 1987. The functional responses of adaptive consumers of two resources. *Theoretical Population Biology* 32:262-288.
- Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology* 60:76-84.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* 115:151-170.
- Comins, H. N., and M. P. Hassell. 1987. The dynamics of predation and competition in patchy environments. *Theoretical Population Biology* 31:393-421.
- DeAngelis, D. L. 1992. Dynamics of nutrient cycling and food webs. Chapman & Hall, London.
- Grover, J. P. 1990. Resource competition in a variable environment: phytoplankton growing according to Monod's model. *American Naturalist* 136:771-789.
- . 1991. Resource competition in a variable environment: phytoplankton growing according to the variable-stores model. *American Naturalist* 138:811-835.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197-229.
- . 1983. Optimal foraging and the form of the predator isocline. *American Naturalist* 122:521-541.
- . 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124:377-406.
- . 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77-88 in R. Ricklefs and D. Schluter, eds. *Community diversity: historical and geographical perspectives*. University of Chicago Press, Chicago.
- Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. *American Naturalist* 130:412-430.
- Holt, R. D., and J. H. Lawton. 1993. Apparent competition and enemy-free space in host-parasitoid communities. *American Naturalist* 142:623-645.
- Hutson, V., and R. Law. 1985. Permanent coexistence in general models of three interacting species. *Journal of Mathematical Biology* 21:285-298.
- Jeffries, C. 1976. Stability of predation ecosystem models. *Ecology* 57:1321-1325.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134:922-949.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* 104:413-423.
- . 1976. Spatial patterning and the structure of ecological communities. *Lectures on Mathematics in the Life Sciences* 8:1-35.
- MacArthur, R. H. 1972. Coexistence of species. Pages 253-259 in J. Behnke, ed. *Challenging biological problems*. Oxford University Press, New York.
- Murdoch, W. W., and J. Bence. 1987. General predators and unstable prey populations. Pages 17-30 in W. C. Kerfoot and A. Sih, eds. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, N.H.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* 9:1-131.
- Nisbet, R. M., and W. S. C. Gurney. 1982. *Modelling fluctuating populations*. Wiley, New York.
- Nisbet, R. M., C. J. Briggs, W. S. C. Gurney, W. W. Murdoch, and A. Stewart-Oaten. 1993. Two-patch metapopulation dynamics. Pages 125-135 in S. A. Levin, T. M. Powell, and J. H. Steele, eds. *Patch dynamics*. Springer, Berlin.
- Oksanen, L. 1992. Evolution of exploitation ecosystems. I. Predation, foraging ecology and population dynamics in herbivores. *Evolutionary Ecology* 6:15-24.

- Reader, R. J. 1992. Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology* 73:373-376.
- Roughgarden, J., and M. Feldman. 1975. Species packing and predation pressure. *Ecology* 56:459-492.
- Schmitt, R. J. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. *Ecology* 68:1887-1897.
- Schoener, T. W. 1986a. Overview: kinds of ecological communities—ecology becomes pluralistic. Pages 467-479 in J. Diamond and T. J. Case, eds. *Community ecology*. Harper & Row, New York.
- . 1986b. Mechanistic approaches to community ecology: a new reductionism. *American Zoologist* 26:81-106.
- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58:338-348.
- . 1980. Resources: a graphical-mechanistic approach to competition and predation. *American Naturalist* 116:362-393.
- . 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- . 1987. The importance of the mechanisms of interspecific competition. *American Naturalist* 129:769-774.
- . 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117-142 in J. B. Grace and D. Tilman, eds. *Perspectives on plant competition*. Academic Press, San Diego, Calif.
- Vance, R. R. 1978. Predation and resource partitioning in one predator-two prey model communities. *American Naturalist* 112:797-813.
- Yodzis, P. 1989. *Introduction to theoretical ecology*. Harper & Row, New York.

Associate Editor: Peter Chesson