Predation, Apparent Competition, and the Structure of Prey Communities

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It is argued that alternate prey species in the diet of a food-limited generalist predator should reduce each other's equilibrial abundances, whether or not they directly compete. Such indirect, interspecific interactions are labeled *apparent competition*. Two examples are discussed in which an observed pattern of habitat segregation was at first interpreted as evidence for direct competition, but later interpreted as apparent competition resulting from shared predation. In order to study the consequences of predator-mediated apparent competition in isolation from other complicating factors, a model community is analyzed in which there is *no* direct interspecific competition among the prey. An explicit necessary condition for prey species coexistence is derived for the case of one predator feeding on many prey species. This model community has several interesting properties: (1) Prey species with high relative values for a parameter r/a are "keystone" species in the community; (2) prey species can be excluded from the community by "diffuse" apparent competition; (3) large changes in the niche breadth of the predator need not correspond to large changes in predator density; (4) the prey trophic level as a whole is regulated by the predator, yet each of its constituent species is regulated by both the predator and available resources; (5) increased productivity may either increase, decrease, or leave unchanged the number of species in the community; (6) a decrease in density-independent mortality may decrease species diversity. These conclusions seem to be robust to changes in the prey growth equations and to the incorporation of predator satiation. By contrast, adding prey refugia or predator switching to the model weakens these conclusions. If the predator can be satiated or switched, the elements a_{ij} comprising the community matrix may have signs opposite the long-term effect of j upon i. The effect of natural selection upon prey species coexistence is discussed. Unless r_i, K_i, and a_i are tightly coupled, natural selection within prey species i will tend to decrease the equilibrial abundance of species j.

INTRODUCTION

During the past decade the theory of competition has played an increasingly important role in both the development of general ecological theory and the interpretation of field data. In standard models of interspecific competition,

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the growth rate of each population is represented by a first-order differential (or difference) equation:

$$dN_i/dt = F_i(N_1, N_2,..., N_i,...).$$

Species i and species j are said to compete directly if $\partial F_i/\partial N_j < 0$ and $\partial F_j/\partial N_i < 0$ at equilibrium (May, 1973). The matrix comprised of these negative partial derivatives is an important special case of the community matrix (*sensu* May, 1973, p. 22), a construct at the heart of recent theoretical discussions of community structure. To connect this body of ecological theory to field data, one must measure the elements of the community matrix or at least determine their signs. The only direct way to measure these elements is to perform perturbation experiments. Indeed, such experiments are the best method for demonstrating interspecific competition (e.g., Putwain and Harper, 1970; Gilpin and Ayala, 1973).

Unfortunately, few natural communities are suited for this sort of careful, manipulative experiment. Hence, ecologists interested in the mechanisms regulating community structure have had to resort to a second, more indirect kind of evidence for competition. This evidence consists of static patterns such as density changes in sympatry compared to allopatry, patterns which can be observed in comparative studies or "natural experiments" and are predicted from models of interspecific competition (e.g., Schoener, 1974a).

However, mechanisms other than interspecific competition may also cause these static patterns. One mechanism which is likely to be particularly important is shared predation. In this paper I argue that in many reasonable circumstances a predator necessarily imposes reciprocal equilibrial abundances upon its alternative prey species, even if these species are otherwise independent. To distinguish cases in which predation is the cause of these relations from cases in which direct competition is to blame, I say that two species are in *apparent competition* whenever the presence of either species leads to a reduced population density for the other species at equilibrium. A pair of species may exhibit an apparent competition relation because they compete directly, or share a predator, or are linked through the food web by some other indirect causal chain. The existence of disparate alternative mechanisms that lead to the same ecological pattern obviously makes it more difficult to correctly infer the dynamical causes underlying observed static patterns. Some ecologists use the word "competition" in a way which encompasses both direct and apparent competition (e.g., Williamson, 1972). Were we to classify interspecific interactions solely by effects, rather than by processes, the models of apparent competition discussed below could be taken as the machinery of one particular kind of competition. But most ecologists seem to use the word "competition" in a more restricted sense; typically, the term is used for direct inhibitory interactions or for more indirect inhibitory effects arising from the sharing of resources in short supply

(e.g., Pianka, 1974; Whittaker, 1975). In this paper I use the unadorned word "competition" in this restricted sense and "apparent competition" for other kinds of indirect interactions.

Predator-mediated apparent competition may place constraints on the kind and number of prey species which can coexist in a predator's diet. These constraints may be as important in the determination of community structure as those constraints which arise from resource competition. For a particular predator–prey model, I first discuss the explicit conditions which allow new prey species to pack into the community, and then apply these conditions to species diversity patterns and a discussion of evolution in predator–prey communities. (Throughout this paper I use the term "species diversity" in the loose sense of "number of species.") I also discuss some ways of changing the assumptions of the model, and I examine the effects of these changes upon apparent competition among prey in the diet of a single predator.

In all the models discussed in this paper, alternate prey species do not compete in the absence of the predator. There are two reasons for making this assumption. First, by studying the separate effects of competition and predator-mediated apparent competition, we may be led to a fuller understanding of those situations in which both are acting. In another paper I will discuss models that include both; the addition of direct competition does not change my conclusions in any essential way. Second, there may be natural communities in which competition is relatively unimportant. The protozoan communities studied by Addicott (1974) seem to be one example. Guilds of host-specific insects may provide others. Models of apparent competition could provide important tools for understanding the structure of such communities.

COMPETITION, OR APPARENT COMPETITION?

Consider a community consisting of a predator, with density P, and its two prey species, with densities R_1 and R_2, respectively. The two prey species may or may not directly compete. I assume that the population growth of each species can be characterized by a differential equation:

$$dR_i/dt = F_i(R_1, R_2, P), \qquad i = 1, 2 \tag{1}$$

$$dP/dt = F(R_1, R_2, P). \tag{2}$$

Given an explicit form for each of these three equations, we could solve for the population densities at equilibrium and test the stability character of each solution. As noted above, the two prey species compete directly if both $\partial F_1/\partial R_2$ and $\partial F_2/\partial R_1$ are negative. But even if these derivatives are not negative, the presence of either species may reduce the other's equilibrial density. If the

predator is strictly food-limited and is not self-damped, its per-capita growth rate can be written as follows:

$$\frac{1}{P}\frac{dP}{dt} = F_p(R_1, R_2).$$ (3)

$F_p(R_1, R_2)$ combines the functional and numerical responses of the predator. At equilibrium,[1]

$$F_p(R_1{}^*, R_2{}^*) = 0.$$ (4)

For any given F_p, this equation implicitly relates the equilibrial densities of the two prey species and thereby describes the set of all possible equilibrial prey communities. Of course, the one that actually occurs, if any, also depends upon the dynamics of each prey species and the stability character of each solution. Nonetheless, without explicitly considering F_1 or F_2, from the form of F_p alone we may make a general assertion about the net effect of one prey species upon another's equilibrial density. I now argue that at equilibrium the alternate prey species of most food-limited predators should exhibit apparent competition.

By the chain rule of differentiation,[2] at the zero isocline

$$\frac{\partial F_p}{\partial R_1} + \frac{\partial F_p}{\partial R_2}\frac{dR_2}{dR_1} = 0 \quad \text{or} \quad \frac{dR_2}{dR_1} = -\left(\frac{\partial F_p/\partial R_1}{\partial F_p/\partial R_2}\right).$$ (5)

dR_2/dR_1 is always negative if both $\partial F_p/\partial R_1$ and $\partial F_p/\partial R_2$ are positive; dR_2/dR_1 is positive only if $\partial F_p/\partial R_1$ or $\partial F_p/\partial R_2$ is negative. The latter is likely only if the predator is rather pathological. If $\partial F_p/\partial R_i < 0$, then the introduction of a small quantity of additional prey to the community induces a *negative* growth rate for the predator—an incremental increase in its food acts like a poison! Such a predator is clearly mal-adapted to the prey it eats. In this paper the only F_p functions discussed satisfy the following condition:

$$\partial F_p/\partial R_i \geqslant 0, \quad \forall_i,$$ (6)

all along the zero isocline (e.g., lines 1 through 3 in Fig. 1). So far as I am aware all of the equations which have ever been proposed for predator population growth satisfy this condition. There may be circumstances in which it is reasonable to expect isoclines violating (6), in which case the arguments in this paper will not apply.

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[1] Asterisks denote equilibrial values.
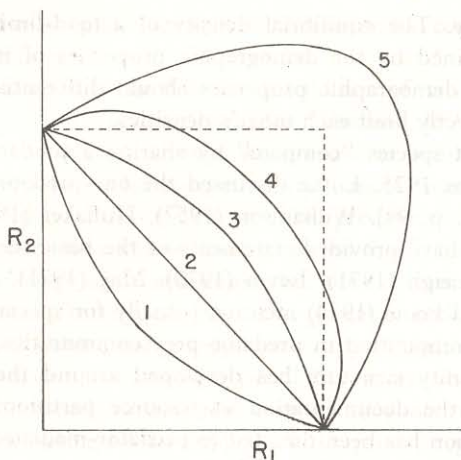[2] I thank S. Levin for suggesting the use of the chain rule to demonstrate the main result.

FIG. 1. The zero isoclines of five food-limited predators ($F(R_1^*, R_2^*) = 0$). When prey densities are in the region between an isocline and the origin, the population of the predator declines in density; when prey densities are outside the isocline, the predator increases in density. Isoclines 1 through 3 satisfy condition (6). Along these isoclines, an increase in R_1^* necessarily causes a decrease in R_2^*.

Hence, as long as $\partial F_p/\partial R_i > 0$ along the line $F_p(R_1^*, R_2^*) = 0$, the two species of prey will always appear to compete at equilibrium whether they compete directly, or do not. (The direct interspecific effects $\partial F_1/\partial R_2$ and $\partial F_2/\partial R_1$ may be negative, zero or even positive.) If the predator can stably coexist with either prey species 1 or 2 alone (species 1 and 2 allopatric), or with both (species 1 and 2 sympatric), then each prey will show a reduced density in sympatry as compared with allopatry. Were one unaware of the importance of the shared predator, it would be easy—but wrong—to ascribe this pattern of reduced densities to direct competitive interactions between the two species.

We can generalize our conclusion to include communities comprised of a food-limited predator and its n prey species. The predator's per-capita growth rate is $(1/P)(dP/dt) = F_p(R_1, R_2,..., R_n)$. ($R_i$ is the density of prey species i.) At equilibrium, $F_p(R_1^*, R_2^*,..., R_n^*) = 0$. By the chain rule, at the zero isocline

$$\frac{\partial F_p}{\partial R_i} + \sum_j \left(\frac{\partial F_p}{\partial R_j}\right)\left(\frac{\partial R_j}{\partial R_i}\right) = 0 \qquad (7)$$

If $\partial F_p/\partial R_i > 0$, then at least one of the terms $\partial R_j/\partial R_i$ must be negative.

The basic mechanism of predator-mediated apparent competition is quite simple. Feeding on only a single prey type, a food-limited predator is maintained at a certain equilibrial density, as is the prey. The introduction of a second prey species increases the density of the predator; the original prey suffers heavier levels of predation because of the increased density of predators and equilibrates

at a lower density. The equilibrial density of a food-limited predator is in large part determined by the demographic properties of its prey. Prey with different intrinsic demographic properties should differentially affect predator density, and indirectly limit each other's densities.

The notion that species "compete" by sharing a predator has had a long history. As early as 1925, Lotka discussed the one-predator two-prey species case (Lotka, 1925, p. 94). Williamson (1957), Huffaker (1966), and Huffaker and Laing (1972) have provided statements of the basic idea, and MacArthur (1969a,b, 1972), Leigh (1971), Levin (1970), May (1971), Barbchenn (1969), Janzen (1973), and Poole (1974) mention (usually for special cases) what I am calling apparent competition in predator–prey communities. Yet, while a rich theory of community structure has developed around the idea of resource competition, and the documentation of resource partitioning has proceeded apace, little attention has been directed to predator-mediated apparent competition by either theoretical or field ecologists.

I know of two cases in which habitat exclusion was observed, explained at first as an outcome of resource competition, but later explained as the result of shared predation; there may be other cases of which I am unaware.

The first could be called "The Case of the Missing Hares." An important source of indirect evidence for competition has been the study of habitat expansions and contractions of species on islands as compared with the same species on mainland areas. Before the introduction of the showshoe hare (*Lepus americanus*) onto Newfoundland, the arctic hare (*Lepus arcticus*) occupied not only tundra—its normal habitat on the mainland—but also many wooded areas (Cameron, 1958). Since the introduction of the snowshoe hare, the arctic hare has contracted its habitat and is now found only near boulder fields in the tundra. MacArthur (1968) has used this situation as an example of evidence for competition. But Bergerud (1967) has suggested that increased lynx predation may better explain the habitat contraction of the arctic hare. Subsequent to the introduction of snowshoe hares, the lynx population greatly increased. Bergerud believes that the defense tactics employed by the arctic hare may make it a particularly vulnerable target. The introduction of an abundant, alternate food source—the snowshoe hare—may have greatly increased the density of lynx; the arctic hare may have been eaten out of the wooded portions of its range. Thus, one hare may have excluded the other by means of a predator feeding on both. Since all of the available evidence is circumstantial, it is impossible to dismiss out of hand the possibility of direct competition, too. (Grant, 1972, has also discussed this example.)

Large and small zooplankton species often show disjunct distributions. In 1965, Brooks and Dodson proposed a twofold explanation for this distributional pattern. They suggested that fish or other vertebrate predators selectively devour large zooplankters, leaving the lake to small ones. But if these predators are absent, Brooks and Dodson reasoned, the greater feeding efficiency of

large species relative to small species should lead to the competitive exclusion of the latter by the former.

Dodson later showed that the disjunct distribution of two species of *Daphnia* was not due to direct competitive exclusion (Dodson, 1974). The smaller of the two species, *D. minnehaha*, thrived when caged in ponds populated by the larger *D. middendorffiana*. These experiments demonstrated that interspecific competition was either weak or absent. The predatory copepod *Diaptomus shoshone* also occurs in these ponds. Dodson found that it feeds most effectively on prey in the size range of *D. minnehaha*, but does consume small individuals of the larger species. He suggests that the predator excludes *D. minnehaha* from small ponds, thereby causing a pattern of apparent competitive exclusion. Although Dodson does not discuss the possibility, it may be true that the two prey species are indirectly interacting even if they are not competing for resources—by contributing to the support of the predator population, the less preferred of the two prey species may be implicated in the exclusion of its congener.

In both of the above examples, one can interpret an observed pattern of habitat exclusion as being due to either resource competition or a shared predator. To decide which is the more reasonable explanation, one probably should carry out field experiments (as did Dodson) and explicitly try to refute one of the two hypotheses.

Limits to Species Packing in Prey Communities

Ecologists have recently become concerned with the impact of predators and parasites on the realized niches of prey and host species (for reviews see Colwell and Fuentes, 1975, and Connell, 1975). A predator specialized to a single species of prey may drastically restrict the range of habitats occupied by that prey. A classic example is the habitat restriction of the Klamath weed (*Hypericum perforatum*) forced upon it by the herbivory of *Chrysolina* beetles (Huffaker, 1957). In the two examples discussed above, the distribution of a single species of prey was probably determined by a generalized predator. The impact of a generalist upon a single species of its prey, however, should depend upon the properties of other species in the generalist's diet. In this section I discuss the way a generalized predator structures a model prey community in the absence of interspecific resource competition. I begin with a derivation of a necessary condition for the existence of any given prey species in the community; this condition is a function of properties of all the other prey species in the predator's diet.

The model is one invented by MacArthur (1969b, 1970, 1972) to analyze

resource competition within a guild of predators. The equations are as follows:

predator:
$$\frac{1}{P}\frac{dP}{dt} = B\left[\sum_i a_i b_i R_i - C\right];$$
(8)

prey:
$$\frac{1}{R_k}\frac{dR_k}{dt} = r_k - \frac{r_k}{K_k}R_k - a_k P,$$
(9)

where

P = the population density of the predator,

R_i = the population density of prey species i,

a_i = the per-predator *per-unit prey* rate of encountering and capturing prey species i,

b_i = the caloric value of a captured individual of species i,

B = a conversion factor relating the energetic intake of the predator to its birth rate,

C = the energetic cost of maintenance and replacement,

r_k = the intrinsic rate of growth of prey species k,

K_k = the carrying capacity of prey species k.

It is assumed that in the absence of the predator each prey species subsists on its own resource base and, when alone, obeys a logistic growth equation. The predator's expected rate of energy intake depends upon both the rate at which prey are encountered and captured, and the caloric value of each capture. (This rate is $\sum_i a_i b_i R_i$.) Density-independent mortality is incorporated as part of the parameter C. The per-capita growth rate of the predator is proportional to its net rate of energy intake. The parameter a_i need not be a constant. It may, for example, vary with changes in prey density. In this section, however, I assume that a_i is a species-specific constant.

At equilibrium, the predator constrains the prey populations, causing them to lie along the hyperplane $\sum a_i b_i R_i^* = C$. The population density of prey species k is

$$R_k^* = \frac{C}{a_k b_k} - \sum_{j \neq k} \frac{a_j b_j}{a_k b_k} R_j^*,$$
(10)

which has the linear form characteristic of competition equations at equilibrium:

$$N_k^* = K - \sum_{j \neq k} a_{kj} N_j^*.$$
(11)

($N_k{}^*$ is the equilibrial density of the kth competitor, K_k is its carrying capacity, and α_{kj} is the competition coefficient.) The ratio a_jb_j/a_kb_k seems analogous to the competition coefficient α_{kj}.

The linear form of Eqs. (8) and (9) facilitates solving for prey density. At equilibrium, the density of prey species k is

$$R_k{}^* = \frac{\dfrac{C}{a_kb_k} - \sum_{j\neq k}^{n} \left\{\left(\dfrac{a_jb_j}{a_kb_k}\right) K_j \left(1 - \dfrac{r_k/a_k}{r_j/a_j}\right)\right\}}{1 + \sum_{j\neq k}^{n} \left(\dfrac{a_jb_j}{a_kb_k}\right)\left(\dfrac{K_j}{r_j/a_j}\right)\left(\dfrac{r_k/a_k}{K_k}\right)}. \tag{12}$$

Despite its inelegance, this expression has several virtues: (1) It implicitly contains the positivity conditions for the one-predator n-prey species community; (2) it allows an explicit analysis of the effect evolution in one species has on the densities of the other species. (The stability character of the point equilibria given by Eqs. (12) and (14) is discussed in Appendix I.)

As is intuitively reasonable, species with equal r_i, K_i, $a_i \equiv a$, and $b_i \equiv b$ have the same density at equilibrium; when there are n such species, $R_i{}^* = (1/n)(C/ab)$. In this special case there is no intrinsic limit to the number of coexisting prey species, except the limit set by the stochastic extinction of small populations for large n (or moderate n and small C/ab). If only K_i varies among the species, then from (12) the density of species k is $R_k{}^* = (K_k/\sum K_j)(C/ab)$. The predator just rescales prey densities, without changing their pattern of relative abundance.

More generally, we expect species to differ in their values for r_i, a_i, and b_i. From (12), species k will be present in positive numbers only if

$$C > \sum_{j\neq k}^{n} a_jb_jK_j \left(1 - \frac{a_j}{r_j}\frac{r_k}{a_k}\right). \tag{13}$$

The existence of a particular species in the community is independent of its own K yet may critically depend upon the K_i of other species in the predator's diet.

These positivity conditions can be put into a form with more biological meaning. Solving for r_k/a_k, we find that species k will be present only if

$$\frac{r_k}{a_k} > \frac{\sum_{j\neq k} a_jb_jK_j - C}{\sum_{j\neq k} a_j{}^2b_jK_j/r_j}. \tag{14}$$

The right-hand side of this expression is the equilibrial density of the predator in the absence of prey species k. Call P^* evaluated in the absence of species k, $P_k{}^*$. The positivity condition (13) may now be written as $r_k > a_kP_k{}^*$. But this is just the condition that must be satisfied if species k is to invade the equilibrium

community consisting of the predator and the other prey species. Hence, the positivity conditions are also conditions for invading the community. This interpretation of (13) is reminiscent of one interpretation of positivity conditions in n-species Lotka–Volterra competition communities (see Strobeck, 1973).

Condition (13) is always satisfied if, for each choice of j, the term $(1 - (a_j/r_j)(r_k/a_k))$ is negative or zero. This occurs if, for each j, $r_k/a_k \geqslant r_j/a_j$. The prey species with the highest relative value for the ratio r_i/a_i is *certain* to be present in the equilibrial community. The fate of species with lower values for r_i/a_i is less certain.

A species with lower r_i/a_i coexists with the species with highest r/a only if

$$C > a_1 b_1 K_1 \left(1 - \frac{a_1}{r_1} \frac{r_2}{a_2}\right) \quad \text{or} \quad \frac{r_2/a_2}{r_1/a_1} > 1 - \frac{C}{a_1 b_1 K_1}. \tag{15}$$

The permissible dissimilarity in the two species' relative abilities to withstand predation (r/a) is set by $C/(a_1 b_1 K_1)$—the equilibrium density of species 1, expressed as a fraction of its carrying capacity. A prey species with a high relative value for r/a is a "keystone" species in the community (*sensu* Paine, 1969), inasmuch as its properties both control the density of the predator and restrict the range of parameters open to other prey.

Given a particular distribution of the parameters of the model among a number of prey species, by substituting into (13) we can determine which combinations of species are compatible. The species can be ranked in order of decreasing r_i/a_i and labeled according to rank order. A species can coexist with species 1 (the species with the highest r_i/a_i) if (15) holds; perforce, it can live with any other single species of lower rank order. Nonetheless, this species can be excluded from the full community (see Fig. 2). This is a "diffuse" form of apparent competitive exclusion. If a predator is found to exclude a given species from a habitat, it may not be possible to attribute that exclusion to a single, particularly prolific prey species—to some extent, *all* the species in the predator's diet will be to blame.

The permissible variance in r/a decreases as the number of species in the diet increases. As one example of this general phenomenon (Fig. 2 depicts another), consider a community in which all species but one have the same values for r_i, K_i, etc., and the nonidentical species has a lower value for r/a. From (14) it can be seen that this species invades the community only if

$$\frac{r_k}{a_k} > \frac{r}{a}\left[1 - \left(\frac{1}{n}\right)\frac{C/ab}{K}\right] = P^*(n). \tag{16}$$

As n increases, it becomes increasingly unlikely that species with $r_k/a_k < r/a$ will be able to invade. A similar result holds if species have different values for their growth parameters.

The expression for $P^*(n)$ has an interesting property. For n greater than some moderate value, the density of the predator is almost independent of its niche breadth. Two widely used measures of niche breadth B are

$$\log B = - \sum_i p_i \log p_i \quad \text{and} \quad B = \frac{1}{\sum_i p_i^2} ,$$

in which p_i is the proportion of the diet comprised by resource i. For either measure, if n resources are equally abundant, then $B = n$. If prey species all have the same values for r_i, K_i, etc., all have the same equilibrial abundance.
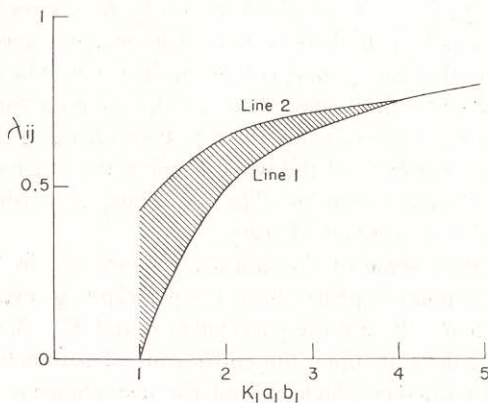
FIG. 2. Parameter spaces allowing invasion into the community ($\lambda_{ij} = (r_i/a_i)/(r_j/a_j)$. $K_1 a_1 b_1$ is plotted in units of C. Line 1 plots the minimum value of λ_{21} satisfying (12). Species 2 cannot invade if the combination of parameters is to the right of line 1. A third species can invade if (1') $C > a_1 b_1 K_1 (1 - (a_1/r_1)(r_3/a_3)) + a_2 b_2 K_2 (1 - (a_2/r_2)(r_3/a_3))$. For example, if $\lambda_{21} = 0.75$ and $a_1 b_1 K_1 = a_2 b_2 K_2$, the minimum value of λ_{31} allowing invasion is shown by line 2. A third prey species with λ_{31} in the cross-hatched region can exist with either 1 or 2, but not with 1 and 2 together.

For example, if $(C/ab)/K = 0.5$, then changing from a diet with $n = 10$ to a diet with $n = 1000$ increases P^* by less than 5%. The reason for this phenomenon is that when feeding on a large number of species our generalized predator overexploits them all and restricts the total productivity of its food supply.

In this model community high species diversity may be permitted for two reasons: (1) All the prey may have very similar abilities to withstand predation —the ratio $r_i/a_i \simeq$ the same constant for all of the species; (2) if there is a high variance in r_i/a_i, species with high relative values for r_i/a_i must have quite low absolute values for K_i or b_i.

Gilpin (1975a) has noted that in randomly constructed real matrices (including a large number of predator–prey interactions), an increase in the

number of species decreases the likelihood that a randomly chosen set of parameters leads to a community with all species present in positive numbers. The above results, based on standard ecological equations, are a particular instance of this general phenomenon.

This analysis may clarify some issues arising out of the controversy between Hairston *et al.* (1960) and their critics, Murdoch (1966) and Ehrlich and Birch (1967). These authors present arguments and counter-arguments about the regulation of whole trophic levels, as well as arguments about the regulation of single populations. In the predator–prey community characterized by (8) and (9), it is clear that the prey trophic level *as a whole* is predator-limited, since at equilibrium $\sum_i a_i b_i R_i^* = C$. If $a_i b_i \equiv ab$, then the total density of prey is a constant: $\sum_i R_i^* = C/ab$. If $a_i b_i$ varies, $\sum_i R_i^*$ varies from $C/\max(a_i b_i)$ to $C/\min(a_i b_i)$. Yet as long as there is more than one prey species present, it is simultaneously true that each *species* is food-limited, too. The carrying capacity of species k enters into the denominator of the solution for R_k^* (see (12)). If this species has the highest value for r/a, then changing K_k from close to zero to a very large number, all the while keeping the other species the same, changes R_k^* from almost zero to $C/(a_k b_k)$. Thus, increasing the resources available to species k increases its density.

The model displays some of the ambiguities inherent in "limiting factor" terminology. At any point in phase space, the per-capita growth rate of species i depends only upon R_i, P, and the parameters r_i and K_i. But the equilibrium density of species i depends upon the entire suite of parameters characterizing the community. Parameters which control the instantaneous growth rate of a prey species may be irrelevant to the determination of its equilibrial density (e.g., any common multiple of the intrinsic rates of growth), whereas factors not in its growth equation at all may nonetheless set its density (e.g., other species' values for K_i). To understand what controls a species' density, one must take care to examine the entire community in which that species is embedded.

It may be necessary to develop a broad understanding of entire predator–prey communities if we are to arrive at optimal solutions to some applied ecological problems. For example, one may want to know whether or not a specialist is preferable to a generalist as a control agent for agricultural pests (Huffaker *et al.*, 1969). One's decision depends upon the characteristics of alternate prey which may be available to the predator. By manipulating the alternate prey, one may be able to greatly reduce the density of the pest. Putnam and Herne (1966) argued that the phytoseiid *Typhlodromus caudiglans* maintained a low endemic density of the pestiferous mite *Panonychus ulmi* in peach orchards, even though *T. caudiglans* largely subsisted on other sources of food. Since alternate prey can increase the density of *Typhlodromus* (Collyer, 1964), this appears to be an example of pest control maintained by apparent competition among prey species.

Predation and Species Diversity Patterns

The study of species diversity patterns is an active area of ecological research. It has often been argued that when productivity is high (Connell and Orias, 1964), or when the environment is stable or "benign" (Sanders, 1969), species diversity will be high. In the predator–prey community characterized by (5) and (6), however, an increase in productivity or "benignness" over ecological time may cause a *decrease* in species diversity.

Imagine that at one time several prey species coexist in a predator's diet. If we know how changes in r_i and K_i reflect changes in given environmental parameters, we can predict changes in the structure of the community from (9); we can determine whether a rise in productivity or decrease in stressful circumstances relaxes apparent competition, or increases its severity.

First, assume that, in the absence of the predator, saturation densities (K) are set by intraspecific inhibitory activities, such as aggressive interactions and the accumulation of metabolic wastes. An increase in productivity will not strongly affect K_i but may change r_i. Since the intrinsic growth rates r_i control densities as ratios r_i/r_j, any increase in productivity which multiplies each r_i by the same constant will not affect prey abundance or change the invasibility conditions. Or, an increase in productivity may *add* the same amount to each r_i, in which case $(r_i/a_i)/(r_k/a_k)$ approaches a_k/a_i. If $a_k \approx a_i$, the increase in productivity makes the community more invasible.

Now, assume that, in the absence of the predator, saturation densities are controlled by the availability of food resources, but r_i is fixed. An increase in productivity increases K_i. Multiplying each K_i by the same constant *decreases* the abundance of species with low relative r/a. As the general economy improves, "the rich get richer, and the poor get poorer." Leigh (1971) and Levin (1970) have also pointed out that when food sources are superabundant (i.e., $K_i \to \infty$ $\forall_i$), only one species of prey can persist in a predator's diet. Thus, an increase in productivity may either increase diversity or decrease diversity, depending upon how productivity affects growth rates.

Presumably, to say that habitat A is harsher than habitat B is to claim that density-independent mortality is higher in A than in B. Density-independent mortality is a component in both r and C. If conditions become more "benign," r is increased and C is decreased. A lower C leads to a higher predator density. Hence, prey species with low r/a may become extinct when their habitat becomes more benign, and species diversity may decrease. (This point is developed more fully in Appendix II.) This decrease is a multispecies analog of Volterra's "third law" for predator–prey systems. This "law"—"The Law of the Disturbance of Averages"—states that "if the mortality of both predator and prey are increased [decreased] simultaneously, by some other factor acting on both, then the number of prey will increase [decrease], but those of the predator will decrease [increase]" (Williamson, 1972). In the absence of interspecific

competition among the prey in a predator's diet, any environmental change increasing the density of the predator may decrease prey species diversity.

OTHER POSSIBLE WORLDS

In this section I discuss the sensitivity of my conclusions to changes in some of the restrictive assumptions built into Eqs. (8) and (9). Three categories of reasonable modifications are briefly explored: (1) changes in the assumptions about prey dynamics; (2) changes in the trophic interaction; (3) changes in the factors limiting the predator. As is argued below, incorporating the third kind of modification into the model may drastically alter the interprey interactions. By contrast, adding the first two types of changes seems to modify only the details of apparent competition among prey. I do not discuss other important assumptions in the model—the lack of spatial or temporal heterogeneity, age structure, etc.—but I do have one programmatic suggestion for ecologists interested in predator–prey models. For each new wrinkle added to a predator–prey model, it seems a worthwhile goal to try to understand the impact of that change upon the conditions for prey species' coexistence. Like null hypotheses, the expression for equilibrium density (12) and the criterion for species packing (13) can serve as yardsticks with which we can gauge the significance of each novel twist in the model.

(i) *Prey dynamics.* It was assumed that prey populations followed logistic growth equations in the absence of the predator. Relaxing this assumption does not seem to greatly affect the qualitative conclusions drawn from the model. Let Eq. (8) describe the predator's growth rate, and write the per-capita growth rate of prey species i as follows:

$$\frac{1}{R_i}\frac{dR_i}{dt} = F_i(R_i) - a_iP. \tag{17}$$

For $F_i(R_i)$ to be a reasonable model of population growth, $F_i(R_i)$ must be bounded, and there must be a maximum R_i (call it $\tilde{K}_i$) above which F_i is zero or negative. Assume that $\partial F_i/\partial R_i < 0$ between 0 and $\tilde{K}_i$. This implies that the maximum value of $F_i(R_i)$ occurs at $R_i = 0$. Let $F_i(0) \equiv \tilde{r}_i$. At equilibrium, $P^* = F_i(R_i^*)/a_i$. Species i will be present only if $F_i(R_i^*) - a_iP^* = 0$ for a positive value for R_i^*. By assumption, $\tilde{r}_i > F_i(R_i^*)$ for $R_i^* > 0$. Species i can be present only if

$$\tilde{r}_i/a_i > P^*. \tag{18}$$

Since a_i is assumed to be a constant, if we decrease R_i^* from K_i to 0 (say by decreasing C), P^* monotonically increases from 0 to $\tilde{r}_i/a_i$. Hence, the maximum

possible value for P^* is $\max_i(\tilde{r}_i \, a_i)$ ($\max_i$ ranges over all species in the predator's diet). Species k can invade if $r_k - a_k P_k^* > 0$, which is assured if $\tilde{r}_k/a_k > \max_{i \neq k}(\tilde{r}_i/a_i)$. This demonstrates that that prey species with largest $\tilde{r}_i/a_i$ will surely be present in the community. By contrast, if $\tilde{r}_i/a_i < \tilde{r}_k/a_k$, species i may be excluded from the community. R_k^* may vary from 0 to $C/a_k b_k$. The *minimum* density for the predator feeding on species k is

$$P^* = \frac{F_k(C/a_k b_k)}{a_k} \, . \tag{19}$$

Substituting from (18), we arrive at a necessary condition for the inclusion of species i in the community:

$$\frac{\tilde{r}_i}{a_i} > \frac{F_k(C/a_k b_k)}{a_k} \, . \tag{20}$$

When there are three or more prey species, "diffuse" apparent competition makes coexistence more difficult than would be predicted from expression (20). If an increase in environmental productivity increases $F_i(R_i)$ for $R_i > 0$, but does not increase $\tilde{r}_i$, some prey species may become extinct. For n prey species with identical $F_i(R_i) = F(R)$, $R_i^*(n) = (1/n)(C/ab)$ and $P^*(n) = F((1/n)\,C/ab)/a$.

$$\frac{\partial P^*}{\partial n} = \frac{\partial P^*}{\partial R} \cdot \frac{\partial R}{\partial n} = \frac{-C}{n^2 a^2 b} \frac{\partial F}{\partial R} > 0,$$

since $\partial F/\partial R < 0$. The sensitivity of the predator's density to changes in its niche breadth should tend to decrease as n increases.

Some species reach their maximum per-capita growth rates at densities *greater* than zero: $\partial F_i/\partial R_i > 0$ for $0 < R_i < \hat{R}_i < K_i$, and $\partial F_i/\partial R_i < 0$ for $\hat{R}_i < R_i < K_i$. Watt (1968) discusses several examples of populations with "Allee-type" growth rates, and Rosenzweig (1969) has argued that "humped" $F_i(R_i)$ should be common in nature. With such prey species, alternate non-invasible communities become possible.

Consider two prey species with *identical* growth curves: $F_1(R_1) = F_2(R_2)$ whenever $R_1 = R_2 \equiv R$. Figure 3 depicts the zero isoclines of both species and the predator for two possible examples of humped $F(R)$ curves. If $a_1 = a_2 \equiv a$ and $b_1 = b_2 \equiv b$, then the equilibrial densities of species 1 and the predator are $R_1^* = C/ab$ and $P^* = F(R_1^*)/a$. In the examples drawn in Fig. 3, $P^* > \tilde{r}/a$. This implies that species 2 cannot invade the community. Since in these examples the identity of the original prey species does not matter in the determination of P^*, there can be at least two alternate noninvasible communities. For either curve in the figure, the community comprised of the predator and one-prey species is stable (see Appendix I). For F', the three-species community is also locally stable. Thus, if the per-capita growth rate
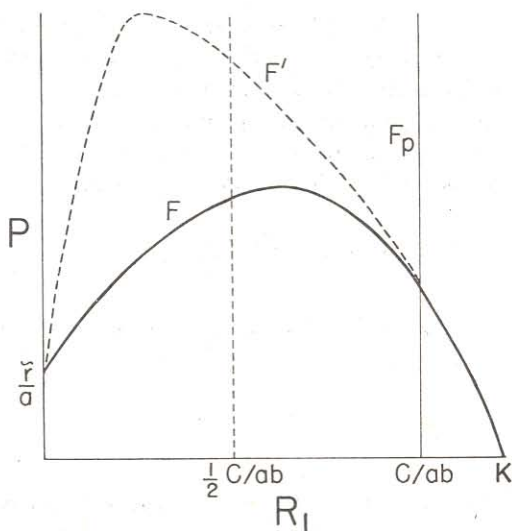
FIG. 3. Apparent competitive exclusion between prey species with identical growth curves. The vertical line F_p is the zero isocline of the predator. F and F' are two different prey isoclines. The intersection of F_p with F or F' gives the equilibrial densities of both species. If two prey species are present, $R_1^* = (0.5)(C/ab)$. For F' at this density, $\partial F'/\partial R_1 < 0$. (See text for further explanation.)

falls off rapidly at low densities—as does F'—there may be three alternate communities. Similarly, we might expect a large number of possible alternate communities if the predator is feeding on n prey species with humped $F_i(R_i)$. Several ecologists have emphasized the likelihood of multiple stable states in communities (e.g., Levin, 1973). Sutherland (1974) has argued that historical events may critically determine the structure of natural communities. If prey often have Allee-type growth curves, we should expect sequences of colonization to determine the composition of particular prey communities.

   (ii)   *The trophic interaction.*   I have been assuming both that the per-capita predation rate $(-a_iP)$ is independent of prey density, and that the per-capita growth rate of the predator is a linear function of prey densities. Neither assumption is true if prey have refuges from predation, or if predators exhibit complex functional responses to changes in prey density. In the following paragraphs I outline several ways in which the addition of these touches of realism to Eqs. (8) and (9) might modify my earlier conclusions.

   Refuges may affect the structure of prey communities in several ways. For example, individual prey may enter and leave refuges at a constant per-individual rate, thereby ensuring the safety of a constant *fraction* of the population at any

one time. The larger is this fraction, the lower will be the parameter a_i. Thus, the model can directly incorporate temporary refuges.

Alternatively, a constant *number* of individuals may live in refuges. If each prey species in the community has its own refuge, then the shared predator can never cause the extinction of any one of them. In such a community, constraints on growth curves (e.g., inequality (13)) are not likely to be important determinants of community structure. The crucial proviso here is that *each* prey species have a refuge. If some species have refuges and others do not, the "haves" may exclude the "have-nots." This can be demonstrated with a simple modification of Eqs. (8) and (9). Assume that $\hat{R}_i$ is the maximum number of individuals in species i able to live in refuges free from predation; the predator must subsist on the surplus E_i above $\hat{R}_i$. Thus, $R_i = \hat{R}_i + E_i$, $R_i > \hat{R}$; $R_i = R_i$, $R_i \leqslant \hat{R}_i$. E_i ranges from 0 to $K_i - \hat{R}_i$. Equation (8) for the predator becomes

$$dP/dt = BP \left[\sum_i a_i b_i E_i - C \right],$$ (21)

whereas the growth equation for prey species i may be written

$$\frac{dR_i}{dt} = R_i \left(r_i - \frac{r_i}{K_i} R_i \right) - a_i E_i P.$$ (22)

In Eqs. (21) and (22), the parameter a_i is to be interpreted as the per-predator, per-unit prey rate of capture of individuals in the surplus population E_i. If, for all i, $\hat{R}_i > 0$, apparent competition will be expressed only through changes in E_i^*.

Assume that there are only two prey species, and that in the absence of refuges species 1 excludes species 2:

$$\frac{r_2}{a_2} < \frac{r_1}{a_1} \left(1 - \frac{C/a_1 b_1}{K_i} \right).$$

Moreover, assume that species 2 has a refuge protecting $\hat{R}_2$ individuals, and that species 1 does *not* have a refuge. At equilibrium, (i) $a_1 b_1 R_1^* + a_2 b_2 E_2^* = C$; (ii) $r_1 - (r_1/K_1) R_1^* - a_1 P^* = 0$; and (iii) $R_2^*(r_2 - (r_2/K_2) R_2^*) - a_2 E_2^* P^* = 0$. From (iii), for $P^* > 0$, then $E_2^* > 0$. With (i) this implies that $R_1^* < C/a_1 b_1$. Species 1 is excluded if $r_1/a_1 < P_1^*$, in which case $E_2^* = C/a_2 b_2$. But from (iii)

$$P_1^* = \frac{r_2}{a_2} \left(\frac{R_2^*}{E_2^*} \right) \left(1 - \frac{R_2^*}{K_2} \right) = \frac{r_2}{a_2} \left(\frac{\hat{R} + C/a_2 b_2}{C/a_2 b_2} \right) \left(1 - \frac{\hat{R} + C/a_2 b_2}{K_2} \right).$$

The last expression can be made greater than any given r_1/a_1 if K_2 is large relative to $(\hat{R} + (C/a_2 b_2))$ and $C/a_2 b_2$ is small enough. From the above analysis we can draw two conslusions: (1) If a prey species is in the community by

virtue of its refuge from predation, and $\hat{R}_i < K_i$, then its presence will decrease the density of other prey species; (2) refuges may reverse dominance in apparent competition relations between prey species.

If species 1 has a refuge, and species 2 does not, the condition for coexistence is

$$\frac{r_2}{a_2} > \frac{r_1}{a_1} \left(\frac{\hat{R}_1 + C/a_1 b_1}{C/a_1 b_1} \right)\left(1 - \frac{\hat{R}_1 + C/a_1 b_1}{K_1}\right). \tag{23}$$

Figure 4 compares (23) to (15), the condition for coexistence in the absence of a refuge. It is straightforward to show that if $C/a_1 b_1 > (0.5) K_1$, coexistence is made easier by the presence of the refuge, whereas if $C/a_1 b_1 < (0.5) K_1$, coexistence is *more* difficult for small $\hat{R}_1$. In Fig. 4b, along a gradient in $\hat{R}_1$,
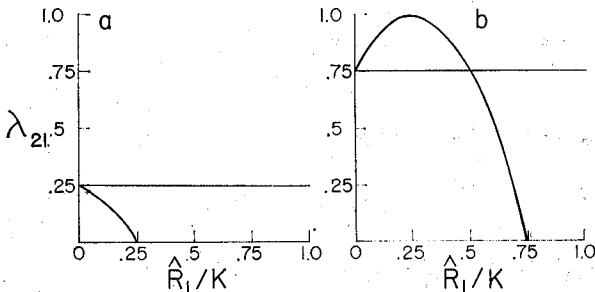

FIG. 4.   Refuges and apparent competition. In both (a) and (b) the straight line is the lowest permissible value for λ_{21} (see Fig. 2) with $C/a_1 b_1 = 0.75\,K_1$ in (a) and $= 0.25\,K_1$ in (b). The curved lines are plots of minimum λ_{21} as a function of $\hat{R}_1$, from inequality (23). Species 2 cannot invade if its value of r_2/a_2 leads to a λ_{21} below these curves. In (a), refuges for species 1 always relax apparent competiton. But when predation is more intense, on species 1, as in (b), refuges may make invasion more difficult. For low $\hat{R}$, refuges allow the predator density to remain high despite the high rate of exploitation of accessible prey.

species 2 may be present at both ends of the gradient yet absent in the middle. Clearly, wherever refuges from predation are present, one cannot use (13) to make accurate predictions about the structure of the prey community. Instead, one must know the distribution of both refuges and population growth parameters among the members of the community.

In the analysis of Eqs. (8) and (9) I assumed that a_i was independent of prey density. This is not true if predators can be satiated or can switch. Introducing predator satiation ($\partial a_i/\partial R_0 < 0$; Holling's Type 2 response) seems to affect the details of prey community structure without greatly changing its qualitative features, at least when a stable point equilibrium exists. The reason is that in a food-limited species no individual will be very satiated at equilibrium. Hence, predator satiation should not greatly affect the relations between prey species. This conclusion can be borne out by analyzing predator–prey equations that

explicitly include satiation. Let h_j be the time required to attack, to capture, and to consume an individual of species j, and let a_j' be the per-individual, per-unit search time rate of capture by a predator. The number of individuals of j captured per-unit time is $n_j = R_j a_j'(1 - \sum_i n_i h_i)$. This expression leads to the following equation for the rate of growth of the predator:

$$\frac{1}{P}\frac{dP}{dt} = B\left[\frac{\sum_i a_i' b_i R_i}{1 + \sum_i a_i' h_i R_i} - C\right] \tag{24}$$

(modified from Maynard Smith, 1975). At equilibrium,

$$R_k^* = \frac{C}{a_k'(b_k - Ch_k)} - \sum_{j \neq k} \frac{a_j'(b_j - Ch_j)}{a_k'(b_k - Ch_k)} R_j^*. \tag{25}$$

Prey mortality is a function of the densities of all the species in the predator's diet:

$$\frac{1}{R_k}\frac{dR_k}{dt} = r_k - \frac{r_k}{K_j} R_k - a_k(R_1, R_2, ...) P, \tag{26}$$

where $a_k(R_1, R_2, ...) = a_k/(1 + \sum_i a_i' h_i R_i)$. Over short time periods these prey species exhibit mutualism: $\partial F_i/\partial R_j > 0$ and $\partial F_j/\partial R_i > 0$. At equilibrium, however, the numerical response of the predator imposes apparent competition relations among its prey—as long as $b_i > Ch_i$ for all i. It can be shown that this is assured if we require that $\partial F_p/\partial R_i > 0$, $\forall i$. (The latter requirement picks out diets that are identical to the diets predicted from optimal diet models (Holt, in preparation).) A reviewer has pointed out that the functional response built into (24) and (26) tends to destabilize this system. The above remarks apply to point equilibria; I do not know what happens when the system exhibits more complex behavior.

If predators concentrate their attention on whichever prey species is temporarily most abundant, and ignore rare species, no prey can be excluded from the equilibrium community. A predator is said to "switch" if it alters its attack parameters a_i concordant with changes in the *relative* frequency of species i. There is a burgeoning literature on switching (e.g., Krebs, 1974; Murdoch and Oaten, 1975); here I can touch on only a few facets of this complex phenomenon.

It is clear that condition (13) is irrelevant to the determination of community structure if rare prey are not being preyed upon at all, i.e., $\lim_{R \to 0} a_k(R_1, R_2, ...) = 0$. If a predator switches, then

$$\partial a_k/\partial R_k \geqslant 0 \quad \text{and} \quad \partial a_i/\partial R_k \leqslant 0 \quad (i \neq k). \tag{27}$$

After a change in prey density, a predator behaving adaptively should change

its attack parameters $a_i(R_1, R_2, ...)$ only if, in so doing, its rate of energy intake is increased, or at the very least not decreased. From (6) and (8),

$$\frac{\partial F_p}{\partial R_k} = \frac{\partial}{\partial R_k} \left(\sum_i a_i b_i R_i \right) = a_k b_k + b_k R_k \frac{\partial a_k}{\partial R_k} + \sum_{i \neq k} b_i R_i \frac{\partial a_i}{\partial R_k} \geqslant 0. \quad (28)$$

If $\lim_{R_k \to 0} a_k = 0$ and $\partial a_k / \partial R_k$ is bounded, then at $R_k = 0$, inequality (28) becomes

$$\sum_{i \neq k} b_i R_i \frac{\partial a_i}{\partial R_k} \geqslant 0. \quad (29)$$

The two inequalities (27) and (29) are jointly satisfied if, and only if,

$$\frac{\partial a_i}{\partial R_k} \bigg|_{R_k = 0} = 0, \qquad \forall i \neq k. \quad (30)$$

Using this criterion we can reject certain functional forms for $a_i(R_1, R_2, ...)$. For example, if a_i' and Z are both positive constants, the functional response $a_i(R_1, R_2, ...) \equiv a_i'(R_i / \sum R_j)^Z$ violates (30). Hence, predators with this functional response are exhibiting mal-adaptive behavior.

Smith (1972) has argued that in spatially heterogeneous system the probability of capture per-unit prey item should decrease as the density of prey decreases, so that the last few individuals are nearly free of predation. One way to model this effect near equilibrium is to let $a_i(R_i)$ be a linear function of prey densities:

$$a_i(R_i) \equiv a_i' R_i. \quad (31)$$

No prey species can be directly excluded from the community. Nonetheless, alternate prey may exhibit strong apparent competition relations. For example, if there are just two prey species, by substituting the identity (31) into Eqs. (8) and (9) and solving for R_1^* it can be shown that $\partial R_1^* / \partial K_2 < 0$ and $\partial R_1^* / \partial r_2 < 0$. If both K_1 and K_2 are very large, $a_1' = a_2'$, and $b_i = b_2$, then

$$R_1^* \cong \left(\frac{C/a'b}{1 + (r_2/r_1)^2} \right)^{1/2}.$$

The equilibrial density of species 1 is in part determined by the demographic properties of species 2.

(iii) *Mechanisms regulating predator density.* Predator-mediated apparent competition will be relaxed by any ecological factor that restricts the predator to an equilibrial density below the density set by its available food. For example, intraspecific interference may depress the predator's density. If predators

interact whenever they meet, and each individual loses an amount of energy I at each encounter, the per-capita growth rate of the predator declines as P increases. This may be represented in the growth equation as follows:

$$\frac{1}{P}\frac{dP}{dt} = B\left[\sum_j a_j b_j R_j - C - IP\right]. \tag{32}$$

MacArthur (1970) briefly discussed this equation. He pointed out that near equilibrium the prey equations resemble competition equations "in which the best competitor is the one which can withstand the greatest predator pressure." As interference intensifies, apparent competition among the prey is relaxed. There may be yet other types of interference that more sharply restrict the importance of apparent competition.

By embedding the predator–prey model of (8) and (9) in a more complex food web model, one may drastically alter the relations among the prey. For instance, consider a community in which the predator is itself the sole prey of a higher-order food-limited predator. The simplest way to modify the original model so as to include this predator is to add a mortality term to (8),

$$\frac{1}{P}\frac{dP}{dt} = B\left[\sum_j a_j b_j R_j - C\right] - a'P',$$

and incorporate an equation for the higher-order predator:

$$\frac{1}{P'}\frac{dP'}{dt} = B'[a'b'P - C'].$$

At equilibrium, P^* is constrained to the density $C'/a'b'$. If the a_i are constant coefficients, the prey equations are decoupled. Prey species i can invade if $r_i - (C'/a'b') > 0$.

An increase in productivity or a decrease in density-independent mortality should ease the difficulties of invasion, as well as increasing the equilibrial density of those prey species already present. These effects are opposite those expected in the absence of the higher-order predator. If the lower-level predator may be sated, or switches, its prey will exhibit "apparent *mutualism*" at equilibrium.

Some ecologists have suggested that all $(-, -)$ relations between species should be labeled "competition," all $(+, -)$ relations "predation," all $(+, +)$ relations "mutualism," and so forth (e.g., Odum, 1959). This classificatory scheme seems inappropriate when the relationship is imposed, as it were, by the structure of the food web. As was noted in the introduction, the elements $a_{ij} \equiv \partial F_i/\partial R_j$ making up the community matrix embody all the direct pairwise interactions occurring in a community at equilibrium. In multispecies com-

munity models, however, the sign of a_{ij} may bear little relation to the *net* effect of species j upon species i at equilibrium; the latter reflects the structure of the entire community. This is particularly clear when $a_{ii} = 0$. Figure 5 depicts several examples. Closed circles in the figure represent populations with self-regulation ($a_{ii} < 0$); open circles are species with $a_{ii} = 0$. If a_{ij} is nonzero, an arrow is drawn from species j to species i. In Fig. 5a, species 4 increases the
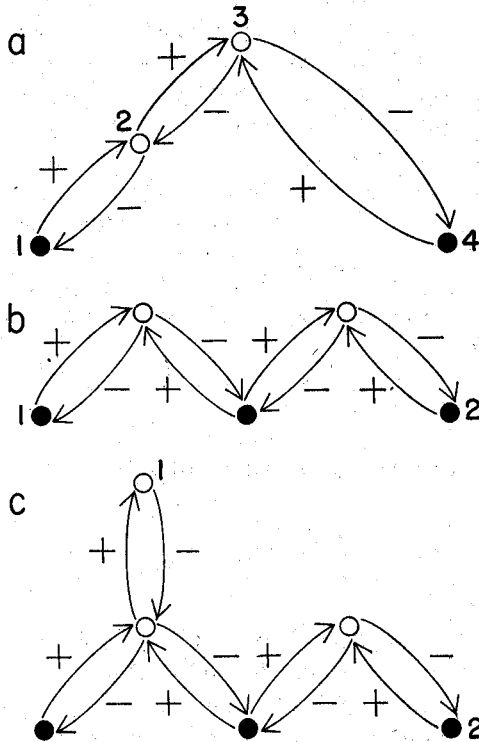
FIG. 5. Indirect interactions in complex food webs. The sign beside each arrow is the sign of a_{ij}. For the examples discussed in the text, the sign of the net effect of i upon j is the same as the sign of $(a_{ki}a_{lk} \cdots a_{rq}a_{jq})$. (Jeffries, 1974, and Levins, 1975, discuss other uses of food web diagrams in ecological theory.)

density of species 3, thereby decreasing species 2 and indirectly increasing 1. Species 1 maintains species 2 and indirectly augments the numbers of species 3, thus decreasing the density of species 4. Species 1 and 4 have a $(+, -)$ relation, yet it is misleading to call this indirect interaction "predation"; I suggest that such indirect $(+, -)$ relations are better termed "apparent predation." In like manner, species 1 and 2 in Fig. 5b may be said to exhibit "apparent symbiosis." Species 1 and 2 in Fig. 5c provide a baroque example of "apparent competition."

Levins' technique of "loop analysis" (Levins, 1975) may prove to be a useful tool for the elucidation of indirect interactions in complex communities.

The distinction between "direct competition" and "apparent competition" is closely related to a distinction between two time scales—on the one hand, the characteristic time required for growth rates to respond to changes in density, and, on the other hand, the time required for the full system to equilibrate subsequent to the addition of a new species. If the latter is much greater than the former, indirect interactions filtered through long chains in the food web may be washed out in the noise of environmental fluctuations. An important task for future work is to investigate the relation between models of direct interactions and apparent interactions arising in multispecies communities. For some purposes it may be legitimate to mimic the indirect interaction between two species with a model in which the two directly interact.

Evolution and Apparent Competition among Prey

Does natural selection within a prey species sharpen the difficulties of prey species' coexistence, or does natural selection tend to relax apparent competition among prey? Until there is a more intimate relation between population ecology and population genetics than exists today there can be no satisfactory answer to this question. Conceptually, the simplest way to wed ecology with genetics is, first, to assume that genetic variants are expressed only through their effect on parameters entering into the per-capita growth equation (1), and then, to assert that a rare genetic variant which increases an arbitrary parameter α_i will be selected only if

$$\partial F_i/\partial \alpha_i > 0 \tag{33}$$

(Rosenzweig, 1972; Levins, 1975). (This may be made more rigorous if one identifies per-capita growth rates with the absolute selective values of alternate alleles at a single locus (e.g., Roughgarden, 1971; Gilpin, 1975a,b).) In this section (33) is used to develop a feeling for the community-level effect of selection on the parameters of Eqs. (8) and (9). Evaluating $\partial R_j^*/\partial \alpha_i$ will allow us to ascertain the impact of selection in species i upon the density of species j.

If r_i, K_i, and a_i are not coupled (i.e., $\partial r_i/\partial K_i = 0$, etc.), then, from Eq. (9): $\partial F_i/\partial r_i > 0$, $\partial F_i/\partial K_i > 0$, and $\partial F_i/\partial a_i < 0$. Natural selection in species i should increase r_i and K_i, and decrease a_i. (If the first two possibilities are referred to as r- or K-selection (Roughgarden, 1971), perhaps the third could be called "a-selection.") Rosenzweig (1972) has argued that the equilibrial population density of a prey species does *not* reflect selection within that species to increase either its intrinsic rate of growth or its carrying capacity. In like manner, Levins (1975) has stated that "species populations just below the top

of the trophic structure will increase only by selecting for predator avoidance."
This conclusion critically depends upon an implicit assumption made by these
authors—that the predator has but a single species of prey in its diet. If there
are two or more species sharing the predator, by differentiating Eq. (12) it can
be seen that $\partial R_i^*/\partial r_i > 0$, $\partial R_i^*/\partial K_i > 0$, and $\partial R_i^*/\partial a_i < 0$.

Both $\partial R_j^*/\partial r_i < 0$ and $\partial R_j^*/\partial K_i < 0$ $(i \neq j)$. Hence, selection acting on
either r_i or K_i makes the coexistence of prey species more difficult. But
"a-selection" has a more ambiguous effect. It is well known that the yield
from an exploited population decreases when the cropping rate increases
beyond a certain level (see, e.g., Watt, 1968). The predator density is set by
the equilibrial yield from its prey; if the predator begins to overexploit its prey,
the predator's density will decline. Conversely, the predator's density may
increase if its overexploited prey is selected to lower a_i. From (14),

$$\partial P^*/\partial a_i < 0 \qquad \text{if} \quad (0.5)\,r_i < a_i P^*. \tag{34}$$

Prey species i is being overexploited if predation upon it consumes more than
half of its intrinsic rate of increase. In the regime of overexploitation (expres-
sion (34)), natural selection within species i to decrease a_i increases the predator's
density $(\partial P^*/\partial(-a_i) > 0)$ and sharpens the impact of species i upon species j.

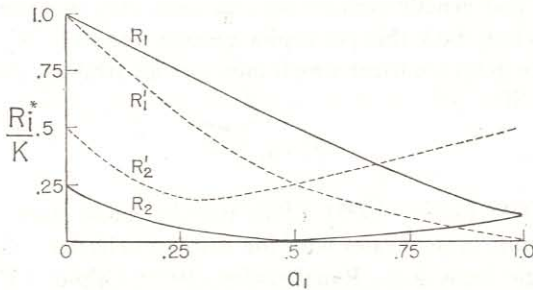Figure 6 shows a hypothetical example of this effect. The predator consumes

FIG. 6. R_1^* and R_2^* as functions of a_1. The lines marked R_1 and R_2 are Eq. (12)
with $a_2 = 1$; lines R_1' and R_2' were computed with $a_2 = 0.5$. The minimum value for
R_2^* is reached when $R_1^* = 0.5K$.

two prey species which have the same values for r_i, K_i, and b_i. It is imagined
that prey species 1 evolves so as to decrease a_i, whereas the predator and
species 2 do not change. In Fig. 6, R_i^* is shown as a function of a_1, with
$C/b = (0.25)\,K$. The solid lines are R_1^* and R_2^* for $a_2 = 1$; the dotted lines
give equilibrial densities for $a_2 = 0.5$. A decrease in a_1 increases the predator
density as long as $R_1^* < (0.5)\,K$. At $a_1 = 0.25$, the density of species 2 is less

than half of what it would be in the absence of species 1. Yet at this value for a_1, the predator cannot subsist on species 1 alone (see Fig. 7). This illustrates how those prey species to which the predator is poorly adapted (low a_i) may be critical determinants of prey community structure.

The above conclusions seem to hold for the more general class of predator–prey models comprised of Eqs. (8) and (17). An increase in the productivity of species i ($F_i(R_i)$) increases the equilibrial density of the predator, thereby
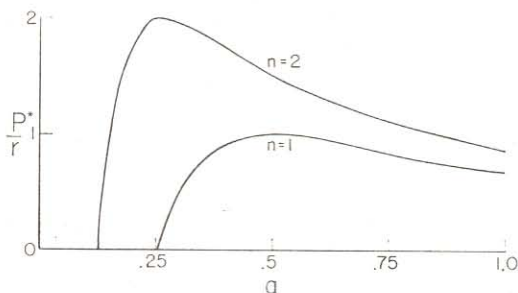
FIG. 7. The equilibrial density of the predator as a function of the parameter a. Both curves are drawn from Eq. (16) with $C/b = 0.25K$. The upper curve may represent either the predator's density when a second prey species is present, or the effect of doubling K or halving C when only a single prey species is present.

increasing predation upon other prey species. From Eq. (17), $F_i(R_i^*) = a_i P^*$. As a_i increases, R_i^* decreases. But $F_i(R_i)$ is bounded, so that as a_i grows larger P^* must eventually begin to decrease with increasing a_i. In these regimes of overexploitation, selection that lowers a_i increases apparent competitive pressures between prey species.

When r_i, K_i, and a_i are uncoupled, natural selection within one prey species will often make prey species coexistence more difficult. In general, we expect these parameters to be coupled. There are two distinct reasons for this expectation. First, in attempting to build up single-species population models from explicit biological assumptions, one often finds that the same parameters enter into the expressions for saturation density and intrinsic rate of growth (T. Schoener, personal communication), usually leading to a positive correlation between the two quantities.

A second, more biological reason for expecting *negative* correlations among r_i, K_i, and a_i stems from "The Principle of Allocation." One argues that an organism has a certain amount of time and energy at its disposal which it must divide among several disparate activities; moreover, an organism can increase its effectiveness at one endeavor, such as escaping predators, only at the expense of its abilities in other activities. A detailed appraisal of the effect of natural selection upon apparent competition depends upon a knowledge of the intrinsic

functional relationships between parameters. Over evolutionary time the structure of the prey community will be molded by the detailed form of these functional relationships. For example, imagine that prey species can be ordered along a single phenotypic axis z and that a_i is a function of z. Examples of such axes might be body size, body shading, or the position of hiding places along an environmental gradient. Consider a predator that is most adept at a single point $\hat{z}$ along the z-axis and that becomes less proficient as $|z_i - \hat{z}|$ increases, as in Fig. 8. At time 0, prey species 1 is imagined to be characterized by $z_1 < \hat{z}$
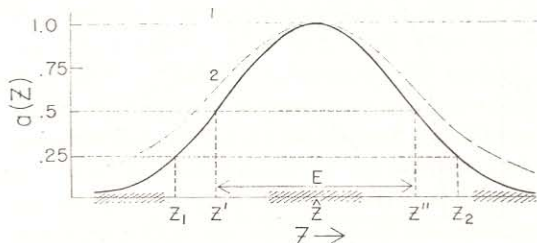

FIG. 8. Character divergence and apparent competitive exclusion. If z_1 and z_2 are located between the shaded regions of the axis, there is an excluded zone E centered at $\hat{z}$. This zone reaches its maximum extent at $a(z_1) = 0.25$. The same will be true if z_1 and z_2 are congruent on one side of $\hat{z}$. (See the text for further explanation.)

and species 2 by $z_2 > \hat{z}$. For simplicity, we assume that $a(z)$ is symmetrical around $\hat{z}$ and that at any given time the two prey species have the same values for a_i, K_i, and b_i. This implies that $|z_1 - \hat{z}| = |z_2 - \hat{z}|$. Natural selection should cause this species pair to diverge away from $\hat{z}$. We would like to understand the significance of this divergence for a third prey species with an intermediate phenotype, $z_1 < z_3 < z_2$.

If $a_i(z_i)$ is functionally related to r_i and K_i, it should be possible to write the growth parameters as functions of z. The dashed lines in Fig. 8 represent two possible forms for $r_i(z)$, assumed to be the same for all three prey species. For a flat $r(z)$ (line 1 in the figure), species 3 is excluded if $1 \leqslant a(z_3) P^*$. P^* evaluated from Eq. (16) (with $n = 2$) is shown as a function of $a = a(z_1) = a(z_2)$ in Fig. 7. Setting $C/b = (0.25) K$ (as in Fig. 7), a third species with $z_3 = \hat{z}$ ($a(\hat{z}) = 1$) is excluded if $0.15 < a < 0.8$. P^* reaches its maximum at $a = 0.25$; for this value of a the third prey species can be present only if $a(z_3) < 0.5$. Hence, when z_1 and z_2 are at the positions shown in the figure, a third species with z_3 between z' and z'' will be excluded from the community. The excluded zone E rapidly decreases as a declines below 0.25. In this hypothetical example, the effects of apparent competition are maximal at intermediate levels of character divergence. This conclusion does not hold if the prey can never be overexploited, or if $r(z)$ has the form of line 2 in the figure. For example, if $C/b = K$, or $a(\hat{z}) = 0.25$, P^* declines monotonically as z_1 and z_2 move apart. Similarly, if r_i

declines with a_i so that r_i/a_i is nearly constant for all values of z (line 2 in Fig. 8), P^* decreases as $|z_1 - z_2|$ increases. Prey species can be packed all along the phenotypic axis if the predator is ineffective—low $a(\hat{z})$ and high C compared to bK—or if r_i and a_i are strongly correlated.

Several ecologists have suggested that prey species "compete" for "escape space" or color patterns and that this "competition" leads to gaps between species' characters (Richlefs and O'Rourke, 1975; Gilbert and Singer, 1975). As mechanisms for such "competition," these authors discuss only apostatic selection due to switching predators able to form search images. The situation depicted in Fig. 8 provides another mechanism for producing gaps between the characters exhibited by alternate prey.

Of course, to understand fully the effects of selection upon apparent competition, we would have to analyze evolutionary changes in the predator, too. As prey species lower their respective values for a_i, the predator is expected to respond by shifting $\hat{z}$ or modifying the shape of $a(z)$. The community-level effects of these evolutionary changes should depend upon the interplay of demographic parameters such as C, B, and the a_i (Eq. (8)). Prey species which diverged so that $\partial a_j/\partial a_i < 0$ could force their predator to become more specialized. Since the predator should be selected to increase a_i only if $\sum_j b_j R_j^*(\partial a_j/\partial a_i) > 0$, the predator will tend to specialize on prey with high relative values for r_i and K_i, thus sparing rarer prey species. I suggest that if we are to develop a deep understanding of the relation between coevolution and community ecology, we must develop our evolutionary arguments in the context of explicit population dynamic models. If we do not, the implications of selection on particular traits (e.g., a_i) may be equivocal; a single selective event may have qualitatively different effects in two different communities.

Conclusion

Ecologists have begun to explore the interplay of predation and competition in the determination of community structure (Schoener, 1974b). Often, it has been argued that predation relaxes competitive pressures by reducing the density of competing prey species, thereby allowing a much higher species diversity than is possible in predator-free communities (Paine, 1966; Harper, 1969; Connell, 1970; but see Cramer and May, 1971). Recently, these verbal arguments have been sharpened into explicit analyses of limiting similarity in guilds of competing species cropped by predators (May, 1974; Roughgarden and Feldman, 1975). These works implicitly or explicitly compare conditions for coexistence in communities *with* a predator to conditions for coexistence in the same communities *without* a predator.

By contrast, in this paper I have deliberately explored the implications of models in which direct competition is absent; whatever the resource base, it was

assumed to be perfectly partitioned among the species of prey. I have compared the equilibrial states of model communities which differ only in the composition of their prey "guilds." In these model communities, apparent competition alone structures relations among the prey. The conditions for coexistence depend upon the degree to which each species limits its own growth (K), as well as the ability of each species to transform resources into offspring (r) and to escape the predator (a). I have argued that the conditions for coexistence become more stringent, the more productive or less harsh is the environment, or the more diverse is the prey community. Since there is always some interspecific variance in parameters such as r, K, and a, there may be a limit to the number of prey species which can coexist in the diet of a food-limited predator.

There may be some natural communities in which direct competition is weak or entirely absent and in which apparent competition plays a primary role in the structure of the community. But in most natural communities, the realized patterns of abundance probably reflect both direct and apparent competition. When a particular community is investigated, one should be aware of the possible importance of both mechanisms. For example, it may be true that a generalized predator permits the coexistence of pair of competitively incompatible species, yet simultaneously it may be true that each species of prey would be better off were it alone in the predator's diet. These two, distinct effects of shared predation may both be important. Apparent competition may play an important and as yet poorly recognized role in natural communities.

Appendix I

This paper has explored some features of the "comparative statics" of predator–prey models. But discussing the properties of point equilibria may be misleading if the equilibria are dynamically unstable. The following result from the theory of qualitative stability allows a rapid assessment of the stability character of several of the models herein discussed (Jeffries, 1974). Recall that $a_{ij} = (\partial F_i / \partial N_j)^*$. The asymptotic stability of the community is assured if the following five conditions are jointly satisfied: (i) $a_{ii} \leqslant 0$ for all i; (ii) $a_{ij}a_{ji} \leqslant 0$ for all $i \neq j$; (iii) $a_{ij}a_{jk} \cdots a_{qr}a_{ri} = 0$ for three or more distinct indices; (iv) $\det\{a_{ij}\} = 0$ ($\{a_{ij}\} \equiv$ the matrix comprised of elements a_{ij} in row i and column j); (v) the community "fails" a "color test." Jeffries (1974) details condition (v); there is no need to discuss it here, for it is satisfied by all the models discussed in this paper.

For Eqs. (8) and (9) it is apparent that conditions (i), (ii), and (iii) all hold. Det$\{a_{ij}\}$ is proportional to the equilibrial densities of all the prey, and is nonzero if P^* and each R_i^* are positive. If all the species can be present in positive densities, we can conclude that the equilibrial community is locally stable.

From expression (14), $P^* > 0$ if $\sum_i a_i b_i K_i > C$—the condition which must be satisfied if the predator is to invade the predator-free community.

Given that the predator and all its n prey species can coexist, all of the possible equilibria on "edges" (one or more population at zero density) are unstable. Let $P_{ij...}^*$ denote the predator's density in the absence of species i, species j,.... Since $R_i^* > 0$, $r_i/a_i > P^*$. Manipulating the expression for P^*, it can be shown that $P^* > P_i^*$. Consider a community in which only species k is absent.

Since for all i, $r_i/a_i > P^* > P_k^*$, all the remaining $n - 1$ prey species have positive densities; it follows that $r_i/a_i > P_{ki}^*$ and $P_k^* > P_{ki}^*$. Iterating, we find that $r_k/a_k > P_k^* > P_{kj}^* > \cdots$. Species k can invade all equilibrial communities from which it is absent. Since k was arbitrary, all the "edge" equilibria are unstable.

Assuming only that $b_i \equiv b$ and that the positivity conditions are satisfied, Aiken and Lapidus (1973) have constructed a Lyapunov function for Eqs. (8) and (9). For this important special case of the model the point equilibrium is globally stable. Using an expression derived by Aiken and Lapidus, we find that for n prey species with equal r_i, K_i, and a_i a small disturbance will return halfway to equilibrium in a time $t = n(2Kb/r)$. As diversity increases, the ability of the community to withstand disturbance decreases. This is reminiscent of the general theme that increased diversity tends to decrease stability (May, 1973).

Several other predator–prey models discussed in this paper are qualitatively stable. The model made up of Eqs. (8) and (17) is stable, as are the models incorporating refuges (Eqs. (21) and (22)), interference (Eq. (31)), or the higher-level predator. By contrast, models in which the prey curve has a "hump" or in which the predator satiates need not be locally stable.

APPENDIX II

To examine the effect of changes in density-independent mortality, we must re-parameterize the model. Following Wilson and Bossert (1971), let the per-capita birth rate of prey species i be given by $b_i - k_{bi}R_i$, the per-capita death rate by $d_i + k_{di}R_i + a_iP$, and the predator's cost of maintenance and replacement by $M + D$. M reflects maintenance costs, and D is the per-capita death rate of the predator. The per-capita growth rate of prey species i may be written

$$\frac{1}{R_i} \frac{dR_i}{dt} = (b_i - k_{bi}R_i) - (d_i + k_{di}R_i + a_iP). \tag{A}$$

In the absence of the predator, Eq. (A) reduces to a logistic equation in which

$$r_i \equiv b_i - d_i \quad \text{and} \quad K_i \equiv \frac{b_i - d_i}{k_{di} + k_{bi}}.$$

A pair of prey species whose growth parameters are the same, except for b_i, can coexist if

$$b_2 > b_1 - \frac{k_{b1} + k_{d1}}{ab} (M + D).$$ (B)

A uniform decrease in density-independent mortality decreases D, shrinking the permissible difference between b_1 and b_2; prey species with low per-capita birth rates may become extinct as a result of decreased density-independent mortality.

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