TRADE-OFFS AND COEXISTENCE IN CONSUMER-RESOURCE MODELS: IT ALL DEPENDS ON WHAT AND WHERE YOU EAT

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Abstract.—The study of interactions between consumers and their resources has led to three important but largely separate bodies of theory: optimal foraging theory, density-dependent habitat selection, and consumer-resource theory. In this article, we draw on all three to study mechanisms of coexistence, uniting these fields of theory via a set of related models based on Holling's disc equation and four different types and arrangements of resources. Using established rules for optimal behavior and habitat selection within a framework of consumer-resource models, we explore how unavoidable trade-offs in conversion efficiency, handling time, and encounter efficiency affect coexistence between species. When resources are nutritionally substitutable and spatially mixed, our model predicts that only trade-offs in encounter efficiency can promote coexistence. For spatially separate substitutable resources, any trade-off in encounter, conversion, or handling efficiency allows coexistence. For essential resources, whether mixed or separate, only trade-offs in conversion efficiency can promote coexistence. Since trade-offs that promote coexistence vary depending on the type of resource, this indicates that mechanisms of coexistence can differ depending on how consumers view their resources and how resources are distributed in the environment.

Consumer-resource theory (Fretwell and Lucas 1970; Tilman 1980, 1982; Abrams 1988) has provided a useful conceptual and empirical framework for proposing and testing mechanisms of species coexistence based on exploitation competition. To determine the outcome of competition among consumer species, two relationships need to be considered. The first is the fitness response of consumers to resource consumption (i.e., consumer growth functions), and the second is the consumption traits adopted by these consumers. From the first, zero-net growth isoclines are derived; from the second, consumption vectors (Tilman 1982).

At least three different properties can influence these relationships to alter the outcome of competition: the nutritional quality of the resources (e.g., essential resources, perfectly substitutable resources; Tilman 1982), the distribution of resources in the environment (e.g., co-occurring within patches vs. occurring

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in separate patches), and the foraging traits of adaptive consumers (i.e., consumers that modify consumption in response to the distribution and abundance of resources). These elements of consumer-resource relationships have been used before in various combinations in consumer-resource models (Tilman 1980, 1982; Abrams 1987a, 1987c, 1988), habitat selection models (MacArthur and Pianka 1966; Fretwell and Lucas 1970; Rosenzweig 1981, 1985; Brown 1990), and optimal foraging models (Pulliam 1974; Sih 1984; Stephens and Krebs 1986; Abrams 1987b; Brown 1989).

Although nutritional, spatial, and consumption properties of consumer-resource interactions have been examined in previous work, consumer-resource models of coexistence have focused on the impact of resource nutritional status (e.g., Tilman 1982; Abrams 1987a, 1988) but have not explicitly considered how consumer traits and resource distribution affect competition for resources. Conversely, habitat selection models of coexistence have focused on adaptive behavior (e.g., Rosenzweig 1981, 1985) but have not explicitly considered different resource distributions and nutritional types. We feel that the scope of consumer-resource properties covered by foraging theory, habitat selection theory, and consumer-resource theory can be examined profitably together to understand how consumer traits interact with the distribution and nutritional nature of resources to affect consumer coexistence.

In determining the outcome of competition among consumers, it is generally assumed that each consumer species must face an unavoidable competitive trade-off (e.g., Tilman 1982). That is, a species that is a superior competitor for one resource must be an inferior competitor for another resource. If this is not the case, the analysis of coexistence is trivial since a "superspecies" with no trade-offs will displace all competitors (Tilman 1982). For this reason, we constrained the foraging traits of the consumers in our model such that competence at using one resource is only gained at the expense of competence on other resources. Note that foraging traits consist of behavioral, physiological, and morphological adaptations, and they are not strictly behavioral properties of consumers.

In this article, we consider four scenarios that result from all combinations of resources that are nutritionally substitutable versus essential with resources that co-occur versus occur in separate habitats. These scenarios allow us to determine which trade-offs in foraging traits can promote coexistence via exploitation competition on these resources. By examining foraging traits common to all four scenarios, we are able to bring together models of coexistence that were in largely separate domains. Bringing together these disparate bodies of work will enhance our understanding of how trade-offs can promote coexistence between consumer species and will foster a means of communication between diverse modeling approaches. We show how the nutritional relationship and the spatial arrangement influence whether trade-offs in a given foraging trait can or cannot promote coexistence.

MODELS

We present four related consumer-resource models, using examples that contain two resources and any number of consumers. These models are characterized

by the nutritional and spatial properties of the resources: substitutable-mixed, essential-mixed, substitutable-apart, and essential-apart. Tilman (1982, p. 18) defines substitutable resources as resources that can sustain reproduction when others are lacking and essential resources as resources that are required for growth and are unable to substitute nutritionally for other resources. Thus, with substitutable resources, both resources limit consumer fitness, but with essential resources, consumer fitness is constrained by the most limiting essential resource. These two different models of fitness are further divided into diet selection models and habitat selection models when the two resources are mixed or apart, respectively. Under a diet selection scenario, resources have no patch structure and occur mixed together in such a way as to be encountered at random by a searching forager. The forager does not know the type of resource item until it is encountered, at which time the forager can reject it or handle and consume it. Under a habitat selection scenario, each kind of resource occurs in distinct habitats, and the forager allocates its search and handling time efforts to each distinct patch of resource.

   Common among all four scenarios are the parameters governing resource harvest and utilization: encounter efficiency, handling time, and resource utilization efficiency. We call these resource-garnering traits and assume that consumer species are distinguished by these traits. We assume that consumer species must search for and handle resource items to gain benefit from their utilization. When foods co-occur (mixed), the harvest rate of a consumer can be described by the two-resource extension of Holling's disc equation (Holling 1959), and the consumer has the behavioral choice whether to accept or reject an encountered food item. When foods occur in separate habitats or places, then a one-resource disc equation governs the consumer's harvest while in a given habitat. In this case, the consumer must decide what fraction of time or effort to devote to each habitat (assuming no travel time or travel costs among habitats). We call these behavioral decisions strategies, and we assume that consumers adaptively accept or reject items (when mixed) and adaptively allocate time among habitats (when apart) to maximize fitness. We also assume a trade-off will occur based on the parameters governing harvest and utilization (Kotler and Brown 1988), such that an increase in the ability to acquire or use one resource necessarily results in the loss of some ability on another resource.

   We begin our analysis with a discussion of zero net growth isoclines and consumption vectors used in our models since both of these components provide necessary conditions for coexistence between consumers (Tilman 1982). Following this, we discuss how parameters contained in the zero net growth isoclines and the consumption vectors can affect the outcome of competition for each of our four models. Notation for these models follows Tilman (1980, 1982) for consumer-resource notation and most work on foraging theory (e.g., Stephens and Krebs 1986) for harvest rates and functional responses.

Zero Net Growth Isoclines

   A consumer's zero net growth isocline (ZNGI; Tilman 1980) gives all of the combinations of resource abundances such that a consumer's per capita growth
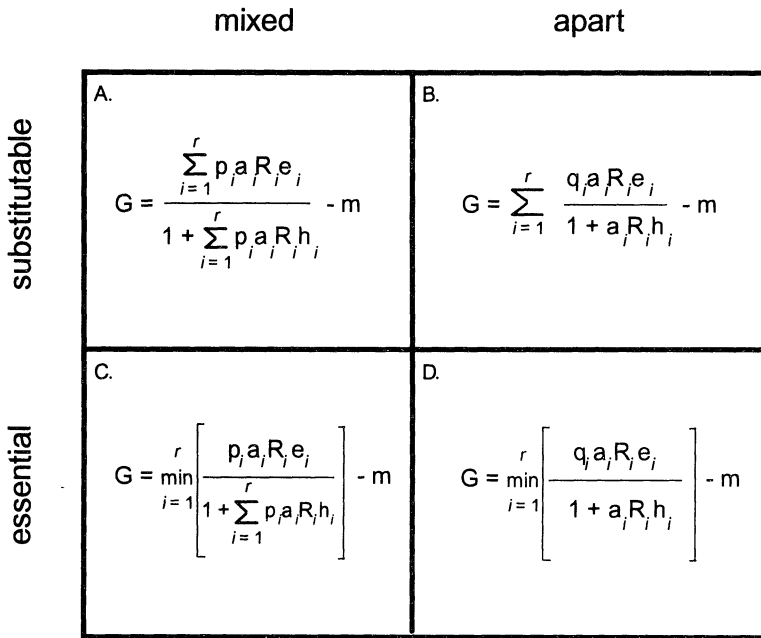
mixed   apart

$$A. \qquad G = \frac{\displaystyle\sum_{i=1}^{r} p_i a_i R_i e_i}{1 + \displaystyle\sum_{i=1}^{r} p_i a_i R_i h_i} - m$$

$$B. \qquad G = \sum_{i=1}^{r} \frac{q_i a_i R_i e_i}{1 + a_i R_i h_i} - m$$

$$C. \qquad G = \min_{i=1}^{r}\left[\frac{p_i a_i R_i e_i}{1 + \displaystyle\sum_{i=1}^{r} p_i a_i R_i h_i} \right] - m$$

$$D. \qquad G = \min_{i=1}^{r}\left[\frac{q_i a_i R_i e_i}{1 + a_i R_i h_i} \right] - m$$

Fig. 1.—Growth or fitness functions for a single consumer population consuming any number of resources. Growth is expressed in the form of Holling's (1959) disc equation for resources, $i = 1, \ldots r$, where we set $r = 2$. Also, G, per capita growth rate; a, encounter efficiency; e, utilization efficiency; R, resource density; h, handling time; m, per capita mortality; p, probability of accepting an encountered resource item; q, proportion of foraging effort in each patch. Here p and q are defined according to rules for adaptive foragers (fig. 2).

rate is zero. In the resource state space, the ZNGI gives the subsistence levels of resources. To determine each consumer's ZNGI, we first consider the consumer's fitness function as it is influenced by its resource-garnering traits (encounter efficiency $[a_i]$, handling time $[h_i]$, and utilization efficiency $[e_i]$) on each of the resources $i = 1, 2$. Next we consider the optimal behavioral strategy of the consumer with respect to accepting or rejecting encountered food items and with respect to allocating effort among habitats. Finally, we use the fitness function of the adaptive consumer to determine the consumer's ZNGI as a function of a_i, h_i, and e_i. In what follows, these steps will be taken for the four scenarios generated by resources occurring mixed or apart and by resources acting as nutritionally essential or substitutable.

Step 1.—The fitness of each consumer is determined as growth minus mortality (fig. 1). Mortality, m, is assumed constant. Fitness is determined by the consumer's harvest rate of resources and the reproductive potential gained from resource consumption (utilization efficiency, e_i). When resources occur mixed, the consumer's harvest rate is given by the multiple-resource Holling's disc equation weighted by the probabilities p_i of accepting encountered resource items. When resources occur apart, the consumer's harvest rate is given by the sum of

mixed   apart

substitutable

A.

For $\dfrac{e_1}{h_1} > \dfrac{e_2}{h_2}$, $p_1 = 1$ and

$p_2 = 1$ if $R_1 < \dfrac{e_2}{a_1(e_1h_2 - e_2h_1)}$

$p_2 = 0$ otherwise.

$G = \dfrac{a_1R_1e_1 + p_2a_2R_2e_2}{1 + a_1R_1h_1 + p_2a_2R_2h_2} - m$

B.

$q_2 = (1 - q_1)$

$q_1 = 1, q_2 = 0$ if: $\dfrac{a_1R_1e_1}{1+a_1R_1h_1} > \dfrac{a_2R_2e_2}{1+a_2R_2h_2}$

$q_1 \mathcal{E} (0, 1)$ if: $\dfrac{a_1R_1e_1}{1+a_1R_1h_1} = \dfrac{a_2R_2e_2}{1+a_2R_2h_2}$

$G = \left[\dfrac{q_1a_1R_1e_1}{1+a_1R_1h_1} + \dfrac{q_2a_2R_2e_2}{1+a_2R_2h_2}\right] - m$

essential

C.

Resource 1 limiting if: $\dfrac{a_2R_2}{a_1R_1} > \dfrac{e_1}{e_2}$

$p_1 = 1, p_2 = \dfrac{a_1R_1e_1}{a_2R_2e_2}$

$G = \dfrac{a_1R_1e_1}{1 + a_1R_1(h_1 + \frac{e_1}{e_2}h_2)} - m$

Resource 2 limiting if: $\dfrac{a_2R_2}{a_1R_1} < \dfrac{e_1}{e_2}$

$p_2 = 1, p_1 = \dfrac{a_2R_2e_2}{a_1R_1e_1}$

$G = \dfrac{a_2R_2e_2}{1 + a_2R_2(h_2 + \frac{e_2}{e_1}h_1)} - m$

D.

$q_2 = (1 - q_1)$ and $0 < q_1 < 1$

$q_1 = $

$\dfrac{a_2R_2e_2(1 + a_1R_1h_1)}{a_1R_1e_1(1+a_2R_2h_2)+a_2R_2e_2(1+a_1R_1h_1)}$

$G = $

$\dfrac{a_1a_2R_1R_2e_1e_2}{a_1R_1e_1(1+a_2R_2h_2)+a_2R_2e_2(1+a_1R_1h_1)}$

$- m$

FIG. 2.—Growth or fitness functions for an adaptive consumer on two resources, showing calculations of p and q. A, Foragers on substitutable-mixed resources follow the zero-one rule (Pulliam 1974); B, on substitutable-apart, an ideal free distribution (Fretwell and Lucas 1970) is formed; on essential resources, whether (C) mixed or (D) apart, adaptive foragers are equally limited by each resource (Tilman 1982, 1988). Variables are defined as in figure 1; subscripts identify resource 1 or 2. See the text for additional explanation.

one-resource disc equations weighted by the allocation of effort q_i among habitats. The reproductive potential gained from resource harvest is then found by weighting the harvest of each resource by its utilization efficiency, e_i. For substitutable resources, fitness equals the sum of fitness gains across all resources. For essential resources, fitness equals the minimum fitness gained across all of the resources.

Step 2.—We incorporate the consumer's foraging behavior by specifying values for the strategies p_i (probability of accepting an encountered resource item) and q_i (allocation of effort among habitats) that maximize the fitness functions given in figure 1. For resources that are mixed and substitutable (fig. 2A), optimal values for p_i will be either one or zero (Pulliam 1974). The more profitable resource will always be consumed ($p_1 = 1$ if $e_1/h_1 > e_2/h_2$), and the less profitable

resource will either be always accepted ($p_2 = 1$) or always rejected ($p_2 = 0$). Utilization of the less profitable resource occurs when the fitness from a mixed diet is greater than the fitness from a specialized diet. This, in turn, depends on whether the abundance of the more profitable resource is below or above a threshold value, $e_2/(a_1[e_1h_1 - e_2h_2])$. For resources that are apart and substitutable (fig. 2B), the consumer should devote all of its foraging effort (q_i) to the habitat that yields the highest reproductive fitness; that is, $q_1 = 1$ and $q_2 = 0$ if habitat 1 offers the higher reward, or $q_1 = 0$ and $q_2 = 1$ if habitat 2 offers the higher reward. If both habitats offer the same reward, then any value of $q_1 = (1 - q_2)$ ≥ 0 is optimal. This results in the ideal free distribution of Fretwell and Lucas (1970).

An adaptive consumer of essential resources should always harvest in a ratio that equalizes the fitness gain from all resources (i.e., all resources are equally limiting; Tilman 1982, 1987; Abrams 1987c). This ratio of harvest of resources 1 and 2 is given by e_1/e_2. This is because the fitness gain on each resource is the product of e_i and the harvest rate (H_i) on that resource where the harvest rate is determined by Holling's disc equation. Thus, for equally limiting resources (e_1H_1 $= e_2H_2$), the harvest ratio is $H_2/H_1 = e_1/e_2$. When essential resources are mixed (fig. 2C), resource 1 is limiting for $a_2R_2/a_1R_1 > e_1/e_2$, where R_i is the density of resource i. In this case, resource 1 is always accepted ($p_1 = 1$), while only a fraction of encountered items of resource 2 are accepted such that the optimal harvest ratio H_2/H_1 is maintained. An opposite situation exists whenever resource 2 is limiting ($a_2R_2/a_1R_1 < e_1/e_2$). When essential resources are apart (fig. 2D), foraging effort must be split among habitat types. Since total foraging effort must be allocated among patch types, $q_2 = 1 - q_1$. This constraint does not alter the fact that the adaptive forager allocates effort among habitats to maintain $q_1H_1/q_2H_2 = e_1/e_2$. Substituting the consumer's behavioral strategy for p_i and q_i into the fitness functions of figure 1 yields the fitness functions for adaptive consumers in figure 2.

Step 3.—The consumer's ZNGI is derived by setting the fitness functions of figure 2 equal to zero and solving for R_2 (or R_1, as applicable). When resources are mixed and substitutable, the ZNGI appears as a straight line with negative slope in the state space of R_1 and R_2 (fig. 3A). For apart and substitutable resources, the ZNGI is formed by the segments inside the intersection of the two components of the fitness function (fig. 3B). For mixed and essential resources, the ZNGI is formed by the segments outside the intersection of the two components of the optimal fitness function (fig. 3C). For apart and essential resources, the ZNGI is a smooth curve concave to the origin (fig. 3D). This curve is hyperbolic and does not intersect the axes.

Consumption Vectors

Consumers remove resources from the environment. This process is modeled by a set of resource equations given in figure 4. (Note that in fig. 4 we introduce superscript $j = 1, \ldots, n$ to denote multiple consumer species. We follow previous work [Vincent and Brown 1987] in denoting consumer species by superscript. We defer further discussion of multiple consumers to the next section.)

mixed   apart

A.

For $p_1 = 1$, $p_2 = 1$

$$R_2 = -\left[\frac{a_1(e_1 - mh_1)}{a_2(e_2 - mh_2)}\right] R_1$$

$$+ \frac{m}{a_2(e_2 - mh_2)}$$

B.

For $R_2 \leq \dfrac{m}{a_2(e_2 - mh_2)}$

$$R_1 = \frac{m}{a_1(e_1 - mh_1)}$$

For $R_1 \leq \dfrac{m}{a_1(e_1 - mh_1)}$

$$R_2 = \frac{m}{a_2(e_2 - mh_2)}$$

C.

For R_1 limiting:

$$R_1 = \frac{m}{a_1 e_1 - a_1 m(h_1 + \frac{e_1}{e_2} h_2)}$$

For R_2 limiting:

$$R_2 = \frac{m}{a_2 e_2 - a_2 m(h_2 + \frac{e_1}{e_2} h_1)}$$

D.

$$R_2 =$$

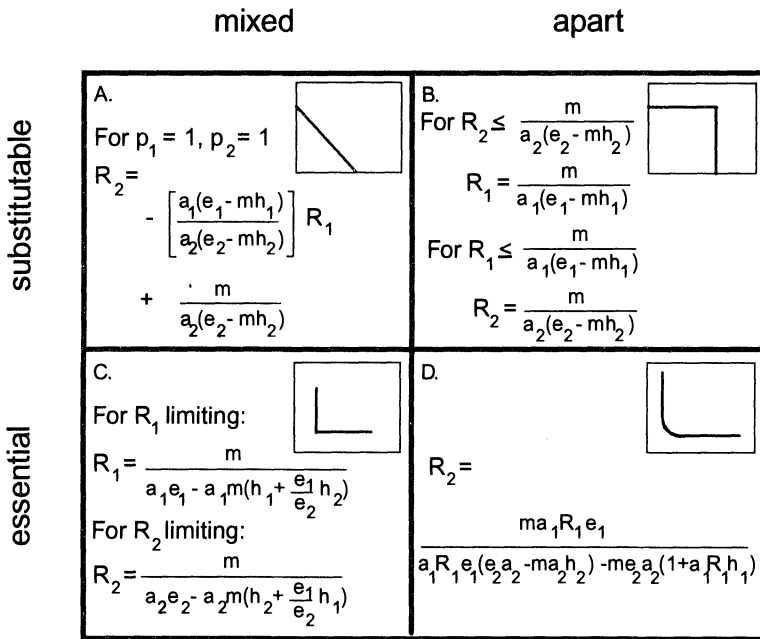$$\frac{m a_1 R_1 e_1}{a_1 R_1 e_1 (e_2 a_2 - ma_2 h_2) - me_2 a_2 (1 + a_1 R_1 h_1)}$$

Fig. 3.—Zero net growth isoclines calculated from the growth functions of optimal consumers on two resources given in figure 2. When resources are (A) mixed, $p_1 = p_2 = 1$ and when they are (B) apart, $q_1 \in (0, 1)$ at equilibria. For essential resources, whether (C) mixed or (D) apart, optimal foragers are equally limited by each resource (fig. 2). Variables are defined as in figure 1; subscripts indicate resource 1 or 2.

Resource supply is calculated by a density-dependent "chemostat" model in which the rate at which resources become available is proportional to the total amount of resource that could exist in the absence of consumers ($\hat{R}_i$) minus the amount of resource currently available for consumption (R_i). The total amounts of all resources that could exist in the absence of all consumers defines the resource supply point. Resource depletion is based on a modified disc equation such that depletion is a function of harvest rate and is thus determined by encounter efficiency a_i, handling time h_i, and adaptive behavior p_i or q_i, but not utilization efficiency e_i, which figures only in consumer fitness.

   Consider the resource dynamics generated by a single consumer species. For an equilibrium consumer population to exist, resource renewal must equal resource consumption (i.e., resources must be at equilibrium). This occurs at the point on the consumer's ZNGI where the vector of resources consumed equals the vector of resources supplied (Tilman 1982, p. 69). For two resources, the slope of the consumption vector equals the ratio of consumption of resource 2 divided by the consumption of resource 1 (Tilman 1982, p. 77).

   Mixed-substitutable resources.—The slope of the consumption vector of a single consumer for this scenario at equilibrium can be determined by setting the growth rates of resources 1 and 2 equal to zero (using the equation in fig. 4A)

mixed   apart

substitutable

A.

$$\dot{R}_i = g(\hat{R}_i - R_i)$$

$$- \sum_{j=1}^{n} N^j \frac{p_i^j a_i^j R_i}{1 + \sum_{i=1}^{r} p_i^j a_i^j R_i h_i^j}$$

B.

$$\dot{R}_i = g(\hat{R}_i - R_i)$$

$$- \sum_{j=1}^{n} N^j \frac{q_i^j a_i^j R_i}{1 + a_i^j R_i h_i^j}$$

essential

C.

$$\dot{R}_i = g(\hat{R}_i - R_i)$$

$$- \sum_{j=1}^{n} N^j \frac{p_i^j a_i^j R_i}{1 + \sum_{i=1}^{r} p_i^j a_i^j R_i h_i^j}$$

D.

$$\dot{R}_i = g(\hat{R}_i - R_i)$$

$$- \sum_{j=1}^{n} N^j \frac{q_i^j a_i^j R_i}{1 + a_i^j R_i h_i^j}$$

FIG. 4.—Resource dynamic equations. Each resource is replenished according to a resource renewal function, g, and depleted by each consumer species j according to consumer growth functions (cf. fig. 1). Note that we follow previous work (Vincent and Brown 1987) for superscript notation. Here $\dot{R}$ denotes change in resource density per unit time; $\hat{R}$ represents the resource supply point (Tilman 1982); N is the consumer population size; n is the number of consumer species. Other variables are defined in figure 1.

and solving for N^* (the equilibrium population size of the consumer). The two expressions for N^* are set equal to each other and solved for the ratio of supply of resource 2 over the supply of resource 1 (fig. 5A). The right-hand side of the equation now gives the slope of the consumption vector at equilibrium. Note that at equilibrium, the value of p_i is always equal to one (mixed diet). This is because each resource type must be able to sustain a consumer population at equilibrium; otherwise, we cannot consider it a resource. For example, given that resource 1 is the most profitable (i.e., $e_1/h_1 > e_2/h_2$), resource 2 will not be taken ($p_i = 0$) only if the gain from resource 1 is greater than the gain from both resources. That is, e_2/h_2 must be less than m at equilibrium. However, this means that resource 2 cannot support population growth and thus cannot be considered a resource at equilibrium. If resource 2 can support some population growth (i.e., the gain from both resources is greater than the gain from resource 1), it will always be included in the diet at equilibrium. Thus, both resources are always taken upon encounter ($p_1 = p_2 = 1$) at any equilibrium. The slope of the consumption vector with values of $p_i = 1$ is given in figure 5A.

Apart-substitutable resources.—When foods occur in separate habitats and habitat selection is cost free, a population of consumers should allocate effort so

FIG. 5.—Equilibrium conditions showing the ratio of resource supply as equal to the ratio of resource consumption. For a single consumer j, the ratio of consumption is the slope of the consumption vector (m_{cj}) on two resources. Note that for (B) substitutable-apart resources, the slope of the optimal consumption vector is zero, infinity, or follows the ideal free distribution (IFD). Slopes of consumption vectors were obtained by substituting the expression for the optimal ps or qs (fig. 2) into the resource equation at equilibrium and simplifying.

as to equalize the fitness rewards between habitats. Under equilibrium conditions, the consumption vector will have a slope defined by an ideal free distribution (the reward rate in habitat 1 equals that of habitat 2), or it will have a slope of zero or infinity depending on the location of the resource supply point (Tilman 1982, p. 70). This can be derived by setting the growth rates of resources 1 and 2 equal to zero (using the equation in fig. 4B) and following the procedure as given in mixed-substitutable resources. Substituting q_i (fig. 2B) into the equations gives a consumption vector with a slope of zero, infinity, or equal reward rates (fig. 5B).

  Essential resources, apart or mixed.—An adaptive consumer on essential resources will always consume the two resources in the appropriate ratio of e_1/e_2 items of resource 2 per item of resource 1. This holds whether resources occur mixed or apart. The consumption vector at equilibrium can be found by setting the resource growth equations equal to zero and setting the rate of resource supply equal to the rate of consumption. Dividing the expression for resource 2 by the expression for resource 1 gives the slope of the consumption vector (fig. 5C, D). Substituting the consumer's behavioral strategy, p_i or q_i (fig. 2C, D), into these equations gives e_1/e_2 for the slope of the consumption vector.
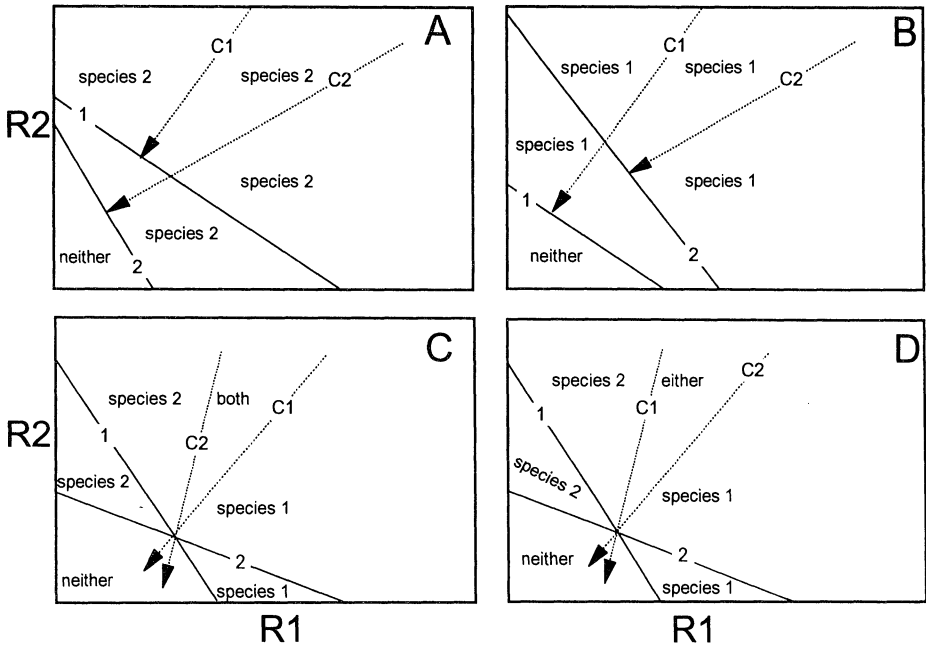
FIG. 6.—A graphic presentation of a consumer resource model for two consumers and two substitutable-mixed resources (modified from Tilman 1980). Species and their ZNGIs are numbered 1 or 2; vectors of consumption for each species are indicated as C_1 or C_2. In the region outside the ZNGIs, either species can survive in the absence of the other. Regions where the location of a particular resource supply point leads to the survival of species 1, species 2, both, or one or the other (either) at equilibrium are indicated. Inside the ZNGIs, only the indicated species can survive at equilibrium, or neither species can survive. The outcome of competition depends on two conditions. First, the ZNGIs must cross to provide an equilibrium point where both species coexist. This condition is not met in A, where species 2 can draw resource levels below the ZNGI of species 1, or in B, where the reverse is true. Second, the consumption vectors (C_1, C_2) must be sloped so as to delimit a region of coexistence (see text for details). This condition is met in C, creating a region where both species 1 and species 2 coexist, but it is not met in D where the intersection of the ZNGIs defines the only point of coexistence. This coexistence point is unstable. Initial conditions in the region labeled *either* determine the outcome of competition for this case.

MECHANISMS OF COEXISTENCE: THE OUTCOME OF COMPETITION BETWEEN CONSUMERS

When two species compete for the same resources, four distinct equilibrium scenarios are possible (Tilman 1982, p. 73). Properties of the ZNGIs and the consumption vectors for consumers determine both the conditions for coexistence and the regions in resource space where coexistence is the equilibrium outcome of competition (Tilman 1980, 1982). Figure 6 depicts the regions in resource state space where the location of the resource supply point leads to either the existence of two, one, or neither species at equilibrium. In two cases, only one species exists at equilibrium because it is able to deplete the resources below

the other species' ZNGI (fig. 6A, B). Thus, the first condition for coexistence is that all potentially coexisting species' ZNGIs must cross at one point (cf. fig. 6A, B with 6C, D). In the other two cases, the slope of each species' consumption vector at equilibrium relative to the other species' becomes important in determining whether the equilibrium point is stable or unstable (contrast fig. 6C with 6D). Thus, given that the ZNGIs cross, the second condition for coexistence is that the resource supply point must lie within a region defined by the slopes of the consumption vectors at equilibrium. For coexistence to be stable, appropriate conditions must be met. Tilman (1982, p. 77) stated these conditions as "each species consumes more of the resource that more limits its own growth." Mathematical stability analysis in Tilman (1980) defines this relationship between the consumption vectors of competing species. From this, we derive conditions for coexistence in each nutritional scenario presented in the following sections.

If a resource-garnering trait (encounter efficiency, handling time, or conversion efficiency) is included in the ZNGI equations (fig. 3), then trade-offs in this trait necessarily affect the shape of the ZNGI and thus can affect whether ZNGIs cross at an equilibrium point. Given that an equilibrium point exists, if a resource-garnering trait can change the slope of the consumption vector (fig. 5), then trade-offs in this trait can affect coexistence between species. Likewise, if a resource-garnering trait is not included in these equations, trade-offs in this trait cannot affect the outcome of competition.

Mixed-Substitutable

The ZNGI for this case is a function of each of the three foraging traits (a, e, and h; fig. 3A). Thus, the ZNGIs can be made to cross by trade-offs in any foraging trait, and therefore no trait by itself can limit conditions for coexistence. This leaves only the slopes of the consumption vectors for consideration.

For mixed-substitutable resources, the only resource-garnering trait that influences the slope of the consumption vector is encounter efficiency a_i (fig. 5A). Although the slope is a function of the behavioral strategies p_i, equilibria can only occur in regions of resource space where $p_1 = p_2 = 1$ since each resource type must remain profitable for each consumer type at equilibrium. Since neither conversion efficiency nor handling time can affect the slope of the consumption vector, a trade-off in e_i or h_i is not sufficient to allow coexistence. At least a trade-off in a_i is required for coexistence since a_i can influence both ZNGIs and the slope of the consumption vectors.

As shown in figure 6, a trait that affects the consumption vectors may affect the stability of coexistence. Under what circumstances will trade-offs in encounter efficiency result in a zone of attraction to a stable coexistence point? By convention, we ranked species according to the slope of their ZNGIs, designating the species with the most negatively sloped ZNGI species 1 (fig. 7A). Given that an equilibrium point exists, for there to be a region of attraction to the two-species equilibrium point, the slope of the consumption vector of species 1 must be less (less positively sloped) than that for species 2 (fig. 7A). These conditions result in a region of coexistence and meet the requirements expressed by Tilman (1980,

1982). The naming convention thus gives the inequality

$$m_{ZNGI}^1 < m_{ZNGI}^2,$$

where m_{ZNGI}^j indicates the slope of the ZNGI of consumer j. (Equations for the ZNGIs are given in slope-intercept form in fig. 3.) From figure 5A, we derive the inequality necessary to meet the restriction on slopes of the consumption vectors:

$$\frac{a_2^1}{a_1^1} < \frac{a_2^2}{a_1^2}. \tag{1}$$

Trade-offs in encounter efficiency that satisfy this inequality will also satisfy $m_{ZNGI}^1 < m_{ZNGI}^2$, when trade-offs in other traits are not present (i.e., when $e_i^1 = e_i^2$ and $h_i^1 = h_i^2$). No trade-offs in e_i or h_i will satisfy inequality (1). Thus, for substitutable and mixed resources, only trade-offs in the encounter efficiencies that satisfy inequality (1) provide a mechanism of coexistence. Note that when consumers have a shared ability for encountering a particular resource (e.g., when $a_1^1 > a_2^1$ and $a_1^2 > a_2^2$), coexistence is possible, but the maximum size of the region where resource supply points can produce coexistence is reduced because each consumer species' ratio of consumption lies on the same side of a 45° line. Where consumers have distinct abilities for encountering a particular resource (e.g., when $a_1^1 > a_2^1$ and $a_1^2 < a_2^2$), the maximum size of the region where resource supply points can produce coexistence is much expanded since the two ratios of consumption lie on opposite sides of a 45° line.

Apart-Substitutable

This case contrasts sharply with all other cases because conditions for coexistence are determined only by whether and where the ZNGIs cross and not by the slopes of the consumption vectors (fig. 7B). Regions of resource space are divided into sections where the slopes of the consumption vectors are zero, infinity, or follow the ideal free distribution. In the region surrounding the equilibrium point, each species is a specialist on a different resources and thus does not compete with the other species. Only when both species are located directly on the equilibrium point will adaptive foragers use both resources. This point is stable under all conditions since small perturbations off it make each species a specialist that drives the system back to the equilibrium point. This means that the region of resource space where the location of a supply point leads to coexistence is not defined by the slopes of the consumption vectors. Therefore, the only limitation on coexistence is that the ZNGIs must cross. From figure 3 we see that the ZNGI can be influenced by trade-offs in any of the three traits, a_i, e_i, or h_i.

We now examine conditions in which trade-offs in a_i, e_i, and h_i lead to a region of coexistence. First, we ranked species according to the level to which each could profitably deplete resource 1 (this level is denoted by R_1^{j*}; Tilman 1982; figs. 3B, 7B) and designated the species with the highest R_1^* as species 1. Thus,

$$a_1^1(e_1^1 - mh_1^1) < a_1^2(e_1^2 - mh_1^2)$$

and (2)

$$a_2^1(e_2^1 - mh_2^1) > a_2^2(e_2^2 - mh_2^2)$$

give the conditions for coexistence. When resources are apart and substitutable, trade-offs in encounter efficiencies, handling times, and utilization efficiencies can all provide a mechanism of coexistence.

Mixed-Essential

As for the substitutable cases, the ZNGIs for consumers of essential-mixed resources contain all three foraging traits a_i, e_i, and h_i (fig. 3C). Figure 5C shows the slope of the consumption vector, in which only conversion efficiencies e_i appear.

To examine coexistence on essential resources, we again ranked species according to the level to which each could profitably deplete resource 1 (R_1^{j*}; Tilman 1982) and designated the species with the highest R_1^* as species 1 (fig. 7C). Given that an equilibrium point exists, this convention results in the inequality

$$R_1^{1*} > R_1^{2*}$$

or (3)

$$a_1^1\left[e_1^1 - m\left(h_1^1 + \frac{e_1^1}{e_2^1}h_2^1\right)\right] < a_1^2\left[e_1^2 - m\left(h_1^2 + \frac{e_1^2}{e_2^2}h_2^2\right)\right]$$

(the ZNGI when resource 1 is limiting indicates R_1^{j*}; fig. 3C). As expressed in Tilman (1980, 1982), conditions for coexistence are that, given that the ZNGIs cross, the species with the higher R_1^* must also have a shallower slope for the consumption vector. Following our naming this convention, this requires

$$\frac{e_1^1}{e_2^1} < \frac{e_1^2}{e_2^2}.$$ (4)

Fig. 7.—Consumer-resource competition for four scenarios differentiated by the nutritional and spatial properties of the resource. Solid lines labeled *1* and *2* are ZNGIs for species 1 and 2, respectively. Resources in *A* are perfectly substitutable and spatially mixed. Dotted lines labeled C_1 and C_2 show the slopes of the consumption vectors (of species 1 and species 2, respectively) at equilibrium and delimit regions of coexistence. The dashed line to the right indicates the boundary below which resource 2 should be harvested by a rate-maximizing forager according to the zero-one rule (fig. 2). Resources in *B* are perfectly substitutable but spatially separate. Dotted lines labeled *1* and *2* divide resource space into different behavioral regions. Arrows labeled 0_1, ∞_1, and IFD_1 indicate slopes of consumption vectors for species 1, and those with subscript 2 indicate slopes of consumption vectors for species 2, where IFD is the ideal free distribution (fig. 5). The outcome of competition is indicated for each region. Resources in *C* are nutritionally essential and spatially mixed, while those in *D* are essential but separate. For both scenarios, dotted lines labeled C_1 and C_2 show the slopes of consumption vectors (for species 1 and species 2, respectively) at equilibrium and delimit regions of coexistence.

Unlike substitutable-mixed resources, this inequality does not automatically sat-isfy inequality (3) when trade-offs in other traits are not present (i.e., when $a_i^1 = a_i^2$ and $h_i^1 = h_i^2$). Nonetheless, it is clear that only a trade-off in utilization efficiency can satisfy equation (4). Conditions that satisfy both equations (3) and (4) may be relatively restricted. One condition that may be more likely to satisfy both equations (3) and (4) is if species 1 were less efficient at utilizing resource 1 than species 2 ($e_1^1 < e_1^2$).

Apart-Essential

Like the other three scenarios, the ZNGI specified in figure 3D contains all three foraging traits. Figure 5D shows the slope of the consumption vector. As for the essential-mixed case, consumers of essential-apart resources have con-sumption vector slopes that depend only on conversion efficiency e_i.

Given that an equilibrium point exists, conditions for coexistence require that the species with the higher R_1^* (species 1) must also have a shallower consumption vector (Tilman 1980, 1982; fig. 7D). That is,

$$R_1^{1*} > R_1^{2*}, \tag{5}$$

and, for coexistence to be stable,

$$\frac{e_1^1}{e_2^1} < \frac{e_1^2}{e_2^2}. \tag{6}$$

Coexistence will result when inequalities (5) and (6) are both met. Inequality (6) will clearly be met only when the appropriate trade-off in utilization efficiency exists. As for essential-mixed resources, meeting inequality (6) does not guaran-tee that inequality (5) is satisfied. While a trade-off in e_i must exist for coexistence to occur at equilibrium on essential-apart resources, this trade-off can only result in coexistence when other aspects of the resource-garnering traits satisfy inequal-ity (5). Conditions for coexistence when resources are essential are thus restric-tive relative to substitutable resource scenarios.

DISCUSSION

We include essential features of optimal foraging and habitat selection models in a consumer-resource framework, which allows us to analyze how trade-offs in foraging traits (which depend on resource distribution and nutritional type) act as potential mechanisms of coexistence. There are a number of conditions for which an organism might face foraging trade-offs, either behavioral or evolution-ary, in encounter efficiency, handling time, or conversion efficiency. For exam-ple, killer whales feeding on marine mammals hunt silently (Morton 1990; Saulitis 1993) as marine mammal prey often will leave the water if they realize killer whales are in the vicinity (e.g., harbor seal [Stacey and Baird 1989]; leopard seal [Smith et al. 1981]). However, when feeding on fish, killer whales echolocate frequently (Morton 1990; Barrett-Lennard 1992). Hence, encounter efficiencies with each resource decline when hunting the other. In this case, selection on

resource-garnering traits may have resulted in the evolution of distinct and non-competing subspecies (i.e., resident and transient killer whales [Baird et al. 1992]). Bluegills and bass face a trade-off in handling efficiency (Werner 1984). Bluegills are more efficient at handling small prey items than large prey items because of their small, protrusible mouths, while bass are more efficient at handling large prey than small prey because of their large mouths. Conversion efficiency trade-offs may be evident in impala and African buffalo. Larger rumen and lower metabolism in buffalo allow the more efficient digestion of low-quality forage (Jarman and Sinclair 1979), while smaller rumen in impala may allow for more efficient digestion of protein from fruits and seeds.

Given such trade-offs, two conditions must be satisfied for stable, two-species coexistence to occur in consumer-resource models described by Tilman (1980, 1982). The first condition is that the ZNGIs of all potentially coexisting species must cross. For all nutritional/distribution cases that we discuss, the ZNGIs (fig. 3) are functions of each foraging trait (a, e, or h), as well as functions of the adaptive behavioral strategy for allocation of foraging effort (p or q). Thus, any trade-off in encounter efficiency, handling time, or utilization efficiency has the potential to alter the position of consumer ZNGIs and allow them to cross, thereby creating an equilibrium point (coexistence). But, with the exception of apart-substitutable resources, this is not sufficient. The slopes of the consumption vectors are determined by resource-garnering traits (for a discussion of how adaptive foraging can alter consumption rates, see Abrams 1987b) and also affect regions of coexistence in resource state space. The impact of different resource-garnering traits on the slopes of the consumption vectors differs depending on the nutritional and spatial status of the resources.

Thus, consumers of substitutable resources are expected to have different mechanisms of coexistence than consumers of essential resources. This is likewise true for consumers of mixed versus spatially separate resources. Coexistence on substitutable-mixed resources requires at least an appropriate trade-off in encounter efficiencies. For substitutable-apart resources, since only the ZNGIs affect coexistence between species and all resource-garnering traits are included in the ZNGIs, trade-offs in any trait (a, e, and h) might lead to coexistence between species. Coexistence on essential resources requires at least an appropriate trade-off in utilization efficiencies.

We simplified our analysis by assuming that mortality is constant across foraging activities (i.e., mortality risk is the same while searching and handling, and it is the same for each resource). However, when activities or resources vary in risk, safety acts as a complementary resource to food, which will alter the decision rule of when to be selective or opportunistic and which can shift diet or habitat preferences (Brown et al. 1988; Lima and Dill 1990). An article focusing on the resource utilization trade-offs that promote coexistence when resources are complementary remains to be written. However, regions of coexistence when risk varies will be influenced by the resource utilization traits (a, e, or h) retained in calculating the mortality, m.

We also assumed no travel costs to moving between habitat patches existed. Travel time is not relevant when resources are mixed. When resources are sepa-

rate, travel time adds a cost to moving between resource patches, which makes foragers reluctant to switch habitats. For nondepletable patches of substitutable resources, any allocation of effort among patches is optimal at equilibrium, and hence there will be no effect of adding travel costs to the model. When resources are essential, selection would presumably favor a forager that had to move between patches as little as possible. While analyses of this case would require additional assumptions, it seems likely that the need to switch habitats will be tied to resource storage ability, which might be considered a component of resource utilization efficiency, e. As utilization efficiency is already the single trade-off necessary for coexistence in this case, the addition of travel time seems unlikely to alter our conclusions.

Can our prediction that mechanisms of coexistence differ among nutritional and spatial resource types shed light on the structure of "real" consumer communities? We found that for consumers of substitutable resources, the spatial distribution of resources influences which resource-garnering traits can affect coexistence. When substitutable resources are mixed, resources can only be partitioned among species with different encounter efficiencies. When substitutable resources occur in different habitats, then resources can be partitioned among species with different encounter efficiencies, conversion efficiencies, or different handling times. For example, desert rodents are consumers of nutritionally substitutable resources such as seeds. Mechanisms of coexistence have been studied extensively for many desert rodent communities (Rosenzweig 1977; Brown 1989; Abramsky et al. 1990; and many others). One of the interesting puzzles yet to be resolved is why the species richness of desert rodents (and indeed many other organisms) has a decreasing phase with increasing productivity (Rosenzweig and Abramsky 1993). One explanation is that habitat heterogeneity declines as productivity increases and that habitat heterogeneity allows resources to be partitioned among more species (Owen 1988; Rosenzweig and Abramsky 1993). However, a more specific mechanism of coexistence may be posited from our analysis. At low productivity, desert rodent resources (plants, seeds) may be more likely to occur in separate patches. As productivity increases, plants grow closer together and resources become more mixed. If this is true, then this analysis predicts that at low productivity (resources separate), trade-offs in encounter efficiency, handling time, or conversion efficiency could promote coexistence between species. At high productivity (resources mixed), only trade-offs in encounter efficiencies could promote coexistence. With fewer available dimensions or "niches" for coexistence, fewer species are expected to coexist (Hutchinson 1957; Abrams 1983).

For competing species on apart-substitutable resources, opportunities for coexistence will exist if specialized morphologies result in trade-offs in encounter efficiency, handling time, or utilization efficiency. For example, locomotor and sensory morphology may impose trade-offs in resource encounter efficiency, feeding morphology may affect resource handling and ingestion, and physiology may affect conversion efficiency (Emerson et al. 1994). However, the same cannot be said for species that compete for mixed-substitutable resources. In this case, we expect a mechanism of coexistence based on just locomotor and sensory

morphology, including such things as body size. This may explain why phylogenetic guilds of predators show variation in body size as well as diet partitioning as a mechanism of coexistence (e.g., felids and canids [Rosenzweig 1966]) rather than variation in feeding morphology (handling trait) or physiology (conversion efficiency trait).

Equations for growth on essential resources are often used to model plant competition, since plants require such essential nutrients as light, nitrogen, phosphorous, and so forth (Tilman 1980, 1982, 1988; Reynolds and Pacala 1993). The resource-garnering traits, a, h, and e, that we use to describe how consumers acquire and use resources can be applied to plants as well as animals since all consumers face limits in encountering resources (a), processing resources (h), and converting those resources to new biomass (e). Plants solve these problems differently than animals. Search and capture efficiency can be affected by morphological and physiological structures of roots and shoots. Handling time is time spent handling one resource during which uptake of the next resource item cannot take place (e.g., competition for uptake sites on roots). Conversion efficiency is the efficiency with which the physiological process of converting a particular resource into new biomass is carried out.

From our models we concluded that for both mixed and separate resources, trade-offs in the efficiency with which resources can be converted to new biomass are required to allow coexistence. Work by Tilman (1988, chap. 4) supports this conclusion. He modeled a system with two essential resources (light, nitrogen) and six consumer species that differed only in allocation to root, leaves, and stems but not to respiration and other parameters such as reproduction. Tilman found that allocation differences among these species did not lead to stable coexistence between pairs of species. Reynolds and Pacala (1993) found this to be true with their analytical version of the same problem. Tilman (1988, chap. 4) explains that these species cannot coexist because each consumes more of the resource that did not limit it at equilibrium, and he suggests that other factors such as trade-offs in tissue nutrient levels might encourage stable coexistence between plants. Here, we point out that only trade-offs in conversion efficiency can affect coexistence. Allocation to roots, leaves, and stems does not affect the efficiency of converting a resource into new biomass, although physiological traits such as tissue nutrient levels may (Chapin 1980; Vitousek 1982; Field and Mooney 1986).

We note that plants, consumers of essential resources, also show a similar diversity-productivity pattern to desert rodents in which there is a decreasing phase of species richness with increasing productivity (e.g., Rosenzweig and Abramsky 1993; Tilman and Pacala 1993). We have concluded that for consumers of essential resources, only trade-offs in utilization efficiency can affect coexistence between species regardless of whether resources occur together or in separate patches. Thus, decreasing resource patchiness with increasing productivity cannot explain the loss of diversity. However, Tilman and Pacala (1993) suggest that light limitation is unavoidable to plants in highly productive habitats. Light limitation offers a number of ways in which species richness could be restricted that are not considered by our models of competition for two resources (e.g.,

reduced heterogeneity in resource supply rates, reduced number of plants per unit area [Tilman and Pacala 1993]; litter-germination interactions [Tilman 1993]).

By creating a set of related models that deal with the spatial and nutritional aspects of resources, we found that mechanisms of coexistence may not be universal for consumers of different kinds of resources. These models suggest that plants (as consumers of essential resources) have fewer options for coexistence based on resource use than animals (as consumers of substitutable resources). Therefore, mechanisms that promote coexistence via resources in plants may be less likely than mechanisms that promote coexistence via other life-history aspects (e.g., resistance to herbivory, stress or disturbance, dispersal abilities, etc.). For animals, consumers of mixed-substitutable resources have fewer options for coexistence than consumers of apart-substitutable resources, especially if there are no sharp trade-offs in encounter efficiency. Thus, assumptions about the nature of how resources are consumed can influence our conclusions about the nature of coexistence between species. Testing these assumptions and predictions may be an enlightening avenue of research, and we hope that our conclusions here will help integrate results from the diverse array of coexistence studies.

LITERATURE CITED

Abrams, P. A. 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics 14:359–376.

———. 1987a. Alternative models of character displacement and niche shift. I. Adaptive shifts in resource use when there is competition for nutritionally nonsubstitutable resources. Evolution 41:651–661.

———. 1987b. The functional responses of adaptive consumers of two resources. Theoretical Population Biology 33:262–288.

———. 1987c. The nonlinearity of competitive effects in models of competition for essential resources. Theoretical Population Biology 32:50–65.

———. 1988. Resource productivity-consumer species diversity: simple models of competition in spatially heterogeneous environments. Ecology 69:1418–1433.

Abramsky, Z. N., M. L. Rosenzweig, B. Pinshow, J. S. Brown, B. Kotler, and W. A. Mitchell. 1990. Habitat selection: an experimental field test with two gerbil species. Ecology 71:2358–2369.

Baird, R. W., P. A. Abrams, and L. M. Dill. 1992. Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*. Oecologia (Berlin) 89:125–132.

Barrett-Lennard, L. 1992. Echolocation in wild killer whales (*Orcinus orca*). Master's thesis. University of British Colombia, Vancouver, B.C.

Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1–20.

———. 1990. Habitat selection as an evolutionary game. Evolution 44:732–746.

Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia (Berlin) 76:408–415.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233–260.

Emerson, S. B., H. W. Greene, and E. L. Charnov. 1994. Allometric aspects of predator-prey interactions. Pages 123–139 in P. C. Wainwright and S. M. Reilly, eds. Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago.

Field, C. B., and H. A. Mooney. 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25–55 in T. J. Givnish, ed. On the economy of plant form and function. Cambridge University Press, Cambridge.

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 41:385–398.

Hutchinson, G. E. 1957. Concluding remarks: population studies: animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427.

Jarman, P. J., and A. R. E. Sinclair. 1979. Feeding strategy and the pattern of resource-partitioning in ungulates. Pages 130–163 in A. R. E. Sinclair and M. Norton-Griffiths, eds. Serengeti: dynamics of an ecosystem. University of Chicago Press, Chicago.

Kotler, B. P., and J. S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics. 19:281–307.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603–609.

Morton, A. B. 1990. A quantitative comparison of the behavior of resident and transient forms of the killer whale off the central British Columbia coast. Report of the International Whaling Commission, Special Issue 12:245–248.

Owen, J. G. 1988. On productivity as a predictor of rodent and carnivore diversity. Ecology 69:1161–1165.

Pulliam, H. R. 1974. On the theory of optimal diets. American Naturalist 108:59–75.

Reynolds, H. L., and S. W. Pacala. 1993. An analytical treatment of root-to-shoot ratio and plant competition for soil nutrient and light. American Naturalist 141:51–70.

Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. Journal of Mammalogy 47:602–612.

———. 1977. Coexistence and diversity in heteromyid rodents. Pages 89–99 in B. Stonehouse and C. Perrins, eds. Evolutionary ecology. Macmillan, London.

———. 1981. A theory of habitat selection. Ecology 62:327–335.

———. 1985. Some theoretical aspects of habitat selection. Pages 517–540 in M. L. Cody, ed. Habitat selection in birds. Academic Press, New York.

Rosenzweig M. L., and Z. Abramsky. 1993. How are diversity and productivity related? Pages 52–65 in R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago.

Saulitis, E. L. 1993. The vocalizations and behavior of the "AT"-group of killer whales (Orcinus orca) in Prince William Sound, Alaska. Master's thesis. University of Alaska, Fairbanks.

Sih, A. 1984. Optimal behavior and density-dependant predation. American Naturalist 123:314–326.

Smith, T. G., D. B. Siniff, R. Reichle, and S. Stone. 1981. Coordinated behavior of killer whales, Orcinus orca, hunting a crabeater seal, Lobodon carcinophagus. Canadian Journal of Zoology 59:1185–1189.

Stacey, P. J., and R. W. Baird. 1989. Harbour seal reaction to killer whales. Victoria Naturalist 45:16–17.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Monographs in behavior and ecology, ed. J. R. Krebs and T. Clutton-Brock. Princeton University Press, Princeton, N.J.

Tilman, D. 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. Further thoughts on competition for essential resources. Theoretical Population Biology 32:442–446.

————. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.

————. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? Ecology 74:2179–2191.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago.

Vincent, T. L., and J. S. Brown. 1987. Evolution under non-equilibrium dynamics. Mathematical Modelling 8:766–771.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. American Naturalist 119:553–572.

Werner, E. E. 1984. The mechanisms of species interactions and community organization in fish. Pages 360–382 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, eds. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, N.J.

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