

## Consumer Functional Response and Competition in Consumer-Resource Systems

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This study investigates the effect of the functional response of resource consumers on the relationship between resource overlap and competition for some two-consumer, two-resource models. Two measures of competition are examined:  $\alpha$ , the competition coefficient, and  $\beta$ , an index of the ease of invasion by the second consumer species when the first is at its carrying capacity. A comparison of systems with linear (type-1) and decelerating (type-2) functional responses shows that: (1) Competition coefficients are functions of the population densities of consumers or resources in systems with type-2 responses. (2) Competition coefficients may differ substantially in magnitude between systems with type-1 and type-2 functional responses. (3) The relative handling time of different resources is important in determining the relationship between overlap and competition. Positive correlations between capture rates (per unit resource) and handling times cause the system with type-2 functional responses to exhibit a higher level of competition for a given level of overlap than for the case of negative correlation. (4) If the functional response is type-2 it may be possible to obtain a priority effect in which either consumer species can exclude the other. (5) Invasion may be easier in a system with type-1 functional responses than in a similar system with type-2 functional responses, even when competition coefficients are larger in the former. Accelerating functional responses also affect the relationship between overlap and competition, but realistic models of such responses are likely to be very complex. Several currently accepted ideas in competition theory depend upon the assumption of a linear functional response, and are unlikely to be generally valid.

### I. INTRODUCTION

The relationship between overlap in resource utilization and interspecific competition is a topic of relevance to both theoretical (MacArthur, 1972; May, 1973; Abrams, 1975) and empirical (e.g., Cody, 1974; Pianka, 1974) studies in population ecology. The justification usually given for the many studies of resource partitioning (see partial list in Schoener, 1974a) is that they are relevant to understanding competition. To draw conclusions about competition from data on overlap, however, it is necessary to know the relationship between

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overlap and competition. This function is believed to be increasing, but to derive an exact relationship, it is necessary to have a model of how consumers and resources interact. The consumer-resource model which has been most widely discussed in the literature (Schoener, 1974a, b; Lawlor and Maynard Smith, 1976; Holt, 1977) is one proposed by MacArthur (1968, 1970, 1972). In his model, resource consumers compete by their common exploitation of logistically renewing resources. Among the assumptions of this model is the provision that the functional response of resource consumers to resource densities is linear (i.e., a plot of the resource consumption rate of a consumer individual vs the amount of resource available for consumption is linear). This assumption seems particularly restrictive considering current understanding of functional responses. Because all organisms have a finite capacity to process resources, the functional response must decrease if resource densities become sufficiently high. This is a type-2 or decelerating functional response (Holling, 1965). The functional response can also be accelerating over at least a certain range of resource densities. Therefore, the assumption of linearity is at best a reasonable approximation for a limited range of resource densities.

The purpose of this study is to present a preliminary analysis of how the functional response of resource consumers can change the relationship between overlap and competition. The bulk of the paper is devoted to type-2 functional responses. The approach used is to analyze a family of simple two-consumer, two-resource models for which it is possible to obtain some results analytically. Analysis of such simple models, while not yielding generally applicable formulas, can illustrate phenomena which may occur for more general multiconsumer, multiresource models. Results presented below suggest that both the type of the functional response and the specific parameters of the response have an important effect on the relationship between overlap and competition.

In the models analyzed here, the two resources are assumed to have identical population growth equations in the absence of consumers. Each of the two consumers species has a higher electivity (consumption rate per unit resource) on a different resource. Electivities may change as a function of resource density, but the ratio of the two is assumed constant. The ratio of the electivity for the preferred resource to that for the nonpreferred resource is equal for the two consumers. Because of this symmetry the two resource types have equal abundances at equilibrium when the population densities of the two consumers are equal. The per capita growth rate of each consumer population is a function ( $g$ ) of the total amount of resource consumed. The two resources are assumed to be of equal value to the consumers. The general form of the model is, therefore,

$$\begin{aligned}\frac{1}{R_1} \frac{dR_1}{dt} &= f(R_1) - \mathcal{C}_1(R_1, R_2) N_1 - \mathcal{C}_2(R_1, R_2) N_2, \\ \frac{1}{R_2} \frac{dR_2}{dt} &= f(R_2) - \mathcal{C}_1(R_2, R_1) N_2 - \mathcal{C}_2(R_2, R_1) N_1,\end{aligned}$$

$$\begin{aligned}\frac{1}{N_1} \frac{dN_1}{dt} &= g_1(\mathcal{C}_1(R_1, R_2) R_1 + \mathcal{C}_2(R_1, R_2) R_2), \\ \frac{1}{N_2} \frac{dN_2}{dt} &= g_2(\mathcal{C}_1(R_2, R_1) R_2 + \mathcal{C}_2(R_2, R_1) R_1).\end{aligned}\quad (1)$$

Here  $f$  is a function describing the per capita growth rate of the resource,  $R_i$  is the density of resource  $i$ ,  $N_i$  is the population density of consumer  $i$ ,  $\mathcal{C}_1$  is the consumption rate per unit resource on the preferred resource types, and  $\mathcal{C}_2$  is the consumption rate per unit resource on the nonpreferred resource. The population density of consumer  $i$  reaches an equilibrium when its per capita resource supply (i.e., the amount of resource consumed per unit time per individual consumer) is equal to an amount  $T_i$ . Resource population processes are assumed to occur at a rate much faster than consumer population processes. As a result, the equations above may be solved for steady-state resource abundances (denoted  $\bar{R}_i$ ) by setting  $dR_i/dt = 0$ .

## II. MEASURING OVERLAP AND COMPETITION

### A. *Measuring Overlap*

Resource utilization by a given species is usually described in the theoretical literature by a resource utilization curve (which becomes a histogram for the case of a finite number of discrete resource types). Resource overlap between two species is measured by a function of their resource utilization curves (histograms). Two different definitions of resource utilization curve have appeared in the literature. The first is that a resource utilization curve represents a plot of the percentage of the total utilization by the consumer consisting of each different resource type. The second (MacArthur, 1972) is that the utilization curve is a plot of relative electivities on different resource types. The electivity is defined as the amount of a resource type consumed divided by the amount available. It is convenient in theoretical applications to multiply each electivity by a constant so that the total area under the utilization curve is unity. Species are thus defined by their relative electivities on different resource types.

It has been common in the theoretical literature (e.g., MacArthur, 1972; May, 1973; Abrams, 1975) to treat overlap in resource utilization as a characteristic of two competing species. In other words, it is assumed that utilization curves do not change as the population densities of resource consumers change. This assumption only makes sense when utilization curves are defined as plots of relative electivities. If utilization curves represent percentage of total utilization in each category, they necessarily change as relative resource abundances change, which in turn occurs whenever relative consumer densities change. This makes it impossible to speak of a single utilization curve or resource overlap value. Overlap and utilization in this article therefore refer to electivity

curves. It is quite probable that the electivity curves of most real organisms change when resource densities change, due to changes in consumer foraging methods. It is, however, not logically necessary that electivity curves change as resource densities change. The case of constant electivity is the only one for which overlap can be specified as a single number. Analyzing a model with constant electivities is also justifiable on the basis that it is necessary to understand the simplest situations before studying more complex ones.

A number of different formulas have been proposed for quantifying overlap of utilization curves (Abrams, 1979). The area in common under the two curves (histograms) is the simplest of these and will therefore be used here. For the two-consumer, two-resource system described above, overlap works out to be

$$\frac{2\mathcal{C}_2}{\mathcal{C}_1 + \mathcal{C}_2} \quad (2)$$

This measure ranges from 0, when each consumer only utilizes its preferred resource, to 1, when both consumers utilize both resources at equal rates, resulting in complete overlap.

### B. *Measuring Competition*

In general, a competitive interaction cannot be characterized by a single number. In the present analysis, two alternative measures of competition are examined:

The competition coefficient is probably the most widely used measure of competition, at least in the theoretical ecology literature. It is defined by Schoener as "a number giving the degree to which an individual of one species affects through competition the growth or equilibrium level of a second species population relative to the effect of an individual of the second species" (Schoener, 1974b). For the model analyzed here, per capita growth rate of the population is a function of per capita resource supply alone, so the competition coefficient may be calculated by

$$\alpha_{12} = \frac{\frac{\partial}{\partial N_2} (\text{per capita resource supply of species 1})}{\frac{\partial}{\partial N_1} (\text{per capita resource supply of species 1})} \quad (3)$$

For the present model, this expression is unchanged if "equilibrium density" is substituted for "per capita resource supply." In general,  $\alpha$  will vary with the population densities of resource consumers. In this case, it is convenient to compare different systems by comparing the value of the competition coefficient when the competitors are at their equilibrium densities. In general, the competition coefficient is a measure of how closely coupled the

population densities of two species are; a change of  $X$  in the density of species 2 results in a change of  $\alpha_{12}X$  in the population density of species 1.

The competition coefficient is a useful measure of the degree of coupling of the consumer populations. Nevertheless, it does not describe the competitive interaction completely.

A second possible measure of the competitive interaction is an index of the ease of invasion by a second species when one species is present in a system at its equilibrium density. If two species are to coexist, it is necessary that each be able to increase when it is rare and the other is at its carrying capacity. Coexistence is comparatively difficult to achieve when the per capita resource requirements ( $T_1$  and  $T_2$ ) of the two species must be vary nearly equal to allow invasion. The ease of invasion may therefore be measured as follows. Designate the species with the lower per capita resource requirement ( $T$ ) to be species 1. Then the two species will coexist if species 2 can increase when it is rare and species 1 is present at its carrying capacity. Species 1's per capita resource supply at carrying capacity will be  $T_1$  by definition. Define  $\beta$  as the ratio of species 2's per capita resource supply (when 1 is at carrying capacity) to  $T_1$ . Then for coexistence it is necessary that  $\beta T_1 > T_2$ . If  $\beta < 1$ , invasion is impossible (since it was assumed  $T_2 \geq T_1$ ). The larger  $\beta$  is, the larger the range of  $T_2$  values which will allow species 2 to invade. High values of  $\beta$  thus represent relatively low ratios of inter- to intraspecific competition. If all else is equal,  $\beta$  increases as overlap decreases.

The analysis presented below largely consists of examining how these two measures ( $\alpha$  and  $\beta$ ) vary as a function of overlap in models which incorporate different functional response types.

### III. CASE 1: LINEAR FUNCTIONAL RESPONSE: LOGISTIC RESOURCE GROWTH

Under these assumptions, the model is simply a symmetrical, two-consumer, two-resource version of the model presented by MacArthur (1972). The resource growth equations are

$$\begin{aligned}\frac{1}{R_1} \frac{dR_1}{dt} &= \frac{r}{K} (K - R_1) - C_1 N_1 - C_2 N_2, \\ \frac{1}{R_2} \frac{dR_2}{dt} &= \frac{r}{K} (K - R_2) - C_1 N_1 - C_1 N_1.\end{aligned}\tag{4}$$

MacArthur (1972) and Schoener (1974b) present methods for calculating the competition coefficient in this system. The competition coefficient is given by  $2C_1C_2/(C_1^2 + C_2^2)$ . The fact that the form is so simple depend son the assumptions of equal  $K$ 's and  $r$ 's and equal values to the consumer of both resources. Table I gives values of the competition coefficient as a function of overlap.

TABLE I

Competition Coefficient as a Function of Overlap for the System with  
Linear Functional Response and Logistic Resource Growth

	Overlap									
	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
$\alpha$	.105	.219	.329	.471	.600	.724	.835	.923	.980	1.0

In this model, the competition coefficient is independent of the population densities of resource consumers. This is true in general for MacArthur's model. Parameters should be restricted so that neither resource is driven extinct by the consumers. This requires that parameters be restricted so that  $C_1N_1 + C_2N_2 < r$  and  $C_2N_1 + C_1N_2 < r$ , for all  $N_1$  and  $N_2$  that can be reached from reasonable initial values.

When consumer species 1 is present alone, its per capita resource supply at equilibrium is  $C_1\hat{R}_1 + C_2\hat{R}_2$ . ( $\hat{R}$  denotes the steady-state resource density when the consumer species are at equilibrium.) At this single-species equilibrium,  $\hat{R}_1$  and  $\hat{R}_2$  are related by  $(K - \hat{R}_1)/(K - \hat{R}_2) = C_1/C_2$ . Therefore, the per capita resource supply may be rewritten in terms of  $\hat{R}_1$  alone;

$$C_1\hat{R}_1 + \frac{C_2}{C_1}(C_1K - C_2K + C_2\hat{R}_1). \quad (5)$$

The per capita resource supply of an invading member of species 2 at this point is  $2C_2\hat{R}_1 + C_1K - C_2K$ . Thus, the ratio  $\beta$  is

$$\frac{2C_1C_2\hat{R}_1 + (C_1^2 - C_1C_2)K}{(C_1^2 + C_2^2)\hat{R}_1 + (C_1C_2 - C_2^2)K}. \quad (6)$$

For any fixed value of  $\hat{R}_1$  this is a decreasing function of overlap (assuming  $C_1 + C_2$  is a constant). If overlap is unity,  $\beta$  is also equal to 1; i.e., for two species to coexist with complete overlap, they must have identical per capita resource requirements. As  $C_2$  approaches 0,  $\beta$  approaches its maximum  $K/\hat{R}_1$ . Unlike  $\alpha$ ,  $\beta$  is dependent on equilibrium resource density. For a given overlap expression (6) is a decreasing function of  $\hat{R}_1$ , which approaches 1 as  $\hat{R}_1$  approaches  $K$ . This means that it is easier for consumers to coexist when their density is high and resource density is low than when the reverse is true. This has been pointed out for a model similar to the one analyzed here by Abrams (1977).

These results for the type-1 functional response model are useful for comparison with the results derived for a similar model with type-2 functional responses analyzed in the next section.

## IV. CASE 2: TYPE-2 FUNCTIONAL RESPONSE; LOGISTIC RESOURCE GROWTH

Murdoch and Oaten (1975) give a general form for a type-2 functional response for a system with two resource types. Their expression with slightly altered notation is

$$\begin{aligned} & \text{(Amount of resource 1 consumed per consumer, per unit time)} \\ &= \frac{C_1 R_1}{1 + C_1 \eta_1 R_1 + C_2 \eta_2 R_2}. \end{aligned} \quad (7)$$

In Murdoch and Oaten's model,  $C_i$  represents the capture rate of resource  $i$  per unit of search time, and  $\eta_i$  is the handling time for resource type  $i$ .  $\eta_i$  may also be regarded as an empirical constant which determines how rapidly the consumption rate per unit resource declines as the density of resource  $i$  increases.

The complete equations for the rate of change of the resource populations are

$$\begin{aligned} \frac{1}{R_1} \frac{dR_1}{dt} &= \frac{r}{K} (K - R_1) - \frac{C_1 N_1}{1 + C_1 \eta_1 R_1 + C_2 \eta_2 R_2} - \frac{C_2 N_2}{1 + C_1 \eta_1 R_2 + C_2 \eta_2 R_1}, \\ \frac{1}{R_2} \frac{dR_2}{dt} &= \frac{r}{K} (K - R_2) - \frac{C_2 N_1}{1 + C_1 \eta_1 R_1 + C_2 \eta_2 R_2} - \frac{C_1 N_2}{1 + C_1 \eta_1 R_2 + C_2 \eta_2 R_1}. \end{aligned} \quad (8)$$

To preserve the symmetry of the system it is assumed that species 1's handling time for resource 1 is equal to species 2's handling time for resource 2 ( $\eta_1$ ). Similarly species 1's handling time for resource 2 equals species 2's for resource 1 ( $\eta_2$ ). If  $\bar{R}_1$  and  $\bar{R}_2$  are the steady-state resource abundances, then the per capita resource supply of species 1 is

$$\frac{C_1 \bar{R}_1 + C_2 \bar{R}_2}{1 + C_1 \eta_1 \bar{R}_1 + C_2 \eta_2 \bar{R}_2}. \quad (9)$$

If this quantity is substituted into expression (3) for the competition coefficient, the result is that

$$\begin{aligned} \alpha_{12} = & \frac{\frac{\partial \bar{R}_1}{\partial N_2} (C_1 + C_1 C_2 \eta_2 \bar{R}_2 - C_1 C_2 \eta_1 \bar{R}_2) + \frac{\partial \bar{R}_2}{\partial N_2} (C_1 + C_1 C_2 \eta_1 \bar{R}_1 - C_1 C_2 \eta_2 \bar{R}_1)}{\frac{\partial \bar{R}_1}{\partial N_1} (C_1 + C_1 C_2 \eta_2 \bar{R}_2 - C_1 C_2 \eta_1 \bar{R}_2) + \frac{\partial \bar{R}_2}{\partial N_1} (C_2 + C_1 C_2 \eta_1 \bar{R}_1 - C_1 C_2 \eta_2 \bar{R}_1)}. \end{aligned} \quad (10)$$

It is possible to solve for the partial derivatives in (10) by setting both  $dR_i/dt$  equal to zero in (8) and differentiating implicitly with respect to  $N_i$ . This results in the following cumbersome expression for the competition coefficient (when  $N_1 = N_2$  so that  $R_1 = \bar{R}_2$ ).

$\alpha_{12} =$ 

$$\frac{\left[ \begin{aligned} &(1 + C_2\eta_2\bar{R} - C_2\eta_1\bar{R})\{-C_1C_2(C_1 + C_2)(1 + C_1\eta_1\bar{R} + C_2\eta_2\bar{R}) \\ &- (K - \bar{R})(C_1^3C_2\eta_2 - C_1C_2^3\eta_2) \\ &+ (1 + C_1\eta_1\bar{R} - C_1\eta_2\bar{R})\{-C_1C_2(C_1 + C_2)(1 + C_1\eta_1\bar{R} + C_2\eta_2\bar{R}) \\ &- (K - \bar{R})(C_1C_2^3\eta_1 - C_1^3C_2\eta_1) \} \end{aligned} \right]}{\left[ \begin{aligned} &(1 + C_2\eta_2\bar{R} - C_2\eta_1\bar{R})\{-C_1^2(C_1 + C_2)(1 + C_1\eta_1\bar{R} + C_2\eta_2\bar{R}) \\ &- (K - \bar{R})(C_1^2C_2^2\eta_1 - C_1^4\eta_1)\} \\ &+ (1 + C_1\eta_1\bar{R} - C_1\eta_2\bar{R})\{-C_2^2(C_1 + C_2)(1 + C_1\eta_1\bar{R} + C_2\eta_2\bar{R}) \\ &- (K - \bar{R})(C_1^2C_2^2\eta_2 - C_2^4\eta_2)\} \end{aligned} \right]}. \quad (11)$$

This expression simplifies considerably if  $\eta_1 = \eta_2$ . In this case,

$$\alpha_{12} = \left( \frac{2C_1C_2}{C_1^2 + C_2^2} \right) \times \left[ \frac{(1 + C_1\eta\bar{R} + C_2\eta\bar{R})}{(1 + C_1\eta\bar{R} + C_2\eta\bar{R}) + (K - \bar{R})(C_1\eta + C_2\eta) - 2C_1C_2\eta(C_1 + C_2)/(C_1^2 + C_2^2)} \right]. \quad (12)$$

When  $N_1 \neq N_2$  (so  $\bar{R}_1 \neq \bar{R}_2$ ), competition coefficients were calculated by computer simulation of (8). Before analyzing these results, it is necessary to note that there are restrictions on the values of the parameters in expressions (11) and (12).

The handling times  $\eta_i$  are restricted by adaptive utilization criteria. It would be unrealistic to assume that an organism consumed a resource type if, in so doing, it decreased its average intake below what it would be if the resource were ignored. Restricting the diet to the resource with the smaller handling time will be adaptive unless the following criteria are satisfied:

$$\begin{aligned} \eta_1 &< \eta_2 + \frac{1}{C_2\bar{R}_2}, \\ \eta_2 &< \eta_1 + \frac{1}{C_1\bar{R}_1}. \end{aligned} \quad (13)$$

For these criteria to apply over the entire range of possible steady-state resource densities, it is necessary that

$$\begin{aligned} \eta_1 &< \eta_2 + \frac{1}{C_2K}, \\ \eta_2 &< \eta_1 + \frac{1}{C_1K}. \end{aligned} \quad (14)$$

Thus, the larger the  $C_i$  or  $K$ , the more nearly equal handling times must be.



In addition, there are restrictions on  $\bar{R}$  due to the assumption (also made in analyzing the type-1 model) that consumer densities are not such as to drive one or both resources extinct. These are discussed in the Appendix. They result in the restriction that

$$\bar{R} > \text{Max} \left[ \frac{K(C_1\eta_1 + C_2\eta_2) - 1}{C_1\eta_1 + C_2\eta_2}, \frac{K(C_1C_2 - C_2^2)}{C_1^2 + C_1C_2 + K(C_1^2C_2\eta_2 - C_1^2C_2\eta_1 + C_1C_2^2\eta_1 - C_1C_2^2\eta_2)} \right]. \quad (15)$$

A complete analysis of the behavior of  $\alpha$  as a function of all the variables and parameters in Eq. (8) would be involved and not especially useful. Instead, this section illustrates several aspects of the behavior of  $\alpha$  that differ from the corresponding model with linear functional responses.

(1) *The competition coefficient is a function of consumer and resource densities.* It is clear from the form of expressions (11) and (12) that  $\alpha$  depends on the steady-state resource densities. Because  $\bar{R}$  is determined by consumer densities,  $\alpha$

TABLE II

Values of the Competition Coefficient  $\alpha_{12}$  as a Function of the Population Densities of the Competing Consumers in a System with a Type-2 Functional Responses<sup>a</sup>

	$N_2$										
$N_1$	0.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
0.0	.2195	.2277	.2372	.2482	.2611	.2764	.2954	.3194	.3514	.3969	.4696
.1	.2159	.2240	.2335	.2443	.2571	.2724	.2914	.3155	.3479	.3945	.4704
.2	.2120	.2202	.2294	.2402	.2529	.2682	.2871	.3114	.3442	.3920	.4716
.3	.2080	.2160	.2251	.2358	.2484	.2636	.2826	.3070	.3402	.3894	.4733
.4	.2037	.2115	.2206	.2311	.2436	.2587	.2776	.3021	.3358	.3865	.4757
.5	.1991	.2068	.2157	.2260	.2384	.2534	.2722	.2969	.3311	.3836	.4790
.6	.1940	.2015	.2102	.2204	.2326	.2475	.2662	.2910	.3258	.3803	.4837
.7	.1885	.1958	.2043	.2142	.2262	.2408	.2595	.2843	.3198	.3769	.4902
.8	.1823	.1894	.1976	.2072	.2189	.2332	.2516	.2764	.3126	.3730	.5007
.9	.1751	.1819	.1897	.1990	.2102	.2241	.2422	.2668	.3037	*	*
1.0	.1666	.1729	.1801	.1883	.1993	.2125	.2297	.2545	.2980	*	*

<sup>a</sup> Overlap is .2.  $\alpha_{21}$  is given by transposing the rows and columns of the table. Other parameter values are:  $r = 1$ ;  $K = 1$ ;  $C_1 + C_2 = 1$ ;  $\eta_1 = \eta_2 = 1$ . The competition coefficient for the linear system with the same overlap is .2195. Entries marked with an asterisk violate condition (15).

TABLE III

Values of the Competition Coefficient  $\alpha_{12}$  as a Function of the Population Densities of the Competing Consumers in a System with Type-2 Functional Responses<sup>a</sup>

	$N_2$										
$N_1$	0.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
0.0	.3227	.3346	.3482	.3641	.3830	.4058	.4342	.4709	.5211	.5954	.7233
.1	.3095	.3210	.3341	.3494	.3676	.3897	.4127	.4530	.5021	.5756	.7042
.2	.2960	.3069	.3195	.3342	.3517	.3730	.3997	.4344	.4824	.5549	.6845
.3	.2820	.2925	.3045	.3185	.3353	.3557	.3814	.4151	.4618	.5330	.6640
.4	.2675	.2774	.2889	.3023	.3182	.3377	.3623	.3948	.4401	.5105	.6427
.5	.2525	.2618	.2726	.2852	.3003	.3189	.3423	.3734	.4172	.4863	.6202
.6	.2366	.2454	.2554	.2672	.2814	.2988	.3210	.3506	.3927	.4602	.5963
.7	.2199	.2279	.2371	.2481	.2612	.2775	.2982	.3260	.3662	.4318	.5708
.8	.2020	.2092	.2175	.2274	.2393	.2541	.2731	.2989	.3366	.3999	.5426
.9	.1822	.1885	.1958	.2044	.2149	.2280	.2449	.2680	.3024	.3623	.5098
1.0	.1597	.1647	.1706	.1776	.1861	.1967	.2106	.2298	.2589	**	*

<sup>a</sup> Overlap and parameters are the same as for Table II except that  $\eta_1 = 13/9$  and  $\eta_2 = 5/9$ . The entry marked with \*\* is missing because the numerical method for determining  $\alpha$  did not converge fast enough at this set of population densities. The entry marked \* violated condition (15).

may also be expressed as a function of consumer densities  $N_1$  and  $N_2$ . If  $N_1 \neq N_2$ ,  $\alpha$  depends on the relative numbers of the two consumer types as well as their total population density. Tables II, III, and IV give values of  $\alpha$  for different population densities of resource consumers. The off-diagonal elements in these tables may be regarded as either nonequilibrium values of  $\alpha$  for a system in which  $\hat{N}_1 = \hat{N}_2$  or as equilibrium values for a system in which  $\hat{N}_1 \neq \hat{N}_2$ . The variation of  $\alpha$  with consumer population density can be substantial; the maximum and minimum values for the system of Table III differ by more than a factor of 4. For the case of  $N_1 = N_2$  it may be shown that  $\alpha$  either increases as  $\bar{R}$  decreases (this pattern occurs if  $\eta_1$  is greater than a threshold value which is less than  $\eta_2$ ) or decreases initially as  $\bar{R}$  decreases from  $K$  and then increases for  $\bar{R}$  beneath some threshold.

(2)  $\alpha$  can differ substantially from a similar system with type-1 function responses. In a system with linear functional responses which had the same overlap as those of Tables II through IV,  $\alpha$  would equal .2195. Values in the tables range from .1312 to .7322. A simple analysis of expression (12) (which assumes equal handling times) shows that the ratio of  $\alpha$  for the type-2 system to that for the

TABLE IV

Values of the Competition Coefficient  $\alpha_{12}$  as a Function of the Population Densities of the Competing Consumers in a System with Type-2 Functional Responses<sup>a</sup>

$N_1$	$N_2$										
	0.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.
0.0	.1312	.1355	.1403	.1457	.1518	.1589	.1671	.1768	.1887	.2035	.2227
.1	.1387	.1433	.1485	.1543	.1610	.1687	.1777	.1884	.2014	.2179	.2396
.2	.1462	.1512	.1567	.1631	.1703	.1786	.1885	.2002	.2147	.2330	.2574
.3	.1537	.1591	.1651	.1720	.1798	.1889	.1996	.2124	.2284	.2489	.2764
.4	.1613	.1671	.1736	.1809	.1894	.1992	.2109	.2250	.2426	.2656	.2966
.5	.1690	.1752	.1821	.1900	.1991	.2098	.2225	.2380	.2576	.2833	.3184
.6	.1767	.1833	.1907	.1993	.2091	.2207	.2345	.2516	.2733	.3023	.3418
.7	.1845	.1915	.1995	.2086	.2193	.2318	.2469	.2658	.2900	.3230	.3687
.8	.1923	.1998	.2084	.2182	.2296	.2433	.2599	.2807	.3081	.3456	.4157
.9	.2001	.2081	.2173	.2279	.2403	.2551	.2734	.2966	.3275	**	**
1.0	.2080	.2166	.2264	.2378	.2512	.2676	.2888	**	**	**	*

<sup>a</sup> Overlap and parameters are the same as for Table II except that  $\eta_1 = 5/9$  and  $\eta_2 = 13/9$ . The entries marked with \*\* are missing because the numerical method for determining  $\alpha$  did not converge fast enough at these population densities. The entry marked \* violated condition (15).

linear system can approach infinity. Expression (12) increases as  $\bar{R}$  decreases. The maximum value of (12) for any given level of overlap is achieved when both constraints incorporated in expression (15) are satisfied simultaneously. At this point

$$\alpha = \frac{2C_1^3 + 2C_1^2C_2}{3C_1^3 + 3C_1C_2^2 - C^3 - C_1^2C_2}. \quad (16)$$

This is an increasing function which approaches  $\frac{2}{3}$  as overlap approaches 0, and approaches 1 as overlap approaches 1. Thus, for low overlap, the competition coefficient in the type-2 system can be many times larger than that for the type-1 system, provided the steady-state resource density is sufficiently small.

There can also be large differences between competition coefficients in linear and type-2 systems when  $\bar{R}$  is large. As  $\bar{R}$  approaches  $K$ , expression (11) approaches

$$\alpha = \frac{(1 + C_2\eta_2K - C_2\eta_1K)(-C_1C_2) + (1 + C_1\eta_1K - C_1\eta_2K)(-C_1C_2)}{(1 + C_2\eta_2K - C_2\eta_1K)(-C_1^2) + (1 + C_1\eta_1K - C_1\eta_2K)(-C_2^2)}. \quad (17)$$

If  $\eta_1 > \eta_2$  this is an increasing function of  $K$ . The maximum  $K$  is set by the

adaptive utilization criteria (14). When  $K$  attains its maximum of  $1/(C_2(\eta_1 - \eta_2))$ ,  $\alpha = C_1/C_2$ , which is always greater than 1. Because  $\alpha_{12} = \alpha_{21}$ ,  $\alpha > 1$  means that the equilibrium point is unstable and either species can exclude the other (a priority effect). This is discussed in more detail later. A sufficiently large  $K$  will make  $\alpha$  greater than 1 for any system in which  $\eta_1 > \eta_2$  and  $\bar{R}$  is close to  $K$ , regardless of the degree of overlap. Table V presents a numerical example.

TABLE V

The Competition Coefficient  $\alpha$  as a Function of Overlap for Various Values of Overlap and Equilibrium Resource Density<sup>a</sup>

R	Overlap								
	.9	.8	.7	.6	.5	.4	.4	.2	.1
.3	1.0044	*	*	.9022	.8273	.7295	.6055	.4498	*
.4	1.0113	.9982	.9594	.8943	.8028	.6857	.5444	.3812	.1987
.5	1.0199	1.0109	.9705	.8984	.7959	.6667	.5159	.3501	.1760
.6	1.0301	1.0271	.9876	.9109	.8004	.6619	.5039	.3355	.1652
.7	1.0416	1.0464	1.0094	.9301	.8128	.6663	.5014	.3295	.1601
.8	1.0542	1.0682	1.0353	.9544	.8313	.6771	.5053	.3289	.1582
.9	1.0678	1.0924	1.0648	.9833	.8547	.6928	.5135	.3317	.1583
1.0	1.0823	1.1186	1.0975	1.0161	.8823	.7123	.5250	.3369	.1597

<sup>a</sup>  $\alpha$  is calculated assuming equal population densities of both consumer species. Parameters are:  $K = 1$ ;  $r = 1$ ;  $C_1 + C_2 = 1$ ;  $\eta_1 = 1.5$ ;  $\eta_2 = .5$ . Entries marked with an asterisk did not satisfy condition (15).

Not only is it possible for  $\alpha$  in a type-2 system to be substantially greater than in a similar type-1 system, but it can also be substantially smaller. Tables II, III, and IV all contain values that are significantly less than .2195, the  $\alpha$  for the type-1 system. If  $\eta_2 > \eta_1$ ,  $\alpha$  is a decreasing function of  $\bar{R}$ , and (17) is a decreasing function of  $K$ . When  $K$  reaches its maximum permissible value of  $1/(C_1(\eta_2 - \eta_1))$ ,  $\alpha = C_2/C_1$ , which is always less than the value for the linear system of  $2C_1C_2/(C_1^2 + C_2^2)$ . The ratio of the two values approaches a minimum of  $\frac{1}{2}$  as overlap becomes small. Low values of  $\alpha$  were obtained for  $\eta_1 \geq \eta_2$  when  $N_1 \neq N_2$ , but none of the values calculated were less than one-half of the value for the type one system.

(3) *The handling times for the two resource types are important in determining competition coefficients.* Because relative handling times do not affect relative electivities, this statement implies that a simple knowledge of utilization curves is insufficient to determine the competition coefficient in even as simple a model as the one presented here. That handling times are important in determining

the competition coefficients should be evident from the form of expressions (11) and (12) and from the discussion of the previous section. It is possible to show that if all other variables are held constant, (12) is an increasing function of handling times. If handling times are not equal, it can be shown (from expression (11)) that the competition coefficient is an increasing function of the ratio  $\eta_1/\eta_2$  assuming that the sum of the handling times is constant. The numerical results for systems in which  $N_1 \neq N_2$  suggest that for most (but not all) consumer population densities, competition coefficients tend to be larger when the  $\eta_i$  and  $C_i$  are positively correlated. Some intuitive feeling for this result may be gained by noting that consumers compete by their effects on both the resource densities and each other's absolute electivities. The competitive effect of reduced resource densities is partially offset by the fact that reduced resource densities mean higher electivities. Because  $\mathcal{C}_1 > \mathcal{C}_2$ , intraspecific competitors (of species 1) affect  $R_1$  more than  $R_2$ , and interspecific competitors (species 2) affect  $R_2$  more than  $R_1$ . When  $\eta_1$  is greater than  $\eta_2$ , the compensatory effect of increased electivities is therefore greater for intraspecific than interspecific competition. This increases  $\alpha$  which is a ratio of inter- to intraspecific competition. Similarly, if  $\eta_i$  and  $C_i$  are negatively correlated,  $\alpha$  is reduced compared to the case of equal handling times. It should be noted that this intuitive explanation has assumed that both species have similar absolute electivities. In the present symmetrical model this is true for  $\bar{R}_1$  and  $\bar{R}_2$  approximately equal. If  $N_1$  is close to carrying capacity and  $N_2$  is close to zero, however,  $\bar{R}_1$  will be much less than  $\bar{R}_2$ . Thus if  $\eta_1 > \eta_2$  species 1 will have a higher absolute electivity than species 2. This implies that intraspecific competition will be relatively large (when compared to the case of equal  $\bar{R}_i$ ) and  $\alpha$  will be relatively small. By the same argument, if  $\eta_2 > \eta_1$  species 2 will have the higher absolute electivity, interspecific competition will be relatively large, and  $\alpha$  will be relatively large. This accounts for the fact that  $\alpha$ 's for very high  $N_1$  and low  $N_2$  are larger in Table IV ( $\eta_2 > \eta_1$ ) than in Table III ( $\eta_1 > \eta_2$ ).

(4) *It is possible to have a priority effect whereby either of two competitors can exclude the other, depending on initial densities.* That this could occur was noted under point (2) in the preceding discussion, where it was noted that  $\alpha_{12}$  and  $\alpha_{21}$  could both be greater than one. This is impossible in the comparable type-1 functional response model. For a priority effect to occur in the type-2 model, it is necessary that:

- (a) the resource with the higher capture rate per unit resource have a higher handling time ( $\eta_1 > \eta_2$ );
- (b) the resource-carrying capacity be larger than a threshold value given by

$$\frac{C_1 - C_2}{2C_1C_2(\eta_1 - \eta_2)} \quad (18)$$

(this value is very large if overlap is low or handling times are similar);

(c)  $\bar{R}$  be greater than a threshold value that can be derived from (11) by setting  $\alpha = 1$  and solving the resulting quadratic equation.

It is possible for a priority effect to occur for any nonzero amount of overlap. For low overlap values, however, this requires that resource carrying capacities be very high and equilibrium resource abundances be very near their carrying capacity. Table V gives a numerical example showing the range of values of the equilibrium resource density and overlap values which result in a priority effect in one specific system. The existence of a priority effect may also be shown by an analysis of the second measure of competition  $\beta$ .

If the density of resource 1 when consumer species 1 is present alone at its carrying capacity is denoted by  $\hat{R}_1$ , then the percapita resource supply of species 1 at carrying capacity is equal to

$$\frac{C_1 \hat{R}_1 + C_2 K - (C_2^2/C_1) K + (C_2^2/C_1) \hat{R}_1}{1 + C_1 \eta_1 \hat{R}_1 + C_2 \eta_2 K - (C_2^2 \eta_2/C_1) K + (C_2^2 \eta_2/C_1) \hat{R}_1}. \quad (19)$$

This expression was derived in the same manner as expression (5). By definition (19) is equal to  $T_1$ . Similarly, the per capita resource supply of an invading member of species 2 is

$$\frac{2C_2 \hat{R}_1 + C_1 K - C_2 K}{1 + C_2 \eta_2 \hat{R}_1 + C_2 \eta_1 \hat{R}_1 + C_1 \eta_1 K - C_2 \eta_1 K}. \quad (20)$$

$\beta$  is simply expression (20) divided by expression (19). Table VI gives values of  $\beta$  calculated for the three systems of Tables II, III, and IV and for a comparable system with linear functional responses.

Like  $\alpha$ ,  $\beta$  is a function of resource densities, and therefore of consumer densities. However, this is also true for  $\alpha$  in the system with type-1 functional responses. Table VI suggests that, as in the linear functional response system,  $\beta$  for the type-2 system decreases as  $\bar{R}$  increases. This is true even for some systems in which  $\alpha$  decreases as  $\bar{R}$  increases. If  $\eta_1$  is sufficiently large relative to  $\eta_2$  it is possible for  $\beta$  to have a relative minimum at intermediate resource densities when overlap is sufficiently high.

Table VI also shows that  $\beta$  can differ significantly between similar systems with linear or type-2 functional responses. It can be shown that for  $\beta$  to be greater in a type-2 system than in a comparable type-1 system, it is necessary that

$$\eta_1/\eta_2 < C_2/C_1. \quad (21)$$

This result is independent of the function  $f$  specifying resource growth. Thus there are some systems (such as the cases of low  $N$  in Table IV) in which  $\alpha$  is lower in the type-2 system than the linear system, but invasion is more difficult.

Relative handling times are clearly important in determining  $\beta$ . It is possible to show that if  $\eta_1 + \eta_2$  is a constant,  $\beta$  decreases as  $\eta_1/\eta_2$  increases. Thus invasion

TABLE VI

Values of  $\beta$  as a Function of  $\bar{R}$  for Four Systems with an Overlap of .2<sup>a</sup>

Resource density	System			
	(1)	(2)	(3)	(4)
0.0	9.0	5.444	4.381	7.031
.1	4.556	2.993	2.471	3.670
.2	3.098	2.140	1.849	2.570
.3	2.374	1.739	1.544	2.025
.4	1.941	1.501	1.365	1.700
.5	1.653	1.344	1.247	1.484
.6	1.448	1.233	1.166	1.331
.7	1.294	1.151	1.107	1.219
.8	1.174	1.089	1.062	1.128
.9	1.078	1.039	1.027	1.057
1.0	1.0	1.0	1.0	1.0

<sup>a</sup> System (1) has a linear functional response. Systems (2), (3), and (4) have type-2 functional responses and correspond to the systems analyzed in Tables II, III, and IV, respectively.

is relatively difficult in systems in which capture rates and handling times are positively correlated. Such systems also have relatively large  $\alpha$ .

If two species have equal  $T$  values a priority effect will result whenever  $\beta < 1$ . This should be clear from the definition of  $\beta$ . It is possible to show that the conditions for  $\beta$  to be less than one are identical to those given previously for  $\alpha$  to be greater than one.

Thus, although lower competition coefficients do not always imply that invasion will be easier, the results of an analysis of  $\beta$  generally agree with results arrived at for  $\alpha$ .

## V. MODELS WITH NONLOGISTIC RESOURCE RENEWAL

This section addresses the question of whether the previous results depend on the logistic resource renewal assumed in the previous section. This seemed useful for two reasons: (1) logistic population growth is seldom observed (Abrams, 1980), and (2) a large fraction of the possible parameter space in the previous model was ignored because it would have implied extinction of one of the resources. This is somewhat artificial, because consumers in nature do not

necessarily follow rules which prevent them from driving one of their resources to extinction. This section examines one alternative resource renewal model in some detail and also makes some more general comments. The resource renewal model examined in this section is one in which resources do not reproduce themselves. It has been presented in more detail elsewhere (Abrams, 1977). The overall consumer-resource model is still assumed to have the basic form of Eqs. (1). The per capita growth rate function of the resource is assumed to be  $(F/R) - S$ , where  $F$  represents an entry rate of resources into the system and  $S$  is an exit rate constant of resources from the system. It is impossible for the consumers to drive either of the resources to extinction in this system. Thus, the only constraints on the parameter values of the system are those imposed by the adaptive utilization criteria. These are still given by (14) if  $F/S$  is substituted for  $K$  ( $F/S$  being the equilibrium resource abundance in the absence of consumers).

It is possible to derive an expression for the competition coefficient in this system, but it is even more unwieldy than expression (11). Table VII gives values for the competition coefficient as a function of consumer density for one level of overlap. The variation in  $\alpha$  as a function of consumer density is quite different from the pattern illustrated by the comparable system with logistic growth (Table II). For example, in Table VII  $\alpha_{12} > \alpha_{21}$  when  $N_1 > N_2$ , but  $\alpha_{12} < \alpha_{21}$  for this case in Table II.

TABLE VII

The Competition Coefficient  $\alpha_{12}$  for the Model with Nonlogistic Resource Growth<sup>a</sup>

$N_1$	$N_2$										
	0.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
0.0	.2195	.2106	.2013	.1933	.1865	.1809	.1761	.1720	.1684	.1652	.1624
.1	.2947	.2477	.2157	.1963	.1840	.1757	.1696	.1649	.1611	.1581	.1554
.2	.4126	.3164	.2535	.2171	.1957	.1820	.1728	.1662	.1611	.1572	.1541
.3	.5565	.4065	.3081	.2513	.2179	.1970	.1832	.1735	.1664	.1610	.1567
.4	.7120	.5090	.3741	.2948	.2477	.2182	.1988	.1853	.1755	.1681	.1624
.5	.8695	.6176	.4472	.3450	.2833	.2444	.2186	.2006	.1876	.1779	.1705
.6	1.0236	.7282	.5247	.3998	.3231	.2743	.2416	.2187	.2022	.1898	.1804
.7	1.1711	.8380	.6044	.4579	.3663	.3071	.2672	.2392	.2189	.2037	.1919
.8	1.3107	.9455	.6850	.5181	.4119	.3438	.2951	.2617	.2373	.2190	.2049
.9	1.4420	1.0498	.7654	.5795	.4593	.3795	.3247	.2858	.2572	.2357	.2191
1.0	1.5651	1.1502	.8849	.6417	.5080	.4181	.3559	.3113	.2785	.2536	.2343

<sup>a</sup> Overlap is .2. Other parameters are:  $F = 1$ ;  $S = 1$ ;  $C_1 + C_2 = 10$ ;  $\eta_1 = \eta_2 = 1$ .



If handling times for the two resources are assumed to be equal, the expression for the competition coefficient simplifies to the following expression:

$$\frac{2C_1C_2}{(C_1^2 + C_2^2)} \left[ \frac{-(F/\bar{R}^2)(1 + C_1\eta\bar{R} + C_2\eta\bar{R})}{-(F/\bar{R}^2)(1 + C_1\eta\bar{R} + C_2\eta\bar{R}) + (F/\bar{R} - S)(C_1\eta + C_2\eta)[(C_1 - C_2)^2/(C_1^2 + C_2^2)]} \right]. \quad (22)$$

It can be shown that this is always greater than the  $\alpha$  for the corresponding system with a linear functional response. It is also possible to show that it has a maximum at an intermediate value of  $\bar{R}$  between 0 and  $F/S$ , and that it approaches the value for the linear system as  $\bar{R}$  approaches 0 or  $F/S$ . This pattern may be seen in Table VIII by examining those values for  $N_1 = N_2$ . This behavior contrasts with that of the equivalent system with logistic resource growth for which small values of  $\bar{R}$  resulted in competition coefficients much larger than those for the type-1 system.

Numerical results for systems with unequal handling times show that the competition coefficient at equilibrium increases as the ratio of the handling time of the preferred to the handling time of the nonpreferred resource increases. This result is independent of the form of the function  $f$ .

The second measure of competition,  $\beta$ , reveals the same general picture. In particular, inequality (21) still applies, since its derivation is independent of the function  $f$ . Also, in the model with nonlogistic growth, it is possible to have a priority effect ( $\beta$  less than one) if overlap is sufficiently high and  $\eta_1/\eta_2$  is sufficiently high.

Thus, it appears that the general conclusions outlined in the previous section do not depend on the assumption of logistic resource renewal.

## VI. ACCELERATING FUNCTIONAL RESPONSES

Although physical constraints ensure that every functional response must become decelerating at sufficiently high prey densities, there may be a wide range of densities over which the functional response accelerates. A functional response which is accelerating at low prey densities, but decelerating at higher densities is generally termed a type-3 functional response (Holling, 1965). One possible cause of an accelerating functional response is increased efficiency with experience on the part of the resource consumers. Oaten (1977) has recently shown that an accelerating functional response can also result when prey are patchily distributed and there is a finite transit time between patches. When these phenomena are incorporated into models of the functional response, they generally result in very complex expressions. In addition, the situations which give rise to accelerating functional responses generally result in the relative electivities for different resources changing as a function of resource densities.

For example, learning how to find or capture prey type A will not necessarily result in any greater efficiency in capturing type B. Unless the prey are captured in identical ways, it seems likely that the consumers' relative electivities on A and B will change with changes in the relative densities of A and B. If the accelerating response is due to Oaten's (1977) mechanism, relative electivities will change unless different resource types have identical spatial distributions. Therefore, the analysis of accelerating functional response assuming constant electivities outlined below is not likely to be a realistic situation. The simplest possible assumption leading to an accelerating functional response is the assumption that per unit resource consumption rates increase linearly with resource densities. This leads to the following two-consumer, two-resource model,

$$\begin{aligned}\frac{1}{R_1} \frac{dR_1}{dt} &= f(R_1) - C_1(1 + C_1\eta_1 R_1 + C_2\eta_2 R_2) N_1 \\ &\quad - C_2(1 + C_1\eta_1 R_2 + C_2\eta_2 R_1) N_2, \\ \frac{1}{R_2} \frac{dR_2}{dt} &= f(R_2) - C_2(1 + C_1\eta_1 R_1 + C_2\eta_2 R_2) N_1 \\ &\quad - C_1(1 + C_1\eta_1 R_2 + C_2\eta_2 R_1) N_2.\end{aligned}\tag{23}$$

Parameters are the same as for system (8) except that the  $\eta_i$ 's should be regarded as empirical constants describing the rate of increase of the per unit resource consumption rates as a function of the density of resource  $i$ . This form is essentially the inverse of the functional form assumed for the type-2 functional response. It may be shown that unless the  $\eta$  value for the preferred resource is sufficiently lower than that for the nonpreferred resource, invasion will be easier and competition coefficients will be less for the type-3 system than for a linear system. This is essentially the opposite of the result for the type-2 functional response system. Although the form assumed for the type-3 functional response here is unrealistic, this brief analysis nevertheless shows that the relationship between overlap and competition when functional responses are accelerating is likely to differ significantly from that for systems with linear or type-2 responses.

## VII. DISCUSSION

The range of bilogically plausible consumer-resource models is quite large, and it is unlikely that the difference in the behavior of a model with a type-2 functional response and an analogous model with a linear functional response will be similar for all possible models. In multiresource models with comparable rates of change in consumer and resource populations there is a possibility of limit cycle behavior, in which case neither  $\alpha$  nor  $\beta$  is a good measure of competition. However, the qualitative conclusions given in Section V are certainly

not restricted to two-consumer, two-resource symmetrical systems in which resources are always at a steady state relative to consumer populations. None of the general results regarding  $\beta$  depend on the assumption that resources are always at a steady state relative to consumer populations. That  $\alpha$  and  $\beta$  depend on consumer densities, that handling times influence both parameters, and that positive correlations between handling times and capture rates make invasion more difficult and coupling higher than negative correlations were observed in all simulations of a number of multiconsumer, multiresource versions of (8) and similar models using the nonlogistic model of Section V.

Priority effects due to the mechanism described here may be somewhat less general in their occurrence. Evolutionary considerations suggest that if there is any flexibility in handling times they should evolve so that resources which were caught most often were handled most efficiently. If a resource which was captured frequently required a large handling time by one consumer species, it would most likely require a large handling time by a second species which captured the resource less frequently. It may therefore be that the conditions required for a priority effect are seldom met. However, more field data on functional responses of sympatric competitors are needed to evaluate this possibility.

Whatever the range of applicability of the present conclusions, field ecologists should be aware of the possibility that the functional responses of competitors may be important in determining observed patterns of niche overlap. It should also be noted that it is not necessary that consumers spend large amounts of time handling resources for the form of the functional response to be important in determining the level of competition. For the logistic resource model, the greatest deviation between linear and type-2 systems in the values of  $\alpha$  often occurred when resource density was very low (i.e., when very little time would be spent in handling resource).

The relation between predation on or harvesting of resource consumers and the level of competition between or ease of coexistence of competing consumers is a topic of considerable interest in theoretical population ecology (Pianka, 1972; Abrams, 1977; Yodzis, 1977). The discussion of the variation of the competition measures as a function of resource density is relevant to this question, because higher levels of harvesting or density-independent mortality on consumers result in higher steady-state resource densities. For most of the possible parameter values of the models analyzed here,  $\beta$  decreases as resource density increases, suggesting that invasion becomes more difficult as consumer densities drop and resource densities increase. On the other hand, for the case of  $\eta_2 \geq \eta_1$  (which seems biologically more likely than the reverse inequality), competition coefficients decrease as resource densities increase when resource renewal is logistic. In the nonlogistic model, however, whether harvesting increases or decreases the competition coefficient depends on current consumer and resource densities. There are unlikely to be any generally valid statements about the effect that harvesting of consumer species has on competition between them.

The present analysis also has implications for other theoretical studies in ecology. Competition theory is largely based upon the Lotka-Volterra model, which can only be derived from a consumer-resource model by assuming a linear functional response. As a result, some theories that depend on a linear functional response have apparently been generally accepted. For example, in an article on interference competition, Case and Gilpin (1974) state that "the incorporation of interference competition into niche theory helps to explain other competitive phenomena. First, unstable equilibrium points, such as those that occur in laboratory *Tribolium* systems, are impossible to explain with the resource or niche overlap approach. If the elements of the community matrix are solely the  $\alpha$ 's from resource overlap, it is impossible for the product  $\alpha_{12}\alpha_{21}$  to exceed unity, a necessary condition for the existence of an unstable equilibrium point." The result of the present analysis of exploitative competition with type-2 functional responses shows that unstable equilibrium points do not require interference competition.

The results presented here are also relevant to theories of the limiting similarity of competing species. Most analyses of the limiting similarity of competitors (e.g., MacArthur and Levins, 1967; May and MacArthur, 1972; May, 1973; Roughgarden, 1974) assumed a Lotka-Volterra model in which competition coefficients were calculated from resource utilization curves using a formula originally proposed by MacArthur and Levins (1967). This formula has been justified on the basis that a similar expression may be derived from MacArthur's (1972) consumer-resource model. The basic conclusion of these initial studies was that there was a limit to the similarity of competitors arranged on a single resource axis corresponding to a pattern in which the means of the species' utilization curves were separated by a distance approximately equal to the standard deviation of the curves. I have shown earlier (Abrams, 1975) that this conclusion is dependent upon using MacArthur and Levins' formula for the competition coefficient. In general, this formula requires the assumption of logistic resource renewal. Other forms of resource renewal result in other expressions for the competition coefficient and less stringent limits to similarity. Also, even when resource renewal is logistic, different interpretations of the utilization curves result in different formulas for the competition coefficient. In spite of this, many subsequent theoretical papers have continued to use MacArthur and Levins' formula to calculate the competition coefficient. For example, May (1976) reiterates his earlier conclusions, and refers to Abrams (1975) as a "good review" without mention of the effect that alternative formulas for the competition coefficient may have on his conclusion. Works by Yoshiyama and Roughgarden (1977) and Christiansen and Fenchel (1977) also use MacArthur and Levins' formula unquestioningly. The present analysis of consumer functional response and competition should serve to cast additional doubts on this theory. Unless the functional response of resource consumers is linear, MacArthur and Levins' formula for the competition coefficient can-

not be justified. Depending on the relative values of handling times and capture rates, the level of species packing predicted using a model with a type-2 functional response may be greater or less than that predicted from a model with linear functional responses. This further supports the conclusion that there is no universal limit to the similarity of competitors.

Finally, it is worth noting that the Lotka-Volterra model will not generally be a good approximation of reality unless functional responses are linear and resources renew logistically. Nonlinear functional responses cause competition coefficients between two consumers to depend upon the population densities of the two consumers and upon the densities of any other consumers which overlap in resource use with these two. Even with linear functional responses, a constant competition coefficient will depend on logistic resource renewal, so variation in  $\alpha$  with consumer and resource density is not a unique feature of systems with nonlinear functional responses. However, even if other assumptions are such as to make it possible to have constant competition coefficients, nonlinear functional responses will result in  $\alpha$  being a function of population densities.

#### APPENDIX: RESTRICTIONS ON STEADY-STATE RESOURCE DENSITY IN EXPRESSIONS (11) AND (12)

In the model presented here, if one resource went extinct, this would imply that at least one consumer would also go to zero population density. It would seem desirable to restrict parameter values so that this does not occur. However, the provision that resources are at steady-state densities relative to consumers means that if the initial consumer populations are large enough, resources which renew logistically will be driven extinct. For certain sets of parameter values and initial densities, the functions describing consumer population growth must be known to derive conditions that the resources not go extinct. It would seem desirable, however, that at least two conditions be satisfied for all possible cases:

(1) *It Should be Possible to Have an Equilibrium at Which Both Resources Are Present with a Single Consumer.* When consumer species 1 is present alone,  $\hat{R}_1 < \hat{R}_2$ , so that the requirement that neither resource go extinct becomes  $\hat{R}_1 > 0$ . For this to be the case, it is necessary that

$$\hat{R}_2 > \frac{C_2}{C_1} (C_1 K - C_2 K). \quad (A1)$$

This implies that

$$T_1 > \frac{C_2[(C_2/C_1)(C_1 K - C_2 K)]}{1 + C_2 \eta_2 [(C_2/C_1)(C_1 K - C_2 K)]}. \quad (A2)$$

When two consumers are present in equal densities at equilibrium

$$T_1 = \frac{C_1 \hat{R} + C_2 \hat{R}}{1 + (C_1 \eta_1 + C_2 \eta_2) \hat{R}} \quad (\text{A3})$$

Combining (A2) and (A3) results in the requirement that

$$\hat{R} > \frac{K(C_1 C_2 - C_2^2)}{C_1^2 + C_1 C_2 + K(C_1^2 C_2 \eta_2 - C_1^2 C_2 \eta_1 + C_1 C_2^2 \eta_1 - C_1 C_2^2 \eta_2)} \quad (\text{A4})$$

(2) *If Both Consumers are Present in Equal Densities, Each Resource Should Be Able to Increase When It Is Near Zero Population Density Regardless of the Density of the Other Resource.* Conditions for increase are most stringent when both resources are near zero. In this case the condition for  $dR_i/dt$  in (8) to be positive is that  $(C_1 + C_2)N < r$ . If  $N_1 = N_2$ , and  $\bar{R}_1 = \bar{R}_2$ , an expression for  $\bar{R}$  may be derived from (8) by solving a quadratic equation. The constraint  $(C_1 + C_2)N < r$  can then be shown to imply

$$\bar{R} > \frac{K(C_1 \eta_1 + C_2 \eta_2) - 1}{C_1 \eta_1 + C_2 \eta_2} \quad (\text{A5})$$

It may be shown by a stability analysis of the linearized version of (8) that (A5) also ensures that the two-resource steady state is locally stable. Thus it is necessary that  $\bar{R}$  in expression (11) or (12) be greater than the larger of the right-hand sides of (A4) or (A5). It should be noted that (A4) is necessary only when  $\alpha$ 's are calculated at the consumer species' equilibrium densities, but (A5) applies for all steady-state resource densities.

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#### REFERENCES

- ABRAMS, P. A. 1975. Limiting similarity and the form of the competition coefficient, *Theo. Pop. Biol.* 8, 356-375.
- ABRAMS, P. A. 1977. Density independent mortality and interspecific competition; a test of Pianka's niche overlap hypothesis, *Amer. Natur.* 111, 539-552.
- ABRAMS, P. A. 1979. Some comments on measuring niche overlap, *Ecology*, in press.
- ABRAMS, P. A. 1980. Are competition coefficients constant? Inductive vs. deductive approaches, *Amer. Natur.*, in press.
- CASE, T. J. AND GILPIN, M. E. 1974. Interference competition and niche theory, *Proc. Nat. Acad. Sci. USA* 31, 3073-3077.

- CHRISTIANSEN, F. B. AND FENCHEL, T. M. 1977. "Theories of Populations in Biological Communities," Springer-Verlag, Berlin.
- CODY, M. L. 1974. Competition and the Structure of Bird Communities," Princeton Univ. Press, Princeton, N. J.
- HOLLING, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation, *Mem. Entomol. Soc. Canad.* **45**, 1-60.
- HOLT, R. D. 1977. Predation, apparent competition and the structure of prey communities, *Theor. Pop. Biol.* **12**, 197-229.
- LAWLOR, L. R. AND MAYNARD SMITH, J. 1976. The coevolution and stability of competing species, *Amer. Natur.* **110**, 79-99.
- MACARTHUR, R. H. 1968. The theory of the niche, in "Population Biology and Evolution" (R. Lewontin, Ed.), Syracuse Univ. Press, Syracuse, N.Y.
- MACARTHUR, R. H. 1970. Species packing and competitive equilibria for many species, *Theor. Pop. Biol.* **1**, 1-11.
- MACARTHUR, R. H. 1972. "Geographical Ecology," Harper & Row, New York.
- MACARTHUR, R. H. AND LEVINS, R. 1967. The limiting similarity convergence, and divergence of coexisting species, *Amer. Natur.* **101**, 377-385.
- MAY, R. M. 1973. "Diversity and Stability in Model Ecosystems," Princeton Univ. Press, Princeton, N.J.
- MAY, R. M. 1976. "Theoretical Ecology: Principles and Applications," Saunders, Philadelphia.
- MAY, R. M. AND MACARTHUR, R. H. 1972. Niche overlap as a function of environmental variability, *Proc. Nat. Acad. Sci. USA* **69**, 1109-1113.
- MURDOCH, W. W. AND OATEN, A. 1975. Predation and population stability, *Advan. Ecol. Res.* **9**, 1-131.
- OATEN, A. 1977. Transit time and density-dependent predation on a patchily distributed prey, *Amer. Natur.* **111**, 1061-1075.
- PIANKA, E. R. 1972.  $r$  and  $K$  selection or  $b$  and  $d$  selection? *Amer. Natur.* **106**, 581-589.
- PIANKA, E. R. 1974. Niche overlap and diffuse competition, *Proc. Nat. Acad. Sci. USA* **71**, 2141-2145.
- ROUGHGARDEN, J. 1974. Species packing and the competition function with illustrations from coral reef fish, *Theor. Pop. Biol.* **5**, 163-186.
- SCHOENER, T. W. 1974a. Resource partitioning in ecological communities, *Science* **185**, 27-39.
- SCHOENER, T. W. 1974b. Some methods for calculating competition coefficients from resource utilization spectra, *Amer. Natur.* **108**, 332-340.
- YODZIS, P. 1977. Harvesting and limiting similarity, *Amer. Natur.* **111**, 833-841.
- YOSHIYAMA, R. M. AND ROUGHGARDEN, J. 1977. Species packing in 2 dimensions, *Amer. Natur.* **111**, 107-121.