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Source: *Ecology*, Vol. 56, No. 4 (Jul., 1975), pp. 881-892

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1936298>

Accessed: 26/01/2010 12:07

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A MODEL FOR TROPHIC INTERACTION¹

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Abstract. A nonlinear function general enough to include the effects of feeding saturation and intraspecific consumer interference is used to represent the transfer of material or energy from one trophic level to another. The function agrees with some recent experimental data on feeding rates. A model using this feeding rate function is subjected to equilibrium and stability analyses to ascertain its mathematical implications. The analyses lead to several observations; for example, increases in maximum feeding rate may, under certain circumstances, result in decreases in consumer population and mutual interference between consumers is a major stabilizing factor in a nonlinear system. The analyses also suggest that realistic classes of consumer-resource models exist which do not obey Kolmogorov's Criteria but are nevertheless globally stable.

Key words: *Consumer-resource models; Kolmogorov Criteria; limit cycle; predator-prey relation; trophic interaction.*

INTRODUCTION

Development of ecosystem models has become an increasingly active area of research in ecology. The models produced almost universally consider consumer and macrodecomposer processes involving trophic interactions between components of the system. As a result of intensive modeling efforts, particularly within the International Biological Program, numerous mathematical expressions have been presented to simulate feeding relationships. Few of these expressions have been subjected to analysis sufficiently detailed to provide a clear understanding of the implications of the mathematical formulation of the model. As ecosystem models begin to be applied to environmental problems, it will become increasingly important to investigate the mathematical properties of individual functions in the models.

The earliest expressions for trophic interaction (Lotka 1925, Volterra 1928) considered the feeding rate, F , as directly proportional to the product of the magnitudes of consumer supply, x_2 , and food supply, x_1 ,

$$F = fx_1x_2 \quad (1)$$

where f is a proportionality constant. The magnitudes were ordinarily expressed as numbers of individuals, but a similar relationship applies for units of biomass per unit area. Extensive analyses are available for models utilizing Eq. (1) (e.g., Goel et al. 1971).

However, this formulation has serious conceptual shortcomings, as pointed out by Smith (1952) and

Minorsky (1962). Equation (1) appears inadequate under conditions of abundant food supply where feeding rate should become proportional only to the consumer population, x_2 . When food is superabundant, consumers will feed at a maximum rate per unit consumer biomass, and further increases in food supply will not be reflected in increased feeding rates. Therefore, modifications of Eq. (1) have been suggested (Ivlev 1961, Gallopin 1971a, b) of the form

$$F = fx_2(1 - e^{-cx_1}) \quad (2)$$

where f and c are constants. An alternative expression,

$$F = fx_1x_2/(c + x_1) \quad (3)$$

where f and c are constants, has been offered by Watt (1959) and Holling (1959a) and has recently been examined in the more general case where multiple food species are present (Marten 1973). Equations (2) and (3) both permit feeding rate to become proportional to consumer populations as food supply becomes abundant. Gallopin (1971a, b) has provided a mathematical analysis of a model utilizing Eq. (2).

Equations (2) and (3) extend the range of values for x_1 and x_2 over which the feeding term is realistic. However, situations can occur in which consumer population density increases, but F will not increase proportionally as a result of mutual interference between consumers. Predation efficiency therefore decreases. Experimental studies on the feeding of the ciliate *Woodruffia metabolica* on species of *Paramecium* (Salt 1967) and *Didinium nasutum* on *Paramecium aurelia* (Salt 1974) indicate that feeding rates per unit consumer, F/x_2 , react strongly to changes in the density of the consumers. The reasons for this are not understood and may result from

¹ Manuscript received 25 September 1973; accepted 17 January 1975.

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behavioral characteristics. As Salt (1967, 1974) points out, such dependence of F/x_2 on x_2 is likely to be a general phenomenon. Hassell (1971) has shown that the searching efficiency of the insect parasite, *Nemeritis canescens*, decreases at high parasite densities. This appears to be primarily a result of mutual interference. Wynne-Edwards (1962) provides numerous examples of intraspecific social behavior, many of which appear to cause a dependence of F/x_2 on consumer density.

Therefore, both on intuitive and experimental ground, dependence of F/x_2 on x_2 is suggested. However, the feeding rate, F , defined by Eq. (2) or (3) has the property that F/x_2 is independent of x_2 . It follows that a more general formulation of F is necessary.

INCLUSION OF CONSUMER INTERFERENCE

The term introduced in this paper differs from the above-mentioned models by including negative effects of increased consumer biomass on the feeding rate. A model of two-species interaction based on this term is analyzed. The equilibrium values and stability of the system are studied as functions of the parameter values of the model, and the ecological significance of the observed relations is discussed.

A term which is simple enough for detailed analysis yet which might adequately simulate many cases of trophic interaction characterized by consumer interference is the following:

$$F = f_{12}x_1x_2 / (b_2 + x_2 + W_{12}x_1) \quad (4)$$

where f_{12} , b_2 , and W_{12} are parameters of the model measured in units of time^{-1} , consumer population density, and consumer population density/food population density, respectively. The food and consumer populations, x_1 and x_2 , may be measured either in units of density of individuals or density of biomass. The parameters of Eq. (4), discussed in detail below, will be considered as constants throughout our analyses. Application of Eq. (4) to real situations would require that the parameters be expressed as functions of environmental variables such as temperature or population characteristics such as age structure.

We present the trophic interactions function as an empirical relationship and, therefore, we will not make an attempt to derive the term. The parameters of the term can be evaluated by fitting the term to experimental data. We have found the function to be consistent with the data of Salt (1974) for *Didinium nasutum* feeding on *Paramecium aurelia*.

The parameters can be interpreted ecologically by examining what happens to the trophic interaction function as each of the terms in its denominator becomes large relative to the other terms.

The parameter W_{12} is an empirical weighting

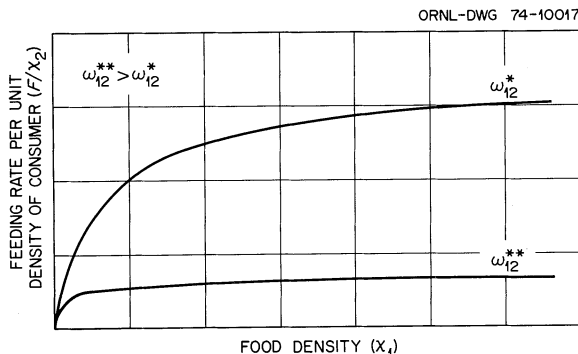


FIG. 1. Feeding rate per unit consumer density, F/x_2 , vs. food density, x_1 . F/x_2 approaches a different limiting value, as $x_2 \rightarrow \infty$, for each of two arbitrarily selected parameter values, W_{12}^* , and W_{12}^{**} .

factor which is a measure of the abundance of food relative to the consumer population and the environment in which the food and consumer interact. If $W_{12}x_1 \gg b_2 + x_2$, then food is superabundant; i.e., an increase in food density, x_1 , will not increase the rate of feeding per unit consumer, F/x_2 . For this condition, F/x_2 is a constant equal to f_{12}/W_{12} . Hence, if we examine feeding rate per unit consumer as a function of food density for different values of W_{12} (Fig. 1), we note that as W_{12} increases, feeding rate per unit consumer saturates at lower food densities and the maximum value of F/x_2 decreases.

If consumer population density, x_2 , is increased while the food population density, x_1 , is held constant, then when $x_2 \gg W_{12}x_1 + b$, the trophic interaction term, F , becomes $f_{12}x_1$, a linear donor-dependent function where f_{12} is the rate constant. Also, the feeding rate per unit consumer population density varies inversely with consumer population density (Fig. 2). If this behavior is a result of mutual interference among consumers, then this mutual interference is affected by food density as well as consumer density, since x_2 must be much

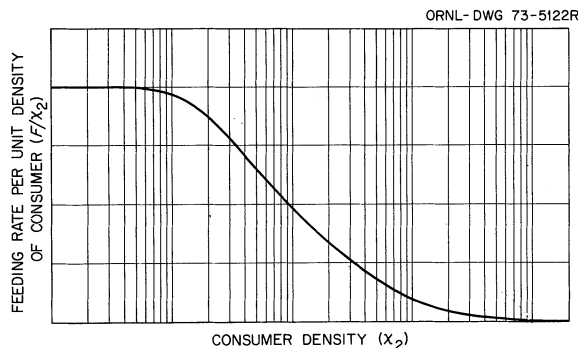


FIG. 2. Feeding rate per unit consumer density, F/x_2 , vs. consumer density, x_2 . The limiting value of F/x_2 as $x_2 \rightarrow 0$ is a function of x_1 . $F/x_2 \rightarrow 0$ as $x_2 \rightarrow \infty$.

greater than $W_{12}x_1$ before mutual interference becomes most effective in reducing the feeding rate per unit consumer.

The parameter f_{12} can be determined directly by measuring feeding rate at high consumer population densities. If f_{12} has been determined, W_{12} can be estimated by measuring feeding per unit consumer at high food densities.

The parameter b_2 relates the densities of food and consumer to the environment in which they interact. If the b_2 parameter were not present in the denominator of the trophic interaction term (Eq. 4), then the feeding rate per unit consumer, F/x_2 , would be solely a function of the relative densities of food and consumer populations, x_1/x_2 , and independent of the absolute densities of the populations. The feeding rate per unit consumer density should depend on the absolute as well as the relative densities of the populations. Feeding rate is affected by whether food and consumer densities are high or low within the environment in which interaction occurs. For instance, even if the weighted density of food, $W_{12}x_1$, greatly exceeds the consumer density, x_2 , the food may not be superabundant to the consumer unless the density of food is high within the environment. The magnitude of b_2 is a measure of the abundance of food and consumer relative to the environment in which they interact. When $b_2 \gg W_{12}x_1 + x_2$, the trophic interaction term, F , becomes functionally identical to the standard Lotka-Volterra interaction term (Eq. 1).

In order to investigate the behavior of an ecological model based on Eq. (4), it is necessary to incorporate the trophic interaction term into a set of differential equations which expresses the rate of change of trophically related populations. Analyses are performed on the special case of a two-level, two-population system.

$$\begin{aligned} \dot{x}_1 &= \left[a_1 - \frac{f_{12}x_2}{b_2 + x_2 + W_{12}x_1} - d_1 - g_1x_1 \right] x_1 \\ &\equiv K_1(x_1, x_2)x_1 \end{aligned} \tag{5}$$

$$\begin{aligned} \dot{x}_2 &= \left[\frac{e_{12}f_{12}x_1}{b_2 + x_2 + W_{12}x_1} - d_2 - g_2x_2 \right] x_2 \\ &\equiv K_2(x_1, x_2)x_2. \end{aligned} \tag{6}$$

The feeding input to species one is a_1x_1 ; that is, species one is assumed to feed on an autotroph in abundant supply. The parameter e_{12} is a conversion factor measured in units of population density of species two/population density of species one. The conversion factor equals the fraction of species two produced per unit of species one as a result of a predation event. In the numerical calculations in the text, we assume that the conversion factor cannot exceed unity. This is obviously true when population

densities are measured in quantities that are conserved, such as energy or biomass. However, for a nonconserved quantity such as number of individuals, it is possible that the conversion factor could exceed unity. The analytical inequalities related to stability that are derived in the next section are valid for all values of $e_{12} > 0$.

The parameters d_i and g_i are measured in units of time⁻¹ and (time × population density of species i)⁻¹, respectively. The parameter d_i is the rate constant for linear (i.e., density-independent) nonpredatory losses of population i . The parameter g_i is the rate constant for quadratic (Verhulst, density-dependent) nonpredatory losses of population i . The use of a quadratic loss term produces a sigmoid growth curve for x_1 in the absence of predation. If the populations are measured in units of individuals, then nonpredatory losses would only refer to mortality. If the units were biomasses, then the losses would include other processes, such as respiration.

The parameters d_i and g_i can be determined by considering the nonpredatory loss rate per unit population density, $d_i + g_ix_i$. As x_i approaches zero, the loss rate per unit population approaches a constant d_i , which is the density-independent loss rate. The parameter g_i is the slope of the line showing increasing loss per unit population density with increasing density, x_i . Both parameters can therefore be estimated from linear regression of nonpredatory loss rate per unit population density as a function of population density. Note that the estimation of g_i does not depend on the measurement of a parameter corresponding to carrying capacity of the environment, a measurement which is difficult or impossible to make for most situations.

MATHEMATICAL ANALYSIS

The major goal of this and the next few sections is the determination of the biomass equilibrium values, x_1^* and x_2^* , and stability of the system.

Investigation of the pair of nonlinear Eq. (5) and (6) is most conveniently carried out in a two-dimensional state space in which x_1 and x_2 form the coordinate axes.

The mathematical analysis of Eq. (5) and (6) that follows will lack generality only in that the $g_2x_2^2$ term, representing intraspecific density-dependent effects on the consumer, will be considered negligible; however, its qualitative effects will be considered. If x_1 represents herbivores and x_2 represents carnivores, it seems valid to assume that food is the principal limiting factor on x_2 (Hairston et al. 1960).

From Eq. (5) and (6) it is obvious that the coordinate axes are zero isoclines, curves in the state plane where the derivative of one or the other of the variables vanishes. But the most important zero

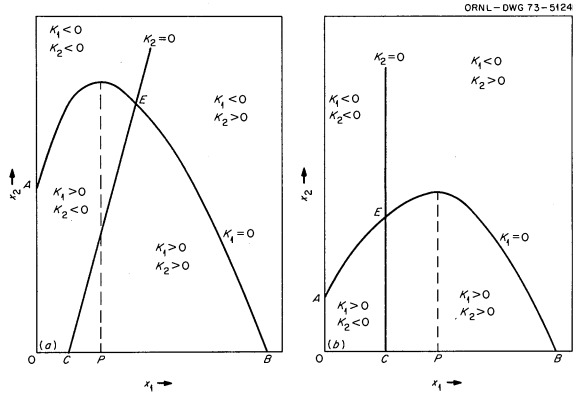


FIG. 3. State plane diagrams. (a) is appropriate to Eq. (7) and (8) when the maximum possible feeding rate by x_2 on x_1 is greater than the intrinsic growth rate of x_1 ($f_{12} > a_1 - d_1$). (b) is appropriate to the case when Eq. (9) is used as the trophic interaction term. In both cases g_2 is assumed negligible. K_1 and K_2 are abbreviations for $K_1(x_1, x_2)$ and $K_2(x_1, x_2)$; note they alternate signs in the four regions defined by the zero isoclines $K_1 = 0$ and $K_2 = 0$. A , B , C , and E are defined in the text and P denotes the position of the peak of the $K_1 = 0$ isocline.

isoclines characterizing the state plane are the following:

$$K_1(x_1, x_2) = 0$$

$$x_2 = \frac{(b_2 + W_{12}x_1)(a_1 - d_1 - g_1x_1)}{f_{12} - a_1 + d_1 + g_1x_1} \quad (7)$$

and

$$K_2(x_1, x_2) = 0$$

$$x_2 = -b_2 + (1/d_2)(e_{12}f_{12} - W_{12}d_2)x_1. \quad (8)$$

The zero isoclines divide the plane into regions in which the variables x_1 and x_2 are either increasing or decreasing (Fig. 3a and 4).

When $f_{12} > a_1 - d_1$ (which means that the maximum feeding rate by x_2 is greater than the intrinsic growth rate of x_1), the isoclines (Fig. 3a) are similar to those pictured by Rosenzweig (1971) (see his Fig. 1 and our Fig. 3b). One noticeable difference is the slope of the line defined by $K_2(x_1, x_2) = 0$. In Rosenzweig's model this isocline is represented by $x_1 = C$, where C is a constant. This latter behavior is characteristic of models where the feeding rate,

$$f_{12}x_1x_2/(b_2 + x_1), \quad (9)$$

of Holling (1959a) and Watt (1959) is used. The positively sloping curve of the $K_2(x_1, x_2) = 0$ isocline in our model reflects the additional effects of consumer interference.

If the intrinsic growth rate of the food is greater than the maximum consumption rate of x_2 (i.e., $f_{12} < a_1 - d_1$), there exists a certain minimum level, $x_1 = (a_1 - d_1 - f_{12})/g_1$, below which the equilibrium density of species one cannot fall (Fig. 4).

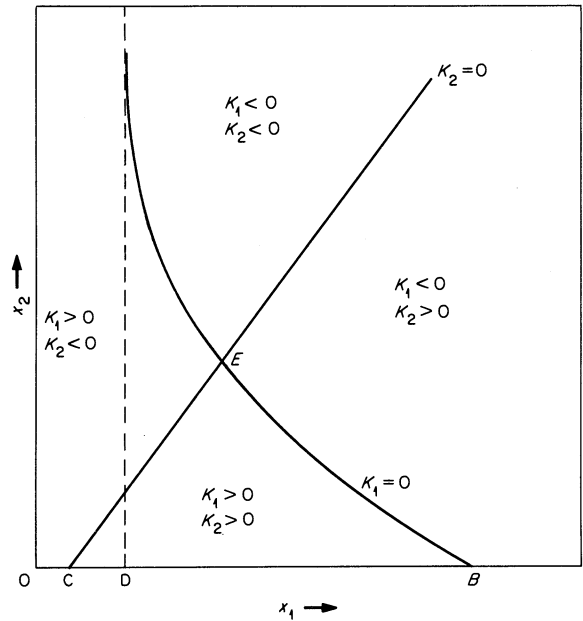


FIG. 4. State plane diagram appropriate to Eq. (7) and (8) when the maximum possible feeding rate by x_2 on x_1 is smaller than the intrinsic growth rate of x_1 ($f_{12} < a_1 - d_1$). K_1 and K_2 are abbreviations for $K_1(x_1, x_2)$ and $K_2(x_1, x_2)$. A , B , C , and E are defined in the text and $x_2 \rightarrow \infty$ as x_1 approaches D from the right.

BIOMASS EQUILIBRIA

The point at which the two zero isoclines intersect (Fig. 3 and 4) is the biomass equilibrium point, denoted by $E = (x_1^*, x_2^*)$. There are several other important points on the graphs at which the isoclines intersect the coordinate axes or approach asymptotes. These are noted in Fig. 3 and 4 and are easily derived from Eq. (7) and (8):

$$K_1(0, A) = 0 \Rightarrow A = \frac{b_2(a_1 - d_1)}{f_{12} - (a_1 - d_1)} \quad (10a)$$

$$K_1(B, 0) = 0 \Rightarrow B = (a_1 - d_1)/g_1 \quad (10b)$$

$$K_2(C, 0) = 0 \Rightarrow C = d_2b_2/(e_{12}f_{12} - W_{12}d_2) \quad (10c)$$

for $f_{12} < a_1 - d_1$,

$$x_2 \rightarrow \infty \text{ as } x_1 \rightarrow D = (a_1 - d_1 - f_{12})/g_1. \quad (10d)$$

Points B and 0 in Fig. 3 and 4 are also equilibrium points, since both derivatives vanish. However, B represents a condition where x_2 is extinct and 0 represents a condition where both x_1 and x_2 are extinct. In this paper, we will confine our discussion to the properties of E .

Examination of Fig. 3 and 4 leads to the following conclusion: for the equilibrium point E to exist in the first quadrant ($x_1^* > 0$, $x_2^* > 0$), it must be true that both

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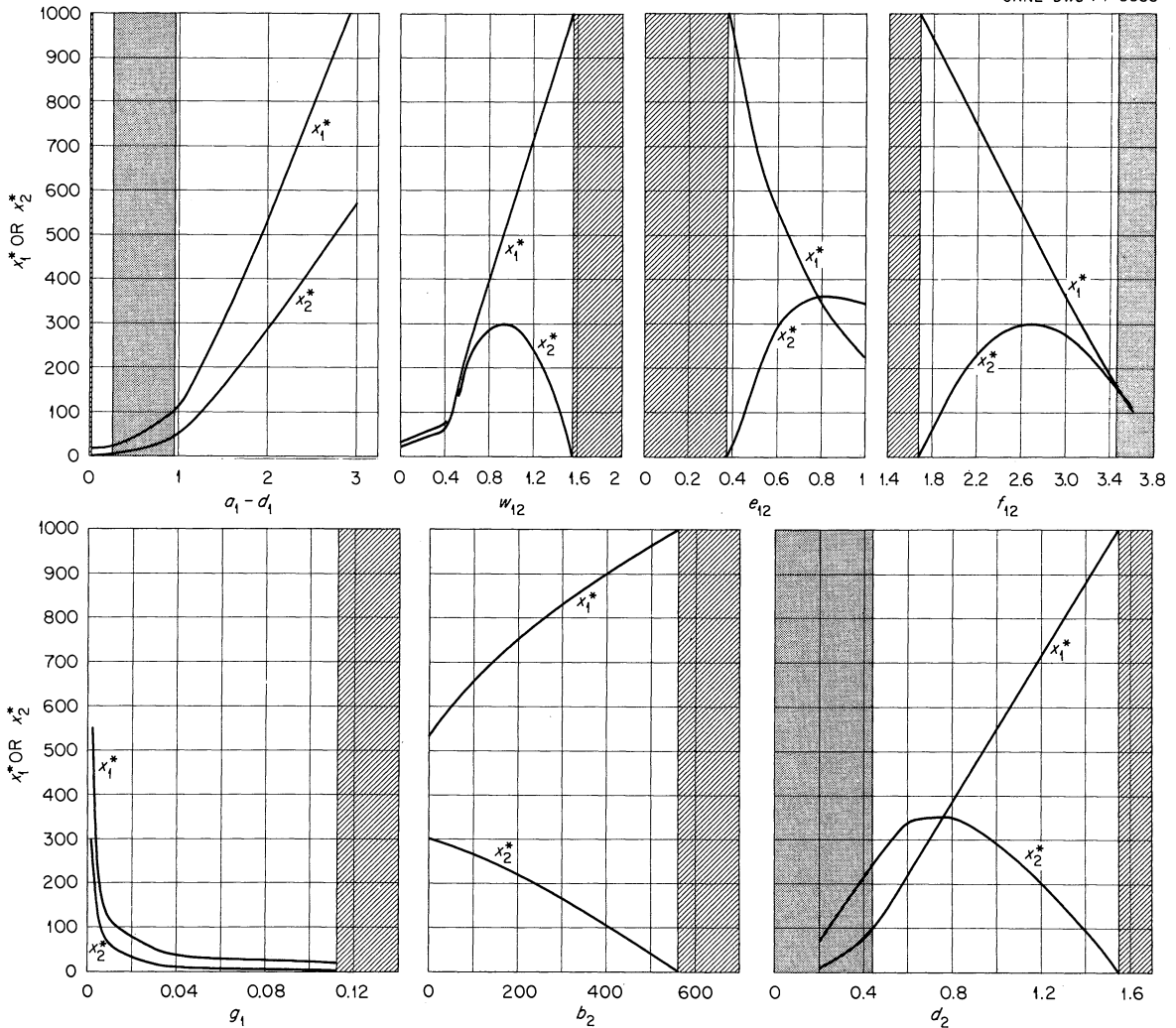


FIG. 5. Equilibrium biomasses x_1^* and x_2^* as functions of parameters of the model. Each of seven parameters is varied; in the graphs where particular parameters are not varied, they have the values (in arbitrary units): $a_1 - d_1 = 2.0$, $g_1 = 0.002$, $g_2 = 0.0$, $f_{12} = 2.6$, $e_{12} = 0.6$, $W_{12} = 1.0$, $d_2 = 1.0$, and $b_2 = 10$. Hatched regions represent parameter values for which x_2 becomes extinct. Dotted regions represent parameter values for which equilibrium point is unstable and a stable limit cycle solution exists.

$$e_{12}f_{12} > W_{12}d_2 \tag{11a}$$

and

$$B > C. \tag{11b}$$

Ecologically, (11a) asserts that maximum conversion by x_2 must be greater than respiration and mortality. The second inequality can be interpreted to mean that, in the presence of abundant prey, the rate of increase in predator density resulting from feeding must exceed the loss rate caused by mortality. These are obvious constraints, but they verify that the model is reasonable.

Biomass equilibrium can be expressed analytically from Eq. (7) and (8):

$$x_1^* = \frac{1}{2} \left(\frac{a_1 - d_1}{g_1} - \frac{e_{12}f_{12} - W_{12}d_2}{g_1e_{12}} \right) + \frac{1}{2} \left[\left(\frac{a_1 - d_1}{g_1} - \frac{e_{12}f_{12} - W_{12}d_2}{g_1e_{12}} \right)^2 + \frac{4b_2d_2}{g_1e_{12}} \right]^{\frac{1}{2}} \tag{12a}$$

$$x_2^* = \frac{(a_1 - d_1 - g_1x_1^*)(b_2 + W_{12}x_1^*)}{f_{12} - a_1 + d_1 + g_1x_1^*}. \tag{12b}$$

We examine the effects on the equilibrium values of variations of the model's parameters (Fig. 5) by choosing a set of values for the parameters and then

varying each parameter while holding the rest constant.

Intrinsic Growth Rate, $a_j - d_1$ (Fig. 5).

An increase in $a_1 - d_1$, the intrinsic growth rate of x_1 , while the other parameters are held constant is accompanied by an increase in the value of the equilibrium point x_1^* . Because of the coupling through predation, x_2^* increases as well, though at a slower rate. There is a value of $a_1 - d_1$ below which E does not exist; at this point the equilibrium biomass of x_2^* goes to zero. There is also a range of values of the intrinsic growth rate for which E is unstable. What is very interesting is that E is stable for values of intrinsic growth rate both below and above this range. (It will be shown later that if E exists, the equations are globally stable; hence, when E is unstable, there exists a stable limit cycle.)

Density-dependent Mortality and Respiration, g_1 (Fig. 5).

As g_1 is increased, the density-dependent feedback on x_1 increases, and both x_1^* and x_2^* decrease. There is a value of g_1 at which x_2^* goes to zero and above which E vanishes. Since $a_1 - d_1$ and g_1 are closely related to the so called "r" and "K" parameters, respectively, connections can be drawn between our results and the extensive body of knowledge on r and K parameters.

Feeding Parameter, f_{12} (Fig. 5).

There is a value of f_{12} at which x_2^* is zero and below which E does not exist. As f_{12} increases above this value, x_1^* decreases monotonically whereas x_2^* increases at first and then decreases; the equilibrium point eventually becoming unstable. The criteria for such instability is discussed in the next section. The reason for the peak in x_2^* has to do with the nature of the feedback relationship between x_1 and x_2 . The population of x_2 which can be sustained depends on x_1 and f_{12} , which Holling (1959b) would call "basic" and "subsidiary" components, respectively. If f_{12} is increased to a large enough value, x_1^* decreases significantly and, through feedback, causes x_2^* to decrease. There is a particular value of f_{12} for which a maximum value of x_2 exists.

Mortality and Respiration Rate, d_2 (Fig. 5).

There is a value of d_2 below which E is unstable; an increase in d_2 above this value causes both x_1^* and x_2^* to increase. The fact that x_2^* increases as its rate of loss increases is counterintuitive but can be explained in terms of feedback from x_1^* . An increased loss rate of x_2 allows x_1^* to reach high population levels, which is of net advantage to increased x_2^* . As d_2 exceeds a certain value, how-

ever, the increased attrition begins to reduce x_2^* . Again, there is a particular intermediate parameter value which maximizes x_2^* . If d_2 is continued to be increased, eventually x_2^* goes to zero.

The last two results may be of importance to both ecological theory and the practical problems of resource management. An increase in the mortality rate of a species, or a decrease of its maximum feeding rate, can, according to this model, lead to an increase in the equilibrium biomass of the species in question. The fact that there is a value of f_{12} for which x_2 is maximized is suggestive of the "prudent predator" concept of Slobodkin (1962); it is advantageous to x_2 not to overexploit x_1 . The increase in x_2^* with increased d_2 , over certain ranges, indicates the complex effects that feedback introduces into predator control. A one-species model would not show this.

Conversion Efficiency, e_{12} (Fig. 5).

As the efficiency of conversion increases from zero to unity, a point is reached where species x_2 can exist. Continued increase of efficiency causes x_1^* to decrease while x_2^* first increases then levels off and decreases. The same type of feedback mechanisms discussed in connection with f_{12} is at work here in causing the peaking effect in x_2^* .

Food Weighting Factor, W_{12} (Fig. 5).

Increasing W_{12} is assumed, in this model, to correlate with lowering the food density at which feeding saturation occurs and the feeding rate per unit consumer at which saturation occurs for high food densities. As W_{12} increases from zero, x_1^* increases, since the feeding rate per unit consumer population is decreased. The equilibrium point x_2^* increases initially due to increasing x_1^* and then decreases due to decreased feeding rate per unit consumer. Finally a point is reached where x_2^* goes to zero.

Normalization Coefficient, b_2 (Fig. 5).

As b_2 increases, it causes an increase in x_1^* and a decrease in x_2^* since it increases the denominator of the trophic interaction term. In biological terms, an increase in b_2 decreases the abundances of food and consumer populations relative to the environment in which they interact and thus decreases the magnitude of the trophic interaction.

The model based on (9) can be shown to exhibit some of the same behavior as ours does, for example, in the peaking of x_2^* . However, one strong difference is in the behavior of x_1^* [using (9) in place of Eq. (4) in Eq. (5) and (6)] given by

$$x_1^* = (b_2 d_2) / (e_{12} f_{12} - W_{12} d_2). \quad (13)$$

This expression would indicate that x_1^* is indepen-

dent of both the intrinsic rate of growth, $a_1 - d_1$, of x_1 and its density-dependent parameter, g_1 . Thus, x_1^* is completely determined by consumption parameters. This seems an unlikely situation in nature. There is abundant evidence, given by Errington (1967) and Wynne-Edwards (1962) among others, that the equilibrium density of many animal populations is closely related to the carrying capacity of the environment. The equilibrium density of many opportunistic species should bear some relation to their growth rates. This information is not embodied in the simpler equation. The more general term, Eq. (4), appears to be more realistic because it predicts a dependence of x_1^* on $a_1 - d_1$ and g_1 as well as on the predation parameters.

STABILITY OF THE EQUILIBRIUM POINT

The equilibrium point is asymptotically stable if the system tends to return to equilibrium as $t \rightarrow \infty$ following a minor perturbation. The conditions under which E is asymptotically stable can be derived by expanding the derivatives \dot{x}_1 and \dot{x}_2 about E and examining the eigenvalues of the resulting linear equations.

The equilibrium point is asymptotically stable for those situations where the real parts of both eigenvalues are negative. The eigenvalues are given by

$$\lambda_{1,2} = \frac{1}{2} \left\{ \left(\frac{\partial K_1}{\partial x_1} x_1^* + \frac{\partial K_2}{\partial x_2} x_2^* \right) \pm \left[\left(\frac{\partial K_1}{\partial x_1} x_1^* + \frac{\partial K_2}{\partial x_2} x_2^* \right)^2 + 4 \frac{\partial K_2}{\partial x_1} \cdot \frac{\partial K_1}{\partial x_2} x_1^* x_2^* - 4 \frac{\partial K_2}{\partial x_2} \cdot \frac{\partial K_1}{\partial x_1} x_1^* x_2^* \right]^{1/2} \right\} \quad (14)$$

where

$$\frac{\partial K_1}{\partial x_1} = \alpha^{*2} f_{12} W_{12} x_2^* - g_1, \quad (15a)$$

$$\frac{\partial K_1}{\partial x_2} = -\alpha^{*2} f_{12} (b_2 + W_{12} x_1^*), \quad (15b)$$

$$\frac{\partial K_2}{\partial x_1} = \alpha^{*2} e_{12} f_{12} (b_2 + x_2^*), \quad (15c)$$

$$\frac{\partial K_2}{\partial x_2} = -\alpha^{*2} e_{12} f_{12} x_1^*, \quad (15d)$$

and

$$\alpha^{*2} = 1.0 / (b_2 + x_2^* + W_{12} x_1^*)^2.$$

Examination of equation set (15) indicates that the following inequalities are always true:

$$\frac{\partial K_1}{\partial x_2} < 0, \quad \frac{\partial K_2}{\partial x_1} > 0, \quad \frac{\partial K_2}{\partial x_2} < 0.$$

Hence, E will be asymptotically stable for those sets of parameters for which the inequalities

$$\frac{\partial K_1}{\partial x_1} x_1^* + \frac{\partial K_2}{\partial x_2} x_2^* < 0 \quad (16)$$

and

$$\frac{\partial K_1}{\partial x_1} \cdot \frac{\partial K_2}{\partial x_2} > \frac{\partial K_2}{\partial x_1} \cdot \frac{\partial K_1}{\partial x_2} \quad (17)$$

are satisfied at the point (x_1^*, x_2^*) . The latter condition (17) is automatically satisfied if Kolmogorov's

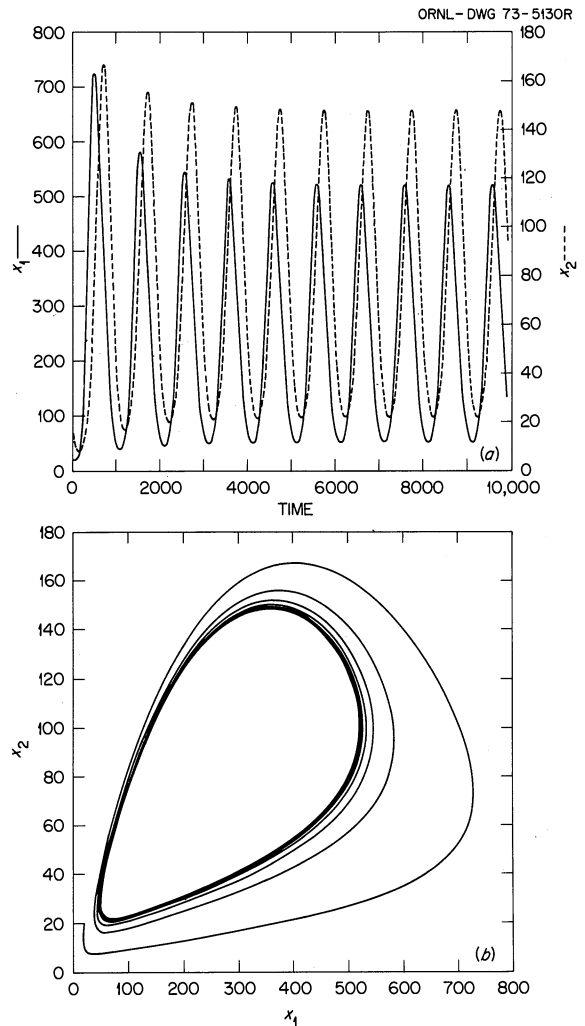


FIG. 6. Computer simulation of Eq. (5) and (6) for parameter values (in arbitrary units): $a_1 - d_1 = 2.0$, $f_{12} = 6.0$, $e_{12} = 0.4$, $W_{12} = 1.0$, $g_1 = 0.002$, $g_2 = 0.0$, $d_2 = 2.5$, and $b_2 = 10$. For these values the equations describe a limit cycle. In (a) the time behavior of x_1 and x_2 is plotted. In (b) the corresponding state plane diagram is exhibited.

Criteria hold. Kolmogorov's Criteria are useful tools in the analysis of sets of nonlinear equations like Eq. (5) and (6) (see Appendix I). If these criteria are satisfied, an equilibrium point, E , exists and the equations are globally stable; that is, no perturbation can cause one or both variables to become negative or to approach zero asymptotically with time. In our model Kolmogorov's Criteria hold except for some cases explicitly accounted for below and in Appendix I. Therefore, the system is always globally stable, implying that neither species can become extinct. If (16) is true, the equilibrium point is also "locally" stable in the sense mentioned at the beginning of this section. If (16) is not true, the local

instability of E will develop into a stable limit cycle (Fig. 6).

In terms of the model's parameters, (16) becomes

$$\frac{f_{12}[W_{12} - e_{12}]x_1^*x_2^*}{(b_2 + x_2^* + W_{12}x_1^*)^2} - g_1x_1^* < 0 \quad (18)$$

which is a necessary and sufficient condition for stability. Examination of (18) shows that a sufficient condition for E to be stable is that the conversion efficiency exceeds the weighting factor,

$$e_{12} > W_{12}.$$

Since $e_{12} < 1$, this requires that W_{12} be less than unity.

A second condition sufficient for stability is

$$\partial K_1 / \partial x_1 < 0.$$

Inspection of Fig. 3 and 4 shows that this inequality is always true when $f_{12} < a_1 - d_1$, and also for $f_{12} > a_1 - d_1$ when the equilibrium point, E , lies to the right of the peak, P (Fig. 3a). Models based on (9) can show unstable equilibria. If Kolmogorov's Criteria are satisfied, the unstable equilibria are evidence of stable limit cycles. Such systems have state plane diagrams of the form illustrated in Fig. 3b. Rosenzweig (1973) proved that state plane configurations of this form are stable for all equilibrium points to the right of P and unstable for all equilibrium points to the left of P . In our model, equilibrium points to the left of P may or may not be stable, depending on whether or not inequality (18) is satisfied. The algebraic stability criterion,

$$\{[W_{12}f_{12}x_2^*x_1^*]/[(b_2 + W_{12}x_1^*)^2]\} - g_1x_1^* < 0, \quad (19)$$

for the interaction term (9) can be compared to the new stability criterion, (18). The factor $W_{12} - e_{12}$ in (18) increases the range of parameters over which the system is stable. Thus, mutual interference between consumers, which reduces consumption efficiency as x_2^* increases, leads to increased stability of the system. It is less likely, therefore, that limit cycle oscillations will occur. Models based on (9) may seriously overestimate the probability of limit cycles.

Inequality (18) contains all information concerning stability of the system as a function of parameter values. Since x_1^* and x_2^* are functions of the parameters, this expression is more complex than it appears. To consider the effects of variations of all the parameters, one should imagine a multi-dimensional space in which the parameters form the coordinates. For regions in that space in which inequalities (11a), (11b), and (18) are true, there exists a stable equilibrium point. For regions where (11a) and (11b) hold but (18) does not, the equilibrium point is unstable but the solution con-

verges to a stable limit cycle (Appendix I). If either (11a) or (11b) is violated, then the equilibrium point, E , does not exist, x_2 goes extinct and the system is unstable. Intuitive feelings about stability lead us to classify the system when limit cycle solutions exist to be qualitatively less stable than when there is a stable equilibrium point. As May (1972) points out, limit cycle trajectories often approach the coordinate axes so closely that one would expect that in a real system x_2 would become extinct.

Since it is impossible to display conveniently more than two dimensions, the results presented are in the form of two-dimensional projections, with f_{12} plotted on the abscissa and other parameters plotted on the ordinate (Fig. 7).

A most intriguing feature is revealed in Fig. 7; for most of the parameters there are regions where, for a given f_{12} , there exists a range of parameter values for which the equilibrium point is unstable, bounded on both ends by ranges where the equilibrium point is stable. If the system lies in this type of region, then the equilibrium point can be made stable by both increasing and decreasing a single parameter while holding the other parameters constant. For example, consider the weighting factors, W_{12} . If $f_{12} = 4.0$, then the equilibrium point is unstable in the range $.64 < W_{12} < 1.5$ and stable in the ranges $0.0 < W_{12} < .64$ and $1.5 < W_{12} < 2.4$. Assume that $W_{12} = 1.0$, then the equilibrium point is unstable. The equilibrium point can now be stabilized by either increasing or decreasing W_{12} while holding the other parameters constant.

Such regions, as described above, may give rise to misleading interpretations of simulation results of complex nonlinear ecosystem models. "Sensitivity analysis" is a method frequently employed to understand the significance of parameters in complex ecosystem simulation models. In this method, after parameter values are determined on the basis of how well the model simulates either experimental data or the ecologist's intuitive feelings about how the system operates or some combination of the two, individual parameters are varied in order to assess how the parameters effect the simulation. Let us assume that this method is being applied to a total ecosystem model which contains trophic interactions employing the nonlinear term introduced in this paper and that a weighting coefficient, W_{12} , has been chosen to be varied. Assume that, under the initial setting of the parameters, the system is in a region of parameter space that is analogous to $f_{12} = 4.0$, $1.5 < W_{12} < 2.4$ in Fig. 7. If W_{12} is decreased gradually, the behavior of the system changes from an asymptotically stable equilibrium point to an unstable equilibrium point. At this stage it might be concluded that decreasing W_{12} (i.e.,

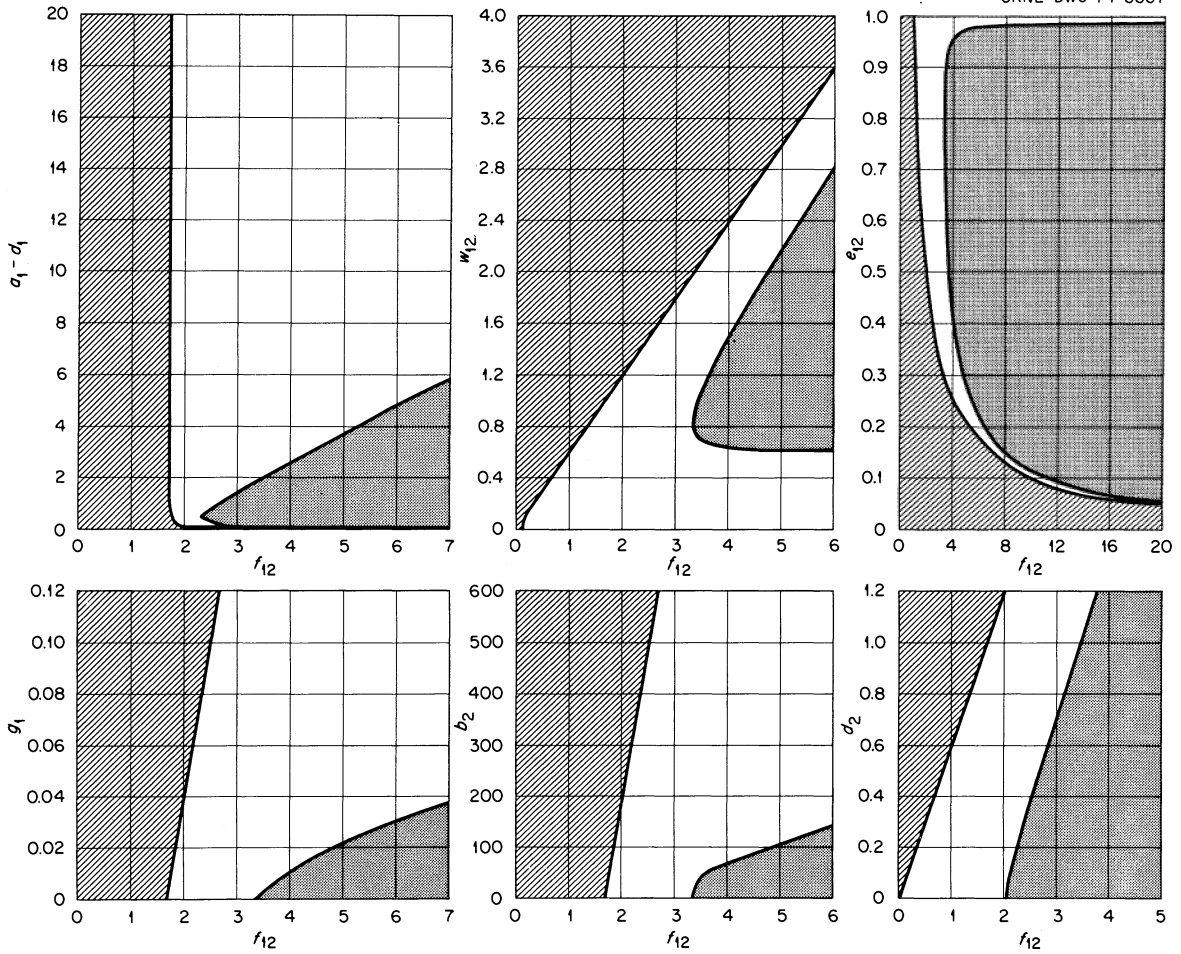


FIG. 7. Regions in parameter space where the equilibrium point is stable or unstable. In the graphs where particular parameters are not varied, they have the values (in arbitrary units): $a_1 - d_1 = 2.0$, $g_1 = 0.002$, $g_2 = 0.0$, $f_{12} = 2.6$, $e_{12} = 0.6$, $W_{12} = 1.0$, $d_2 = 1.0$, and $b_2 = 10$. Hatched regions represent parameter values for which x_2 becomes extinct. Dotted regions represent parameter values for which equilibrium point is unstable and a stable limit cycle solution exists.

removing the effect that when food becomes superabundant, the feeding rate per unit consumer population saturates) decreases stability, and the sensitivity analysis of W_{12} would be terminated. However, in reality, lower values of W_{12} would have re-established the stability of the equilibrium point; in fact, the greatest range of the feeding rate constant, f_{12} , for which both the system and the equilibrium point are stable occurs when $W_{12} = 0$. The above discussion demonstrates the desirability of applying analytical techniques to the major components of complex simulation models.

Because of the existence in parameter space of regions of an unstable equilibrium point surrounded by regions of a stable equilibrium point, it is difficult to make generalizations about how minor changes in the values of parameters will alter the basic stability of the system. One can conclude that, for a

given f_{12} , there are always values of W_{12} , g_1 , b_2 , and d_2 above which x_2 becomes extinct. The greater f_{12} is, the greater are W_{12} , g_1 , b_2 , and d_2 at which the extinction of x_2 occurs. The upper bounds on global stability placed by W_{12} and b_2 are a result of limiting the consumption rate to levels below which x_2 can be supported. The upper bound placed by g_1 is a result of limiting the population of x_1 to levels below which x_2 can be supported. The upper bound placed by d_2 is a result of increasing the rates of mortality and respiration of x_2 to the point where they can no longer be compensated by feeding on x_1 .

It has already been pointed out that when W_{12} is allowed to vary, then the greatest range of f_{12} for which both the equilibrium point and the system are stable occurs at $W_{12} = 0$. This indicates that saturation of feeding rate per unit consumer population for high food densities is not a stabilizing

mechanism in the model. The major factor in the trophic interaction term that stabilizes the model is the mutual interference between consumers as expressed by the consumer population density in the denominator.

As W_{12} decreases, Eq. (5) and (6) approach the form of linear, donor-dependent equations for a wide range of values of x_1 and x_2 ; that is,

$$f_{12}x_2x_1/(b_2 + W_{12}x_1 + x_2) \Rightarrow f_{12}x_1$$

for a wider range of the variables. Since linear, donor-dependent systems are stable, one might expect nonlinear systems to exhibit increasing stability when they approach this condition. The result is also suggestive of situations for which linear, donor-controlled models are a reliable assumption; i.e., feeding rate of consumer population is limited by abundance of food supply.

The effects of g_1 and b_2 on stability are similar. For increases in either g_1 or b_2 , both the width of the region in which the equilibrium point is stable and the width of the region where x_2 becomes extinct increase monotonically. Considering that the rate of increase in the width of the former is greater and that a stable equilibrium point implies qualitatively a more stable system than a stable limit cycle, increases in g_1 and b_2 can be considered to enhance the stability of the system.

Another general observation that can be made from Fig. 7 is that increasing the feeding rate constant, f_{12} , expands the range of the other parameters for which a stable limit cycle exists. Wiegert and Owen (1971) have pointed out that in terrestrial ecosystems, it is often true that $f_{12} \gg a_1 - d_1$; i.e., the maximum consumption rate of a herbivore population, especially insects, is much greater than the growth rate of the dominant autotrophs, trees. However, insect control by predation or density-dependent mortality would tend to stabilize such systems and prevent limit cycle behavior.

It should be cautioned that, although the properties of the parameters discussed in connection with Fig. 7 seem to be true rather generally, not all combinations of parameter values have been explored, and contrary behavior is possible in some regions of parameter values.

NONZERO VALUES OF g_2

When consumer mortality includes intraspecific density-dependent effects (i.e., $g_2 > 0$), Kolmogorov's Criteria are no longer satisfied (see Appendix I) and it would appear that global stability of the system cannot be proven. However, a detailed study shows that inclusion of nonzero g_2 can only increase both the local stability of E and the global stability of the system.

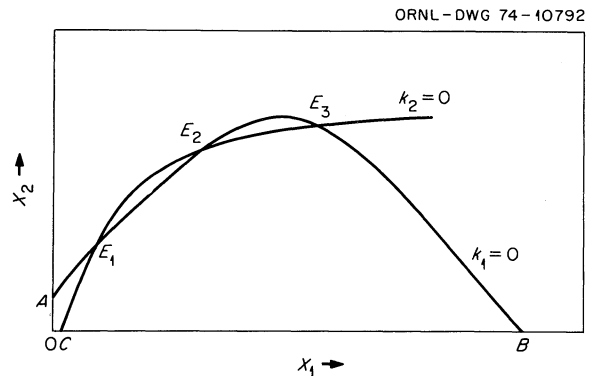


FIG. 8. State plane diagram which can occur when $g_2 > 0$. There are three equilibrium points. E_3 is always stable. E_2 is always unstable. E_1 may or may not be stable, depending on whether conditions (16) and (17) are or are not satisfied at E_1 .

If the $K_2 = 0$ isocline intersects the $K_1 = 0$ isocline to the left of its peak, there is the possibility that three equilibrium points can exist, as pictured in Fig. 8. The equilibrium point on the right-hand side of the peak is, of course, stable, while the point farthest left may be stable or unstable. Since Kolmogorov's Criteria are not satisfied, inequality (18) cannot be used alone but only in combination with (17) to determine the stability of this point, but its likelihood of being stable increases with increasing values of g_2 . The middle equilibrium point is always a saddle point and, therefore, unstable.

CONCLUSIONS

This paper has introduced a trophic interaction model suitable for a wider range of ecological conditions than previously published models. To increase the utility of this model as a component of ecosystem models, extensive analysis was performed to make the behavior of this trophic interaction term explicit and to illustrate what behavior could be expected of a larger-scale model which employed this function as a component. As large-scale ecosystem models are produced, the critical problem becomes our lack of ability to analyze and understand the total model, which may contain scores of parameters. In order to understand the behavior of the total system model, a clear understanding of the behavior of its major component parts and their interactions is valuable.

Analysis of the model revealed several ecological implications, some specific to the model and some not. Since these implications may indicate the usefulness of model analysis for increasing our understanding of system behavior, they are summarized here. (1) In a two-consumer system, the biomass of the higher trophic level may display counter-

intuitive behavior as a function of some of the parameters. Increases in feeding rate and in conversion efficiency and decreases in mortality plus respiration of the higher trophic level may, under certain circumstances, result in a decrease rather than an increase of x_2^* . (2) The assumption of decreased feeding per unit consumer population with increased consumer population density leads to increased system stability. (3) The decrease in feeding rate per unit consumer population as a result of mutual interference between consumers is a more effective mechanism for producing stability than is the saturation of feeding rate per unit consumer population density for superabundant food supplies. (4) If the maximum consumption rate per unit food biomass, f_{12} , is less than the intrinsic growth rate of the food, $a_1 - d_1$, there is some minimum value below which the equilibrium food supply cannot be decreased, no matter how large the consumer population is. (5) Increasing values of the density-dependence factors, g_1 and g_2 , tend to stabilize the system. The argument over the relative importance of density-dependent and density-independent population control has been active for a number of years (Nicholson and Bailey 1935, Smith 1935, Andrewartha and Birch 1954). The present analysis suggests that populations with dominant density-independent mechanisms will tend to destabilize a system. Such populations might occur in highly stable natural systems, such as complex forest communities, where their destabilizing effect is suppressed naturally and kept from disrupting the entire system. (6) Kolmogorov's Criteria are useful in the formulation of globally stable species interaction models. However, globally stable models can be formulated which violate the criteria.

It should be kept in mind that some of these conclusions are implications of the particular model presented here and do not necessarily have general validity. This model, like any other model, presents a hypothesis about the real system which, provided its basic assumptions are kept in mind, is useful in increasing our understanding of complex systems. A major theme of the paper has been development of a thorough understanding of the properties of the model. This is just as important as a well-motivated formulation. In elucidating the behavior of the model as fully as possible, one hopes to evaluate its strengths and weaknesses. Where the model conflicts with observations, or where hypotheses generated by the analysis are proven incorrect, one can more easily determine the invalid assumptions which must be modified. It appears to us that such a careful analysis is required for the full scope of models utilized in ecosystem analysis as an important step in understanding a total system

model and in demonstrating that development and analysis of complex models will be an increasingly important component in the advancement of ecological theory.

ACKNOWLEDGMENTS

The authors thank the Systems Ecology Group, Environmental Sciences Division, Oak Ridge National Laboratory for stimulating discussions. This group includes J. B. Mankin, H. H. Shugart and J. R. Kercher. The research was supported in part by the Eastern Deciduous Forest Biome, US-IBP, funded by the National Science Foundation under Interagency Agreement AG-199, BMS69-01147 A09 with the Atomic Energy Commission-Oak Ridge National Laboratory. Contribution No. 192 from Eastern Deciduous Forest Biome, U.S. International Biological Program. Publication No. 675, Environmental Sciences Division, Oak Ridge National Laboratory, and in part by the U.S. Atomic Energy Commission under contract with the Union Carbide Corporation.

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APPENDIX I: Application of Kolmogorov's theorem

Kolmogorov (1936) proved that under a certain set of conditions the set of differential equations

$$\dot{x}_1 = K_1(x_1, x_2)x_1 \quad (a)$$

$$\dot{x}_2 = K_2(x_1, x_2)x_2 \quad (b)$$

will have either a stable equilibrium point or stable limit cycle in the first quadrant. A limit cycle is an isolated closed trajectory in the phase plane (Fig. 5) and is stable if all nearby trajectories approach it as $t \rightarrow \infty$ (Minorsky 1962). Minorsky (1962) and Rescigno and Richardson (1967) have discussed the relevance of Kolmogorov's theorem to population dynamics modeling. In a recent paper May (1972) has shown that the conditions of the theorem can

be satisfied by several hypothesized predator-prey models. As May notes, instability of the point of equilibrium has often been assumed to result necessarily in the extinction of one or both species. If a stable limit cycle surrounds the unstable equilibrium point, however, periodic fluctuations of the population variables short of extinction may result. The importance of studying the existence of limit cycles is that, for many systems, populations undergo almost periodic fluctuations in size. Such fluctuations resemble limit cycles. Both Minorsky (1962) and May (1972) present lucid discussions as to why the observed fluctuations are more likely to correspond to limit cycles than to be the well-known periodic solutions of the Lotka-Volterra equations.

In this section Kolmogorov's Criteria are applied to the model under study, and a set of conditions is derived which prescribe the parameter ranges for which Kolmogorov's Criteria are satisfied. The conditions are:

$$a_1 - d_1 - f_{12} < 0 \quad (c)$$

$$e_{12}f_{12} - W_{12}d_2 > 0 \quad (d)$$

$$(a_1 - d_1)/g_1 > d_2b_2/(e_{12}f_{12} - W_{12}d_2) \quad (e)$$

$$a^{*2}e_{12}f_{12}b_2x_1 > g_2x_2 \quad (f)$$

Conditions (d) and (e) are identical to (11a) and (11b) in the text. Although May and others (e.g., Rescigno and Richardson 1967) have stressed the importance of Kolmogorov's Criteria, ecologically interesting systems can also be constructed which do not obey these criteria. For example, Gallopin's model (1971a, b), like many other models with extrinsically controlled inputs to the lowest trophic level, fails to satisfy the criteria and yet is a very stable system. Our model, for the case $f_{12} < a_1 - d_1$, violates condition (c), yet is stable. Inequality (f) is true everywhere in the positive quadrant only if $g_2 = 0$. However, the model remains globally stable if (d) and (e) are satisfied and $g_2 > 0$.