

FUNCTIONAL RESPONSE AND STABILITY IN  
PREDATOR-PREY SYSTEMS

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## I. STABILITY IN INCOMPLETELY SPECIFIED MODELS

We here present a criterion and two measures showing the effects of predators on the stability of prey populations. We seek ways of answering such questions as, When does a predator which "switches" tend to stabilize a prey population? Is a patchily distributed prey more likely to be stabilized by predation than a homogeneously distributed one? and Does prey clumping enhance stability?

Discussions of stability usually take place in the context of particular models, which can be investigated graphically (e.g., Rosenzweig 1971) or analytically (for reviews, see May 1972; Holling 1973) for the presence or absence of several different kinds of stability. These have been described by Lewontin (1969), May (1972), Scudo (1971), and others. A brief summary of some of the different kinds of stability follows.

The history of an ecological system can be represented as the path traced by a point on a graph whose axes are the population densities of the species involved. In many models of such systems, there are some "equilibrium points" from which no paths lead away; that is, once the system reaches an equilibrium point, it can be moved away only by some ("random") influence not represented in the model. "Stability" relates to the tendency of the system to return or to be attracted to such points. One can consider *local or neighborhood stability* (does the system return to the equilibrium point after a small perturbation has driven it away?); *global stability* and *domain of attraction* (is there a region of points from which the system will return to the equilibrium point, and can we describe this region?); and *structural stability* (how do the stability properties of the system change with the parameters of the model?). It may also be that there is no equilibrium point but a well-defined "limit cycle", a closed path on the graph which our system never leaves once it is on it. This, too, can be stable or unstable. In all these cases one can also ask how quickly the system returns to equilibrium, giving some idea of the system's invulnerability to frequent, small, random perturbations.

All of the above ways of viewing stability in models assume the existence of an equilibrium point or cycle, and consider whether and how the system returns

to equilibrium after perturbation. In real communities stability is more difficult to define and analyze, and we are usually concerned with the "amount of fluctuation" in population densities or the similarity in species composition through time. While these properties are probably related to the formal types of stability described above, the relationship is not clear or straightforward; indeed, in real populations there is even a problem in defining "equilibrium" and "perturbation" (Murdoch 1970).

In addition, questions like those asked at the beginning of this paper require us to discuss stability without a completely specified model. We want to be able to evaluate the effects of a small number of simple, testable assumptions, which affect only one (or a few) of the many interactions that occur in ecosystems and which may apply in several different systems. We would like to be able to say whether these assumptions, if true, enhance stability, without reference to a particular model.

We began with questions about features of the way predators choose or search for prey. These features may well occur in many different systems but are likely to have their effects (especially short-term effects) almost entirely through the functional response, i.e., the relation between the prey population size and the number of prey eaten per unit time by a single "average" predator. There are other ways for a predator population to respond to changes in prey population size: the predator population can change (numerical response), or the predators themselves can change—grow bigger, for example, or mature faster (developmental response). However, these responses, and their effects, are likely to be slower than the functional response and also dependent on it. Consequently, we feel justified in discussing the stabilizing effects of various types of predator behavior or prey distribution in terms of the stabilizing effects of the resulting functional responses. This reduces our original questions to, Given a functional response, is it stabilizing and how stabilizing is it?

A precise answer to such a question is almost surely impossible. Even if agreement could be reached about the kind of stability to be considered, any functional response will probably be stabilizing in some models and destabilizing in others. More precisely, given any functional response, there will exist both stable and unstable models of which it is a component. Thus any classification into "stabilizing" and "destabilizing" would be misleading. Our best hope seems to be a measure in the form of a number attached to each functional response to indicate *how* stabilizing it is. But this, too, presents difficulties. For example, if  $f$  and  $g$  are two functional responses, it is possible that each is stabilizing in some models where the other is not. If so, how are we to say which is "more stabilizing"?

The impossibility of a precise answer and the desire for *some* answer make it necessary to find some criteria for measuring the *extent* to which a functional response enhances stability and to defend them by arguments rather than proofs.

Throughout what follows,  $H$  stands for the prey population size, and  $f(H)$  for the functional response, i.e., for the number of prey killed per unit time by a

single “average” predator. We first give a criterion according to which a functional response can be said to be stabilizing or not at a particular prey population size and a measure of the extent to which a given functional response is stabilizing. These are supported by arguments which, while not proofs, have (we believe) considerable intuitive force. We then suggest one other measure and try to support all three by reference first to the simplest model involving functional response and then, more vaguely, to more general models.

## II. A CRITERION AND A MEASURE OF STABILITY

Our criterion is a standard one: predation is stabilizing at a prey population size of  $H$  if it causes density-dependent mortality. That is, an increase or decrease in the prey population should result in a greater than proportionate increase or decrease in the rate of predation by a single predator. This means that  $f(H)/H$  (the risk run by the average prey) must increase with  $H$ ; i.e., its derivative must be positive. This requires

$$f'(H) > \frac{f(H)}{H}. \quad (1)$$

See figure 1.

If  $f$  satisfies (1), we will say that  $f$  is stabilizing at  $H$ . There are obvious reasons (Holling 1959) for believing that (1) cannot hold for very large values of  $H$ ; limitations of time and gut capacity will cause  $f$  to level off at some maximum value. This suggests that we might measure the tendency of  $f$  to stabilize by the size of the range of  $H$  over which (1) holds. If it were possible for two functional responses each to satisfy (1) at points where the other did not, this measure would not be very helpful; but virtually every functional response curve either proposed in theory or observed experimentally (i.e., types 1, 2, and 3, [Holling 1965; Murdoch and Oaten 1975]) has either not satisfied (1) at all (types 1 and 2) or has satisfied it over an entire interval,  $(0, H_m)$  (type 3; see fig. 1).

Thus our first measure of *the extent to which  $f$  is stabilizing* is  $H_m$ , the maximum (strictly, the supremum) of the values of  $H$  for which (1) holds:

$$H_m = \sup \left[ H : f'(H) > \frac{f(H)}{H} \right].$$

As shown in figure 1, it is the first point at which the tangent to the curve passes through the origin. Our other measure, which we discuss later, is  $f(H_m)$ .

Arguments supporting the use of (1) and  $H_m$  are obvious and simple. Equation (1) requires that, if  $H$  is the equilibrium, an increase in the prey population results in an increase in predation intensity, so that the risk of the “average” prey individual is increased. That is, each individual member of the prey population has a greater instantaneous probability of being killed by our average predator when the prey population is increased. Conversely, when the prey population is reduced, there is a reduction in the risk, per predator per unit time, of each prey individual. The prey population is at equilibrium at  $H$  if its death

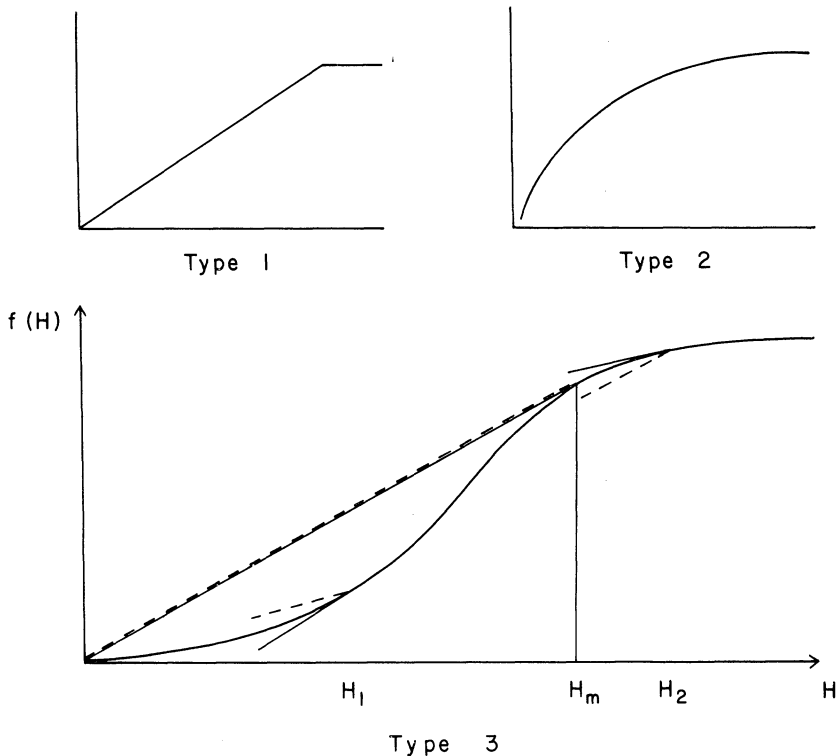


FIG. 1.—The three types of functional response. In the diagram for type 3, the dashed lines indicate the line joining  $[H, f(H)]$  to the origin; the solid lines give the direction of the tangent,  $f'(H)$ . At  $H_1$ ,  $f'(H_1) > f(H_1)/H_1$ , so (1) is satisfied; at  $H_m$  the two lines are identical; at  $H_2$ , the line to the origin has a steeper slope than the tangent. Our measures are  $H_m$  and  $f(H_m)$  (the value of the functional response at  $H_m$ ).

rate and birth rate are equal at this size; the equilibrium is stable if an increase in population size results in the death rate being greater than the birth rate, while a decrease results in the death rate being smaller than the birth rate. Other factors besides predation will affect this, but predation will contribute to this stability if the death rate due to predation increases or decreases with  $H$ . In the short run this death rate will depend on the proportion of prey killed per unit time per predator, i.e., on  $f(H)/H$ , rather than on the number of predators.

The measure  $H_m$  shows how large the prey population can get and still be controlled by the predator in this sense of an increasing per capita death rate. If the prey population increases beyond  $H_m$ , the prey has escaped in the sense that the death rate due to predation will now decrease as prey numbers increase; thus prey numbers would continue to grow until prevented by factors other than predation (shortage of food or space, for example). An increase in the predator population seems less likely to be effective: it depends on the conversion of prey into new predators, which is itself dependent on the functional response, and this conversion takes time. Thus  $(0, H_m)$  can be taken as the range over

which predation is stabilizing: if the equilibrium prey population is in this range, then predation will, in the short run, tend to return the prey population to equilibrium after any perturbation which does not take it out of this range.

### III. THE LOTKA-VOLTERRA MODEL AND TWO MEASURES OF STABILITY

The simplest commonly used model of a predator-prey interaction is the Lotka-Volterra model,

$$\frac{dH}{dt} = aH - bPH; \quad \frac{dP}{dt} = -cP + dPH, \quad (2)$$

where  $H$  and  $P$  are the prey and predator populations. Numerous objections can be and have been made to this model: it assumes that (i)  $H$  and  $P$  are affected by no varying influences but each other; (ii) all effects are instantaneous, no time lag; (iii) there is no randomness; (iv) anything that could be constant is constant: the intrinsic rates of change of the prey ( $a$ ) and predator ( $-c$ ), the proportion of prey eaten by the average predator ( $b$ ), and the value of a consumed prey in terms of new predators ( $d/b$ ).

We can introduce a nonlinear functional response by changing the model to

$$\frac{dH}{dt} = aH - Pf(H); \quad \frac{dP}{dt} = -cP + dPf(H). \quad (3)$$

(Here,  $d$  is the old  $d/b$ .) By doing so, we are ignoring all the above objections except part of (iv).

Standard neighborhood stability analysis finds the equilibrium point,  $(H^*, P^*)$ , where  $f(H^*) = c/d$  and  $P^* = adH^*/c$ , and then takes  $H = H^*(1 + h)$  and  $P = P^*(1 + p)$ , expands  $f(H^* + hH^*)$  in Taylor series, and drops all higher-order terms in  $h$  and  $p$  to get

$$\frac{dh}{dt} = rh - ap; \quad \frac{dp}{dt} = dH^*P^*f'(H^*)h, \quad (4)$$

where  $r = a[1 - H^*f'(H^*)/f(H^*)]$ . The  $h$  and  $p$  are thus small fractional perturbations in population density, and we want to know if they diminish with time. This system of linear differential equations is easy to solve (see, e.g., Murdoch and Oaten 1975, appendix), and the solutions turn out to be locally stable (i.e., return to equilibrium after small perturbations) provided  $r < 0$ .

This condition is exactly the same as (1), providing support for our use of both (1) and  $H_m$ . In addition, if we ask whether a given functional response,  $f$ , yields stability for a model of this form (specified by the parameters  $a$ ,  $c$  and  $d$ ), the answer is that it does if  $H^* < H_m$ ; since  $f$  is increasing (the more prey there are, the more a predator will eat), this is equivalent to requiring  $f(H^*) < f(H_m)$ , i.e.,  $c/d < f(H_m)$ . Thus the larger  $f(H_m)$  is, the greater is the range of values that  $c$  and/or  $d$  can take while still permitting neighborhood stability.

Thus  $f(H_m)$  provides a measure of the size of the class of models for which  $f$  will yield stability: any model, specified by  $(a, c, d)$ , will have a locally stable



solution provided  $c/d < f(H_m)$ . Alternatively, we can take this value as a means of comparison: if  $f_1$  and  $f_2$  have their " $H_m$ " values at  $H_{1m}$  and  $H_{2m}$ , and  $f_1(H_{1m}) > f_2(H_{2m})$ , then  $f_1$  is "more stabilizing" than  $f_2$  in the sense that any model,  $(a, c, d)$ , in which  $f_2$  yields stability will also be stable with  $f_1$ ; but the converse is false—if  $f_2(H_{2m}) < c/d < f_1(H_{1m})$ ,  $f_1$  yields stability but  $f_2$  does not. Thus  $f(H_m)$ , in measuring the allowable variation in parameter values, provides a measure of one aspect of structural stability of the model or, more precisely, of its functional response component.

It may be objected here that, in changing equation (2) to equation (3), we have changed the numerical response as well as the functional response. We would argue that this is justifiable: that an increase in the number of prey eaten will result in a corresponding increase in the number of new predators and that the most evenhanded way of modeling this is to assume a constant rate of conversion. However, it is not essential to do this. Two other simple possibilities are:

a) It may be that, because of alternative prey or limiting factors other than food, the predator population size is little affected by the prey population size. Thus we might be dealing with a system (or part of a system) approximable by  $dH/dt = aH - Pf(H)$ ,  $dP/dt = 0$ , for some fixed  $P$ . Here, (1) is again the relevant criterion: the prey population will return to  $H^*$  after a small perturbation if and only if  $H^* < H_m$ .

b) In general, if we change (2) to

$$\frac{dH}{dt} = aH - Pf(H); \quad \frac{dP}{dt} = -cP + dPg(H), \quad (5)$$

so that the conversion rate is not held constant, then we can proceed as after (3) to get

$$\frac{dh}{dt} = rh - ap; \quad \frac{dp}{dt} = dH^*P^*g'(H^*)h, \quad (6)$$

where  $H^* = g^{-1}(c/d)$ ,  $P^* = aH^*/[f(H^*)]$ , and all other terms are as in (4). Again the solutions are locally stable if and only if (1) holds, provided only that  $g'(H^*) > 0$ , i.e., that predator birth rates increase with increasing prey.

#### IV. MORE GENERAL MODELS

Suppose we are considering several populations,  $N_1, N_2, \dots, N_k$ , whose behavior is determined by the differential equations

$$\frac{dN_i}{dt} = F_i(N_1, \dots, N_k), \quad i = 1, 2, \dots, k; \quad (7)$$

If the system has an equilibrium,  $(N_1^*, \dots, N_k^*)$ , we can investigate the behavior near equilibrium by writing  $N_i = N_i^*(1 + n_i)$ , expanding each  $F_i$  in Taylor series, and dropping all but first-order terms in the  $n_i$ 's. If we do this, we get

$$\frac{dn_i}{dt} = \sum_{j=1}^k a_{ij}n_j, \quad i = 1, 2, \dots, k, \quad (8)$$

where each

$$a_{ij} = N_j^* \frac{\partial F_i^*}{\partial N_j} N_i^{*-1},$$

where the asterisk superscript means the function is evaluated at  $(N_1^*, N_2^*, \dots, N_k^*)$ .

The neighborhood stability (or otherwise) is determined by the characteristic values (or eigenvalues) of the matrix  $[a_{ij}]$ : if these values are all negative, the system is stable. It is not easy to give simple sufficient conditions for this, but a simple necessary condition is that

$$\sum_{i=1}^k a_{ii} < 0.$$

(See, e.g., May 1973, appendix 2.)

This sum will usually depend on other things besides the functional response, but we can get some idea of the influence of the functional response in the predator-prey interaction by considering the two terms that will be affected by it, those representing the predator and the prey, which we will take to be  $N_1$  and  $N_2$ , respectively. We consider three cases, in decreasing order of generality.

For the first, we admit that the number of prey eaten may depend on other populations (e.g., on other populations of prey) besides  $N_1$  and  $N_2$ , though we still take it to be linear in  $N_1$  (the predator) and its effect on the growth rates of both populations to be additive. Thus we take the functional response to be  $f(N_2 | N_3, \dots, N_k)$  and

$$\begin{aligned} F_1(N_1, \dots, N_k) &= cN_1f(N_2 | \dots N_k) + G_1(N_1, N_3, \dots, N_k), \\ F_2(N_1, \dots, N_k) &= -N_1f(N_2 | \dots N_k) + G_2(N_2, N_3, \dots, N_k), \end{aligned} \quad (9)$$

where the  $G$ 's represent all other effects. After approximating, we find

$$a_{11} = cf^* + \frac{\partial G_1^*}{\partial N_1}; \quad a_{22} = \frac{\partial G_2^*}{\partial N_2} - N_1^* \frac{\partial f^*}{\partial N_2}. \quad (10)$$

At this level of generality it is hard to see what characteristics  $f$  should have to yield stability, especially as it has effects, which are not explicit here, on the equilibrium values themselves. Nevertheless, it does seem that the larger  $(\partial f^* / \partial N_2) / f^*$  is, the more likely  $a_{11} + a_{22}$  is to be negative.

However we can simplify slightly: if we can assume that, except for the functional response, the two populations have rates of change which are linear functions of themselves, then

$$\begin{aligned} F_1(N_1, \dots, N_k) &= cN_1f(N_2 | \dots N_k) + N_1g_1(N_3, \dots, N_k), \\ F_2(N_1, \dots, N_k) &= -N_1f(N_2 | \dots N_k) + N_2g_2(N_3, \dots, N_k). \end{aligned} \quad (11)$$

(For constant  $N_3, \dots, N_k$ , this is easily seen to be the same system as [3]). In this case,  $a_{11} = 0$  and  $a_{22} = g_2^* - N_1^*(\partial f^* / \partial N_2)$ ; but since  $F_2^* = 0$  (for equilibrium),  $N_2^*g_2^* = N_1^*f^*$ , so that

$$a_{11} + a_{22} = a_{22} = g_2^* \left[ 1 - \frac{\partial f^*}{\partial N_2} \frac{N_2^*}{f^*} \right],$$

which is negative precisely if (1) holds. This is not, of course, conclusive, since  $f$  will have some effect on the remaining  $a_{ii}$  terms, but it does again suggest that our criterion, (1), is reasonable. This again supports our first measure, " $H_m$ " (in this case,  $N_{2m}$ ), though this measure is no longer clear-cut. In the present context,  $N_{2m}$  is the "maximum" (supremum) of those values of  $N_2$  for which

$$\frac{\partial}{\partial N_2} f(N_2 | N_3, \dots, N_k) > \frac{f(N_2 | \dots N_k)}{N_2}; \quad (12)$$

and this obviously depends on  $N_3, \dots, N_k$ , as well as on  $f$ .

Support for our other measure,  $f(N_{2m})$ , seems weaker here. If the interactions of  $N_1$  and  $N_2$  with other populations in the system are fairly weak,  $g_1^*$  and  $g_2^*$  would be essentially functions of other parameters of the model, not involving  $N_1^*$ ,  $N_2^*$ , or  $f$ . In this case, the dynamics of  $N_1$  and  $N_2$  are essentially determined by (9) with  $g_1$  and  $g_2$  taken as the constants,  $g_1^*$  and  $g_2^*$ ; this is the simple system discussed in the previous section. So we again have that  $f(N_{2m} | N_3^*, \dots, N_k^*)$  is a measure of "how many" functions,  $g_1$  and  $g_2$ , will yield stability with  $f$  in (4), given  $N_3^*, \dots, N_k^*$ . Once again, however, we note that our "measure" is no longer a number but a function of  $N_3^*, \dots, N_k^*$ . It seems also that the more the predator and prey are affected by their interactions with other species, the less meaning  $f(H_m)$  has as a measure of stabilizing tendency; conversely, when other parameters of the model have more effect on the equilibrium values,  $N_1^*$  and  $N_2^*$ , it may be that  $N_{2m}$  becomes an indicator of the range of models in which  $f$  will be stabilizing, thus approaching the role that  $f(H_m)$  plays in the simple system.

#### V. CONCLUDING REMARKS

We have suggested a criterion by which a functional response can be said to be "stabilizing" or not at a particular point, and two measures to indicate how "stabilizing" a functional response is. The criterion is given by (1); and with  $H_m$  as the "largest" (supremum) of the values of  $H$  for which (1) holds, the measures are  $H_m$  and  $f(H_m)$ —in, we believe, decreasing order of importance. The criterion and the measures are illustrated in figure 1.

Note that the condition (1) is essentially unchanged if we consider the predation rate as a function of a multiple of  $H$ , say  $h = \alpha H$ , rather than  $H$  itself. For instance, it may be convenient to use  $h$  = average number of prey in a patch (Oaten, Murdoch, and McNulty 1975), so  $h = H/N$  where  $N$  is the number of patches, or to use  $h$  = instantaneous rate at which the predator contacts prey (Oaten and Murdoch 1975), so  $h = \lambda H$  where  $\lambda$  is the predator's search rate. If  $f(H)$  is the functional response,  $h = \alpha H$ , and  $g(h)$  is the number of prey eaten per unit time as a function of  $h$ , then  $g(h) = g(\alpha H) = f(H)$ . Differentiating with respect to  $H$ : if  $f'(H) > f(H)/H$ , then  $\alpha g'(\alpha H) > g(\alpha H)/H$  so that  $g'(h) > g(h)/h$ ; i.e., the criterion for  $h$  is the same as that for  $H$ . Similarly,  $h_m = \alpha H_m$  and  $f(H_m) = g(h_m)$ .

We have tried to support the use of these measures partly by appeal to intuition and partly by appeal to standard types of mathematical models. We



have not attempted to cover any but the most simple possibilities. Stable limit cycles have not been discussed, partly because the machinery for discussion of these cycles does not exist for more than two dimensions (species) and partly because Kolmogorov's set of sufficient conditions for stability in the two-species case, as given by May (1973, p. 87), are not easily translated into conditions on functional response.

The Kolmogorov equations are  $dH/dt = HF(H, P)$  and  $dP/dt = PG(H, P)$ , of which the first can be rewritten as  $dH/dt = HF(0, 0) - P[F(0, 0) - F(H, P)]H/P$ , which is like (5) with  $f(H, P) = [F(0, 0) - F(H, P)]H/P$  as the "functional response." From this we find that  $\partial F/\partial P = -[f + P(\partial f/\partial p)]/H$  and  $\partial F/\partial H = -P[(\partial f/\partial H) - (f/H)]/H$ . May's condition (i) ( $\partial F/\partial P < 0$ ) is thus satisfied unless interference, the tendency of functional response to decrease as predator numbers increase and predators have to compete for prey, is very strong (essentially, linear or accelerating in  $P$ ). We have assumed it to be negligible, and suspect this is nearer to the truth. Condition (ii),  $H(\partial F/\partial H) + P(\partial F/\partial P) < 0$ , will, if condition (i) is satisfied, certainly be satisfied by  $\partial F/\partial H < 0$ , which is clearly equivalent to our criterion, (I). However condition (vi),  $F(0, A) = 0$  for some  $A > 0$ , in conjunction with condition (v),  $F(0, 0) > 0$ , and the continuity of  $F$ , implies that  $f(H, A) > 0$  for small  $H$ ; thus there are no absolute prey refuges. In addition, condition (vii),  $F(B, 0) = 0$  for some  $B > 0$ , says that the prey population cannot grow indefinitely, even without predation. Thus, although these conditions provide some support for our suggestions, this system is not entirely suitable for analyzing the role of the functional response.

Our measures also have some weaknesses. It is possible, for example, only to compare type 3 responses:  $H_m$  does not exist for type 1 or type 2 responses. Yet stability is undoubtedly possible with such responses if such components as predator interference (Hassell and May 1973) or a logistic prey growth rate are included.

Nevertheless we believe, for the reasons given in the first section of this paper, that there is a need for *some* measure, and that the measures we propose have the virtues of simplicity and intuitive appeal and are the best for simple models.

#### SUMMARY

We propose two measures of how stabilizing a functional response is. We suggest that predation be regarded as stabilizing at a prey density of  $H$  if the predation rate is increasing then—i.e., if  $f(H)/H$  is increasing where  $f$  is the functional response. This is equivalent to asking that an increase in prey density results in an increased chance of a given prey being killed by the predator. With  $H_m$  as the maximum value of  $H$  for which this criterion holds, our measures are  $H_m$  and  $f(H_m)$ . We relate this criterion and these measures to local stability and also to structural stability in a modified Lotka-Volterra model and a general multispecies model. The criteria will be used in detailed models of switching in predators (in the following paper in this issue) and of patchiness.

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