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## CONCEPTS OF STABILITY AND RESILIENCE IN PREDATOR-PREY MODELS

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### INTRODUCTION

Three elementary observations guide our thinking in this paper. First, the populations of most species in many ecosystems appear to fluctuate around characteristic mean levels of abundance. Secondly, the amplitude of the fluctuations around these quasi-equilibria differs markedly in different organisms and thirdly, populations occasionally decrease to such an extent that they do not recover, that is they become extinct. Mathematical models purporting to describe the real world should provide unifying insights into these three basic phenomena.

A now familiar question is to ask how the numerical values attached to the parameters of particular ecological models influence the local (neighbourhood) stability properties of such models (May 1974a; Smith 1974). A reasonable inference is that the persistent, quasi-stable populations which we observe in real ecological communities demand parameter values in their model counterparts which lead to locally stable equilibria or to limit-cyclic behaviour. Combinations of parameter values which produce only negative population equilibria, or which lead to exponential growth or extinction following a small disturbance from a positive equilibrium, are obviously inappropriate and will not be observed in real communities. Demarcating 'feasible' from 'unfeasible' and locally stable from locally unstable regions of parameter space in ecological models has attracted considerable recent attention (e.g. Beddington, Free & Lawton 1975; Hassell & May 1973; Roberts 1974). In parallel, there is an increasing number of studies which show that the parameter values which characterize the interactions of real population systems are very far from being an haphazard selection of all numerically possible values (Hassell, Lawton & May 1976; Price 1974; Rogers & Hubbard 1974; Walters 1975), that certain communities have converged remarkably in structure from different origins (Cody 1974; Stephenson & Stephenson 1972) and that equivalent parameters may change markedly on different community backgrounds (Gilbert & Hughes 1971). However, there are very few unequivocal demonstrations that the observed parameter values and combinations lead to stable equilibria and that other unencountered values and combinations do not, although the inference is an attractive one.

Despite its importance, it is unlikely that a consideration of local stability properties alone will be sufficient for anything but the most general statements about the parameter values that characterize real communities, and those that do not. The fact that most natural populations fluctuate appreciably reminds us that real perturbations, whether by fire, climate, predation, pollution or cropping will rarely, if ever, be arbitrarily small. It is therefore of considerable importance to ask over what range of perturbations will a particular population, or set of populations, return to equilibrium, and at what point do the regulatory mechanisms break down—that is the populations no longer return to the original equilibrium or the original limit cycle? To ask this question is to ask not about

local stability, but about global stability. If all real and persistent ecological systems are, by definition, to be characterized by locally stable models (or perhaps by models showing limit-cycle behaviour), then the really interesting questions about the ‘stability’ of such systems may actually be questions about global stability—how far can a locally stable model be ‘pushed’ before the regulatory mechanisms break down? Not only that, but the length of time taken to return to equilibrium is important. For example, it makes a considerable difference to our thinking if we know that even though a particular combination of parameters defines a locally stable point in phase-space, and that surrounding this point are well defined limits within which any perturbation eventually dies away, nevertheless, the time taken to return to equilibrium is so long that effectively the populations never ‘damp’ within a biologically sensible time-scale. Hence we may need to know not only about the local and global stability properties of population models, but also about their ‘characteristic return times’. Indeed, the rate of return to equilibrium after a perturbation has already entered the experimental literature as a measure of ‘stability’ (Hurd & Wolf 1974; Murdoch 1970).

We can illustrate these ideas on a simple diagram. First, we note that large-scale shocks (or perturbations) to real systems may not only be associated with changes in the numbers of their species populations; in all probability they will also be associated with persistent changes in their parameters. Breakdown may therefore follow from exogenous numerical perturbation, and/or by a move from locally stable to locally unstable regions of parameter space. This point is illustrated in Fig. 1 (suggested to us by P. Diamond) which indicates the presence (or absence) of a locally stable point or cycle in a two-species (prey–predator) model at various positions in parameter space. Along the hypothetical parameter space axis we then position a series of standard phase-plane diagrams to show the limits of global stability of the populations at these points in parameter space. Conceptually this model embraces each of the elementary observations listed in our opening remarks. The quasi-stable equilibria of real populations suggest that they must lie within locally stable combinations of parameter space (or in the ‘shell’ of limit-cycle space which surrounds this zone). Fluctuations will not normally carry them outside their globally stable limits and when this does happen, extinction may occur, or the community may occupy new and clearly different sets of equilibria (Austin & Cook 1974; Sutherland 1974). Finally, within these globally stable limits, the populations have different characteristic return times, defining the rates of return to equilibrium after a perturbation.

Holling (1973) has coined the word *resilience* to describe the ability of ecological systems ‘to absorb changes ... and still persist’. The limits to which the populations in Fig. 1 can be ‘pushed’ before the system breaks down represent the limits of resilience of the system.

In this paper, we attempt to illustrate these ideas with reference to general predator–prey models framed in difference equations. Biological considerations demand that a reasonably realistic population model should incorporate thresholds and hence that the local and global stability properties will be different. Our predation model incorporates such thresholds. However, it is not our intention to produce a model with sufficient realism that very precise predictions can be made about the real world. Rather our aim is to clarify a set of related concepts and ideas that have given rise to considerable confusion in the ecological literature. In order to do this we have tried to effect a compromise between sufficient complexity to produce results that are biologically interesting, and sufficient simplicity to ensure that the ideas are not lost in a mass of mathematical detail.

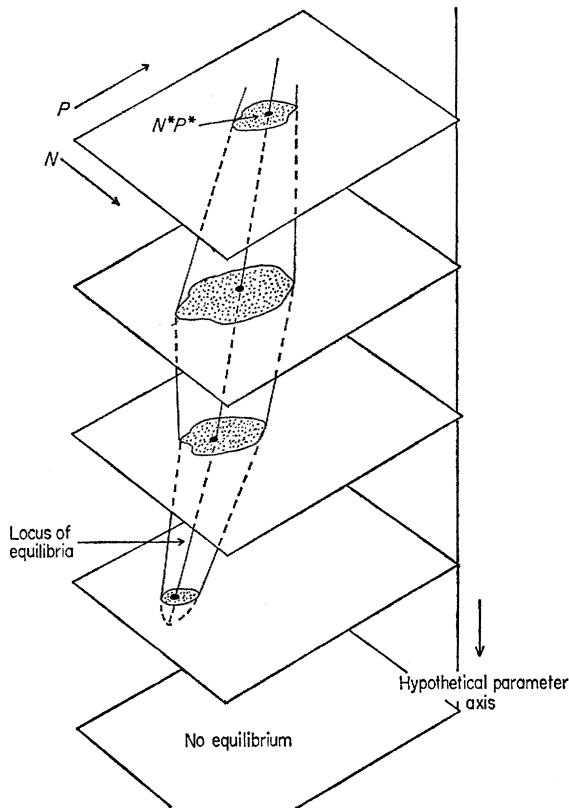


FIG. 1. A hypothetical predator ( $P$ )—prey ( $N$ ) interaction, characterized by a single parameter or combination of parameters. At points on the vertical parameter axis are positioned phase-planes, on which the numerical values taken by the populations can be represented ( $N^*$  = prey equilibrium,  $P^*$  = predator equilibrium). The shaded areas represent the regions of global stability (domains of attraction). Within these limits, numerical perturbations die away; outside them one or both of the populations become extinct. A domain of attraction may surround either a locally stable equilibrium or a limit cycle (see text for further details). A persistence domain is defined as the entire region in parameter and phase space within which the populations persist.

We reiterate that our aim is to provide qualitative insights, not quantitative predictions.

The first part of the paper describes the model (specified fully at eqn (8)), and is followed by a section describing the combinations of parameter values which lead to locally stable equilibria and the characteristic return times of the populations within this locally stable region. We then explore the global stability properties of these equilibria, and in the final section briefly consider the behaviour of the populations in the 'shell' of limit cycle behaviour which lies outside the locally stable zone.

## THE MODEL

### *The model framework*

An excellent mathematical representation of the dynamics of populations with non-overlapping generations may be framed as time-independent difference equations (Beddington *et al.* 1975; Hassell & May 1973; Hassell & Varley 1969; May 1974a, 1975; May & Oster 1976; Nicholson & Bailey 1935).

The general form for a predator-prey model of this type may be written as the system

$$\begin{aligned} N_{t+1} &= N_t f_1(N_t) f_2(N_t, P_t) \\ P_{t+1} &= P_t f_3(N_t, P_t). \end{aligned} \quad (1)$$

Necessarily, these equations are homogeneous (Rescigno & Richardson 1967). They are constructed using three basic functions, as follows:  $f_1(N_t)$  specifies the per capita prey rate of increase as a function of its own density ( $N_t$ );  $f_2(N_t, P_t)$  specifies the proportional survival of  $N_t$  prey confronted with  $P_t$  predators;  $f_3(N_t, P_t)$  specifies the per capita predator rate of increase as a function of its own and the prey density.

These functions may take a variety of specific forms, depending upon particular biological circumstances. We particularly have in mind an arthropod herbivore-predator food chain with discrete generations (typified by many annually reproducing, temperate region arthropods), and have chosen our detailed models accordingly. Our general conclusions, however, are unlikely to be restricted simply to food chains of this type.

#### *Components of the model*

One essential property of any reasonably realistic population model is that it should incorporate a characteristic carrying capacity above which (in the absence of predation) prey density will decline and below which it will increase. In other words, it should incorporate some form of self limitation by the prey population. In this study we use the form

$$f_1(N_t) \equiv \exp(r(1 - N_t/K)) \quad (2)$$

where  $r$  is the unrestricted rate of increase of the prey and  $K$  the carrying capacity. We have chosen eqn (2) in preference to a variety of other similar models for several reasons. It has the desirable feature that it can not generate negative prey populations (unlike certain other, related functions (May 1975)); further, its local stability properties (as a single species model) are completely specified by the single parameter  $r$  and its dynamic properties have been thoroughly investigated by May (1975) and May & Oster (1976) who show its behaviour to be typical of a wide class of other, density dependent single species models. Note, in passing, that it also reduces to the form of  $f_1(N_t)$  implicitly assumed by Hassell & May (1973) as  $K$  tends to infinity, but under these circumstances there is the unrealistic consequence that the prey population grows exponentially at a rate of  $e^r$  when predators are absent.

Hassell & May (1973) have also reviewed a wide variety of forms for the function  $f_2(N_t, P_t)$ . For our analysis we have taken the simplest of these, namely:

$$f_2(N_t, P_t) \equiv \exp(-a P_t) \quad (3)$$

where  $a$  is the 'attack rate' of the predators. In a subsequent publication, we shall explore the consequences of using different alternative forms for the functions  $f_2(N_t, P_t)$ , incorporating the full range of known predator responses (Hassell, Lawton & Beddington 1976). Model components that are crucial to an understanding of the differences between local and global stability have been developed in full and with considerable biological realism, but in the interests of clarity we have allowed other model components to take a simpler form.

If  $f_2(N_t, P_t)$  defines the proportion of prey surviving attack by the predators in genera-

tion  $t$ , then the proportion attacked is  $(1 - f_2(N_t, P_t))$  with the number of prey attacked per predator,  $N_a$ , being given by

$$N_a = \frac{N_t}{P_t}(1 - f_2(N_t, P_t)). \quad (4)$$

For the reasons outlined above, development of the function  $f_3(N_t, P_t)$  is somewhat more complex. First, we note that basal metabolic requirements demand that predators must catch and eat several, usually many, prey before they are able to reproduce. Second, once this threshold has been passed, there need not be a simple one to one relationship between the number of eggs laid and the number of prey eaten per predator. In other words, we expect the relationship between the food energy ingested,  $I$ , and the reproductive output per predator,  $E$ , to be of the form

$$E = \lambda(I - c) \quad (5)$$

where  $c$  is a constant determined by the maintenance energy requirements of the predator and the proportion of ingested food assimilated and  $\lambda$  is the appropriate proportionality constant.

Equation (5) is supported by a variety of data (Fig. 2) and is discussed more fully by Lawton, Hassell & Beddington (1975) and Beddington, Hassell & Lawton (1976). These arguments were specifically developed with only the adult (final instar) stages of predatory arthropods in mind. They may be generalized to embrace all the feeding stages

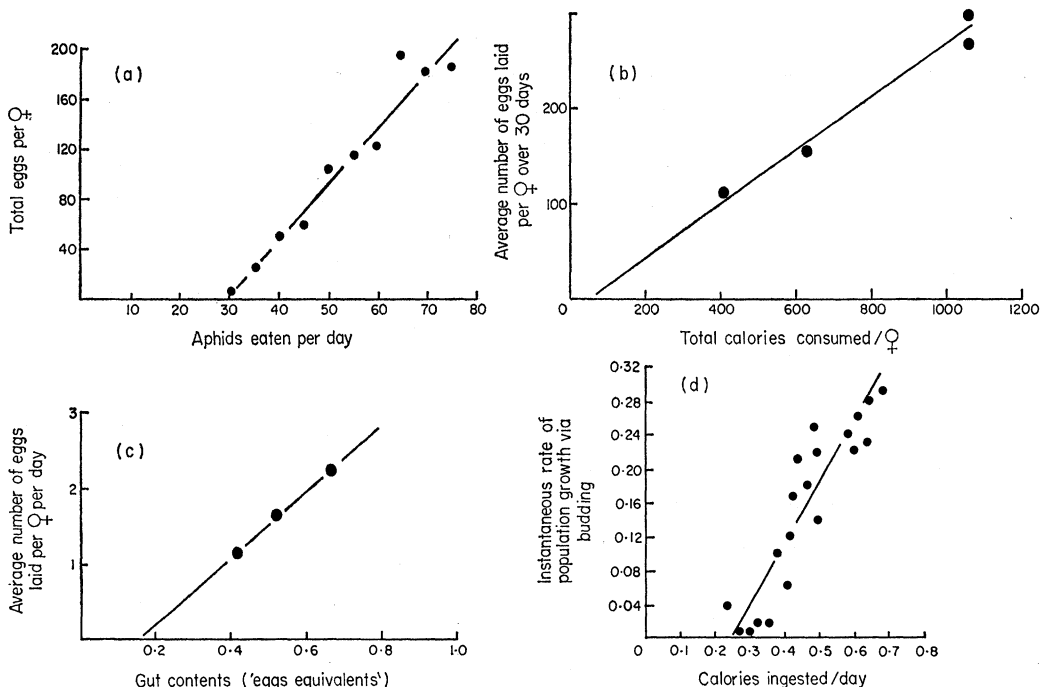


FIG. 2. Reproductive rate as a function of feeding rate in various predators: (a) *Coccinella undecimpunctata aegyptiaca* Reiche (ladybird) (Hodek, 1973); (b) *Podisus maculiventris* (Say.) (bug) (Mukerji & LeRoux 1969); (c) a mite (*Typhlodromus occidentalis* Nesbitt) (Fransz 1974); (d) *Hydra pseudoligactis* Hyman (Schroeder 1969). All are linear relationships of the form specified by eqn (5).

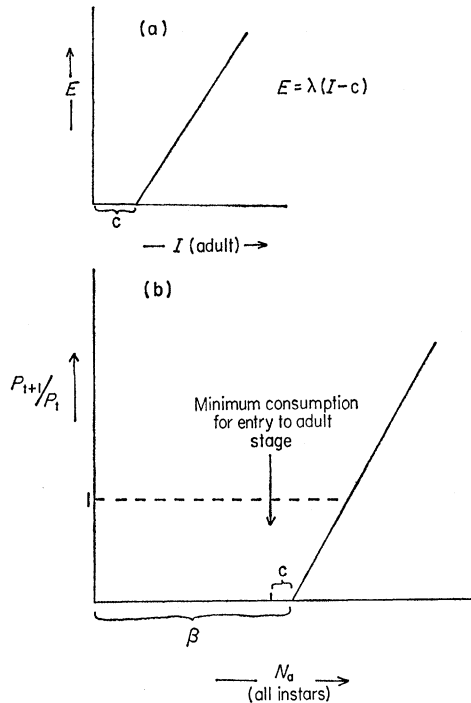


FIG. 3. (a) Diagrammatic representation of the data shown in Fig. 2, for the relationship between the food energy ingested by an adult predator  $I$ , and its fecundity  $E$ . This may be generalized (b) to predict the relationship between prey eaten by all stages in the life of the predator in generation  $t$ , and the number of predators in generation  $t+1$  (see text). The predator equilibrium population,  $P^*$ , is defined where  $P_{t+1}/P_t = 1$ .

within the predator's life-cycle by making the reasonable, if simple, assumption that the rate of increase of the predator population,  $f_3(N_t, P_t)$ , is directly proportional to predator fecundity,  $E$ , and that the basal metabolic requirement should now include all the food that the predator requires between hatching and the onset of reproduction,  $\beta$ . Finally assuming food energy intake,  $I$ , is itself proportional to the number of prey eaten,  $N_a$ , we obtain

$$\begin{aligned} f_3(N_t, P_t) &\equiv \alpha(N_a - \beta), \quad N_a > \beta \\ f_3(N_t, P_t) &\equiv 0, \quad N_a < \beta \end{aligned} \quad (6)$$

where  $\alpha$  is the 'efficiency' with which prey are converted into new adult predators. Figure 3 illustrates these ideas diagrammatically.

Substituting for  $N_a$  (eqn (4)) we now obtain

$$f_3(N_t, P_t) = \alpha \left[ \frac{N_t}{P_t} (1 - f_2(N_t, P_t)) - \beta \right]. \quad (7)$$

Drawing together these arguments, our basic model now takes the form

$$N_{t+1} = N_t \exp(r(1 - N_t/K) - a P_t) \quad (8)$$

$$P_{t+1} = P_t \alpha \left[ \frac{N_t}{P_t} (1 - \exp(-a P_t)) - \beta \right].$$



Emphasizing the caveats which we made in the introduction, this model has enough detail to make it biologically interesting, but it omits a number of well-known attributes of arthropod predator-prey interactions that would add to its realism.

### LOCAL STABILITY

We now proceed to demarcate those regions of parameter space where very small perturbations from equilibrium will die away from those where they will grow. The technique we use is essentially that described by Hassell & May (1973), but can be applied generally to arbitrary sets of non-linear difference equations. Details of the technique are available in Beddington (1974) and are developed for the models (1) and (8) in the Appendix. The underlying logic of the technique is to calculate the possible equilibria of the system ( $N_{t+1} = N_t = N^*$ ;  $P_{t+1} = P_t = P^*$ ) and then by considering the behaviour of a small perturbation from equilibrium to arrive at a linear expression in the perturbations at time  $t+1$  in terms of the perturbations at time  $t$ . If we denote  $\delta_t$  as a column vector containing the perturbations from equilibrium of prey and predator populations, we may express this linear relationship as the matrix equation

$$\delta_{t+1} = \mathbf{M}_\delta \delta_t. \quad (9)$$

The exact form of the relationship is given by the elements of the square matrix  $\mathbf{M}_\delta$ . If we operate eqn (9) from some initial perturbation  $\delta_0$  we arrive at an expression

$$\delta_t = (\mathbf{M}_\delta)^t \delta_0. \quad (10)$$

It is a well known result (e.g. Crow & Kimura (1970), Appendix 8) that we can now express eqn (10) as

$$\delta_t = \lambda_1^t \mathbf{v}_1 + \lambda_2^t \mathbf{v}_2 \quad (11)$$

where  $\lambda_1$  and  $\lambda_2$  are the eigenvalues of  $\mathbf{M}_\delta$  and  $\mathbf{v}_1$  and  $\mathbf{v}_2$  are determined by the initial vector  $\delta_0$ . If we consider the case where the eigenvalues are real and denote the larger eigenvalue as  $\lambda_1$  we obtain, with some rearrangement

$$\delta_t = \lambda_1^t \left( \mathbf{v}_1 + \left( \frac{\lambda_2}{\lambda_1} \right)^t \mathbf{v}_2 \right). \quad (12)$$

By definition  $\left( \frac{\lambda_2}{\lambda_1} \right)^t$  will tend to zero as  $t$  increases and thus the ultimate fate of the vector of perturbations  $\delta_t$  will depend upon the magnitude of  $\lambda_1$ . If the modulus of  $\lambda_1$  exceeds unity the perturbations will grow as  $t$  increases. If  $|\lambda_1|$  is less than unity then the perturbations will decrease as  $t$  increases. Local stability is thus guaranteed if and only if the modulus of the larger eigenvalue of  $\mathbf{M}_\delta$  is less than unity. Similar considerations apply if the eigenvalues are complex numbers.

Accordingly the conditions for local stability depend upon the conditions that the eigenvalues of  $\mathbf{M}_\delta$  lie within the unit circle. It is possible to write the characteristic equation in the eigenvalues of the matrix as the quadratic

$$\lambda^2 + b\lambda + c = 0 \quad (13)$$

Hassell & May (1973) show that the conditions on the coefficients of this equation that guarantee that the roots lie within the unit circles are

$$|b| < 1 + c < 2. \quad (14)$$



Writing these inequalities as equalities defines the limit where the largest eigenvalue is exactly equal to unity. These equalities can thus be used to demarcate locally stable from locally unstable parameter space. The algebraic details of this exercise are given in the Appendix, where the coefficients of the characteristic equation are shown to depend upon three basic parameter combinations. These are  $r$ , the unrestricted rate of increase of the prey population;  $\phi = \alpha\beta$ , which is a combination of the size of the basal metabolic requirements of the predator  $\beta$ , and the efficiency with which prey are converted to adult predators,  $\alpha$ ; and thirdly, a measure of predator hunting efficiency. This latter component can be expressed in one of two ways, either as the combination  $\theta = \alpha\alpha K$  which effectively specifies the efficiency of a predator at catching prey and reproducing, or alternatively as a measure of the predators' ability to depress the prey equilibrium ( $N^*$ ) below its carrying capacity ( $K$ ). We denote this parameter as  $q \equiv N^*/K$ .

#### *Biologically feasible parameter values*

Before proceeding to demarcate stable from unstable parameter space it is necessary to consider the meaningful ranges of the parameter values, as it is manifestly misconceived to establish zones of stable behaviour for parameter values that lie outside the ranges shown by real organisms. Clearly the parameter  $q$  must lie in the range  $0 \leq q \leq 1$  and the only sensible restriction on  $r$  is that it be greater than zero.

#### *Restrictions on $\phi$*

A biologically meaningful range of values for  $\phi = \alpha\beta$  may be derived from the following argument. Define  $z$  as the proportion of food eaten that is used for non-reproductive processes, i.e.

$$z = \beta/N_a. \quad (15)$$

Then at equilibrium, using eqn (A8) for  $P^* > 0$ , we obtain the relationship

$$1 - \alpha(N_a - \beta) = 0. \quad (16)$$

Eliminating  $N_a$  between eqns (15) and (16) gives

$$\phi = \alpha\beta = \frac{z}{1-z}. \quad (17)$$

Approximate values for  $z$  may be obtained by reference to the experimental data summarized in Table 1. This suggests that for a range of different types of predatory arthropods, the proportion of food eaten by the larval instars typically constitutes between 0.1 and 0.6 of the food eaten throughout life. However, we cannot use these figures to obtain  $z$  (and hence  $\phi$ ) directly, for two reasons. First, the reproductive (adult) stage must normally also consume some food before reproduction can take place (equivalent to  $c$  in eqn (5)). Unfortunately the experimental data do not permit us to specify this quantity for most of the organisms listed in Table 1, but its effect will be to raise the proportions shown in the table by some small amount. Second, these figures are for single individuals and make no allowance for mortality within a cohort of predators as it passes from egg to adult. Our simple population model implicitly assumes that a number of young predators never become reproductive adults. The effect of incorporating these unsuccessful individuals will again be to raise the proportion of food eaten by an 'average' individual before reproduction. Consideration of a cohort undergoing both growth and death, for example, raises the figure of 0.19 for the mysid predator *Metamysidopsis* to one of approximately 0.6 (Clutter & Theilacker 1971).

Table 1. *The proportion of a predator's total food intake consumed during larval instars*

Species	Type of predator	Total food eaten/individual by all larval instars		Reference
		Total food eaten throughout life		
♀ <i>Linyphia triangularis</i> Clerck	Spider	0.62		Turnbull (1962)
♀ <i>Paradosa lugubris</i> (Walckenaer)	Spider	0.26		Edgar (1971)
<i>Blepharidopterus angulatus</i> (Fall.)	Hemiptera	0.54		Glen (1973)
<i>Podisus maculiventris</i> (Say)	Hemiptera	0.14 (Max. food supply)		Mukerji & Le Roux (1969)
		0.08 (Min. food supply)		
<i>Coccinella</i> spp.	Coleoptera	c. 0.15-0.4		Hodek (1973)
♀ <i>Metamysidopsis elongata</i> (Holmes)	Mysidacea :	0.19		Clutter & Theilacker (1971)
	Crustacea			
♀ <i>Mytopus morio</i> (F.)	Phalangidae	c. 0.35		Phillipson (1960)

With these considerations in mind, we have chosen an upper limit on  $z$  of 0.8, and hence, from eqn (17), have examined a range of values for  $\phi$  that lie between 0 and 4.

### Restrictions on $\theta$

The function  $g(N^*)$  which specifies the equilibrium prey density in eqn (A8) has two roots, of which one, at  $N^* = K$ , implies  $P^* = 0$ . For a positive value of  $P^*$  it is necessary that the other root of  $g(N^*)$  lie in the range  $0 < N^* < K$ . A consideration of  $g'(N^*)$ , the first derivative of  $g(N^*)$ , enables us to formulate this condition as

$$g'(K) < 0. \quad (18)$$

It can be shown that

$$g'(K) = (r/K)(1 + \phi) - r\alpha\alpha. \quad (19)$$

Hence the condition eqn (18) reduces to

$$\theta > 1 + \phi. \quad (20)$$

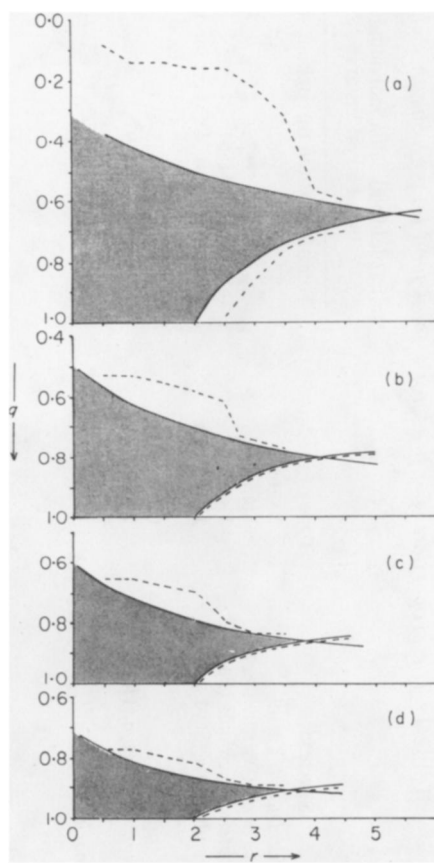


FIG. 4. The solid lines enclose a (shaded) region of parameter space in which the model has a locally stable equilibrium. These boundaries are shown in terms of  $r$  and  $q$  for varying values of  $\phi$  ( $\phi = \alpha\beta$ ): (a)  $\phi = 0$ , (b)  $\phi = 1$ , (c)  $\phi = 2$ , (d)  $\phi = 4$ . The dashed lines in (b) to (d) indicate a numerical approximation to the limits of the biologically feasible region of  $r$ - $q$  space. For parameter combinations falling outside the dashed lines, the population process generates solutions in which the predator becomes extinct. In (a) (no intercept) the dashed lines show, for comparison, the limits beyond which the model is not easily computable ( $N_1, P_1 < 10^{-10}$  or  $N_1, P_1 > 10^{10}$ ).

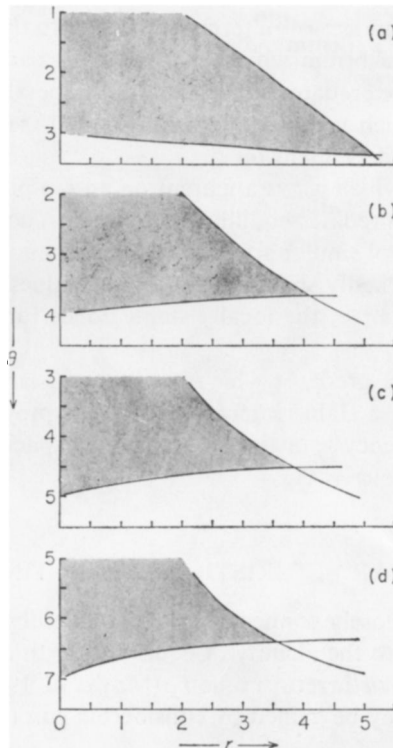


FIG. 5. The boundaries of the locally stable region of parameter space, are replotted in terms of  $r$  and  $\theta$  ( $\theta = axK$ ), for those values of  $\phi$  used in Fig. 4: (a)  $\phi = 0$ , (b)  $\phi = 1$ , (c)  $\phi = 2$  and (d)  $\phi = 4$ . The stable region is shaded. The range of  $\theta$  is not greatly affected by increasing  $\phi$ , but the actual values are offset by the equilibrium condition  $\theta > 1 + \phi$ .

#### *The demarcation of stable from unstable parameter space*

In Figs 4 and 5 we illustrate the stable and unstable zones of parameter space in two different, but complementary, ways. Figure 4 shows the interacting effects of  $r$ , the prey's intrinsic rate of increase, and  $q$ , the extent to which the predator population is able to depress the prey population below equilibrium, for various values of  $\phi$ . The magnitude of  $\theta$  required to effect a particular depression is not shown explicitly. In general terms, high  $r$  values and marked depression of the prey population by the predators both tend to make unstable equilibria more likely. In the absence of predators ( $q = 1$ )  $r$  values greater than 2 are always unstable; with predators, at moderate  $q$  values, the model is stable for rather higher  $r$  values, but there are no stable solutions above  $r \approx 3.5$ –4 (depending on the value of the third parameter  $\phi$ ). Strong depression of the prey population always leads to a marked reduction of the values of  $r$  for which locally stable behaviour is possible.

The effect of increasing the term  $\phi$  is again to decrease the likelihood of the existence of a locally stable equilibrium, particularly for small values of  $q$ . Where  $\phi = 0$ , there is no threshold and each prey attacked contributes proportionally to the next generation. Essentially this describes an insect host–parasitoid system and is the case with the largest region of locally stable behaviour. As  $\phi$  increases, the locally stable zone decreases in size (Fig 4(a)–(d)), but rather surprisingly, not very markedly. Even with  $\phi = 4$  there is still a considerable region of locally stable combinations of  $q$  and  $r$ .

Figure 5 expresses the same results in terms of  $r$  and  $\theta$ . In this case it is the extent of the depression of the prey equilibrium which is implicit. In parallel with Fig. 4, there are upper and lower limits to the predator efficiency which depend on  $r$ . Increasing  $r$  decreases the range of  $\theta$  values for which a stable equilibrium exists. As above, the size of the locally stable zone is not strongly dependent on  $\phi$ .

A feature revealed here which is not apparent on an  $r$ - $q$  plot arises from the condition that  $\theta > 1 + \phi$  for a positive predator equilibrium to exist. A consequence is that, although the locally stable zones are of similar size, the offset introduced by incorporating a basal metabolic requirement markedly shifts the range of  $\theta$  values for which there is a stable equilibrium. Thus, for example, the locally stable zones for  $\phi = 1$  and  $\phi = 4$  do not overlap.

In biological terms, for a predator which needs to eat large numbers of prey before it can reproduce and have a stable interaction with its prey, at least one of the attack rate  $a$ , the conversion efficiency  $\alpha$ , or the prey carrying capacity  $K$  must be higher than is required for the simple case  $\phi = 0$ .

### CHARACTERISTIC RETURN TIMES

A property of the model closely connected to local stability is the speed at which perturbed populations return to the vicinity of equilibrium. In a single species context this has been called the characteristic return time  $T_R$  (May *et al.* 1974; Smith 1974). An understanding of this concept may be gained by considering eqn (12)

$$\delta_t = \lambda_1^t \left( \mathbf{v}_1 + \left( \frac{\lambda_1}{\lambda_2} \right)^t \mathbf{v}_2 \right).$$

For  $|\lambda_1| < 1$  the equilibrium is stable and the rate at which perturbations will die away will be determined by the size of  $\lambda_1$ .

We may define the return time in terms of  $\lambda_1$  as

$$T_R = \frac{1}{1 - |\lambda_1|}. \quad (21)$$

Thus the shortest possible return time is unity (immediate damping between a perturbation at time  $t$ , and  $t+1$ ), corresponding to  $\lambda_1 = 0$ , and the longest return time is infinite, corresponding to  $\lambda_1 = 1$ . Clearly the concept of a characteristic return time has no meaning for an unstable equilibrium. In the same way as a demarcation was made between locally stable and unstable parameter space by considering the constraints specified by eqn (14) upon the characteristic eqn (13) it is possible to demarcate zones of parameter space where the characteristic return times (defined by eqn (21)) are greater or less than any specified value. It may simply be shown that the constraints that the roots of eqn (13) should be less than any arbitrary number  $\rho$  are:

$$|b| < \frac{\rho^2 + c}{\rho} < 2\rho \quad (22)$$

which reduce to eqn (14) when  $\rho = 1$ . For example, if  $\rho = 0.95$ , eqn (22) defines the conditions in parameter space where the return time is greater or less than 20. We illustrate these results for the model in Fig. 6.

Characteristic return times are least about the unique point in  $r$ - $q$  space where  $\lambda = 0$

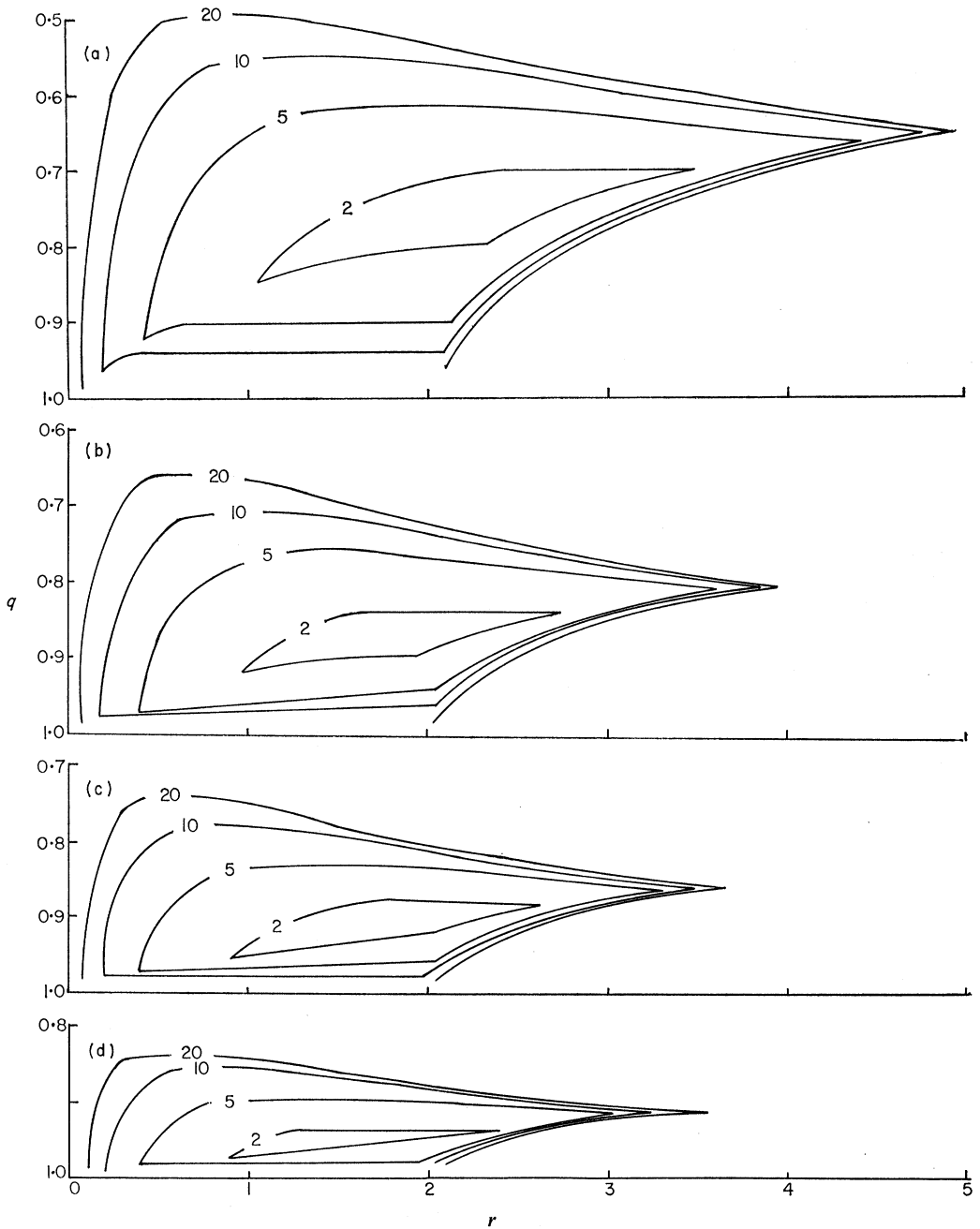


FIG. 6. Within the locally stable space depicted in Fig. 4, the characteristic return time,  $T_R$ , varies with  $r$  and  $q$ . The loci of  $T_R = 2, 5, 10, 20$  are shown for (a)  $\phi = 0$ , (b)  $\phi = 1$ , (c)  $\phi = 2$ , (d)  $\phi = 4$ . The stability boundaries shown in Fig. 4 represent an infinite return time.

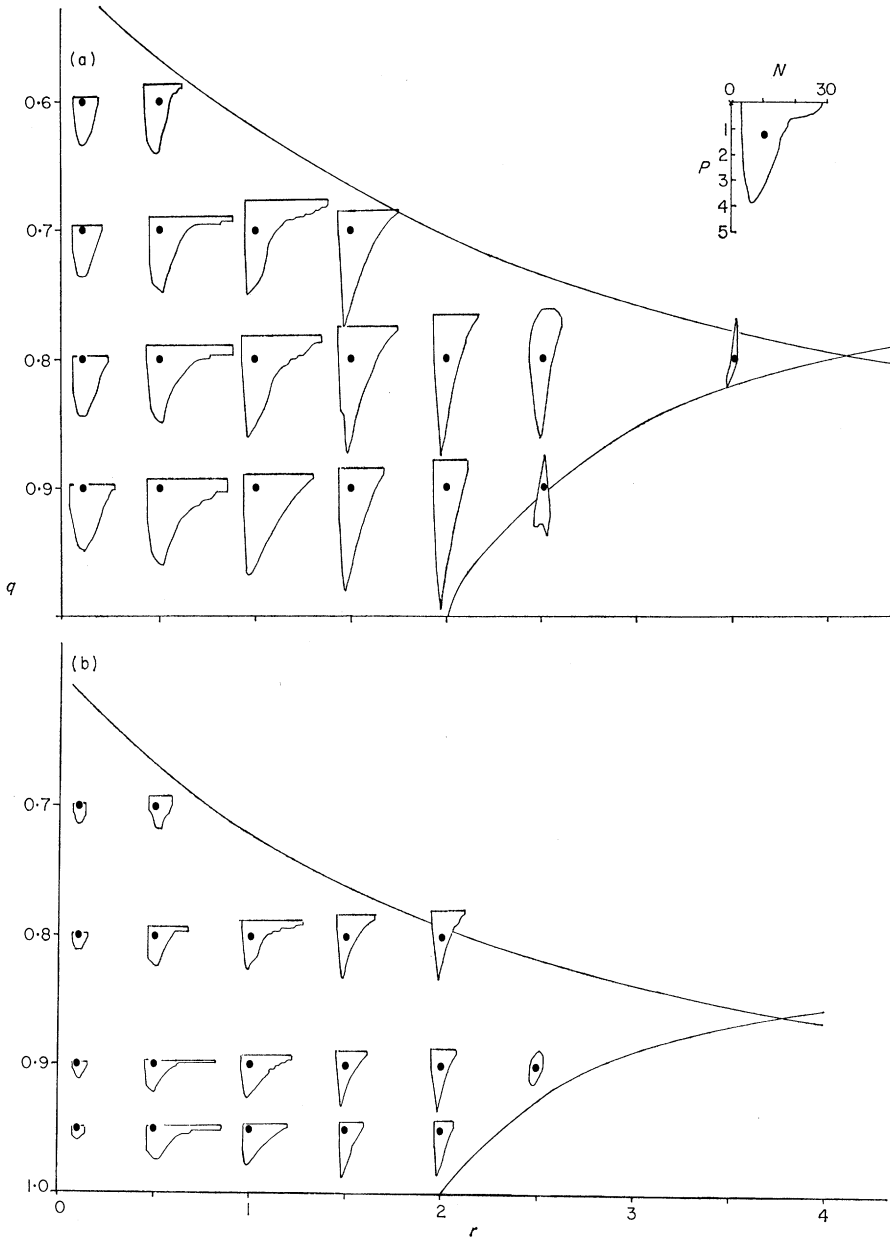
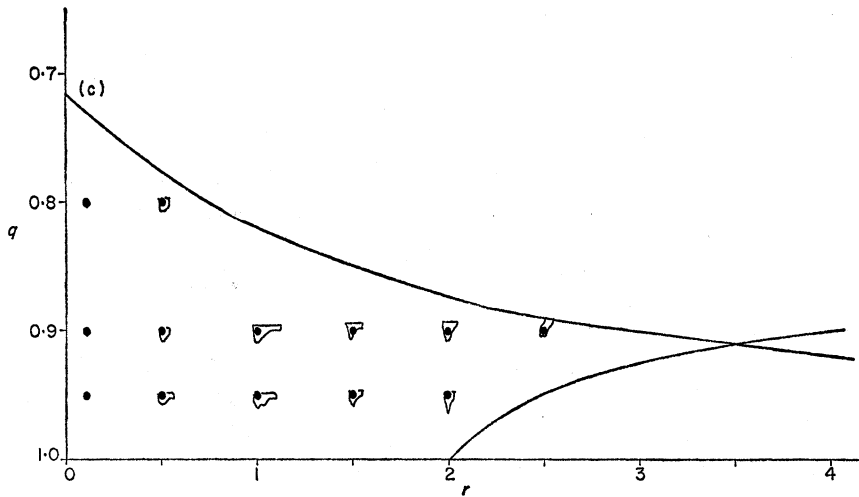


FIG. 7. Domains of attraction (see text) for equilibria derived from a grid of values of  $r$  and  $q$ , and centred so that the equilibrium point on the domain of attraction (shown as a dot) lies on the appropriate point in  $r$ - $q$  space. Sets of domains of attraction, together with the local stability boundaries, are shown for (a)  $\phi = 1$ , (b)  $\phi = 2$ , and (c)  $\phi = 4$ . All are drawn to the same scale, given in the inset to (a), set for the arbitrary carrying capacity  $K = 10$ .



FIG. 7 *cont.*

and  $T_R = 1$ . For  $\phi = 0$ , for example, this region occurs at values of  $q$  and  $r$  of approximately 0.7–0.8 and 2 respectively. As a parameter combination moves away from this central, rapidly damping region, the time taken for the populations to return to equilibrium progressively increases until the boundary defining the limits of local stability is crossed. Note that the rate of change of the characteristic return time with respect to  $\lambda$  is given by  $(1 - |\lambda|)^{-2}$ , so there is very little difference in the return time for large variations in  $r$  and  $q$  about the central region. However, as the boundaries of local stability are approached, the length of time taken to return to equilibrium increases rapidly. Close to the boundaries of the locally stable area, perturbations to populations may take so long to die away that effectively the populations may never return to equilibrium within a biologically meaningful time-span. To that extent, attempts to define feasible and unfeasible combinations of parameter values for ecological models by local stability analysis may give an over-optimistic picture of the range of possibilities open to real organisms in a noisy world.

This foreshadows the results of the next section.

## GLOBAL EQUILIBRIUM BEHAVIOUR

A local stability analysis of the sort we have described above demarcates those points in parameter space where very small perturbations from an equilibrium point will ultimately disappear from those where they will grow. For global stability we need to know for each point in locally stable parameter space what are the limits (if any) beyond which the perturbed populations will no longer return to equilibrium.

There are two ways of investigating the global stability properties of a mathematical model of the form described by eqn (1). The first involves the construction of a Liapunov function (usually numerically) whose properties guarantee the applicability of the local analysis for some range of points in locally stable parameter space and for some (possibly unbounded) domain of phase space. The mathematical literature on this problem is somewhat esoteric and we have found that the published algorithms used to generate

Liapunov functions break down when confronted with a model of even the rather low level of complexity of eqn (1). Interested readers are referred to Siljak & Sun (1971) and the references therein.

The second method, although mathematically inelegant, produces satisfactory results for even quite complicated models; its disadvantage is that it is time consuming. In essence it involves taking a given point in locally stable parameter space and then, using these parameter values, simulating the population process from a set of initial conditions chosen from a grid in phase space. In this way a boundary may be constructed to any specified accuracy within which perturbations from equilibrium will disappear. Clearly this has disadvantages in that it presumes that the boundaries approximated to are continuous; it also involves some arbitrary decision about the maximum perturbations to be considered. Nevertheless it does afford an unequivocal way of characterizing, for any specified perturbation, whether or not a population ultimately returns to its locally stable equilibrium.

The results of our numerical studies are illustrated in Fig. 7. For all the parameter combinations when  $\phi = 0$  we find that the equilibrium values are globally stable up to the extreme perturbation  $N = 0$  and/or  $P = 0$ . This is to be expected given that the condition  $\phi = 0$  is simply saying that there is no lower threshold for prey density below which the predator population goes extinct. The results for values of  $\phi > 0$  are, however, less obvious and more interesting. For a given value of  $\phi$  the size of the stable domains in phase space varies markedly with  $r$ , increasing to a maximum with  $r \simeq 1$ . The parameter  $q$  appears to have little effect upon the size of the domains. Increasing values of the parameter  $\phi$  lead to marked decreases in the size of the stability domains. This result may be compared with the small effect that this parameter has on the local stability properties of the model. Thus for  $\phi = 4$  there is a substantial area of locally stable parameter space, but a vanishingly small domain of phase-space within which the population trajectories will return to equilibrium. In other words, although the local stability analysis suggests that for  $\phi = 4$ , stable coexistence of a predator and prey population is possible over quite a large range of values of  $r$  and  $q$ , this stability is fragile. Any but the smallest numerical perturbations of the populations away from equilibrium will result in the breakdown of the regulatory mechanisms and the extinction of the predator. Clearly such interactions between local and global stability will be important in interpreting the patterns of parameter values existing in real populations.

At this point we digress and consider the parameter  $\phi = \alpha\beta$  in more detail. The results of our local stability analysis indicated that as long as the product  $\alpha\beta$  was constant then the relative contributions of  $\alpha$  and  $\beta$  to the product did not matter. In marked contrast, the global analysis shows that the basal metabolic requirement of the predator  $\beta$  affects the global properties more fundamentally than the predator efficiency  $\alpha$ . Thus appropriate parameter combinations for a local analysis may prove to be entirely inappropriate when considering the global properties of the same model. We illustrate this in Fig. 8 for one point in  $r, q$  and  $\phi$  space which shows how increasing the proportional contribution of  $\beta$  to  $\phi$  (such that  $\alpha\beta$  remains constant and hence local stability is unchanged) considerably reduces the size of the stable region of the model in phase space. The effect is strictly proportional to the decrease in the predator equilibrium  $P^*$ , also caused by the decrease in  $\alpha$ . Indeed, the domains of attraction become identical when they are plotted for perturbations which are proportional to  $P^*$ . These considerations further reinforce the argument of this section that local stability analysis may be quite misleading in predicting or interpreting the behaviour of real populations.

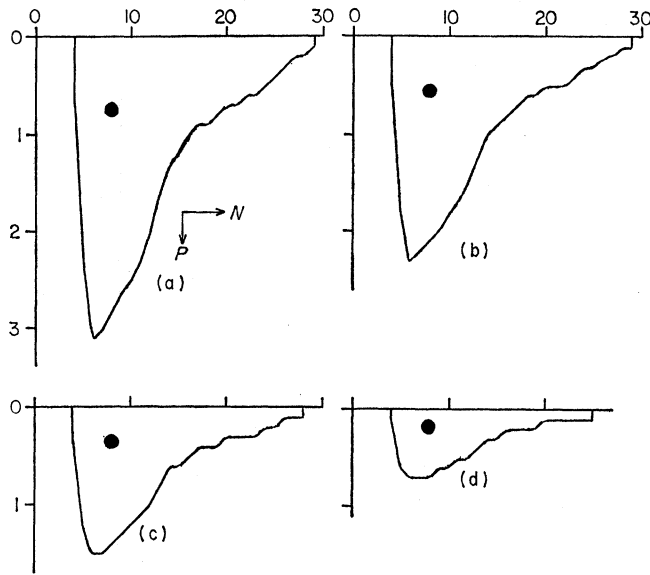


FIG. 8. Domains of attraction for  $r = 1$ ,  $q = 0.8$ ,  $\phi = \alpha\beta = 1$ , with varying  $\alpha$  and  $\beta$ : (a)  $\alpha = 1$ ,  $\beta = 1$ ; (b)  $\alpha = 0.75$ ,  $\beta = 1.333$ ; (c)  $\alpha = 0.5$ ,  $\beta = 2$ ; (d)  $\alpha = 0.25$ ,  $\beta = 4$ . As  $\alpha$  decreases there is a decrease in the range of numerical perturbations that the predator population can withstand, manifested by a shrinking domain of attraction.

### NON-EQUILIBRIUM BEHAVIOUR

It is increasingly recognized that local instability in a population interaction does not imply that coexistence between the component species is impossible. For models framed as differential equations there is an extensive literature cataloguing results that guarantee for a large set of such models the existence of limit cycles in locally unstable parameter space (Hirsch & Smale 1974; Kolmogorov 1936; May 1972). For predator-prey models framed as difference equations, Beddington *et al.* (1975) indicate that there are likely to be three basic types of behaviour in locally unstable parameter space: (1) limit cycles of non-integral period in which the populations follow closed curves in phase space; (2) integer period limit cycles in which there are sets of points in phase space which are visited in turn by the population trajectories; and (3) chaotic behaviour in which there appears to be an unlimited number of points to which the populations move in a well defined domain of phase space.

In considering the non-equilibrium behaviour of the model specified by eqn (8), we shall use the concepts of local and global stability which have already proved to be useful in the equilibrium case. Initially we demarcate the shell of non-equilibrium behaviour in parameter space which is both 'locally stable' (i.e. cyclical or chaotic patterns of behaviour, to which the populations return after a small disturbance) and which permits only positive population values. This is illustrated in Fig. 4. Some care must be taken in interpreting these boundaries as they have been arrived at numerically by first finding the limit cycle or chaotic domain and then investigating the population trajectories following small perturbations away from them. The figure does, however, indicate unsurprisingly that the introduction of a threshold into the population model  $\phi > 0$

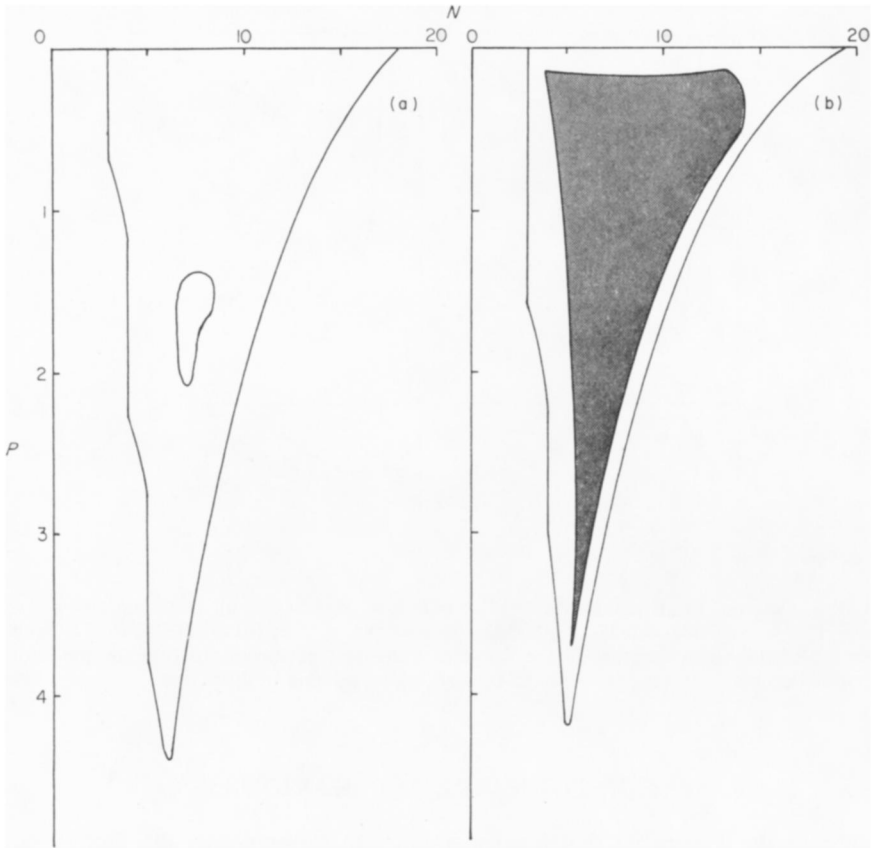


FIG. 9. Domains of attraction for examples of stable non-equilibrium behaviour: (a) limit cycle ( $r = 2.4$ ,  $q = 0.72$ ,  $\phi = 1$ ,  $\alpha = \beta = 1$ ); (b) 'chaos' ( $r = 2.4$ ,  $q = 0.63$ ,  $\phi = 1$ ,  $\alpha = \beta = 1$ ). Whereas the limit cycle lies well within its domain of attraction, the population fluctuations inherent in 'chaotic' behaviour often come close to the boundary. Such behaviour is relatively fragile to the additional fluctuations naturally imposed on a population.

results in a considerable reduction of the domain of parameter space within which non-equilibrium, but strictly positive, population trajectories are followed. R. M. May has pointed out to us that using a different mathematical form for the prey density-dependence  $f_1(N_i)$  might make this reduction less dramatic.

The global stability of these limit cycles and chaotic domains can now be investigated in a similar way, but without the restriction that the perturbations should be small. The results parallel those of the equilibrium case in that we find that local stability is sufficient to guarantee globally stable behaviour for  $\phi = 0$  and that for  $\phi > 0$  there are well defined finite zones of attraction in phase space. Some typical results are illustrated in Fig. 9.

There are no sudden discontinuities in the sizes or shapes of the globally stable region during a transition from locally stable to locally unstable parameter space. Not unexpectedly, the domains of attraction change smoothly and continually across the boundary, the only difference being that on the one side they centre on a point equilibrium and on the other on a very small limit cycle.

## DISCUSSION AND CONCLUSIONS

Our analysis has been linked to a particular type of interaction (predator-prey), a particular mathematical form (difference equations) and to a particular model. In this final section we explore some of the general consequences of the analysis before making some rather speculative comments about particular predator-prey systems.

For a population interaction to persist, the parameters of the appropriate population model should be such that the model implies either a locally stable equilibrium or a limit cycle. However, a central result of our analysis is that this is a necessary, but not sufficient, condition for persistence. Sufficiency may be guaranteed only when the component population densities occur and stay within some well-defined region around the equilibrium or cycle. It is important to note that this region may be vanishingly small and indeed, for any interactions in the real world, it is unlikely to be so large as to be irrelevant.

These ideas, represented pictorially in Fig. 1, allow several interesting inferences about population phenomena to be made. We can speculate, for example, that different kinds of population interactions may have different kinds of persistence domains. Thus we would expect predator-prey interactions to give rise to different forms of persistence domain from those produced by competitive or mutualistic interactions. This is not a somewhat trivial consequence of the fact that different types of interaction involve different parameters (e.g. predation rates and competition coefficients), a problem that may be surmounted by considering interactions in terms of biomass or energy exchange, but rather results from noticing that the dynamic processes involved are essentially dissimilar.

Any particular predator-prey interaction will at some chosen time occupy a particular position in parameter and population space. If this point lies in the persistence domain, in a deterministic world the component populations will eventually return to the appropriate equilibrium or limit cycle. If it does not lie in the persistence domain, ultimately one or both populations will become extinct. However, in the noisy, real world both the parameters of the interaction and the densities of the component populations may alter. We can thus ask of a particular interaction how robust it is to such changes. In essence, this is the question posed by Holling (1973) and Leigh (1975) about the 'resilience' of an ecological system, although they both concentrate only on numerical perturbations to the population. However, it is clear that a simple answer is not possible. Perturbations to population densities in areas of parameter space where characteristic return times are short will tend to dampen quickly and such areas are by definition some distance from the boundaries of locally stable and unstable parameter space. Thus the characteristic return time might be thought to be a measure of the resilience of a system. Indeed this is reinforced by the consideration that a fully stochastic version of the model in which the parameters were treated as random variables would be likely to result in the constraints for stability being more severe and requiring that the eigenvalues of the stability matrix should lie within a subset of the unit circle whose size was determined by the environmental variability (May 1974a, p. 35). That this is not the whole story is apparent from the observation that parameters affect the local and global properties of a model in different ways. Thus a parameter may only weakly affect the local properties and hence the return times, but may have a substantial effect in determining those boundaries in phase space within which perturbations die away. Clearly in the context of our particular model,  $\beta$ , which reflects the basic metabolic needs of the predator, is one such parameter.

Thus one set of parameters will define a particular characteristic return time and a large area of phase space within which perturbations die away, yet a different set of parameters can be chosen which produce the same return time, but which have a considerably smaller stable domain in phase space associated with them. These considerations support the view of May (1974a) that there is no single number or small set of numbers which can characterize the resilience of a system. Nevertheless some guidelines may be laid down for qualitative comparison of particular interactions. Short return times and large domains of attraction in phase space are clearly characteristics of highly resilient populations.

Just as it is impossible to define, simply, the resilience of an ecological system, it is also likely to be impossible to find any one single criterion to judge whether a particular combination of parameter values is, or is not, ecologically feasible. In the introduction we pointed out that there is an increasing number of studies which show that the parameter values which characterize the interactions of real population systems are very far from being a haphazard selection of all numerically possible values. Observed parameter combinations must inevitably be associated with persistent population behaviour, but it should by now be obvious that this is not synonymous with the existence of a locally stable equilibrium. To this extent, attempts to make predictions about expected parameter combinations in real ecological systems on the basis of a local stability analysis will be subject to two kinds of error. On the one hand, such analyses will define locally stable combinations that are improbable when domains of attraction and characteristic return times are also considered, and on the other hand they will exclude locally unstable combinations that give rise to stable limit cycles. Failure to recognize this point is likely to lead to considerable confusion as more empirical data accumulate on the parameter values associated with particular sets of interacting species. Two predictions which arise directly from our model are that in predator-prey interactions at least (and presumably in other sorts of interactions also), we expect to see persistent natural populations that have model counterparts that are locally unstable, and, requiring more data to establish, large regions of locally stable parameter space unoccupied by any real-world populations.

The very existence of a series of mutually interdependent criteria upon which the persistence of populations in the field can be thought to depend also suggests other interesting ideas. For example, what happens at the edge of a species' range? Which of the several possibilities either in isolation or in combination result in it ceasing to exist outside the boundaries of a particular geographical region? Do changing environmental conditions produce changes in parameters such that no locally stable point or cycle exists? Do the vagaries of the environment increase to such an extent that the likelihood of a large perturbation pushing the population outside the limits of its persistence domain become a virtual certainty? Do return times become so long that small numerical perturbations eventually lead to extinction? These questions are clearly answerable, in principle at least, and may provide a unifying set of hypotheses for what is otherwise a well-known, but little-studied phenomenon (Ford (1975) is a notable exception), with no body of theory associated with it.

Reversing the direction of these arguments, we can say that certain combinations of parameter values giving rise to locally stable equilibria or to limit cycles will only be feasible in very constant, predictable environments. This is consistent with the view that these environments tend to have a high diversity of species (May 1974b; Sanders 1969), presumably because a proportion of the organisms are able to occupy highly specialized 'niches', involving interactions with their environment and other members of the community that are characterized by fragile, even bizarre, combinations of parameter values.



As expected, these species-rich systems are extremely vulnerable to even quite small, novel, numerical perturbations (Larsen 1974; Paine 1969).

Although these general insights may be useful, our model ought also to provide some particular insights for those biological circumstances it most closely describes, namely predator–prey interactions. Attempts to establish persistent, self-perpetuating predator–prey systems either in the laboratory or in the field frequently meet with failure (Beirne 1975; DeBach 1974; Gause 1933; Huffaker 1958; Maly 1975; Varley, Gradwell & Hassell 1973). Undoubtedly some of these failures can be attributed to rather obvious causes, for example an environment that is physically unsuitable for one or other of the introduced species, giving rise to  $\alpha$  values = 0. Such locally unstable behaviour may also be produced for more subtle reasons involving particular combinations of predator attack-rates, or prey rates of increase. However, in other cases a locally stable equilibrium (or limit cycle) may in principle have been possible but the numbers of prey and/or predators chosen to start the experiment were wrong; that is they lay outside the globally stable limits of the potential equilibrium. The very precise conditions required to achieve biological control of red spider mite (*Tetranychus*) by *Phytoseiulus persimilis* Athias-Henriot (including both the ratio of prey to predators and the timing of the introductions—see Moreton 1969) may provide an example of this phenomenon. Recognition of this fact may well help to explain the failure of a number of other biological control programmes that on the face of it appeared as though they ‘ought’ to have worked. The much smaller persistence domains shown by predators, compared with parasites, prompts the further prediction that introductions of parasites for biological control should, in general, succeed more often than introductions of predators. Curiously this particular comparison does not appear to have been made in a number of recent reviews (e.g. Beirne 1975), although it is consistent with the view expressed in DeBach (1964, p. 129) that parasites are more successful biological control agents than are predators.

A consideration of the ‘edge of range’ problem in terms of our particular model also appears to provide insights into a study by Whittaker (1971) on the bug *Neophilaenus lineatus* (L.). This species has an annual life-cycle and appears to conform rather closely in the essential features of its biology to the general model specified by eqn (1). Populations in lowland, southern England (the usual habitat) exhibit ‘normal’ density dependence including attack by a pipunculid parasite *Verallia aucta* Fallén. In contrast, a population at the very edge of the species’ altitudinal range in the northern Pennines showed very little evidence of density dependence and when manipulated experimentally, failed to converge toward an unmanipulated control. In other words, characteristic return times were long. Not only that, the Pennine population also fluctuated more in response to natural environmental perturbations than the lowland one. We speculate that the high altitude population can be visualized as lying close to the boundary of a locally stable region in ‘parameter space’ and that it is this which gives rise to the long characteristic return times. The limit of the altitudinal range is crossed when repeated natural environmental perturbations to the population, changes in parameter values with increasing altitude, and long characteristic return times combine to produce such high probabilities of extinction that the population is no longer able to persist.

More exact attempts to equate the predictions of our model with the behaviour of real predator–prey systems must await refinements in the model in those components where it is known to be too simple. These will not alter an essential point of this analysis, namely that a study of the local (neighbourhood) stability properties of ecological models is, at best, likely to provide only limited insights into the workings of the real world. The



utility of such models can be considerably extended by considering global stability properties and the time taken to return to equilibrium, employing techniques similar to those developed in this analysis.

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### SUMMARY

(1) The persistence of populations in the real world depends on their ability to withstand perturbations imposed by either exogenous or endogenous factors.

(2) This paper illustrates the appropriate mathematical concepts for describing persistence by means of a simple predator-prey model framed in difference equations.

(3) Perturbations may be visualized either as a change in the parameters of the model or as alterations to the densities of the component populations.

(4) A local stability analysis is performed to demarcate regions of parameter space in which the model displays locally stable equilibrium behaviour. Within these regions different rates of return to equilibrium occur, some so small that perturbations to populations do not damp within a biologically feasible time-span.

(5) Each point in locally stable parameter space has associated with it a well-defined domain of attraction in phase space outside which perturbed populations do not return to equilibrium. There is considerable variation in the size of these domains. Thus some locally stable equilibria are robust to large displacements of their populations while some parameter combinations define equilibria which are fragile to any but the smallest perturbations.

(6) Ideas of persistence are also applicable in locally unstable parameter space, where the domains of attraction centre on stable limit cycles or chaotic behaviour rather than on stable equilibria.

(7) Analysing the local stability properties of a model is merely the first step in understanding persistence in the real world. Large regions of locally stable parameter space may not be occupied by real populations because of long characteristic return times or very small domains of attraction in phase space. Furthermore, parameter combinations giving rise to locally unstable equilibria may characterize populations showing stable limit cycle behaviour.

(8) There would seem to be no single number, or small set of numbers, capable of describing 'the stability' or 'the resilience' of a population. Characteristic return times are a partial measure of the resilience of a population to perturbation, but a full understanding of persistence requires in addition a description of the non-local stability properties of the interaction.

(9) The qualitative insights which the model provides into two fundamental ecological problems are considered. We ask what happens at the edge of a species' range, and we consider the success and failure of biological control programmes involving predators and parasites.

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## APPENDIX

### Local stability analysis

The general model specified by eqn (1) may be rewritten in an extension of simple matrix notation as

$$\mathbf{v}_{t+1} = \mathbf{M}_{(\mathbf{v}_t)} \mathbf{v}_t \quad (\text{A1})$$

where  $\mathbf{v}_t$  is a column vector consisting of  $N_t$  and  $P_t$ . The matrix  $\mathbf{M}_{(\mathbf{v}_t)}$  is of the form

$$\mathbf{M}_{(\mathbf{v}_t)} = \begin{bmatrix} f_1(N_t)f_2(N_t, P_t) & 0 \\ 0 & f_3(N_t, P_t) \end{bmatrix}. \quad (\text{A2})$$

The subscript  $\mathbf{v}_t$  indicates that the elements of the matrix are functions of the elements of the vector  $\mathbf{v}_t$ . Using this formalism, it is possible to show that the time-path of a perturbation  $\delta_t$  from an equilibrium of the model can be described by eqn (9)

$$\mathbf{v}_{t+1} = \mathbf{M}_\delta \delta_t$$

where

$$\mathbf{M}_\delta = \mathbf{M}_{(\mathbf{v}^*)} + \sum_i \mathbf{M}'_{i(\mathbf{v}^*)} \mathbf{H}_{i(\mathbf{v}^*)} \quad (\text{A3})$$

$\mathbf{M}_{(v^*)}$  is the matrix  $\mathbf{M}_{(v_t)}$  evaluated at equilibrium;  $\mathbf{M}'_{i(v^*)}$  is the first derivative of  $\mathbf{M}_{(v_t)}$  with respect to the  $i$ th element of  $v_t$  evaluated at equilibrium, and  $\mathbf{H}_{i(v^*)}$  is a square matrix with the  $i$ th column the vector  $v^*$  and all other elements zero (Beddington 1974).

Equilibria for the model are obtained by setting  $N_{t+1} = N_t = N^*$  and  $P_{t+1} = P_t = P^*$ , to give

$$\begin{aligned} N^* &= N^* f_1(N^*) f_2(N^*, P^*) \\ P^* &= P^* f_3(N^*, P^*) \end{aligned} \quad (\text{A4})$$

Using eqn (A3),  $\mathbf{M}_\delta$  is of the form

$$\mathbf{M}_\delta = \begin{bmatrix} 1 + N^* [v_2 f_1(N^*) + v_1 f_2(N^*, P^*)] & N^* f_1(N^*) \cdot \pi_2 \\ P^* v_3 & 1 + P^* \pi_3 \end{bmatrix} \quad (\text{A5})$$

$$\text{where } v_i = \left. \frac{\partial f_i(N_t, P_t)}{\partial N_t} \right|_* \quad \text{and } \pi_i = \left. \frac{\partial f_i(N_t, P_t)}{\partial P_t} \right|_*$$

The characteristic equation of  $\mathbf{M}_\delta$  is of the form

$$\lambda^2 + b\lambda + c = 0 \quad (\text{A6})$$

where

$$\begin{aligned} b &= -2 - N^* [v_2 f_1(N^*) + v_1 f_2(N^*, P^*)] - P^* \pi_3 \\ c &= -b - 1 + N^* P^* [f_1(N^*) (v_2 \pi_3 - v_3 \pi_2) + f_2(N^*, P^*) v_1 \pi_3] \end{aligned} \quad (\text{A7})$$

#### *Application to the particular model*

Applying these results to the model specified by eqn (8), it can be seen that three equilibria are possible:

- (i)  $N^* = 0, P^* = 0$
- (ii)  $N^* = K, P^* = 0$
- (iii)  $P^* = \frac{r}{a} \left(1 - \frac{N^*}{K}\right)^*$ , where  $N^*$  is the second root ( $N^* \neq K$ ) of

$$g(N^*) = r \left(1 - \frac{N^*}{K}\right) (1 + \phi) - a\alpha N^* \left[1 - \exp\left(-r \left(1 - \frac{N^*}{K}\right)\right)\right]. \quad (\text{A8})$$

The coefficients of the characteristic equation, specified in eqn (A7), can be shown to reduce to:

$$\begin{aligned} b &= r - 1 + \phi \left(1 + r \left(1 - \frac{N^*}{K}\right)\right) - \eta (1 + \phi) \\ c &= \left(1 - \frac{rN^*}{K}\right) [\eta (1 + \phi) - \phi] + r^2 \frac{N^*}{K} \left(1 - \frac{N^*}{K}\right) (1 + \phi) \end{aligned} \quad (\text{A9})$$

where

$$\eta = r \left(1 - \frac{N^*}{K}\right) / \left[1 - \exp\left(-r \left(1 - \frac{N^*}{K}\right)\right)\right].$$

For the non-trivial equilibrium with  $P^* > 0$ , the coefficients of the characteristic equation can be completely specified by either of two sets of three parameters, these being

$$(i) \quad r, \phi, q = \frac{N^*}{K} \quad (A10)$$

$$(ii) \quad r, \phi, \theta = a\alpha K.$$

The relation between  $q$  and  $\theta$  can be derived from  $g(N^*)$  in eqn (A8) which gives

$$\theta = \eta(1 + \phi)/q. \quad (A11)$$