



Stability in Insect Host-Parasite Models

M. P. Hassell, R. M. May

Journal of Animal Ecology, Volume 42, Issue 3 (Oct., 1973), 693-726.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8790%28197310%2942%3A3%3C693%3ASIIHM%3E2.0.CO%3B2-H>

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Journal of Animal Ecology is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Journal of Animal Ecology
©1973 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2002 JSTOR

STABILITY IN INSECT HOST-PARASITE MODELS

BY M. P. HASSELL AND R. M. MAY*

*Department of Zoology, Imperial College, London S.W.7, and
Department of Theoretical Physics, University of Sydney, Sydney, Australia*

INTRODUCTION

Population submodels for insect parasitism (or predation) abound in the ecological literature. Many of these have been well reviewed by Royama (1971). They have the general form:

$$\begin{aligned} N_s &= N_t f[P_t, N_t]; \\ P_{t+1} &= N_t - N_s; \end{aligned} \tag{1}$$

where N_s represents the survivors after P_t parasites have searched for N_t hosts resulting in P_{t+1} parasite progeny†. All assumptions about parasite searching behaviour are here contained in the function $f[P_t, N_t]$. If we consider the simplest case where the parasite population is specific and synchronized temporally with its host population, we can write the following generalized model for a host-parasite interaction:

$$\begin{aligned} N_{t+1} &= FN_t f[P_t, N_t]; \\ P_{t+1} &= N_t - \frac{N_{t+1}}{F}; \end{aligned} \tag{2}$$

where N and P are now the host and parasite densities in generations t and $t+1$ and F is the rate of increase of the host population. Note that F is not necessarily the average fecundity per adult host, but represents the effective rate of increase of the host after allowing for all mortalities within the generation except parasitism. This is best shown by an example. Let a given host species have an average fecundity of 100 eggs per adult. In this case, $F = 100$ only if there are no other host mortalities. If there are such mortalities, as will usually be the case, F must be reduced accordingly. Thus with an average additional mortality of 90%, F becomes 10; if the mortality is 95%, $F = 5$ and so on. This is important because, as we shall see below, effective rate of increase always has an effect on the stability of an interaction.

General host-parasite models may be judged on several counts, especially on whether the biological assumptions made are valid and whether sufficient assumptions have been made for the outcome to indicate the rôles of parasitism in natural interactions. It is also important that the model is 'useful' which of course depends on the objectives in mind.

* Present address: Department of Biology, Princeton University, Princeton, New Jersey, U.S.A.

† We shall refer in this paper to 'hosts' and 'parasites' (= parasitoids) rather than to 'prey' and 'predators'. This is not because prey-predator interactions are fundamentally different, but they are usually more complex, especially in that the predator reproductive rate is often only loosely dependent on the number of prey eaten and because the immature stages have specific searching characteristics which vary during their development.

Generally, models with a large number of input parameters are difficult to apply to a wide range of natural populations. This application is much easier with some of the simpler models based on much fewer assumptions, which makes it desirable to single out the really important factors affecting the outcome of parasitism. To be useful in pest control, a general model for parasitism should contain only those components which are likely to affect markedly the outcome of a host-parasite interaction.

The models discussed here vary from the very simple such as that of Nicholson & Bailey (1935) to more complex ones involving effects of host and parasite densities and distribution. In each case we place special emphasis on the type of outcome from different models: whether a particular model is always unstable or is stable within certain limits. In the latter case one should know the precise conditions which can lead to stability, since this may be a useful consideration in developing a theoretical basis to biological control (see Discussion). The practical objective is to be able to predict the type of

Table 1. *Brief description of some of the models to be discussed (see text for definition of symbols)*

Model	Parasitism function $N_s = N_t f(P_t, N_t)$	Brief description	Author(s)
A	$N_s = N_t \exp(-a P_t)$	Random search; constant searching efficiency	Nicholson (1933) Nicholson & Bailey (1935)
B	$N_s = N_t \exp\left(-\frac{a' T_t P_t}{1 + a' T_h N_t}\right)$	Random search; searching efficiency dependent on host density	Holling (1959b) Royama (1971) Rogers (1972)
C	$N_s = N_t \exp(-Q P_t^{1-m})$	Random search; searching efficiency dependent on parasite density	Hassell & Varley (1969)
B/C	$N_s = N_t \exp\left(-\frac{a' T_t c P_t^{1-m}}{1 + a' T_h N_t}\right)$	Random search; searching efficiency dependent on host and parasite density	Hassell & Rogers (1972)
D	$N_s = N_t \sum_{i=1}^n [\alpha_i \exp(-a \beta_i P_t)]$	Non-random search; constant searching efficiency	(This paper)
E	$N_s = N_t \sum_{i=1}^n [\alpha_i \exp(-Q(\beta_i P_t)^{1-m})]$	Non-random search; searching efficiency dependent on parasite density	(This paper)

outcome expected from different host-parasite interactions by measuring certain 'key parameters' of the host and parasite. We have, therefore, wherever possible, illustrated graphically the stability boundaries of the different models. Their mathematical derivations are given in the Appendix.

Hassell & Rogers (1972) discuss three basic parasite responses which can affect searching efficiency and should form part of any general host-parasite (or prey-predator) model: (1) the response to host density; (2) the response to other parasites; and (3) the distribution of searching parasites in relation to the host distribution. We shall illustrate the relative importance of these with different models. Initially, we consider simple models where each response is present alone, and then attempt to show how these responses may be combined in more complex models which are more realistic and yet not so complex as to be unwieldy. Table 1 provides a brief description of these different models. Models A, B, C and B/C are all based on random search but differ in the responses to host and parasite density, while models D and E examine the importance of non-random search by including responses to the host distribution,

MODEL A

The Nicholson–Bailey host–parasite model (Nicholson 1933; Nicholson & Bailey 1935) has been included here as a form of ‘control’. It illustrates the properties of a host–parasite model where search is at random and where searching efficiency is independent of both host and parasite density. It is based on the following assumptions, which if generally valid make the model an ideal one.

(1) Each parasite in the population searches at random with respect to both hosts and other parasites.

(2) The average area which one parasite effectively searches in its life-time (the area of discovery [a]) is constant and characteristic for that species.

(3) A parasite always contains sufficient eggs for oviposition in all hosts encountered. This follows on from assumption (2) in that the area of discovery cannot be a constant if egg supply is limiting.

A parasite with these characteristics will encounter hosts in direct proportion to their density. This is shown by the functional responses* in Fig. 1, which clearly imply that

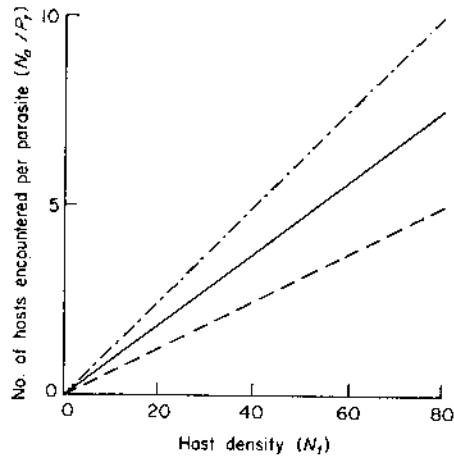


FIG. 1. Examples of functional responses implicit in Nicholson and Bailey's theory. The different slopes are determined by the assumed areas of discovery ($a = N_a/(N_t P_t)$). ---, $N_a/P_t = 0.1N_t$; —, $N_a/P_t = 0.075N_t$; -.-, $N_a/P_t = 0.05N_t$.

parasites do not have a maximum attack rate (Watt 1959) determined by their egg supply or by the time spent ‘handling’ hosts (Holling 1959b). From Fig. 1 we see that the average number of attacks or encounters per host (N_a/N_t) is equal to the product of the area of discovery and the searching parasite density ($N_a/N_t = a P_t$). The way that these attacks are distributed amongst the available hosts has a great bearing on the outcome of the model. Nicholson followed Thompson (1924) by distributing these attacks randomly so that

$$N_{ha} = N_t \left[1 - \exp\left(-\frac{N_a}{N_t}\right) \right] \quad (3a)$$

or

$$N_{ha} = N_t [1 - \exp(-a P_t)] \quad (3b)$$

* A functional response to host density (Solomon 1949; Holling 1959a) is defined as any change in the number of hosts attacked per parasite (or prey attacked per predator) as host density changes.

where N_{ha} is the number of hosts parasitized (whether one or more times) by the parasite population. Clearly, this must be less than the number of encounters with hosts (N_a). We shall see later that eqn (3a) has been widely used in more recent models (see models B and C), but with the derivation of N_a differing from model to model.

By substituting in eqn (2) we have the simple model:

$$\begin{aligned} N_{t+1} &= F N_t \exp(-a P_t); \\ P_{t+1} &= N_t (1 - \exp(-a P_t)). \end{aligned} \quad (4)$$

Such models have only one equilibrium, occurring when host and adult parasite populations are equal to the 'steady densities' (N^* and P^*). These densities depend on the values for the area of discovery (a) and the host rate of increase (F):

$$\begin{aligned} N^* &= \frac{F \ln F}{(F-1)a}; \\ P^* &= \frac{\ln F}{a} \quad \text{or} \quad F e^{-a P^*} = 1. \end{aligned} \quad (5)$$

Any deviation of either N or P from these values leads to host-parasite oscillations of increasing amplitude. Unstable interactions of this kind have been observed only under very simple laboratory conditions. Fig. 2, for example, shows the results of an interaction

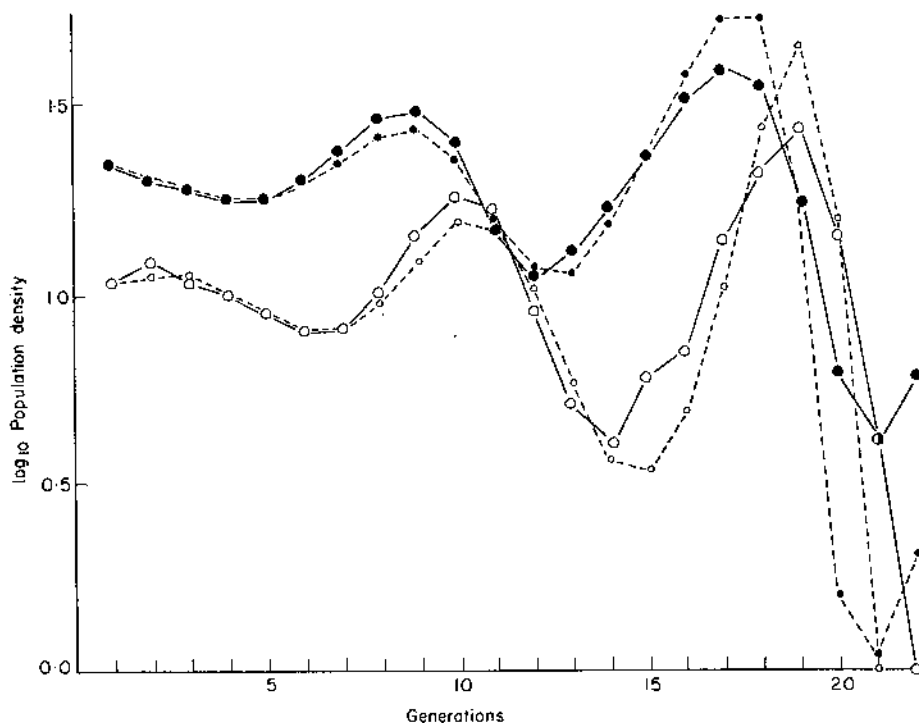


FIG. 2. Observed (—) and calculated (---) results of an interaction between the parasite *Encarsia formosa* (○) and the greenhouse whitefly, *Trialeurodes vaporariorum* (●). The model is calculated on the basis of a constant area of discovery of 0.068 and a host reproductive rate of 2. (After Burnett 1958a.)

between the greenhouse whitefly (*Trialeurodes vaporariorum* (Westw.)) and its parasite, *Encarsia formosa* Gahan, where the host reproductive rate in each 'generation' was artificially made two-fold (Burnett 1958a). Notice that a Nicholson-Bailey model with the area of discovery equal to the mean of those observed over the twenty-one 'generations' follows the results quite closely. Under natural conditions, however, one is struck by the great stability of most host-parasite interactions. Where pronounced host-parasite oscillations do seem to occur as in the case of the black-headed budworm (*Acleris variana* (Fern)) in Canada (Morris 1959), there is no sign that they are increasing in amplitude.

We cannot, however, reject Nicholson's theory as inadequate on these grounds alone since any model based on eqn (4) may be made stable by the inclusion of a suitable density-dependent factor acting on host or parasite population (Varley & Gradwell 1963; Hassell 1969a, b). The real test must be whether the assumptions upon which the model is based—random search and a constant searching efficiency—are biologically valid. The wealth of biological information on parasites indicates that neither of these can be generally true. Perhaps some parasites do effectively search at random throughout their life, but certainly many, and probably most, do not search in this way: they respond to the host distribution (see models D and E below). A constant searching efficiency is even more difficult to accept. Apart from the influence of climate (Klomp 1959), searching efficiency must depend on host density on *a priori* grounds and is also likely to be dependent on parasite density. The effect of host density is included in Model B and that of parasite density in model C.

MODEL B

This model is based on the work of Holling (1959b) and differs from the Nicholson-Bailey model (A) in that searching efficiency is now dependent on the host density. Holling pointed out that there must always be a certain time interval between a host being encountered and search being resumed: this he called the 'handling time'. This handling time progressively reduces the time available for searching (T_s) as more and more hosts are encountered:

$$T_s = T_t - T_h N_a, \quad (6)$$

where T_h is the handling time for a particular host-parasite interaction, and T_t the total time initially available for searching. In model A the total number of encounters with hosts is directly proportional to host density

$$N_a = a N_t P_t \quad (\text{see Fig. 1}). \quad (7)$$

The time spent searching here is assumed to be constant ($T_t = T_s =$ generation time of adult parasites). Eqn (6) shows that this should be modified so that

$$N_a = a' (T_t - T_h N_a) N_t P_t \quad (8)$$

where a' is an attack coefficient representing the instantaneous rate of encountering hosts. (Notice that the area of discovery, a , is equal to $a' T_s$.) The expected functional responses are therefore obtained from

$$\frac{N_a}{P_t} = \frac{a' T_t N_t}{1 + a' T_h N_t}. \quad (9)$$

This is Holling's familiar 'disc equation'—so-called because it was supported by an

experiment in which a blindfolded subject searched for various numbers of sandpaper discs (N_t) on a flat surface. The effect of including a handling time is that with increasing host density the attacks per parasite rise at a decreasing rate towards a maximum defined by $a' T_i$ and T_h . This is illustrated in Fig. 3 where increasing T_h clearly reduces the maximum attack rate. Such curvilinear functional responses are typical of insect parasites and predators (Holling 1959b, 1966). There are considerable data in the literature from which handling times can be calculated and Table 2 shows the extent to which handling times have been found to vary from species to species. Under natural conditions, of course, the maximum rate may also depend on egg-limitation or satiation in the case of predators. In such cases, we may expect the handling time to increase as egg-depletion or satiation is approached.

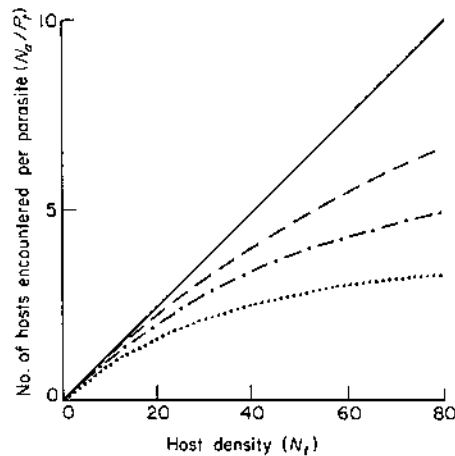


FIG. 3. Functional responses based on eqn (9) where the attack coefficient (a') is 0.01 and the handling time (T_h) (expressed as a proportion of the total time (T_i)) varies as shown for each relationship. —, $T_h = 0$; ---, $T_h = 0.05$; - · -, $T_h = 0.1$; ····, $T_h = 0.2$.

Table 2. Estimated handling times (T_h) from different host-parasite experiments (from Rogers (1972) with the exception of that for *Pleolophus basizonus* (Griffiths 1969) and for *Nemeritis canescens* where T_h was directly observed; the values of T_h/T_i are based on very conservative estimates of adult parasite longevity obtained from the literature)

Parasite species	Host species	Handling time T_h (days)	$\frac{T_h}{T_i}$	Author(s)
<i>Nasonia vitripennis</i> (Walker)	<i>Musca domestica</i> (L.)	0.5	< 0.1	DeBach & Smith (1941)
<i>Chelonus texanus</i> Cress.	<i>Ephestia kuhniella</i> Zeller	0.005	< 0.001	Ulyyett (1949a)
<i>Cryptus inornatus</i> Pratt	<i>Loxostege sticticalis</i> (L.)	0.06	< 0.02	Ulyyett (1949b)
<i>Dahlbominus fuscipennis</i> (Zett.)	<i>Neodiprion sertifer</i> (Geoff.)	0.04	< 0.01	Burnett (1954)
<i>Dahlbominus fuscipennis</i>	<i>Neodiprion lecontei</i> (Fitch)	0.01	< 0.003	Burnett (1958b)
<i>Pleolophus basizonus</i> (Grav.)	<i>Neodiprion sertifer</i>	0.03	< 0.02	Griffiths (1969)
<i>Nemeritis canescens</i> (Grav.)	<i>Ephestia cautella</i> (Walk.)	0.0002	< 0.0001	Hassell & Rogers (1972)

Griffiths & Holling (1969), Royama (1971) and Rogers (1972) have all pointed out that the disc equation can predict only the number of attacks or encounters with hosts (N_a) and not the number parasitized (N_{ha}). This is because the model does not consider the distribution of parasite eggs amongst the available hosts. (In the case of predators

where prey are removed at each encounter (i.e. eaten) the model can only apply to a systematically searching predator which searches a given area only once (Rogers 1972.) The most appropriate way to predict the number of hosts parasitized from eqn (9), which implies random encounters, is to distribute the attacks randomly amongst the available hosts, once again using eqn (3) above. (Non-random distributions are considered later (models D and E).) This makes model B comparable to model A and model C. The function in eqns (1) and (2) must now become

$$f = \exp\left(-\frac{a'T_tP_t}{1 + a'T_hN_t}\right). \quad (10)$$

This model is always less stable than a comparable Nicholson–Bailey model. The reason for this can be appreciated by comparing Figs. 1 and 3. The functional responses in Fig. 1 (implicit in model A) shows a constant proportion of hosts encountered per parasite at all host densities, while the responses in Fig. 3 (model B) are clearly inversely density-dependent. The degree of instability is determined by the values of F (the effective rate of increase of the host) and T_h (the handling time). Increasing the value of either of these leads to greater instability. The value of $a'T_t$ has *no* effect on stability—it is merely a scaling parameter which partly determines the levels about which the populations oscillate.

Models using eqn (8) avoid one of the criticisms of the Nicholson–Bailey theory since they allow searching efficiency to be dependent on host density. The predicted outcome, however, is an even less satisfactory explanation of the apparent general stability of natural interactions. Clearly, we must look for other important components of parasite searching behaviour which may contribute to the stability of such interactions.

MODEL C

Several experiments reported in the literature have shown parasite searching efficiency to be dependent on the density of searching parasites (Hassell 1971a). On the basis of these, Hassell & Varley (1969) proposed a simple inductive model for parasite interference where the area of discovery (a) is exponentially related to parasite density:

$$a = Q P_t^{-m} \quad \text{or} \quad \log a = \log Q - m \log P_t, \quad (11)$$

where Q is the area of discovery when $P_t = 1$ and m (the mutual interference constant) is the slope of the linear relationship between $\log a$ and $\log P_t$. This provides a simple sub-model for parasitism where

$$f = \exp(-Q P_t^{1-m}) \quad (12)$$

may be substituted in eqns (1) and (2). This modification of the Nicholson–Bailey model (which is now a special case when $m = 0$) can completely alter the outcome of a host–parasite model. Instead of always being unstable, this new model is stable over a wide range of conditions depending on the effective rate of host increase (F) and the amount of interference (m). (Q , again contributes to the determination of level but has no effect on stability.) The precise conditions for stability or instability have been derived in the Appendix and are listed in Table 3 and illustrated in Fig. 4. We can see from this figure that, provided that values for F are not very large, even quite small values for m (say $m > 0.25$) will contribute markedly to stability and may even give complete stability. The

Table 3. Stability boundaries for model C

	Description	Condition
(1) Unstable	Populations increase exponentially	$m > 1$
(2) Unstable	Populations oscillate with increasing amplitude	$m < 1 - \left[\frac{F-1}{F \ln F} \right]$
(3) Stable	Populations oscillate with decreasing amplitude	$1 - \left[\frac{F-1}{\ln F} \right] (2F-1-2 \sqrt{F(F-1)}) > m > 1 - \left[\frac{F-1}{F \ln F} \right]$
(4) Stable	Populations approach equilibrium exponentially	$1 > m > 1 - \left[\frac{F-1}{\ln F} \right] (2F-1-2 \sqrt{F(F-1)})$
Stable	Populations approach equilibrium oscillatorily or exponentially	$1 > m > 1 - \left[\frac{F-1}{F \ln F} \right]$
Optimum stability	Most rapid exponential approach to equilibrium which occurs at boundaries of 3 and 4 above	$m = 1 - \left[\frac{F-1}{\ln F} \right] (2F-1-2 \sqrt{F(F-1)})$

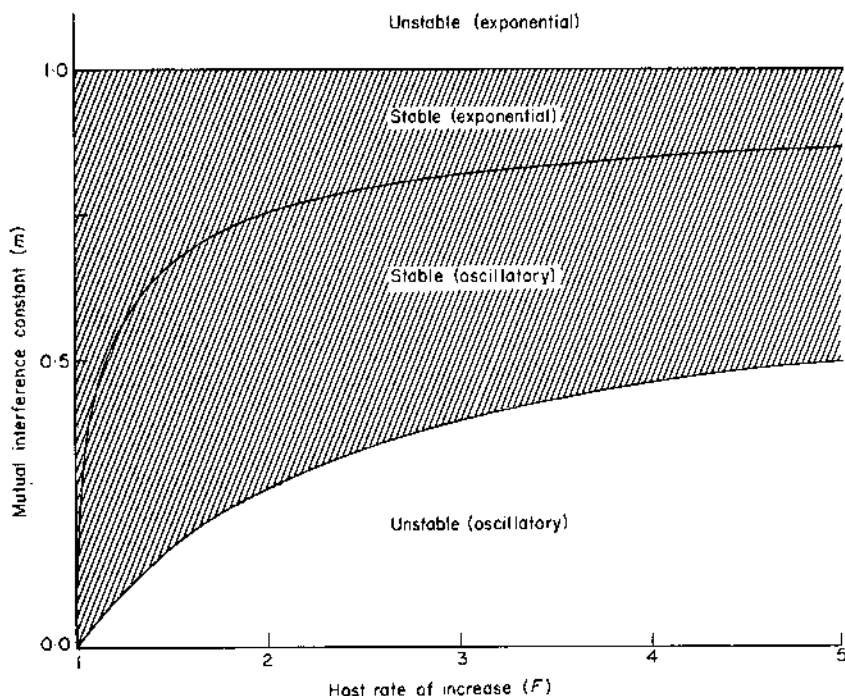


FIG. 4. Stability boundaries (from model C) between the mutual interference constant (m) and the host rate of increase (F). The shaded area denotes the conditions for stability and is divided into two regions (1) where the equilibrium host and parasite populations are approached exponentially; and (2) where there are damped oscillations. The line between these regions indicates the conditions for most rapid approach to the equilibria.

optimum stability is always on the boundary between the zones of exponential and oscillatory stability shown in Fig. 4.

Before the usefulness of this model can be judged we need to know (1) how widespread is interference of some form, and (2) whether eqn (11) is a generally valid description of interference. Table 4(a) shows values of m and their confidence limits obtained from laboratory experiments on six parasite species. In all of the species m was greater than 0.25 and in three cases greater than 0.5. There is less information from interactions in the field. The four parasite species listed in Table 4(b) have comparably high (or higher) values for m , although these cannot be statistically confirmed (Hassell & Varley 1969) and, thus, it is not known at present whether or not the interference found in laboratory experiments is solely due to unnatural conditions. Griffiths & Holling (1969) do not consider interference to be important under natural conditions since the frequency of encounters between parasites will usually be lower than in laboratory experiments. While this is certainly true, they overlook the fact that under field conditions the time 'wasted'

Table 4(a). *Mutual interference constants (m) from laboratory experiments*

Parasite species	Mutual interference constant \pm S.E.	Author(s)
<i>Chelonus texanus</i> Cress.	0.53 \pm 0.12	Ullyett (1949a)
<i>Cryptus inornatus</i> Pratt.	0.38 \pm 0.08	Ullyett (1949b)
<i>Dahlbominus fuscipennis</i> (Zett.)	0.28 \pm 0.06	Burnett (1956)
<i>Encarsia formosa</i> Gahan	0.39 \pm 0.04	Burnett (1958b)
<i>Pseudeucoila bochei</i> Weld.	0.69 \pm 0.05	Bakker <i>et al.</i> (1967)
<i>Nemeritis canescens</i> (Grav.)	0.54 \pm 0.08	Hassell & Huffaker (1969)
	0.66 \pm 0.02	Hassell (1971a, b)
	0.69 \pm 0.02	

Table 4(b). *Mutual interference constants (m) from field studies*

Parasite species	Mutual interference constant \pm S.E.	Author(s)
<i>Apanteles fumiferanae</i> Vic.	0.96 \pm 0.07	Miller (1959)
<i>Telenomus nakagawai</i> Watanabe	0.48 \pm 0.15	Nakasuji, Hokyo & Kiritani (1966)
<i>Cyzenis albicans</i> (Fall.)	0.52 \pm 0.20	Hassell & Varley (1969)
<i>Cratichneumon culex</i> (Muell.)	0.87 \pm 0.19	G. R. Gradwell (personal communication)

after each encounter between two parasites (T_w = 'time wasted')—is almost certain to be more than in laboratory experiments where dispersal is not possible. Thus, omitting any effects of host density, the time spent searching per parasite (T_s) may be represented by

$$T_s = T_t - T_w \text{Encs} \quad (13)$$

where Encs are the encounters per parasite. The same value for T_s can be obtained by large numbers of encounters per parasite with low values for T_w (laboratory conditions) or, conversely, few encounters but large values for T_w (field conditions). For example, Hassell & Rogers (1972) found from laboratory experiments using *Nemeritis canescens* (Grav.) that approximately 25 s represents the average time between leaving a container of hosts following interference and locating a further suitable area. Under natural conditions (within a flour mill) *Nemeritis* will still encounter one another, if only occasionally, since they are attracted to areas of high host density. However, T_w will now be much higher on average since areas of suitable hosts are much more widely dispersed than under laboratory conditions.

We conclude that there are no *a priori* grounds for considering interference to be unimportant under natural conditions. Conversely, its probable importance is supported by its occurrence in some laboratory experiments where parasite density is no greater than that found often in the field, and by the reports of aggressive behaviour between parasite females of some species (Hassell 1971a). Apart from helping to account for the observed stability of so many host-parasite interactions, parasite interference also can account for the frequent coexistence of several parasite species on one host. In such cases, interspecific interference is also possible, but has not yet been considered theoretically. Certainly, some parasites, such as *Rhyssa persuasoria* (L.) (Spradbery 1970), seem to react principally to females of their own species. However, interspecific interference has been clearly reported in a few cases. For example, Hokyō & Kiritani (1966) report 'severe interspecific interference through aggressive behaviour of *Asolcus* [*mitsukurii* Ashmead] female[s] against *Telenomus* [*nakagawai* Watanabe]' under natural conditions.

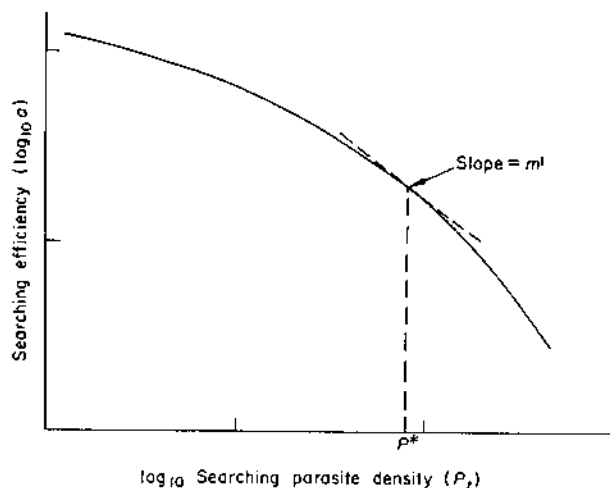


FIG. 5. An arbitrary curvilinear relationship between the searching efficiency ($\log a$) and \log parasite density. The point m^i represents the slope of the curve at the equilibrium parasite density (P^*) (see text for further explanation).

Eqn (11) is an inductive submodel for parasitism based on the approximate description of several sets of data. It has the virtue of being sufficiently simple for the parameters to be measurable from census information on natural populations (Varley & Gradwell 1971). However, its general validity must depend upon the assumptions implicit in eqn (11)—principally on whether m can be a constant for a particular interaction. It is clear that this cannot be the case. It is not possible for m to be constant throughout the range of possible parasite densities. The searching efficiency must tend to become independent of parasite density as the chance of interference becomes very small. Deductive models show that values of m will tend to increase as parasite density increases (i.e. there will be a curvilinear relationship between $\log a$ and $\log P$) (Royama 1971; D. J. Rogers & M. P. Hassell, unpublished). The available data support these models to a greater extent than those where m is a constant. We must conclude therefore, that while model C may remain a very useful submodel for parasitism, it requires further development to be realistic under all conditions.

An advantage of the stability boundaries shown in Fig. 4 is that they may be used whatever interference model is adopted. Fig. 5 shows an arbitrary curvilinear relationship

between $\log a$ and \log parasite density. The slope (m') is no longer a constant in contrast to m above. The procedure for determining stability is now as follows.

(1) Calculate the potential equilibrium density of parasites (P^* in Fig. 5) using the particular model adopted. This is the point where

$$Ff(P, N_t) = 1.$$

(2) Measure the slope (m') of the curve at this point.

(3) The model will be stable if $1 > m' > 1 - \frac{F-1}{F \ln F}$ (see Table 3) and Fig. 4 may be used by substituting m for m' .

MODEL B/C

Our aim here is to explore the effects of both the functional response to host density and

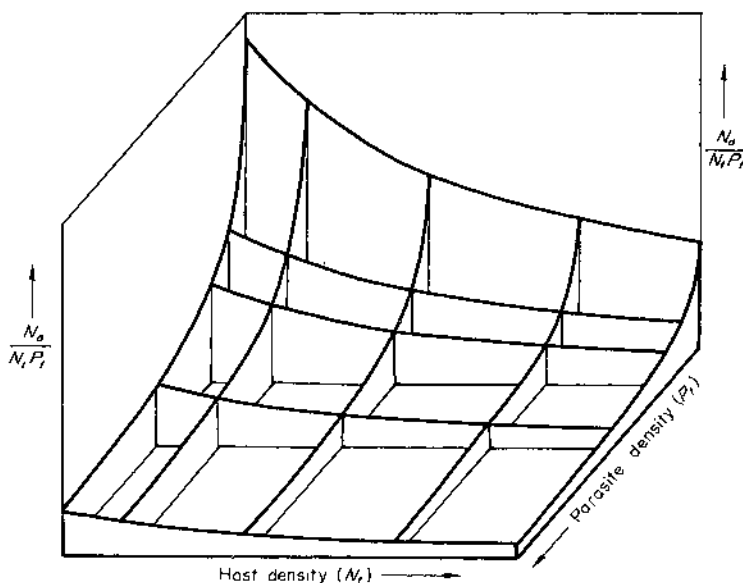


FIG. 6. Diagram of a three-dimensional surface showing how the searching efficiency (expressed as $N_a/(N_t P_t)$) in model B/C is dependent on both host and parasite density.

parasite interference in a single model. Starting with eqn (9) (the 'disc equation'), we have included interference by making the total time (T_t) dependent on parasite density:

$$\frac{N_a}{P_t} = \frac{a' T_t c P_t^{-m} N_t}{1 + a' T_h N_t}, \quad (14)$$

where c and m are constants, m being the mutual interference constant as in model C. This is similar in effect to T_t being constant and the attack coefficient (a') varying with parasite density. Thus, the model reduces to model B if there is no interference ($m = 0$) and to model C if there is assumed to be no handling time ($T_h = 0$). The three dimensional 'surface' in Fig. 6 shows how the searching efficiency (expressed as $N_a/(N_t P_t)$) in this model now varies with both host and parasite densities. Searching efficiency is low

at high host densities due to a high total handling time ($T_h N_a$) and it is low at high parasite densities due to increased interference.

If once again we assume that the attacks (N_a) are distributed randomly amongst the available hosts, we can write the function for parasitism as

$$f = \exp\left(-\frac{Q' P_t^{1-m}}{1+a' T_h N_t}\right), \quad (15)$$

where $Q' =$ the constant $a' T_t c$ from eqn (14). There are three significant parameters affecting stability in a population model based on eqn (15).

(1) ρ , which is defined to be

$$\rho = \frac{a' T_h N^*}{1 + a' T_h N^*}, \quad (16)$$

where N^* is the equilibrium host density and T_h is expressed as a proportion of total time (T_t). This parameter can take any value between zero and unity, and largely characterizes the effect of handling time on stability. Increasing values of T_h give higher values for ρ , as discussed below, while variation in a' has a relatively smaller effect on ρ due to compensating changes in the value of N^* .

(2) m , the interference constant as discussed under model C.

(3) F , the effective host rate of increase which, as in all host-parasite or prey-predator models, must affect the stability of the interaction.

The stability boundaries in Figs. 7 and 8 show the rather complex interaction between these three parameters. The relationships between m and F are plotted in Fig. 7(a, b, c) for three values of ρ (0.2, 0.5 and 0.8) and Fig. 8(a, b, c, d) illustrates the relationships between m and ρ for various values of F (1.1, 1.5, 2.0 and 4.0). Both figures indicate that increasing values of ρ (between 0 and 1) and of F decrease stability, while increasing values of m may make the interaction more stable. Fig. 7(a, b, c) is similar in general form to Fig. 4 from model C where values of m within the range $0 < m < 1$ are shown to increase stability. Now we find that only values of m within the range of $0 < m < 1 - \rho$ make the model more stable.

We saw from model C that marked mutual interference is a powerful stabilizing factor. It is clear from Figs. 7 and 8 that the handling time component can have the opposite effect but only becomes important when ρ is relatively high (say $0.2 < \rho < 1$). We therefore need to know the values of ρ that are likely under natural conditions.

Let us first consider the case where there is no interference ($m = 0$), as in model B. The equilibrium levels here may be written as:

$$\frac{a' T_t P^*}{1 + a' T_h N^*} = \ln F; \quad (17)$$

$$P^* = \frac{(F - 1)}{F} N^*,$$

where P^* and N^* are the equilibrium populations of parasite and host. The parameter ρ , defined above, may now be written as

$$\rho = \frac{T_h}{T_t} \cdot \frac{F \ln F}{F - 1}. \quad (18)$$

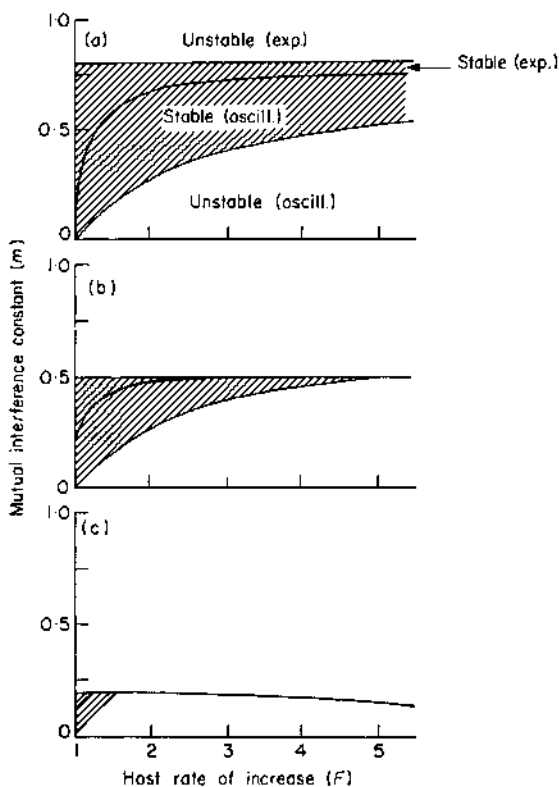


FIG. 7. Stability boundaries (from model B/C) between the mutual interference constant (m) and the host rate of increase (F) for three values of the 'handling time' parameter (ρ): (a) $\rho = 0.2$; (b) $\rho = 0.5$; (c) $\rho = 0.8$. Shaded area indicates conditions for stability.

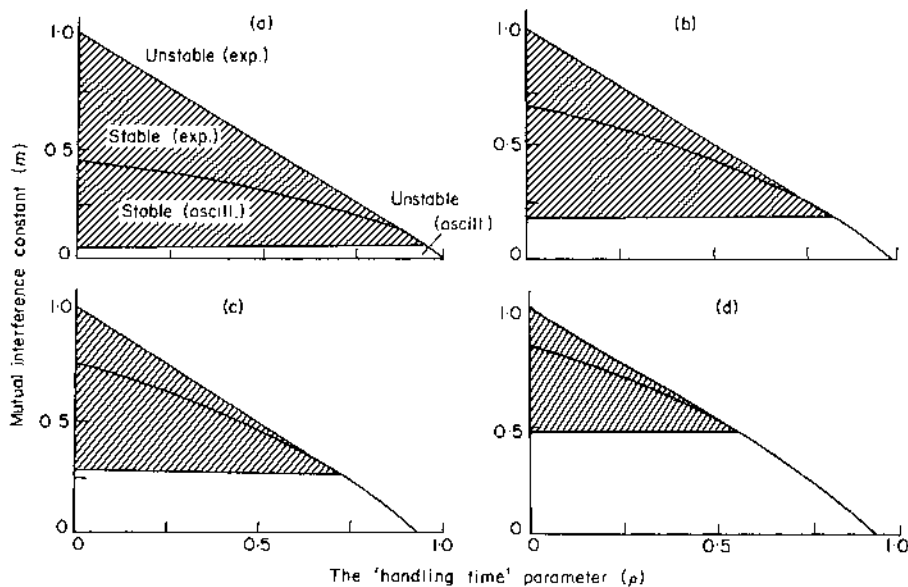


FIG. 8. Stability boundaries (from model B/C) between the mutual interference constant (m) and the parameter, ρ , for various values of the host rate of increase (F): (a) $F = 1.1$; (b) $F = 1.5$; (c) $F = 2.0$; (d) $F = 4.0$. Shaded area indicates conditions for stability.

Now, $\frac{F \ln F}{F-1}$ is always of order unity, from which it follows that $\rho \sim T_h/T_t$. For most parasites the handling time is a very small fraction of the parasite's total searching time (T_t) (see Table 2) and hence it follows that usually $\rho \ll 1$.

This argument remains qualitatively correct when we include some degree of interference ($m \neq 0$). We therefore conclude that in most host-parasite interactions, stability will be affected more by interference and non-random search (to be discussed below) than by handling time.

NON-RANDOM SEARCH

Models A-C assume that parasites search at random. They are all based on a Poisson distribution of the total number of attacks (N_a) amongst N_t hosts, where the probability of an attack on a particular host is equal to $1/N_t$. Thus,

$$P_0 = \exp\left(-\frac{N_a}{N_t}\right) \quad (19)$$

where P_0 is the proportion of hosts unattacked (cf. eqn 3).

The biological assumptions in these equations are straightforward. The distribution of hosts within the whole area is irrelevant when parasites search at random. In other words, hosts within an aggregation are just as susceptible to parasitism as those which are widely spaced out. It is not so easy, however, to relate random search to the actual movements of a parasite, although on average each parasite should spend as much time searching in one sub-unit of the total area as in any other equivalent unit. This means that each parasite will encounter the same *proportion* of hosts in each sub-unit (Rogers 1970, 1972).

We can see that random search is a convenient assumption mathematically; but is it a realistic one? The accumulating information in the literature on the searching behaviour of insect parasites and predators strongly indicates that random search is the exception rather than the rule. This is not surprising when we consider that most host and prey populations tend to be contagiously distributed over the area in which a parasite or predator individual searches. This provides a strong selective advantage for those parasites and predators that tend to aggregate where their food supply is most abundant. There are several types of behaviour that will result in such aggregating of a searching population. For example, individuals may respond over a considerable distance to some product whose concentration is a function of host density. Several examples of this are now known, some of which are listed in Table 5. Alternatively, some species change their searching behaviour after successful parasitism—often by an increased turning rate and thus tend to remain for longer periods in the unit areas where there are most hosts. Fig. 9 illustrates this from an experiment using *Cyzenis albicans*, a tachinid parasite of the winter moth (*Operophtera brumata* (L.)). The track shows the movement of a female parasite in an arena with different densities of small drops of sugar solution per unit area. (*Cyzenis* tends to oviposit on leaves where sap has exuded as a result of feeding by host caterpillars (Hassell 1968).) The increased turning rate has resulted in more time being spent in the area with eight drops than in any lower density area (Murdie & Hassell 1973). Very similar behaviour has been found from an aphid parasite, *Diaeretiella rapae* McIntosh (Hafez 1961); an egg parasite, *Trichogramma evanescens* Westw. (Laing 1937);

MODEL D

We commence with a general formulation. Let the total host and parasite populations produced in each generation be distributed into n areas (where the unit area may be a leaf, a plant, an area of tree canopy, etc.) with the fraction of the host population in the i th area being α_i and the parasite fraction correspondingly being β_i . Thus, the sum of the α_i values and of the β_i values are equal to unity

$$\left(\sum_{i=1}^n \alpha_i = 1; \sum_{i=1}^n \beta_i = 1\right).$$

Model A can now be modified:

$$N_s = N_t \sum_{i=1}^n [\alpha_i \exp(-a \beta_i P_i)]. \quad (20)$$

This model therefore distributes P_t parasites and N_t hosts into n areas in the proportions specified by α_i and β_i . Within each area (i) the exploitation of the hosts is random and the searching efficiency of the parasites is assumed to be independent of host and parasite density so that the effects of different distributions may be more easily shown. We are therefore considering a model similar to model A, but including spatial distributions of hosts and searching parasites. Solution of eqn (20) (see Appendix) shows that, unlike the Nicholson-Bailey model, this model may be completely stabilized if there is an uneven host distribution and marked aggregation of parasites in the unit areas of highest host density. The precise conditions for stability are

$$F \sum_{i=1}^n [\alpha_i (a \beta_i P^*) \exp(-a \beta_i P^*)] < \frac{F-1}{F}. \quad (21)$$

Thus, the key parameters affecting stability in this model are: (1) F , the effective rate of increase of the host population; (2) $\{\alpha_i\}$, the distribution of hosts; and (3) $\{\beta_i\}$ the distribution of parasites.

Eqn (20) provides a completely general model with which to explore the effects of different host and parasite distributions. It requires, however, lengthy calculation for the values of each special set $\{\alpha_i\}$ and $\{\beta_i\}$ that are used. We shall therefore define a further parameter—the 'parasite aggregation index' (μ)—which describes the distribution of the parasite population relative to that of the host:

$$\beta_i = c \alpha_i^\mu \quad (22)$$

where c is a normalization constant such that the β_i values sum to unity

$$(c = [\sum \alpha_i^\mu]^{-1})$$

We have adopted this expression as a simple means of predicting parasite distributions given a particular host distribution. A subsequent paper will consider parasite and predator aggregation more realistically. Fig. 10 shows some special relationships between α_i and β_i ($\mu = 0$; $\mu = 1$ and $\mu > 1$).

(1) $\mu = 0$. This is the special case when there are the same number of parasites in all host areas, irrespective of the host distribution. Thus,

$$\beta_i = \frac{1}{n} \text{ [for all values of } i \text{ from 1 to } n]. \quad (23)$$

Eqn (20) is now exactly comparable to model A where search is at random. Regardless of the host distribution there will be the same (unstable) outcome as in a Nicholson-Bailey model.

(2) $\mu = 1$. This represents the special case where the proportions per unit area of the total parasites searching and the total hosts are the same. Thus,

$$\beta_i = \alpha_i \text{ [for all values of } i \text{ from 1 to } n\text{]}. \quad (24)$$

(3) $\mu > 1$. There is now a differential aggregation of parasites in the areas of highest host density which can be very marked if $\mu \gg 1$. The limiting case, when $\mu \rightarrow \infty$, occurs when all the parasite population aggregates in the single area of highest host density. Thus, all but this particular host area are refuges from parasitism. This is further discussed later in this section.

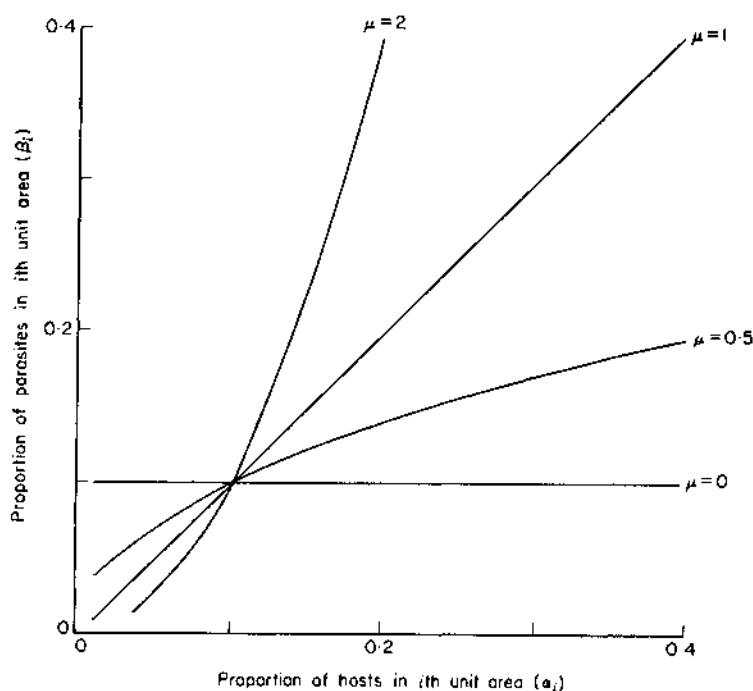


FIG. 10. Some relationships between the proportion of searching parasites (β_i) and the proportion of hosts (α_i) per unit area from eqn (22), assuming different values of the parasite aggregation index (μ) as shown.

At present it is difficult to assess what values of μ may be found under natural conditions since both $\{\alpha_i\}$ and $\{\beta_i\}$ are rarely measured in host-parasite studies. Fig. 11, however, shows the results in one case where these were measured; from laboratory experiments where *Nemeritis canescens* searched for unevenly distributed *Ephestria cautella* larvae (Hassell 1971a, b). Eqn (22) describes the observed data moderately well, with the calculated value for the aggregation index ($\mu = 0.73 \pm 0.04$ (95% confidence limits)) being close to condition (2) above.

Ideally, we should like to produce stability conditions for the parasite response to any set of host distributions. For example:

$$\begin{aligned} \{\alpha_i\} &= 0.4, 0.3, 0.2, 0.05, 0.03, 0.02; \\ \{\beta_i\} &= c\alpha_i^\mu. \end{aligned} \quad (25)$$

Although mathematically straightforward, it is difficult to obtain general insight using such particular examples. Instead, we shall take one particular type of host distribution as an example, since the stability conditions are of the same *general* form for any given $\{\alpha_i\}$ set. The particular host distribution we have selected corresponds to one where hosts are abundant in one area and relatively scarce elsewhere, with α hosts in the high density area and $(1-\alpha)/(n-1)$ hosts in each of the $(n-1)$ low density areas. The degree of parasite aggregation in response to this distribution depends on the aggregation index (μ). Thus for the hosts:

$$\{\alpha_i\} = \alpha; (n-1) \text{ areas with } \frac{1-\alpha}{n-1}; \quad (26)$$

and for the parasites:

$$\{\beta_i\} = \beta; (n-1) \text{ areas with } \varepsilon\beta. \quad (27)$$

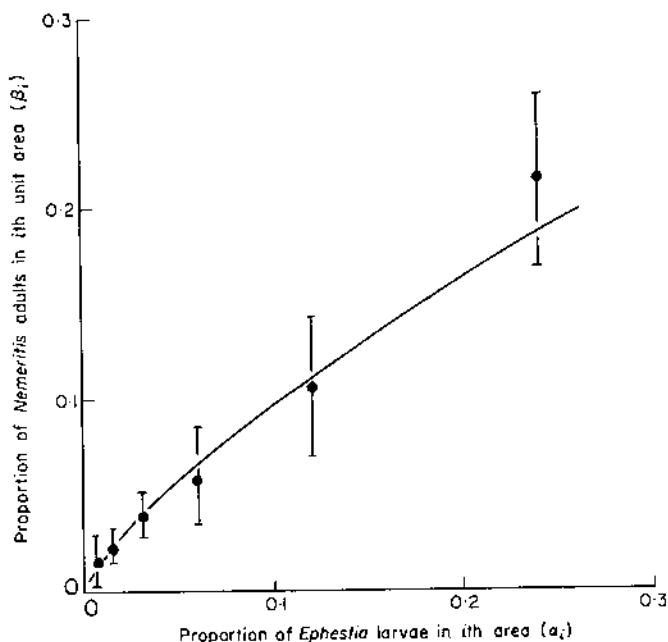


FIG. 11. The relationship between the proportion of searching *Nemeritis canescens* (β_i) and the proportion of *Ephestia cautella* larvae (α_i) per unit area from a laboratory interaction (Hassell 1971a, b). The fitted curve was derived by use of eqn (22). $\beta_i = 0.53 \alpha_i^{0.73 \pm 0.04}$.

The probabilities in eqn (27) for the parasites are related to those in eqn (26) for the hosts by the definition (22):

$$\varepsilon = \left[\frac{1-\alpha}{n-1} \right]^\mu; \quad (28)$$

$$\beta = [1 + \varepsilon(n-1)]^{-1}. \quad (29)$$

There are four parameters which now affect stability, which are (1) μ , the parasite aggregation index, (2) α , the proportion of hosts in the high density area, (3) $(n-1)$,

the number of low host density areas, and (4) F , the host rate of increase. Figs. 12 and 13 illustrate the stability boundaries between μ and F for various values of α and $(n-1)$. These graphs indicate which features of host and parasite distribution have the most impact on stability. There are four obvious trends.

(1) Increasing parasite aggregation (μ) increases stability. This is clear from all the figures. Thus, parasite aggregation alone can sometimes stabilize a model which otherwise is quite unstable.

(2) Given the particular type of host distribution considered, stability is increased if there are more low host density regions. Fig. 12 shows that as $(n-1)$ gets larger, smaller values of μ (less parasite aggregation) are required for stability.

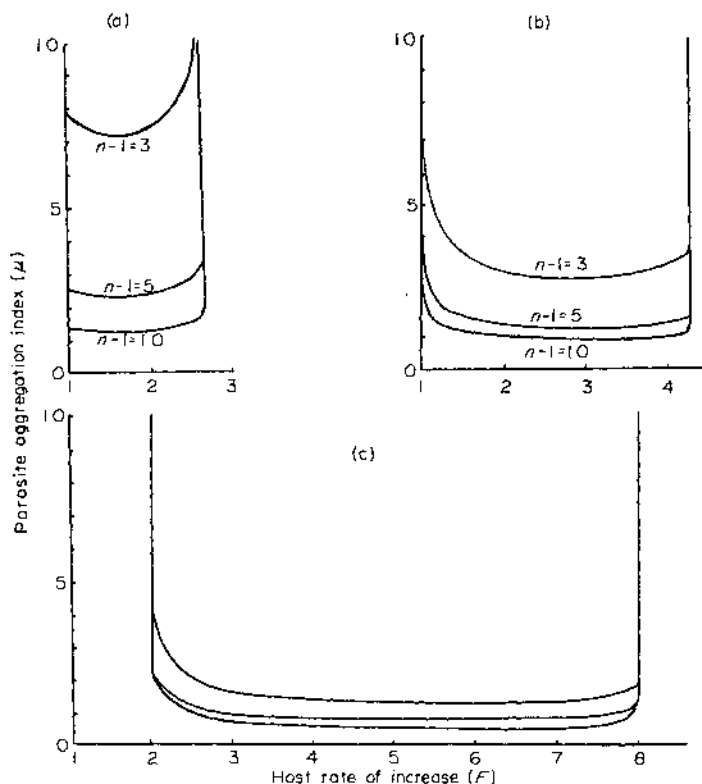


FIG. 12. Stability boundaries (from model D) between the parasite aggregation index (μ) and the host rate of increase (F) for various values for the number of 'low host density areas' ($n-1$) and for the proportion of hosts (α) in the 'high host density area'. Each graph gives the boundaries for three values of $(n-1)$ depending on the value of α : (a) $\alpha = 0.3$; (b) $\alpha = 0.5$; (c) $\alpha = 0.7$.

(3) There is a wider range of stability conditions when α is in the region of 0.5 rather than when it is very small or very large. If α is large (e.g. $\alpha = 0.7$ or 0.8 in Fig. 12c) there is no stability at low rates of host increase (F). On the other hand, as α decreases (e.g. $\alpha = 0.15$ in Fig. 13) stability is only possible with combinations of small values for F and large values for μ .

(4) In each case stability breaks down rather abruptly as F increases.

Bailey, Nicholson & Williams (1962) have previously derived a criterion equivalent to eqn (21) (their equation (17) with their definitions (2) and (10)) for the stability of a host-parasite system in which some hosts are more difficult to find than others. To illustrate the nature of the stability criterion (21) they chose specific host and parasite distributions which are more mathematically elegant than our three-parameter model defined by eqns (22), (26) and (27); but their conclusions are somewhat less biologically transparent. However, examination of the specific distributions of Bailey *et al.* shows them to bear out the main trends remarked above. This is true both for the discrete distributions in their sections 6(ii) and 6(iii), whose stability structure is laid bare in their

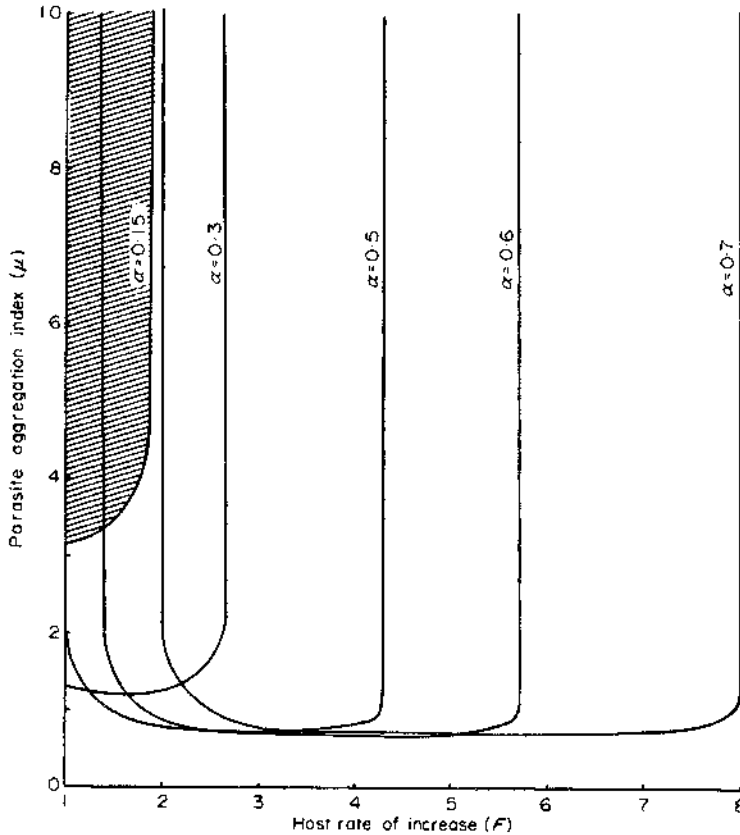


FIG. 13. Stability boundaries (from model D) between the parasite aggregation index (μ) and the host rate of increase (F), for various proportions of hosts (α) in the 'high host density area'. Shaded area indicates conditions for stability where $\alpha = 0.15$.

Figs. 4 I-III and 5, and for the continuous distributions treated in sections 7(i), 7(ii) and Fig. 4 IV-V. Consider, for example, their mathematical statement (comprising their section 7(i)) that the very special continuous 'gamma distribution' relating host and parasite distributions leads invariably to stability if ' $t < 1$ ', and to instability if ' $t > 1$ '. This comes down to the biological statement that this particular model is always stable if there is a wide spread of host densities, with a considerable amount of low density area ($t < 1$, see their Fig. 6), whereas the model is never stable if the host density distribution is relatively flat ($t > 1$).

We may expect, therefore, that the ability of searching parasites to locate the areas of highest host density is an important feature of behaviour promoting stability. The effectiveness of aggregation in this respect depends not only on F but also in part on the type of host distribution ($\{\alpha_i\}$). In this case, stability is increased if something in the region of 50% of the hosts are in a high density region ($\alpha = 0.5$) and the remaining hosts fairly evenly spread over a wide area.

We have chosen this type of host distribution because of the ease with which the stability conditions may be presented as μ varies. Of course, under natural conditions host distributions must vary very considerably and will often depend on the unit areas considered. Thus, the distribution of aphids per plant will usually be quite different from the distribution per leaf. The most meaningful distribution depends on the area searched by the parasite individual. If a parasite tends to remain on a single plant throughout its

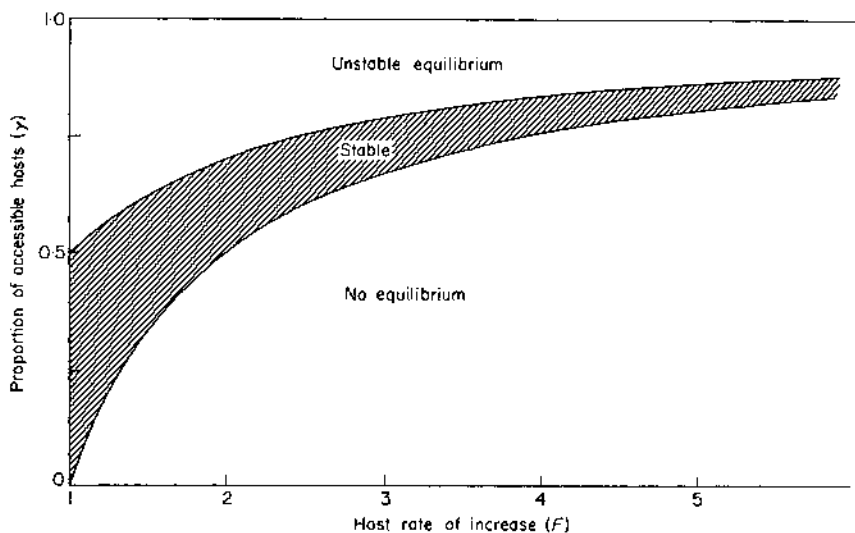


FIG. 14. Stability boundaries (from model D) between the proportions of hosts accessible to parasitism (γ) and the host rate of increase (F). Shaded area indicates conditions for stability.

life, the distribution per leaf, branch, etc. will be most meaningful. On the other hand, the whole plant is likely to be a more useful unit of host distribution where parasites move very readily from plant to plant. These different types of host distribution do not, however, qualitatively change the conclusions already reached. For any given $\{\alpha_i\}$ set, one will still arrive at the general form of relationship between μ and F shown in Fig. 12. The principal difference is that the minimum value for μ required for stability (μ_{\min}) will increase as the $\{\alpha_i\}$ set gets 'flatter' (i.e. as the hosts tend towards a more even distribution). Indeed, if there is too little contrast in the prey population densities in the various 'patches', it can be that no amount of parasite aggregation (not even $\mu \rightarrow \infty$) can stabilize the interaction.

Model D (eqn 20) is also useful in exploring the effect of spatial asynchrony between host and parasite. Fig. 14 shows the precise conditions for stability assuming that the hosts may be divided into a proportion, γ , which are accessible to parasitism and thus a proportion, $1 - \gamma$, that are inaccessible. There are only two parameters affecting stability in this simple model, F and γ . We may conclude from this that increasing the degree of asynchrony ($1 - \gamma$) either spatially or temporally, increases stability only within narrow

limits depending on the effective host rate of increase. In the 'no equilibrium' region marked in the figure there is no kind of equilibrium possible: there is too much refuge from parasitism and both populations must increase. Similar conclusions were obtained by Bailey *et al.* (1962).

Temporal or spatial asynchrony at some level must be a widespread feature in host-parasite interactions and a number of authors have noted that it can contribute to the stability of populations. Varley & Gradwell (1958) listed any protection of hosts from parasitism as a stabilizing factor. Griffiths (1969) studied two ichneumon parasites of the European pine sawfly, one of which was imperfectly synchronized temporally and the other imperfectly synchronized spatially (due to difficulties in locating the host cocoons at any depth in the pine needle litter). He showed by simulation that such asynchrony can contribute to stability. Hassell (1969a) found that 55% of the winter moth larvae in one year were protected from parasitism by *Cyzenis albicans* due to the late emergence of the parasite adults. This was found to be sufficient to stabilize a simple population model based on the observed interaction.

We consider that spatial considerations of the type discussed in this section will often be the dominant factor governing the stability of an interaction (see Discussion).

MODEL E

Using model D we considered the importance of parasite aggregation and host distribution without the complications of functional responses and parasite interference. In this way it was possible to show quite clearly the likely effect of some non-random distributions on the outcome of an interaction. In this section we combine the effects of interference with parasite aggregation and host distribution. To be complete we should also include the functional response from model B which would then give

$$N_s = N_t \sum_{i=1}^n \left[\alpha_i \exp \left(- \frac{a' T_i c (\beta_i P_i)^{1-m}}{1 + a' T_h N_t} \right) \right] \quad (30)$$

in which handling time (T_h), parasite interference (m) and the host and parasite distributions ($\{\alpha_i\}$ and $\{\beta_i\}$) are considered. To avoid a very complex family of stability curves, we have simplified this model by omitting the effect of handling time on the functional response, since most handling times have only a small destabilizing effect on an interaction (see p. 704). Model E, therefore, becomes

$$N_s = N_t \sum_{i=1}^n [\alpha_i \exp (-Q(\beta_i P_i)^{1-m})]. \quad (31)$$

The precise conditions for stability from this model are shown in the Appendix. As expected, the significant parameters are the same as those from model C and model D. Fig. 15 shows how these stability conditions become very extensive even when moderate values for interference and parasite aggregation are combined.

DISCUSSION

It is clear that certain features of parasite searching behaviour can have a marked effect on a host-parasite interaction by determining the form of three basic parasite responses: (1) the functional response to host density; (2) the response to parasite density; and (3) the response to the host distribution.

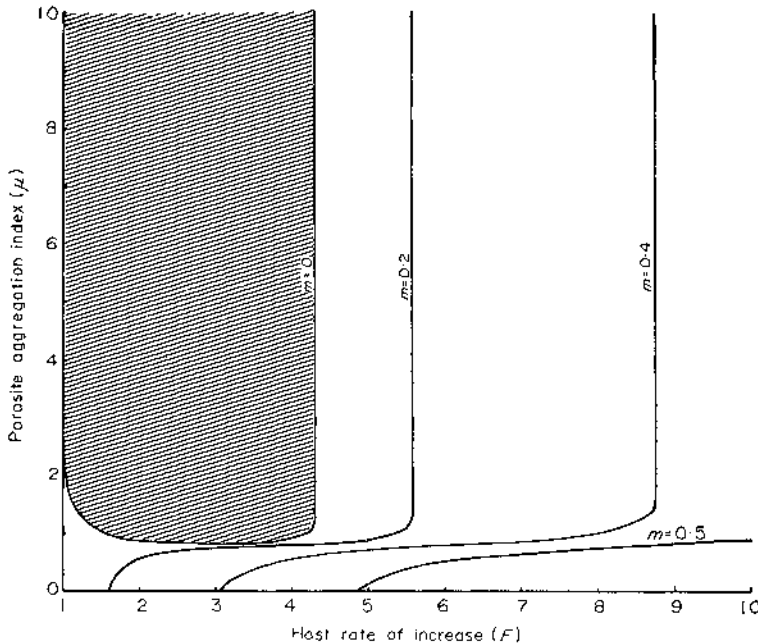


FIG. 15. Stability boundaries (from model E) between the parasite aggregation index (μ) and the host rate of increase (F) for different degrees of mutual interference (m). Shaded area indicates conditions for stability where $m = 0$.

Biological control

The nature of these responses is important to the stability of host and parasite populations as indicated in Table 6. It would be most misleading, however, to imply that only factors affecting stability are important to the outcome of an interaction, since other factors principally have an important effect on the average levels about which the populations fluctuate although they have little or no effect on stability. Both of these categories are important to biological control using insect natural enemies, the success of which depends on the parasites or predators reducing the pest population and maintaining it about a new low level in a stable interaction. These equilibrium levels depend on two factors.

Table 6. *The effect of different parasite responses on population stability*

Response	Parameter	Effect
Functional response to host density	Handling time (T_h) (model B)	Increasing instability as T_h (as a proportion of T_l) increases
Response to parasite density	Interference constant (m) (model C)	Increased stability if m is within the range $0 < m < 1$ with an optimum value as shown in Table 3
Response to host distribution	Aggregation index (μ) (model D)	Increased stability as μ increases, depending on the host distribution (see p. 711).

(1) The effective rate of increase (F) of the host. The value of F depends on the host fecundity, sex ratio and all host mortalities other than parasitism.

(2) The average proportion of hosts parasitized. This proportion depends on the number of searching parasites (which in part depends on the survival of parasite progeny) and all factors affecting the overall searching efficiency (N_a/N_sP_s).

Thus any factors acting on host or parasite populations must have some effect on their average population levels, while only some of these will alter stability.

It is now possible to suggest (see Table 7) how the various searching parameters in models A-E should be optimized for better biological control. Parasites with the following searching characters are the more likely to stabilize their host population at low levels.

Table 7. Some parameters affecting stability and average population levels

Parameter	Optimum for biological control	Effect
a'	High	Reduced average population levels
a		
Q		
T_i^*	High	Reduced average population levels
T_h	Low	Negligible reduction in stability and very slight increase in average population levels
m	Within the range $0 < m < 1$ with an optimum as shown in Table 3	Increase in stability. Some increase in average population levels
μ	High	Increase in stability depending on the host distribution. Some increase in average population levels

* T_i is included in the definition of a and Q .

(1) A high intrinsic searching efficiency (a'). This is necessary to attain the low equilibrium populations.

(2) A small handling time (T_h) relative to the total adult searching life-time (T_i). This minimizes the instability that results from parasite functional responses.

(3) Some degree of parasite interference (m). This contributes to stability if the interference constant falls within the range $0 < m < 1$ (for optimum stability, see Table 3).

(4) A high level of parasite aggregation (μ). This too can contribute markedly to stability but depends very much on the host distribution (p. 711). Generally speaking, higher values of μ are required for stability as the host population tends to become more evenly distributed per unit area. In the extreme case where there is no variation in host density per unit area, no amount of aggregation affects the outcome.

Of course, the success of biological control depends in the first place on the suitability of the chosen natural enemy or enemies within a broader context (Messenger 1971; van den Bosch 1971; Zwölfer 1971). Thus, specific parasites are likely to be more effective than widely polyphagous ones which will interact with their hosts in quite different ways. Their density is less dependent on that of a single host species and their aggregative behaviour is likely to depend on the relative abundance of the different host species. Parasite effectiveness is often limited by *climate*. For example, the introduced parasite, *Aphytis lingnanensis* Compère, has been very effective against the California red scale in the coastal parts of California, but much less so in the more extreme climatic conditions inland where *A. melinus* DeBach is more effective (DeBach, Rosen & Kennett 1971). The

choice of unsuitable *biological races* has hindered some projects such as the early attempts to control the olive scale in California (Doutt 1954). The development of *host resistance* has greatly reduced the effectiveness of *Mesoleius tenthredinis* Morley, an introduced ichneumon parasite of the larch sawfly in Canada (Muldrew 1953). Lack of *synchronization* may be an important factor preventing the establishment of some parasites. Although this can be a powerful stabilizing factor within a narrow range, too much asynchrony prevents any control by the parasite (model D). Other unforeseen circumstances could often be important. For example, it now seems clear that the strong density-dependent pupal mortality of *Cyzenis albicans* in Wytham Woods has prevented it having the important effect on the winter moth populations there that it has had in Nova Scotia (Embree 1966; Hassell 1969b; Varley & Gradwell 1971). Such difficulties are hard to foresee without extensive preliminary studies.

Given, however, that such factors are not limiting, the searching characteristics of the natural enemies become of central importance. The four 'key parameters' listed above are not very difficult to measure experimentally. A series of experiments in which host density is varied will give a measure of a' and T_h or how the searching efficiency ($N_a/N_i P_r = a$) varies with host density (Rogers 1972), and a series where hosts are distributed unevenly and parasite density varied provides estimates of aggregation and interference. Although the precise parameters from such experiments cannot be directly related to field conditions, they would be useful in comparing potential parasites for release. It is hoped that experiments of this kind will become more widespread in the normal screening procedure for possible biological control agents.

ACKNOWLEDGMENTS

We are very grateful to Drs D. J. Rogers, G. R. Conway and G. R. Gradwell for their helpful criticism of the manuscript and to the Ford Foundation for computing facilities at the Imperial College Field Station, Silwood Park.

SUMMARY

(1) Several models for host-parasite interactions are discussed. Some of these are based on random search where searching efficiency is either assumed to be constant or to depend on host and/or parasite density. In the others, the parasites are assumed to search in a non-random way, tending to aggregate in unit areas where host density is high. The most complex model considered includes three basic parasite responses: the functional response to host density, the response to parasite density and the response to the host distribution.

(2) For each of these models, the significant parameters affecting stability are presented and the stability boundaries illustrated where possible. Only mutual interference between searching parasites, aggregation of parasites in unit areas where host density is relatively high and some degree of spatial or temporal asynchrony were found to contribute to stability.

(3) The parameters that affect the equilibrium levels of host and parasite populations and those also affecting stability are discussed in the context of biological control. It is concluded that a high basic searching efficiency, a low handling time, some degree of interference and parasite aggregation are all optimum searching characteristics for biological control.

REFERENCES

- Bailey, V. A., Nicholson, A. J. & Williams, E. J. (1962). Interaction between hosts and parasites when some host individuals are more difficult to find than others. *J. theor. Biol.* **3**, 1-18.
- Bakker, K., Bagchee, S. N., Van Zwet, W. R. & Meelis, E. (1967). Host discrimination in *Pseudeucoila bochei* (Hymenoptera: Cynipidae). *Entomologia exp. appl.* **10**, 295-311.
- Banks, C. J. (1957). The behaviour of individual coccinellid larvae on plants. *Br. J. Anim. Behav.* **5**, 12-24.
- Bedard, W. D., Tilden, P. E., Wood, D. L., Silverstein, R. M., Brownlee, R. D. & Rodin, J. O. (1969). Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. *Science, N.Y.* **164**, 1284-5.
- Benson, J. F. (1972). *Laboratory studies of insect parasite behaviour in relation to population models*. Unpublished D.Phil. thesis, Oxford University.
- Bosch, R. van den (1971). Biological control of insects. *A. Rev. Ecol. Syst.* **2**, 45-66.
- Burnett, T. (1954). Influences of natural temperatures and controlled host densities on oviposition of an insect parasite. *Physiol. Zool.* **27**, 239-48.
- Burnett, T. (1956). Effects of natural temperatures on oviposition of various numbers of an insect parasite (Hymenoptera, Chalcididae, Tenthredinidae). *Ann. ent. Soc. Am.* **49**, 55-9.
- Burnett, T. (1958a). A model of host-parasite interaction. *Proc. Xth int. Congr. Ent.* (1956), **2**, 679-86.
- Burnett, T. (1958b). Dispersal of an insect parasite over a small plot. *Can. Ent.* **90**, 279-83.
- Camors, F. B. & Payne, T. L. (1972). Response of *Heydenia unica* (Hymenoptera: Pteromalidae) to *Dendroctonus frontalis* (Coleoptera: Scolytidae) pheromones and a host-free terpene. *Ann. ent. Soc. Am.* **65**, 31-3.
- Corbet, S. A. (1971). Mandibular gland secretion of larvae of the flour moth, *Anagasta kuehniella*, contains an epideictic pheromone and elicits oviposition movements in a hymenopteran parasite. *Nature, Lond.* **232**, 481-4.
- DeBach, P., Rosen, R. & Kennett, C. E. (1971). Biological control of coccids by introduced natural enemies. *Biological Control* (Ed. by C. B. Huffaker), pp. 165-94. Plenum Press, New York.
- DeBach, P. & Smith, H. S. (1941). The effect of host density on the rate of reproduction of entomophagous parasites. *J. econ. Ent.* **34**, 741-5.
- Dixon, A. F. G. (1959). An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* **28**, 259-81.
- Doutt, R. L. (1954). An evaluation of some natural enemies of the olive scale. *J. econ. Ent.* **47**, 39-43.
- Embree, D. G. (1966). The role of introduced parasites in the control of the winter moth in Nova Scotia. *Can. Ent.* **98**, 1159-68.
- Fitzgerald, T. D. & Nagel, W. P. (1972). Oviposition and larval bark-surface orientation of *Medetera aldrichii* (Diptera: Dolichopodidae): response to a prey-liberated plant terpene. *Ann. ent. Soc. Am.* **65**, 328-30.
- Fleschner, C. A. (1950). Studies on searching capacity of the larvae of three predators of the citrus red mite. *Hilgardia*, **20**, 233-65.
- Griffiths, K. J. (1969). The importance of coincidence in the functional and numerical responses of two parasites of the European pine sawfly, *Neodiprion sertifer*. *Can. Ent.* **101**, 673-713.
- Griffiths, K. J. & Holling, C. S. (1969). A competition submodel for parasites and predators. *Can. Ent.* **101**, 785-818.
- Hafez, M. (1961). Seasonal fluctuations of population density of the cabbage aphid, *Brevicoryne brassicae* (L.), in the Netherlands, and the rôle of its parasite, *Aphidius (Diaeretiella) rapae* (Curtis). *Tijdschr. PZiekt.* **67**, 445-548.
- Hassell, M. P. (1968). The behavioural response of a tachinid fly (*Cyzenis albicans* (Fall.)) to its host, the winter moth (*Operophtera brumata* (L.)). *J. Anim. Ecol.* **37**, 627-39.
- Hassell, M. P. (1969a). A study of the mortality factors acting upon *Cyzenis albicans* (Fall.), a tachinid parasite of the winter moth (*Operophtera brumata* (L.)). *J. Anim. Ecol.* **38**, 329-39.
- Hassell, M. P. (1969b). A population model for the interaction between *Cyzenis albicans* (Fall.) (Tachinidae) and *Operophtera brumata* (L.) (Geometridae) at Wytham, Berkshire. *J. Anim. Ecol.* **38**, 567-76.
- Hassell, M. P. (1971a). Mutual interference between searching insect parasites. *J. Anim. Ecol.* **40**, 473-86.
- Hassell, M. P. (1971b). Parasite behaviour as a factor contributing to the stability of insect host-parasite interactions. *Dynamics of Populations* (Ed. by P. J. den Boer & G. R. Gradwell), pp. 366-79. Centre for Agricultural Publishing and Documentation, Wageningen.
- Hassell, M. P. & Huffaker, C. B. (1969). Regulatory processes and population cyclicity in laboratory populations of *Anagasta kuehniella* (Zeller) (Lepidoptera: Phycitidae). III. The development of population models. *Researches Popul. Ecol. Kyoto Univ.* **11**, 186-210.
- Hassell, M. P. & Rogers, D. J. (1972). Insect parasite responses in the development of population models. *J. Anim. Ecol.* **41**, 661-76.
- Hassell, M. P. & Varley, G. C. (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature, Lond.* **223**, 1133-7.

- Hokyo, N. & Kiritani, K. (1966). Oviposition behaviour of two egg parasites, *Asolcus mitsukurii* Ashmead and *Telenomus nakagawai* Watanabe (Hym., Prototrupoidea, Scelionidae). *Entomophaga*, **11**, 191-201.
- Holling, C. S. (1959a). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Ent.* **91**, 293-320.
- Holling, C. S. (1959b). Some characteristics of simple types of predation and parasitism. *Can. Ent.* **91**, 385-98.
- Holling, C. S. (1966). The functional response of invertebrate predators to prey density. *Mem. entomol. Soc. Can.* **48**, 1-86.
- Klomp, H. (1959). Infestations of forest insects and the role of parasites. *Proc. 15th int. Congr. Zool.* (1958), pp. 797-802.
- Laing, J. (1937). Host-finding by insect parasites. I. Observations on the finding of hosts by *Alysia manducator*, *Mormoniella vitripennis* and *Trichogramma evanescens*. *J. Anim. Ecol.* **6**, 298-317.
- Messenger, P. S. (1971). Climatic limitations to biological controls. *Proc. Tall Timbers Conf. Ecol. Anim. Contr. by Habitat Management*, **3**, 97-114.
- Mitchell, W. C. & Mau, R. F. L. (1971). Response of the female Southern green stink bug and its parasite, *Trichopoda pennipes*, to male stink bug pheromones. *J. econ. Ent.* **64**, 856-9.
- Miller, C. A. (1959). The interaction of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the parasite *Apanteles fumiferanae* Vier. *Can. Ent.* **91**, 457-77.
- Morris, R. F. (1959). Single-factor analysis in population dynamics. *Ecology*, **40**, 580-8.
- Muldrew, J. A. (1953). The natural immunity of the larch sawfly (*Pristiphora erichsonii* [Htg.] to the introduced parasite *Mesoleius tenthredinis* Morley, in Manitoba and Saskatchewan. *Can. J. Zool.* **31**, 313-32.
- Murdie, G. & Hassell, M. P. (1973). Food distribution, searching success and predator-prey models. *The Mathematical Theory of the Dynamics of Biological Populations*, pp. 87-101. Academic Press, London.
- Nakasuji, F., Hokyo, N. & Kiritani, K. (1966). Assessment of the potential efficiency of parasitism in two competitive scelionid parasites of *Nezara viridula* L. (Hemiptera: Pentatomidae). *Appl. Ent. Zool.* **1**, 113-9.
- Nicholson, A. J. (1933). The balance of animal populations. *J. Anim. Ecol.* **2**, 131-78.
- Nicholson, A. J. & Bailey, V. A. (1935). The balance of animal populations. Part 1. *Proc. zool. Soc. Lond.* 551-98.
- Rogers, D. J. (1970). *Aspects of host-parasite interaction in laboratory populations of insects*. Unpublished D.Phil. thesis, Oxford University.
- Rogers, D. (1972). Random search and insect population models. *J. Anim. Ecol.* **41**, 369-83.
- Royama, T. (1971). A comparative study of models for predation and parasitism. *Researches Popul. Ecol. Kyoto Univ. Suppl.* **1**, 1-91.
- Solomon, M. E. (1949). The natural control of animal populations. *J. Anim. Ecol.* **18**, 1-35.
- Spradbery, J. P. (1970). Host finding by *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid wood-wasps. *Anim. Behav.* **18**, 103-14.
- Thompson, W. R. (1924). La théorie mathématique de l'action des parasites entomophages et le facteur du hasard. *Annls Fac. Sci. Marseille*, **2**, 69-89.
- Ulyyett, G. C. (1949a). Distribution of progeny by *Chelonus texanus* Cress. (Hymenoptera: Braconidae). *Can. Ent.* **81**, 25-44.
- Ulyyett, G. C. (1949b). Distribution of progeny by *Cryptus inornatus* Pratt (Hymenoptera: Ichneumonidae). *Can. Ent.* **81**, 285-99.
- Ulyyett, G. C. (1953). Biomathematics and insect population problems. A critical review. *Mem. ent. Soc. sth. Afr.* **2**, 1-89.
- Varley, G. C. & Gradwell, G. R. (1958). Balance in insect populations. *Proc. 10th int. Congr. Ent.* (1956), **2**, 619-24.
- Varley, G. C. & Gradwell, G. R. (1963). The interpretation of insect population changes. *Proc. Ceylon Ass. Advmt Sci.* (1962), **18**, 142-56.
- Varley, G. C. & Gradwell, G. R. (1971). The use of models and life tables in assessing the role of natural enemies. *Biological Control* (Ed. by C. B. Huffaker) pp. 93-112. Plenum Press, New York.
- Watt, K. E. F. (1959). A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *Can. Ent.* **91**, 129-44.
- Wood, D. L., Browne, L. E., Bedard, W. D., Tilden, P. E., Silverstein, R. M. & Rodin, J. O. (1968). Response of *Ips confusus* to synthetic sex pheromones in nature. *Science, N. Y.* **159**, 1373-4.
- Wylie, H. G. (1958). Factors that affect host finding by *Nasonia vitripennis* (Walk.) (Hymenoptera: Pteromalidae). *Can. Ent.* **90**, 597-608.
- Zwölfer, H. (1971). The structure and effect of parasite complexes attacking phytophagous host insects. *Dynamics of Populations* (Ed. by P. J. den Boer & G. R. Gradwell), pp. 405-18. Centre for Agricultural Publishing and Documentation, Wageningen.

(Received 17 November 1972)

MATHEMATICAL APPENDIX

This appendix outlines the mathematical derivation of the various stability results set out in the body of the paper. We first give a formal treatment of the stability character of the general eqn (2), and then apply the consequent formulae to the particular models A–D.

The present account is sketchy. A detailed and lucid analysis of some similar, but simpler, models is in Maynard Smith (1968, Ch. 2). A formal, and in some respects more fully set out, stability analysis of eqn (2) is due to Bailey, Nicholson & Williams (1962); however, these authors have no host dependence in the search function f (i.e. $f(P_t)$ only, not $f(N_t, P_t)$), and their specific applications differ from our models A–D, being somewhat less biologically motivated. For a general account of the stability analysis of population models with difference equations, and their relation to the corresponding analysis for systems of differential equations, see May (1972a, 1973a, b).

General case

The possible time-independent equilibrium populations, N^* and P^* , are found simply by putting $N_{t+1} = N_t = N^*$ and $P_{t+1} = P_t = P^*$ in eqn (2):

$$F P^* = (F - 1) N^*; \quad (\text{A1})$$

$$f(N^*, P^*) = F^{-1}. \quad (\text{A2})$$

These equations may in principle be solved to get N^* and P^* , provided $F > 1$.

In the real world, with its environmental fluctuations, the equilibrium solution will be meaningful only if the system tends to return to these equilibrium populations when perturbed from them. Thus we seek to find whether the equilibrium point N^*, P^* is a stable or an unstable one.

To this end, first write the perturbed populations as:

$$N_t = N^* (1 + x_t); \quad (\text{A3})$$

$$P_t = P^* (1 + y_t). \quad (\text{A4})$$

Here the quantities x_t and y_t measure the initially relatively small perturbations to host and parasite populations, respectively. The dynamics of such perturbations are studied by Taylor-expanding the eqn (2) about the equilibrium point, and discarding terms of relative order x^2 , xy , y^2 or higher, to get

$$x_{t+1} = [1 + v] x_t - \eta(F - 1)y_t; \quad (\text{A5})$$

$$(F - 1) y_{t+1} = F x_t - x_{t+1}.$$

The quantities η and v have been defined for notational convenience:

$$\eta \equiv -N^* (\partial f / \partial P)^*; \quad (\text{A6})$$

$$v \equiv FN^* (\partial f / \partial N)^*. \quad (\text{A7})$$

The partial derivatives of $f(N, P)$ with respect to P and to N are both to be evaluated at the equilibrium point, N^*, P^* . In any biologically sensible model, the fraction of unparasitized hosts, $f(N, P)$, is likely to decrease as P increases, and to increase as N

increases, so that we expect η and ν to be non-negative. However, the formal treatment below encompasses arbitrary η and ν values.

As pointed out in Maynard Smith (1968), Bailey *et al.* (1962), and elsewhere, for linear difference equations such as (A5) it is standard to write the solution in the form:

$$\begin{aligned}x_t &= A_1 (\lambda_1)^t + A_2 (\lambda_2)^t; \\y_t &= B_1 (\lambda_1)^t + B_2 (\lambda_2)^t.\end{aligned}\tag{A8}$$

Here the coefficients A and B are set by the initial perturbations in the generation at $t = 0$, and the time dependence is contained solely in the factors λ^t . The quantities λ_1 and λ_2 are obtained in the usual way by substituting (A8) into (A5), to obtain relations of the form

$$\begin{aligned}(1 + \nu - \lambda) A - \eta(F - 1)B &= 0; \\(F - \lambda) A - (F - 1) \lambda B &= 0.\end{aligned}\tag{A9}$$

This pair of equations are consistent only if their determinant vanishes:

$$\det \begin{vmatrix} 1 + \nu - \lambda & -\eta(F - 1) \\ F - \lambda & -\lambda(F - 1) \end{vmatrix} = 0,\tag{A10}$$

that is

$$\lambda^2 - \lambda(1 + \nu + \eta) + F\eta = 0.\tag{A11}$$

Thus, finally, the quantities λ_1 and λ_2 are given by

$$2\lambda = (1 + \nu + \eta) \pm [(1 + \nu + \eta)^2 - 4F\eta]^{\frac{1}{2}}.\tag{A12}$$

From eqn (A8) it is evident that the perturbations x_t and y_t will die away in time if and only if both λ_1 and λ_2 have modulus less than unity. That is, the overall stability criterion is

$$|\lambda| < 1.\tag{A13}$$

If the factor inside the square brackets in (A12) is positive, both λ_1 and λ_2 are real numbers, and the damping is exponential in character; if this factor is negative, λ_1 and λ_2 are a conjugate pair of complex numbers, and the stability character is oscillations of decreasing amplitude. Likewise if $|\lambda| > 1$, there ensues purely exponential growth or growing oscillations depending on whether this same factor is positive or negative.

It may be shown, after some algebraic manipulation, that application of the stability criterion (A13) to the specific form (A12) leads to the overall stability criterion

$$\frac{\nu}{F - 1} < \eta < \frac{1}{F}.\tag{A14}$$

In addition to this criterion, it is also required that $\eta > -(2 + \nu)/(F + 1)$. However, for biologically reasonable $f(N, P)$ we expect $\nu \geq 0$, $\eta \geq 0$ (as is the case in all the present models, A-E), so that this third condition is automatically fulfilled. Larger values of η outside the range (A14) lead to unstable oscillations, smaller values to unstable monotonic growth. Within the range (A14), the stability is oscillatory or monotonic depending on whether η is greater or less than a critical value η_0 , which is the value for which the term in square brackets in eqn (A12) vanishes, namely

$$\eta_0 = (\sqrt{F} - \sqrt{F - 1 - \nu})^2.\tag{A15}$$

The above constitutes a linearized stability analysis, valid in the neighbourhood of the equilibrium point. For a class of analogous population models where growth is a continuous process, that is where we have differential equations rather than difference equations such as (2), it is possible to show that for a stable equilibrium point the global nonlinear stability character is validly described by the neighbourhood analysis (May 1972). (Conversely those models with no stable equilibrium point may possess a stable limit cycle.) The Poincaré-Bendixson techniques employed in the differential equation case have no immediate analogue for difference equations, and we have no corresponding rigorous proof that the conventional neighbourhood stability analysis characterizes the global stability, for very large perturbations. However, it is plausible that in the comparatively simple models A-D the neighbourhood analysis does describe the global stability character, and this conjecture is strengthened by the fact that extensive numerical studies for these models have invariably displayed the stability character predicted by the linearized analysis.

Model A

Here

$$f(N, P) = \exp(-aP). \quad (\text{A16})$$

The equilibrium populations, eqns (A1) and (A2), are given by:

$$\begin{aligned} a P^* &= \ln F; \\ (F - 1) N^* &= F P^*. \end{aligned} \quad (\text{A17})$$

Consequently the quantities η and ν have the values

$$\nu = 0, \quad (\text{A18})$$

$$\eta = (\ln F)/(F - 1). \quad (\text{A19})$$

But for all $F > 1$, necessarily $\ln F > (F - 1)/F$, which is to say

$$\eta > 1/F. \quad (\text{A20})$$

Therefore the conventional Nicholson-Bailey model A leads to growing oscillations.

Model B

Here $f(N, P)$ is given by eqn (10). First obtaining the equilibrium solutions N^* and P^* from eqns (A1) and (A2), we may then show that again

$$\eta = (\ln F)/(F - 1), \quad (\text{A21})$$

and now

$$\nu = \left[\frac{F (\ln F)^2}{F - 1} \right] \frac{T_h}{T_i}. \quad (\text{A22})$$

It is still true that necessarily

$$\eta > 1/F, \quad (\text{A23})$$

leading to growing oscillations. From eqn (A12) it is seen that the finite value of ν makes such models less stable than the simple Nicholson-Bailey model A.

Model C

The function $f(N, P)$ is here given by eqn (12). The consequent equilibrium populations follow from eqns (A1) and (A2), and the quantities η and ν are

$$\eta = \frac{(1 - m) \ln F}{(F - 1)}, \quad (\text{A24})$$

$$\nu = 0. \quad (\text{A25})$$

Use of the expressions (A24) and (A25) in conjunction with the stability criteria (A14) and (A15) leads directly to the results given in Table 3 and Fig. 4, which give the stability character of the model in terms of the parameters m and F .

Using the form (A24) for η , and putting $\nu = 0$, it may be asked for what value of m (given F) does the stability-determining quantity λ attain its minimum value, corresponding to maximum damping? The answer is seen to be for the value $\eta = \eta_0$ of eqn (A15), that is for m at the interface between stable oscillations and stable exponential damping, as stated in the main text.

More generally, consider the case when $f(N, P)$ is some *arbitrary* function of P alone:

$$f = f(P). \quad (\text{A26})$$

By analogy with the simple model A above, define a generalized 'area of discovery',

$$'a(P)' = -(\ln f(P))/P. \quad (\text{A27})$$

If m' is now *defined* as the (negative) slope of the $(\ln 'a')$ versus $(\ln P)$ curve at the equilibrium point, then from the definition (A6)

$$\begin{aligned} \eta &= \frac{a(P^*) N^*}{F} \left[1 + \frac{P^*}{a(P^*)} \left(\frac{da}{dP} \right)^* \right], \\ &= \frac{(\ln F)}{(F - 1)} (1 - m'). \end{aligned} \quad (\text{A28})$$

That is, the stability analysis is *identical* with that for the straightforward model C above, except that the slope m' , defined as indicated in Fig. 5, now plays the rôle previously played by the m of eqn (12).

Model B/C

By combining the features of finite handling time (model B) and of parasite mutual interference (model C), we obtain the function $f(N, P)$ of eqn (15). As usual the equilibrium populations N^* and P^* are found from eqns (A1) and (A2). From the definition (A6) η is again

$$\eta = \frac{(1 - m) \ln F}{(F - 1)}, \quad (\text{A29})$$

and from eqn (A7) ν may be written

$$\nu = \rho \ln F. \quad (\text{A30})$$

Here ρ is the quantity defined by eqn (16); notice $1 > \rho > 0$, with $\rho \rightarrow 0$ as the handling time becomes very short.

The stability conditions illustrated by Figs 7 and 8 now follow by substituting the expressions (A29) and (A30) for η and ν into the overall stability criterion (A14). We see that this criterion assumes the form

$$1 - \rho > m > 1 - \left(\frac{F-1}{F \ln F} \right) \quad (\text{A31})$$

as illustrated for fixed ρ in Fig. 7, and for fixed F in Fig. 8. The boundary between stable solutions which are damped purely exponentially and those which exhibit damped oscillations is given by the general criterion (A15), or specifically by

$$m = 1 - \frac{(F-1)}{\ln F} [\sqrt{F} - \sqrt{F-1-\rho \ln F}]^2. \quad (\text{A32})$$

Model D

Here we have

$$f(N, P) = \sum_i \alpha_i \exp(-a\beta_i P) \quad (\text{A33})$$

where the normalized sets of probabilities $\{\alpha_i\}$ and $\{\beta_i\}$ are as defined above. As before the equilibrium populations N^* and P^* are given by eqns (A1) and (A2), and thence η and ν by (A6) and (A7):

$$\eta = \left(\frac{F}{F-1} \right) \sum_i \alpha_i (a\beta_i P^*) \exp(-a\beta_i P^*), \quad (\text{A34})$$

$$\nu = 0. \quad (\text{A35})$$

The overall stability criterion (A14) then leads directly to the general result (21) presented in the body of the paper. For any given set of host and parasite proportions $\{\alpha_i\}$ and $\{\beta_i\}$, the stability character for a given F may in principle be determined. Some special cases are worth pursuing.

(i) Explicit refuge

Suppose a proportion γ of hosts are accessible to the parasites, and the remaining $1-\gamma$ are not. That is, $\alpha_1 = \gamma$, $\alpha_2 = 1-\gamma$; $\beta_1 = 1$, $\beta_2 = 0$. The equilibrium parasite population follows from eqn (A2) with (A33):

$$F(\gamma \exp(-aP^*) + 1 - \gamma) = 1. \quad (\text{A36})$$

Unless $F(1-\gamma) < 1$, no equilibrium configuration is possible, which gives one stability boundary in Fig. 14.

If an equilibrium population N^* , P^* does exist, it is seen that eqn (A34) reduces to

$$\begin{aligned} \eta &= \frac{(\gamma F)}{(F-1)} (aP^*) \exp(-aP^*) \\ &= \frac{[1-F(1-\gamma)]}{[F-1]} \ln \left(\frac{\gamma F}{1-F(1-\gamma)} \right). \end{aligned} \quad (\text{A37})$$

Substituting this into the general equations (A14) and (A15) gives the relations between γ and F which determine the upper stability boundaries in Fig. 14.

(ii) *High density/low density*

A typical way of characterizing the differential densities and aggregations of hosts and parasites is by the three parameters α , n and μ of eqns (22), (26) and (27). The equilibrium parasite population is then

$$F[\alpha e^{-x} + (1 - \alpha)e^{-\varepsilon x}] = 1 \tag{A38}$$

where for convenience $x = a\beta P^*$. The stability criterion (21) is now

$$xF[\alpha e^{-x} + \varepsilon(1 - \alpha)e^{-\varepsilon x}] < \frac{F - 1}{F} \tag{A39}$$

Remember, ε is a function of α , n and μ (eqn 27). By eliminating x between the two eqns (A38) and (A39), a relation between μ and F is obtained for given α and n ; such relations are as depicted in Figs. 12 and 13.

(iii) *General result for $F \simeq 1$*

In the limit

$$F = 1 + \Delta; \Delta \ll 1 \tag{A40}$$

it is possible to simplify the stability criterion (21) for arbitrary sets of probabilities $\{\alpha_i\}$ and $\{\beta_i\}$. The limiting assumption (A40) implies that aP^* is relatively small, which forms the basis for an approximate simplification of eqns (A2) and (A21), leading to the stability criterion

$$\sum_i \alpha_i \beta_i^2 > 2 \left(\sum_i \alpha_i \beta_i \right)^2 [1 + O(\Delta)] \tag{A41}$$

The correction terms are of relative order Δ . This approximation gives a good estimate of the stability character even for F as large as two (i.e. Δ around unity).

The trends manifested by this general (but approximate) result are interesting. The easiest way to satisfy (A41) is to have roughly equal numbers of hosts in a few high density areas and in many low density areas, and also to have strong differential aggregation of the parasites in the high density areas. (Try writing down sets of probabilities $\{\alpha_i\}$ and $\{\beta_i\}$, and testing them against equation (A41).)

Model E

Here we use eqn (31) to get

$$f(N, P) = \sum_i \alpha_i \exp[-Q(\beta_i P)^{1-m}] \tag{A42}$$

In conjunction with eqns (A1) and (A2), this gives the equilibrium populations N^* , P^* . From eqn (A7) $v = 0$, and the quantity η of eqn (A6) is now

$$\eta = \frac{(1 - m)F}{(F - 1)} \sum_i \alpha_i z_i \exp(-z_i) \tag{A43}$$

with the definition $z_i = Q(\beta_i P^*)^{1-m}$. The overall stability criterion is, as ever, eqn (A14).

In essence, this differs from the preceding analysis only by the factor $(1 - m)$ in eqn (A43), and all the calculations made above for model D are easily amended to incorporate this additional stabilizing factor. In particular, the computations which give Figs. 12 and 13 now give Fig. 15, with its wider stability zones.

REFERENCES

- Bailey, V. A., Nicholson, A. J. & Williams, E. J. (1962). Interaction between hosts and parasites when some host individuals are more difficult to find than others. *J. theor. Biol.* **3**, 1-18.
- May, R. M. (1972). Limit cycles in predator-prey communities. *Science, N.Y.* **177**, 900-2.
- May, R. M. (1973a). On relationships among various types of population models. *Am. Nat.* **107**, 46-57.
- May, R. M. (1973b). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, N.J.
- Maynard Smith, J. (1968). *Mathematical Ideas in Biology*. Cambridge University Press, London.