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HOST-PARASITOID SYSTEMS IN PATCHY ENVIRONMENTS: A PHENOMENOLOGICAL MODEL

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SUMMARY

(1) A host-parasitoid model is presented which is intermediate in complexity between the Nicholson–Bailey model (in which the parasitoids search independently randomly in a homogenous environment) and complicated models for incorporating environmental patchiness (in which the overall distribution of parasitoid attacks is derived from detailed assumptions about their searching behaviour and about the spatial distribution of the hosts). The model assumes the overall distribution of parasitoid attacks per host to be of negative binomal form. There are consequently three biological parameters: two are the usual parasitoid 'area of discovery', a, and the host 'rate of increase', F; the third is the negative binomial clumping parameter, k. Such intermediate-level models have proved useful in sorting out ideas in the related disciplines of epidemiology and parasitology.

(2) Empirical and theoretical arguments for using the negative binomial to give a phenomenological description of the essential consequences of spatial patchiness in models are surveyed.

(3) A biological interpretation of the parameter k in host parasitoid models is offered. If the parasitoids be distributed *among* patches according to some arbitrary distribution which has a coefficient of variation CV_P, and if the parasitoid attack distribution *within* a patch be Poisson, then the ensuing *compound* distribution can be approximated by a negative binomial which will have the same variance as the exact distribution provided k is identified as $k = (1/CV_P)^2$.

(4) Expressions are obtained for the equilibrium values of host and parasitoid populations. These equilibria are stable if, and only if, $k < 1$; that is, provided there is sufficient clumping.

(5) The dynamical effects of parasitoid aggregation in some respects mimic those introduced by mutual interference among parasitoids; the appropriate coefficient of 'psuedo-interference' is calculated.

INTRODUCTION

Spatial heterogeneities in the distribution of prey and predator populations are of central importance in stabilizing prey-predator interactions. On the empirical side, the stabilizing effects of a patchy environment have been exhibited in quantitative detail in the experiments of Huffaker (1958) and later workers (see Luckinbill 1973, and references therein). Other examples may be argued to arise in many natural prey-predator systems, and in some biological control situations, although here the quantitative proof is lacking (see e.g. the reviews by Krebs 1972, ch. 17 and Huffaker 1971). On the theoretical side,

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several recent studies (Maynard Smith 1974; Hilborn 1975; Hastings 1977; Zeigler 1977; Gurney & Nisbet 1978; and references contained in these works) have considered a hypothetical environment made up of many discrete patches, and shown how the dynamic interplay among empty patches, patches containing only prey, and patches containing both prey and predators could under certain circumstances lead to overall stability of the system. A more general class of prey-predator models that incorporate spatial heterogeneity are reviewed by Levin (1976). One basic mechanism is common to essentially all these laboratory and theoretical studies: if the prey are patchily distributed, and if the predators tend to aggregate in regions of relatively high prey density, then the regions of low prey density constitute a kind of implicit refuge, whereby the prey population is maintained; conversely, the predator population flourishes in the regions of relatively high prey density. Too much implicit refuge for the prey tends to lead to 'runaway', with the prey population ultimately controlled by factors other than predation. Too little implicit refuge tends to produce the diverging population oscillations that characterize simple and spatially homogeneous prey-predator models.

Arthropod host-parasitoid systems constitute an important subclass of prey-predator interactions. In these systems, each host in any one generation *either* is parasitized, thus producing a next-generation parasitoid, *or* escapes parasitism to give rise to F progeny that become the next generation of hosts. As discussed more fully by Hassell (1978), host-parasitoid systems possess two features that make them especially amenable to detailed study. First, because the life cycles of host and parasitoid are so intimately intermeshed, the usual complications of the predator's 'numerical response' (*sensu* Solomon 1949; Holling 1959) are absent; one only has to deal with the predator's 'functional response', which here is expressed by the probability for a host to escape parasitism. Secondly, the small size and relatively short generation time of arthropod hosts and parasitoids permits laboratory studies of a kind that are simply not feasible for vertebrate predators and their prey. (Unlike the first, the second advantage is shared with other arthropod prey-predator systems.)

In the classic Nicholson–Bailey (1935) model, the parasitoids search independently randomly in a homogeneous environment, with the consequence that both host and parasitoid populations exhibit diverging oscillations. Recently, several authors (Hassell & May 1974; Murdoch & Oaten 1975, and references therein) have analysed models in which the hosts are distributed non-uniformly among many patches, and where the parasitoids have searching behaviour that leads to their aggregation in patches with relatively high host density; these model systems may be stable or unstable, depending on the values of the relevant biological parameters. Such studies have the merit of being relatively realistic, with the overall host-parasitoid dynamics being explicitly related to the behavioural mechanisms whereby the parasitoids aggregate. The studies suffer the concomitant disadvantage of containing many parameters, which makes lucid exposition difficult and extension to multispecies situations (such as those with several parasitoid species, or hyperparasitism) intractable.

This paper presents a model of intermediate complexity. All the spatial and behavioural complications that lead to patterns of parasitoid aggregation are subsumed in the single phenomenological assumption that the net distribution of parasitoid attacks upon hosts is of negative binomial form. That is, all these complications are summarized in the single parameter k, which characterizes the degree of clumping or over-dispersion in a negative binomial distribution. The model thus has three parameters: the conventional a and F (respectively representing the 'area of discovery' for a single parasitoid, and the number of

surviving progeny produced by an unparasitized host), and the new k (summarizing the effects of spatial heterogeneity and consequent parasitoid aggregation). Clearly the model bridges the gap between the overly simple two-parameter Nicholson–Bailey model, and the proliferation of parameters that are required in relatively realistic models.

The paper is divided into two main parts. First, some comments are made about the negative binomial. A simple, yet general, biological interpretation of k is given in terms of the variance in the distribution of parasitoids among patches. Some data in support of a negative binomial distribution is marshalled, and a survey is made of the theoretical and empirical evidence that underpins the use of similar phenomenological models in broadly analogous contexts in epidemiology and parasitology. Secondly, the host-parasitoid model itself is presented, and its equilibrium and stability properties are laid bare. Following the suggestion of Free, Beddington & Lawton (1977), it is shown that the dynamical consequences of overdispersion in the distribution of parasitoid attacks are in some respects indistinguishable from those produced by mutual interference among parasitoids, and the coefficient of 'pseudo-interference' is calculated. In conclusion, some potential applications of the model are discussed. Throughout the main text, attention is focussed on the biology; mathematical details and proofs are segregated in appendices.

WHY THIS MODEL?

The negative binomial distribution

In the Nicholson–Bailey model, P parasitoids search independently, and in a random fashion, each discovering hosts at a rate given by the 'area of discovery', a. The probabilities for a given host to be discovered 0, 1, 2, 3 . . . times are therefore given by the terms in a Poisson distribution, with the mean discovery rate being aP. In particular, the probability for a host to escape parasitism is given by the zero term in the Poisson series, namely $\exp(-aP)$.

We now replace this random distribution of parasitoid attacks with an overdispersed distribution, described by a negative binomial with clumping parameter k. The other biological assumptions remain as in the Nicholson–Bailey model, so that the mean attack rate is aP. The probability of escaping parasitism is now the zero term in this negative binomial, namely $(1+aP/k)^{-k}$.

A more full account of the properties of the negative binomial distributions are given from a mathematical standpoint by Anscombe (1950), and from a biological standpoint by Southwood (1966, pp. 24–35). The mathematical meaning of the parameter k may be appreciated by noting that, for a negative binomial with mean m, the coefficient of variation (CV) is

$$CV^2 \equiv \frac{\text{variance}}{(\text{mean})^2} = \frac{1}{m} + \frac{1}{k}. \tag{1}$$

In the limit $k \to \infty$, the random or Poisson distribution is recovered, with the variance equal to the mean. As k becomes smaller, the CV gets larger, with the effect becoming very pronounced for very small k. The geometric series corresponds to $k = 1$, and the log series to the limit $k \to 0$.

A biological interpretation of k *within this model*

In a host-parasitoid context, a biological meaning may be attached to k by considering the following model.

Suppose the parasitoids are distributed *among* a large number of patches according to some specified (but, as yet, arbitrary) distribution; the number of parasitoids in any one patch has mean P and variance σ^2_P. *Within* any patch, the parasitoids search independently randomly, in Nicholson–Bailey fashion, each having an area of discovery a; the attack distribution within a patch is Poisson. The overall distribution of parasitoid attacks in any one patch is thus given by *compounding* the specified among-patch distribution of parasitoids with the Poisson within-patch distribution of attacks. This overall, compound distribution will have some well determined form, dependent on the specified among-patch distribution.

The compound distribution will not, in general, be negative binomial. But it is necessarily overdispersed, and may be approximated by a negative binomial distribution with the same mean and same variance as the exact distribution. If this is done, the approximating negative binomial will have a mean equal to aP, and a clumping parameter k given by

$$k = P^2/\sigma^2_P \tag{2a}$$

This result is proved in Appendix 1. Note that k depends only on parameters of the among-patch distribution of parasitoids. By introducing CV_P to denote the coefficient of variation of the among-patch distribution of parasitoids, we can rewrite eqn (2a) as

$$k = (1/CV_P)^2. \tag{2b}$$

If the among-patch distribution is a Pearson type III (i.e. gamma) distribution, then the compound distribution is exactly a negative binomial (see, e.g. Anscombe 1950, pp. 360–361). Regardless of whether the overall negative binomial is exact or an approximation, eqn (2) interprets k in a way that is direct and biologically meaningful.

Data on parasitoid attack distributions

Griffiths & Holling (1969) have carried out an extensive series of experiments in which ichneumon *Pleolophus basizonus* (Grav.) parasitoids interacted with sawfly *Neodiprion sertifer* (Geoff.) hosts in 1·22 × 2·44 m(4 × 8 ft) cages. The distribution of attacks per host is well described by a negative binomial, as is the number of eggs laid in hosts, with k around 0·8. Surveying fourteen other laboratory host-parasitoid systems, Griffiths and Holling find three have negative binomial attack patterns; the other eleven manifest the 'avoidance' behaviour discussed immediately below. In their laboratory studies of hyperparisitism, Kfir, Podoler & Rosen (1976) show that one of their two hyperparasitoid species, *Cheiloneurus paralia* (Walk.), has an attack distribution that conforms to a negative binomial with k in the range 0.5–1.3. Their other species, *Marietta exitiosa,* shows 'avoidance' (again, see below). Table 1 summarizes some field data from Hassell (unpublished), showing that two measures of the distribution of attacks of *Cyzenis albicans* upon its winter moth hosts are in significant agreement with a negative binomial distribution.

In laboratory studies, it is, however, usually found that attacks are underdispersed; that is, are distributed more evenly than random (see, e.g. the experiments and reviews by Rogers (1975) and by Benson (1973)). This is not surprising. The laboratory cages constitute relatively small and homogeneous single patches, and many parasitoids have behavioural mechanisms whereby they avoid attacking hosts that are already parasitized, leading to underdispersion within a single patch. Even under these circumstances, which are not representative of the patchy environments found in the field, Rogers (1975, p. 632)

TABLE 1. (a) Distribution of *Cyzenis* larvae within their hosts

Distribution	Frequency of winter moth larvae containing the following numbers of *Cyzenis* larvae: 0	1	2	3	4	Chi-square	
Observed	1066	176	48	8	5		
Expected from a negative binomial	1063·2	183·5	42·2	10·5	2·7	3·60	($P>0·5$)
Expected from a Poisson series	1022·0	248·0	30·1	2·4	0·1	206	($P<0·01$)

(b) Distribution of *Cyzenis* eggs on leaves

Distribution	Frequency of leaves with the following number of *Cyzenis* eggs: 0	1	2	3	4	5–12	Chi-square	
Observed	85	33	20	12	7	10		
Expected from a negative binomial	86·0	33·7	18·2	10·7	6·6	11·4	0·55	($P>0·5$)
Expected from a Poisson series	47·6	38·0	15·1	4·0	0·8	0·1	38·9	($P<0·01$)

notes that in some species 'the adult parasites are known to avoid superparsitism but produce random or even clumped egg distributions, suggesting either that more than one egg is laid at each encounter with a host, or that the parasites remain in one part of the host area [references given by Rogers, but omitted here].'

It must be emphasized that the present model is visualized as applying to patchy real world situations, with the overdispersion coming mainly from the way parasitoids distribute themselves among patches (and not usually from the searching behaviour within a patch). Cage studies are thus largely irrelevant. More field data along the lines of Table 1 are needed.

Analogous contexts in which negative binomial distributions arise

Several plausible mathematical models for the transmission dynamics of parasitic infections, such as schistosomiasis, lead to a negative binomial for the distribution of parasites per host. Bradley & May (1977) review these models, and also review corroborative data for helminthic infections in man and other animals. More generally, catalogues of biological mechanisms that can lead to negative binomial distributions for the number of parasites per host have been given by Boswell & Patil (1970) and by Southwood (1966, pp. 31–32). Such negative binomial distributions have been used in parasitologically-oriented discussions of the dynamics of host-parasite interactions by Crofton (1971), May (1977), and Anderson & May (1977). The latter authors tabulate fifteen empirical host-parasite studies in which the distribution of parasites among hosts is described well by a negative binomial, with clumping parameters k ranging from 0.1 to 10.

Southwood (1966) has surveyed yet other pertinent examples, such as the series of counts of a gall-wasp on chestnut trees that were distributed as a Poisson for each single tree, but as a negative binomial when all trees were combined (Ito *et al.*, 1962). Sen, Tourigny & Smith (1974) have given a mathematical treatment, along with some data (in which grouse are the 'prey' and bird-watchers the 'predators'), relating to the use of negative binomial to approximate an overdispersed distribution.

In short, there are both empirical and theoretical reasons for fastening on the negative binomial to approximate the distribution of parasitoid attacks in a patchy environment. Equation (2) provides a plausible biological interpretation of the clumping parameter k, under general assumptions.

PROPERTIES OF THE MODEL

The basic equations

Let H_t denote the number of hosts in generation t, and P_t the corresponding number of parasitoids. The equation relating the number of hosts in successive generations, $t+1$ and t, is then

$$H_{t+1} = F\, H_t (1 + aP_t/k)^{-k}. \tag{3}$$

The parameters F, a and k are as defined earlier. As discussed above, the negative binomial factor is the zero term in the parasitoid attack distribution; that is, it represents the probability of a host escaping parasitism. The number of parasitoids in generation $t+1$ is simply given by those hosts that do *not* escape parasitism:

$$P_{t+1} = H_t - H_{t+1}/F. \tag{4}$$

Equation (4) may, indeed, be taken as defining the meaning of the term 'parasitoid'. (For fuller discussion, see Hassell & May 1973.)

Griffiths & Holling (1969) have studied host-parasitoid interactions in which the number of attacks upon hosts followed a negative binomial distribution. Their numerical studies were, however, not directed toward the dynamical stability of the system. Moreover, their version of eqn (3) roughly corresponds to having P_t/H_t rather than P_t inside the parenthesis on the right hand side of the equation, so that the two studies are not comparable.

Equilibrium

The equilibrium solutions of eqns (3) and (4) is found by putting $H_{t+1} = H_t = H^*$ and $P_{t+1} = P_t = P^*$. Then H^* cancels out of the equilibrium version of eqn (3), to give an expression for the equilibrium parasitoid density:

$$aP^* = k(F^{1/k} - 1). \tag{5}$$

Figure 1 illustrates the way P^* depends on the parameters k and F. In the limit $k \to \infty$, the Nicholson–Bailey or Poisson result, $aP^* = \ln F$, is recovered. For finite values of k, the equilibrium parasitoid density is larger, and increasingly so as k gets smaller.

The equilibrium version of eqn (4) shows H^* and P^* to be simply related by

$$H^* = \left(\frac{F}{F-1}\right) P^*. \tag{6}$$

That is, the equilibrium host density is larger than that of the parasitoid population by a factor depending only on F, exactly as in the Nicholson–Bailey case. H^* and P^* have the same functional dependence on k.

Notice that the parameter a enters only as an overall scaling factor, setting the scale of H^* and P^*.

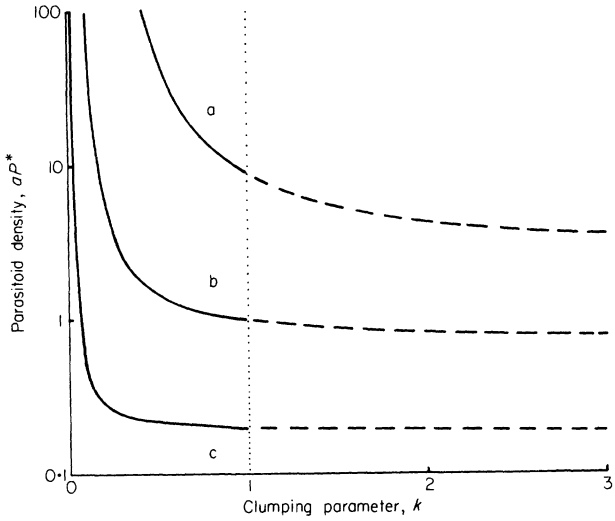

FIG. 1. This figure shows how the (dimensionless) equilibrium parasitoid population, aP^*, depends on the clumping parameter k, for three values of the host fecundity: (a) $F = 1{\cdot}2$; (b) $F = 2$; (c) $F = 10$. Notice the logarithmic scale for aP^*. The solid part of the curves corresponds to stable equilibria; the dashed part corresponds to unstable equilibria, where the host-parasitoid system undergoes diverging oscillations.

Stability

The way the system responds to small perturbations about the above equilibrium may be elucidated by standard techniques. This is done in Appendix 2. The system is stable against small disturbances if, and only if,

$$k < 1. \tag{7}$$

For $k > 1$, arbitrarily small disturbances from the equilibrium configuration lead to diverging oscillations. This is represented in Fig. 1 by drawing solid curves for stable equilibria, and dashed curves for unstable ones. Note that the stability of the system depends only on the clumping parameter k, independent of the values of F and a.

If the system is stable, small disturbances from equilibrium will exhibit either exponential damping or damped oscillations; this question is pursued in Appendix 2. The result (7) follows analytically from a linearized, or local, analysis. The response to large amplitude disturbances requires a nonlinear, or global, analysis, for which no general techniques are available. Extensive numerical simulations, however, suggest the global stability properties are the same as the local ones, with global stability or instability hinging on eqn (7).

We conclude that the host-parasitoid system is stable provided the parasitoid attack distribution is overdispersed to a degree in excess of that manifested by a geometric series distribution ($k < 1$). Such a degree of parasitoid clumping means there is enough 'effective refuge' in regions of low parasitoid density for the host population to reproduce and maintain itself steadily. The stability criterion (7) may be rephrased by using the biological interpretation of k given in eqn (2): the system is stable if, and only if, the coefficient of variation of parasitoids among patches exceeds unity ($CV_P > 1$).

Pseudo-interference

In two important papers, Beddington, Free and Lawton (Free, Beddington & Lawton 1977; Beddington, Free & Lawton 1978) have argued that neither density dependence in the host's intrinsic growth rate, nor biologically plausible amounts of mutual interference among parasitoids, are capable of stably maintaining host populations at levels significantly below the level, K, that would pertain in the absence of parasitoids. On the other hand, Beddington, Free & Lawton (1978) have catalogued many field situations where parasitoids apparently do regulate their host populations at levels well below K. They conclude that spatially heterogeneous host distributions, coupled with parasitoid aggregation in regions of high host density, must be the main stabilizing mechanism. They also suggest that such clumping of parasitoid attacks can be formally described as 'pseudo-interference', mimicking the stabilizing dynamical effects of mutual interference among parasitoids as studied by Hassell & Varley (1969; see also Hassell 1978).

These notions can be applied to the present model, to get a 'pseudo-interference' coefficient of magnitude (see Appendix 3)

$$m' = 1 - \frac{k(1 - F^{-1/k})}{\ln F}. \tag{8}$$

That is, the overdispersion of parasitoid attacks has much the same dynamical consequences as would be produced by pure mutual interference among parasitoids in a homogeneous world; the strength of the equivalent Hassell–Varley mutual interference coefficient m is given by the m' of eqn (8). Using Hassell and May's (1973) analysis of the dynamical effects of mutual interference, it is easy to verify that the 'pseudo-interference' coefficient m' of eqn (8) corresponds to a stable equilibrium if, and only if, $k < 1$. This is a way of rewording the earlier result (7).

DISCUSSION

The main message emerging from the host-parasitoid model developed here is that such systems may be stable, with equilibrium host and parasitoid population densities larger than for the corresponding (but unstable) Nicholson–Bailey system, provided the parasitoid attack distribution is sufficiently clumped. This accords with the conclusions derived from more detailed models (e.g. Hassell & May 1974; Murdoch & Oaten 1975; Hassell 1978).

One advantage of these models is that they can be used as components in the exploration of higher-order systems in patchy environments. In particular, they permit an understanding of some basic aspects of the interactions among one host and two parasitoid species, and of host-parasitoid-hyperparasitoid interactions. These insights can be tested against some data, and hold potentially important implications for biological control (Hassell 1978; May & Hassel, in preparation).

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APPENDIX 1

This appendix establishes eqn (2), which attaches a biological meaning to the parameter k. The appendix makes use of the properties of probability generating functions, or *pgf*; for full explication of these entities see, e.g. Pielou (1969). In particular, note that if a distribution has *pgf* $H(z)$, its mean, m, and variance, σ^2, are given by

$$m = H'(1) \tag{1.1}$$

$$\sigma^2 = H''(1) + H'(1)\,[1 - H'(1)]. \tag{1.2}$$

Here the prime denotes differentiation.

Assume that the distribution of parasitoids among patches is specified by some distribution with *pgf* $G(z)$. Defining P to be the mean number of parasitoids per patch, and σ_P^2 to be the variance, it follows that

$$P = G'(1) \tag{1.3}$$

$$\sigma_P^2 = G''(1) + G'(1)\,[1 - G'(1)]. \tag{1.4}$$

The CV of $G(z)$ is, as defined in the text,

$$CV_P = \sigma_P / P. \tag{1.5}$$

Within any one patch, each individual parasitoid searches in independently random fashion, with an area of discovery a. Thus the within-patch distribution of attacks by an individual parasitoid is Poisson, with the *pgf*

$$g(z) = \exp\,[a(z-1)]. \tag{1.6}$$

The overall distribution of attacks within a patch is then a compound distribution, with *pgf* $H(z)$ given by

$$H(z) = G(g(z)). \tag{1.7}$$

The compound distribution $H(z)$ has mean, m, given via eqns (1.1), (1.3) and (1.6) as

$$m = aG'(1) = aP. \tag{1.8}$$

The variance of $H(z)$, σ^2, follows from eqns (1.2), (1.6) and (1.8) as

$$\sigma^2 = a^2G''(1) + a^2G'(1) + m(1-m). \tag{1.9}$$

Using eqns (1.4) and (1.8) to re-express $G''(1)$ in terms of σ_P^2 and m, we get

$$\sigma^2 = a^2\sigma_P^2 + m. \tag{1.10}$$

The compound distribution $H(z)$ will not in general be a negative binomial. (Indeed, it can easily be shown that $H(z)$ is negative binomial if $G(z)$ is a gamma distribution.) $H(z)$ is, however, overdispersed (its variance exceeds its mean), and we may choose to approximate it by a negative binomial with the same mean, m, and same variance, σ^2, as the exact distribution.

Having the same mean trivially implies that, for the negative binomial, $m = aP$. For the negative binomial, the variance and the parameter k are related by eqn (1): $\sigma^2 = m+m^2/k$. Therefore identifying this variance with the variance of the exact distribution $H(z)$, as given by eqn (1.10), leads to

$$(aP)^2/k = a^2\,\sigma_P^2. \tag{1.11}$$

That is,

$$k = (P/\sigma_P)^2 = (1/CV_P)^2. \tag{1.12}$$

This is the result we sought to prove.

APPENDIX 2

This appendix gives a standard stability analysis of the equilibrium point H^*,P^* with regard to small disturbances (see, e.g. Hassell & May 1973). We write $H_t = H^* + x_t$ and $P_t = P^* + y_t$, and discard all terms of second or higher order in x and y, to arrive at the linearized versions of eqns (3) and (4) for perturbations about the equilibrium configuration:

$$x_{t+1} = x_t - aH^*\,(1+aP^*/k)^{-1}y_t, \tag{2.1}$$

$$y_{t+1} = x_t - x_{t+1}/F. \tag{2.2}$$

Using the routine observation that x_t and y_t in these equations will scale with time as λ^t, and substituting the explicit values of H^* and P^* from eqns (6) and (5) in eqn (2.1), we get

$$(\lambda-1)x_t + \xi y_t = 0 \tag{2.3}$$

$$(\lambda/F-1)x_t + \lambda y_t = 0. \tag{2.4}$$

Here ξ has been defined, for notational convenience, as

$$\xi = kF(1-F^{-1/k})/(F-1). \tag{2.5}$$

Note that necessarily $\xi > 0$, because $F > 1$.

The eigenvalues λ are now the solutions of the quadratic equation

$$\lambda^2 - \lambda(1+\xi/F\ ) + \xi = 0. \tag{2.6}$$

The Schur–Cohn criterion (May 1974, pp. 219–220), which expresses the requirement that both eigenvalues must have modulus less than unity if the disturbance is to be damped back to equilibrium, here becomes

$$2 > 1+\xi > |1+\xi/F|. \tag{2.7}$$

The right half of this inequality is automatically satisfied, because $\xi > 0$ and $F > 1$. The left half of the inequality is fulfilled if $1 > \xi$, that is if

$$1 > k(1 - F^{-1/k})/(1 - F^{-1}). \tag{2.8}$$

It can be seen that the function on the right hand side (i.e. $\xi(k,F)$) is a monotonically increasing function of k for all k in the range $0 < k < \infty$, and furthermore that $\xi = 1$ for $k = 1$. It follows that the stability criterion (2.8) is satisfied if $k < 1$, as stated in eqn (7).

Within the stable region, the boundary between exponential damping and damped oscillations is given by the condition

$$(1 + \xi/F)^2 = 4\xi. \tag{2.9}$$

These details are not elaborated here, but can be worked out along the lines laid down in Hassell & May (1973) and elsewhere.

APPENDIX 3

The concept of 'pseudo-interference', and its biological implications, have been developed by Free *et al.* (1977). The underlying mathematical formalism was earlier introduced by Hassell & May (1973, pp. 702–703, 723), and is very briefly recapitulated here. Consider the general case where the probability for a host to escape parasitism, whatever the biological mechanism whereby this happens, depends only on the parasitoid density:

$$H_{t+1} = F H_t \, \mathrm{f}(P_t). \tag{3.1}$$

It is now possible to define an 'effective area of discovery', $\tilde{a}(P)$, as

$$\tilde{a}(P) = -[\ln \mathrm{f}(P)]/P. \tag{3.2}$$

Thence a quantity m' can be defined as

$$m' = -\left(\frac{P \, \mathrm{d}\tilde{a}^*}{\tilde{a} \, \mathrm{d}P}\right) \tag{3.3}$$

where the asterisk denotes evaluation at the equilibrium point, P^*. In any discussion of the (linearized) dynamical behaviour of the system, the quantity m' plays a rôle that is formally identical with that played by the Hassell–Varley coefficient of parasitoid mutual interference, m.

For the model under discussion here, $\tilde{a}(P)$ has the form

$$\tilde{a}(P) = [k \ln(1 + aP/k)]/P. \tag{3.4}$$

Substituting this into eqn (3.3), and using eqn (5) for P^*, we arrive at eqn (8) for m'.

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