

## THE PERSISTENCE OF HOST-PARASITOID ASSOCIATIONS IN PATCHY ENVIRONMENTS. I. A GENERAL CRITERION

M. P. HASSELL,\* R. M. MAY,\* S. W. PACALA,† AND P. L. CHESSON‡

\*Department of Biology and Centre for Population Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, England; †Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06268; ‡Department of Zoology, Ohio State University, Columbus, Ohio 43210

*Submitted July 13, 1989; Revised July 30, 1990; Accepted August 22, 1990*

*Abstract.*—In this article we show that, for host-parasitoid interactions in a heterogeneous environment and with discrete generations, the dynamic effects of any patterns of distribution of searching parasitoids can be assessed within a common, simple framework. The populations are regulated if the distribution of searching parasitoids is sufficiently heterogeneous. Specifically, the square of the coefficient of variation ( $CV^2$ ) of the searching parasitoids per host must exceed unity. This criterion is demonstrated to apply approximately, in general and also in several specific cases. We further show that  $CV^2$  may be partitioned into a density-dependent component caused by the response of parasitoids to host density per patch and a density-independent component. Population regulation is enhanced as much by density-independent as by density-dependent heterogeneity.

The spatial patterns of parasitism by insect parasitoids, and the importance of these to the population dynamics of host-parasitoid interactions, have been topics of widespread interest in ecology for several years. Many models have been developed in which heterogeneity in the distribution of parasitism has played an important part in population regulation (e.g., Hassell and May 1973, 1974, 1988; Murdoch and Oaten 1975; May 1978; Perry 1987; Reeve 1988). At the same time, data from laboratory and field studies have accumulated and show the patterns of percent parasitism in relation to local host densities per "patch" or other sampling unit. These have recently been reviewed by Lessells (1985), Stiling (1987), and Walde and Murdoch (1988) and categorized under the headings "direct" or "inverse density-dependent" and "density-independent" (fig. 1).

A popular interpretation of these data, guided by the theoretical literature of the time (e.g., Hassell and May 1973, 1974; Murdoch and Oaten 1975), has been that the direct density-dependent patterns are the most important in promoting the stability of the interacting populations. More recently, however, it has been emphasized that in addition to these direct density-dependent patterns, inverse density dependence (Hassell 1984; Walde and Murdoch 1988) and variation in parasitism that is *independent* of host density (Chesson and Murdoch 1986; Hassell and May 1988) can both be important contributors to population regulation. This arises in part because *any* variation in levels of parasitism from patch to

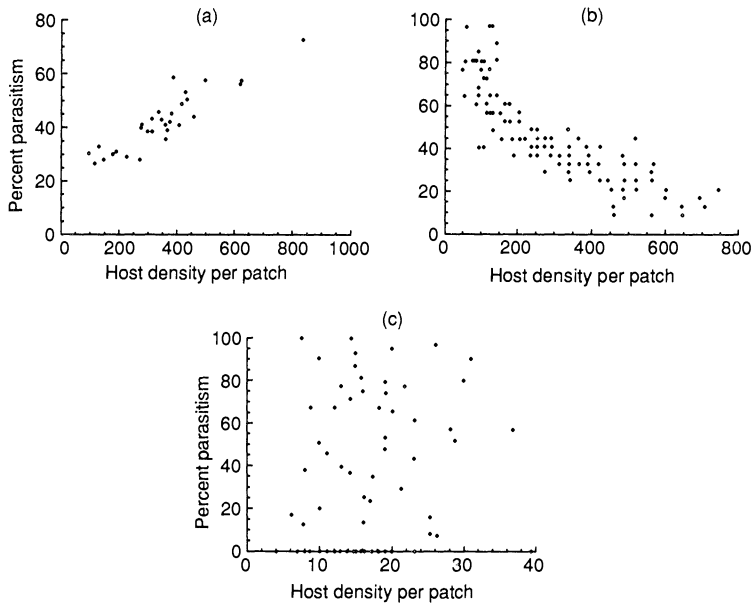


FIG. 1.—Three examples from field studies of different patterns of parasitism from patch to patch. *a*, Direct density-dependent parasitism of the scale insect *Fiorinia externa* Ferris by the eulophid parasitoid *Aspidiotiphagus citrinus* (Craw.) on the lower crown of 30 hemlock trees (McClure 1977). *b*, Inverse density-dependent parasitism of gypsy moth (*Lymantria dispar* [L.]) eggs by the encyrtid parasitoid *Ooencyrtus kuwanai* (Howard; see Brown and Cameron 1979). *c*, Density-independent parasitism of gall midge, *Rhopalomyia californica* (Felt.), by the torymid parasitoid *Torymus baccharidis* (Huber; see Ehler 1987).

patch has the net effect of reducing the per capita parasitoid searching efficiency (measured over all hosts) as parasitoid density increases (the so-called pseudointerference effect of Free et al. [1977]).

It follows that the dynamical consequences of observed, within-generation patterns of parasitism cannot simply be inferred from the shape of the relationships. This led Hassell and May (1988) to suggest an alternative approach in which some simple and measurable quantity, characterizing the way parasitoid attacks are distributed among patches, could provide a guide to the dynamical properties of the host-parasitoid association. Specifically, they conjectured that heterogeneity in the distribution of parasitism may result in the overall population densities of hosts and parasitoids remaining roughly steady (a locally stable interaction) if  $CV^2$  is greater than one, where  $CV$  is the coefficient of variation in the distribution of searching parasitoids among patches. If  $CV^2 < 1$ , the interaction is likely to exhibit cyclic, chaotic, or (in simple cases) diverging fluctuations.

In this article, we show that a criterion very similar to that proposed by Hassell and May (1988) indeed gives an accurate account of the qualitative nature of the dynamics in a variety of models. An overview of this work is also given in Pacala et al. (1990). Specifically, let the density of searching parasitoids about the  $i$ th host be  $p_i$  ( $i = 1, 2, \dots, y$ ), and let the density of such parasitoids in the  $j$ th

patch be  $q_j$  ( $j = 1, 2, \dots, z$ ). Characteristically, models express the distribution of parasitoids and hosts in terms of the  $q_j$  and  $n_j$  (host density in the  $j$ th patch). We show that an approximate condition for locally stable dynamics is that the coefficient of variation squared of the  $p_i$  across the  $y$  hosts exceeds one (rather than the coefficient of variation of the  $q_j$  across the  $z$  patches as in Hassell and May [1988]). Here,  $CV^2$  refers exclusively to the coefficient of variation squared of the  $p_i$ . If  $f(q, n)$  is the joint density function for  $q_j$  and  $n_j$ , the density function for  $p_i$  is given by  $h(p) = \int nf(p, n)dn / \iint nf(n, p)dndp$ . This is the weighted distribution discussed in Chesson and Murdoch (1986) and is the distribution that we use to calculate the  $CV^2$ .

We also show how between-host variation in parasitism can be partitioned between the density-dependent component (both direct and inverse) and the residual variation about this, both contributing in a precise way to population regulation. In the companion article, we show, first, how the same criterion can be applied to the kinds of data that now abound in the literature relating percent parasitism to host density per patch (fig. 1), and second, how this changes our views on the design of field studies aimed at evaluating the role of heterogeneity in population dynamics.

#### THE MODELS

To demonstrate the generality of the suggested rule,  $CV^2 > 1$ , we show that it is approximately the condition for stability in five different models, all based on a familiar discrete-generation host-parasitoid model (Hassell 1978):

$$N_{t+1} = \lambda N_t F(N_t, P_t); \quad (1a)$$

$$P_{t+1} = w N_t [1 - F(N_t, P_t)]. \quad (1b)$$

Here  $N$  and  $P$  are the host and parasitoid populations in successive generations  $t$  and  $t + 1$ ,  $\lambda$  is the host's finite rate of increase in the absence of the parasitoid,  $F(N_t, P_t)$  is a function giving the average proportion of hosts that escape parasitism, and  $w$  is the average number of female parasitoids emerging from each host parasitized (henceforth, we assume that  $w = 1$ ). The functional form of  $F(N_t, P_t)$  depends on all the factors that affect the rate of parasitism of hosts by the  $P_t$  searching adult parasitoids. An internal equilibrium of equation (1) is defined by  $\lambda F(N^*, P^*) = 1$  and  $P^* = N^*(1 - 1/\lambda)$  and is locally stable if

$$-\frac{\lambda^2}{\lambda - 1} P^* \frac{\partial F(N^*, P^*)}{\partial P_t} < 1, \quad (2a)$$

$$\frac{\lambda - 1}{\lambda} \left( \frac{-\partial F(N^*, P^*)}{\partial P_t} \right) > \frac{\partial F(N^*, P^*)}{\partial N_t}. \quad (2b)$$

Many studies of this model have focused on the effects of spatial heterogeneity on stability (reviews in Hassell 1978; Chesson and Murdoch 1986). Typically, the habitat is assumed to be composed of discrete patches, and host density varies from patch to patch either as a random variable or in some other prescribed way.

The density of searching parasitoids in each patch is either a random variable independent of local host density (e.g., May 1978; Chesson and Murdoch 1986) or a deterministic function of local host density (e.g., Hassell and May 1973, 1974). Chesson and Murdoch (1986) labeled models containing the former assumption as *pure-error models* and those containing the latter as *pure-regression models*. These labels stem from the realization that the spatial distribution of the parasitoid may be modeled generally as a regression of local parasitoid on local host density. Covariance between the parasitoid and host is accounted for by the regression function, and heterogeneity in the density of parasitoids that is unrelated to host density is accounted for by the regression error. Although we recognize that this distinction is important, we also feel that the phrase “pure error model” may suggest to some that the heterogeneity is caused only by the limited decision-making abilities of parasitoids (though this “decision error” is certainly one source of “pure error”). We thus adopt the more cumbersome yet accurate labels of *HDI models* and *HDD models*, in which HDI stands for *host-density-independent heterogeneity* and HDD for *host-density-dependent heterogeneity*.

The five models we use to demonstrate the generality of the  $CV^2 > 1$  rule are listed below and described in detail in the ensuing sections.

Model I is an HDI model in which parasitoid density varies from patch to patch as a gamma-distributed random variable. This model reduces to the negative-binomial model of May (1978).

Model II is a corresponding HDD model in which *host* density varies from patch to patch as a gamma-distributed random variable and local parasitoid density is a deterministic function of local host density.

Model III is a general HDI and HDD model of which Model I, Model II, and most other published discrete-generation models are special cases. In Model III, host spatial distribution is arbitrary and HDI and HDD are given by general functional forms. We can analyze Model III if  $\lambda$  is close to one or if there is small variability among the local population densities of both parasitoids and hosts. We include Models I and II, even though these are special cases of Model III, because Models I and II can be analyzed no matter what the value of  $\lambda$  or degree of variability among patches.

Model IV is a model with no spatial structure in the habitat but with variation between individual hosts in their ability to survive parasitism by encapsulating the parasitoid progeny (Godfray and Hassell 1991). This model is included to demonstrate that the  $CV^2 > 1$  rule is valid even with some major changes in the biological assumptions underpinning Models I–III.

Model V is a numerical model that departs from the assumptions of equation (1) in having only a fraction of the parasitoid progeny emerging within a patch enter a “pool” for subsequent redispersal among the patches (Hassell and May 1988; Reeve 1988). The remainder stay on in the patches and reproduce there. The hosts are evenly distributed and the dispersing parasitoids colonize the patches according to a negative-binomial distribution. Model V is thus an HDI model and is included here to demonstrate that the  $CV^2 > 1$  rule is not a result of the phenomenological assumptions about spatial distributions in Models I–III.

*Model I*

Consider a habitat divided into discrete patches, such as food plants for an herbivorous insect, and suppose that both hosts and parasitoids are distributed among the patches. This, for instance, is often the case for univoltine forest Lepidoptera and their specialist parasitoids. We allow the hosts to have any spatial distribution whatsoever, but the distribution of parasitoids is unrelated to that of their hosts. Local densities of searching parasitoids are thus determined by chance and by their responses to environmental cues that are uncorrelated with local host densities. More specifically, we assume that parasitoid density varies as a gamma-distributed random variable from patch to patch. Because host and parasitoid distributions are independent, the distribution of parasitoids from host to host is also gamma. The gamma-probability-density function with unit mean and variance  $1/\alpha$  is

$$g(x) = \alpha^\alpha x^{\alpha-1} e^{-\alpha x} / \Gamma(\alpha),$$

in which  $\Gamma(\alpha)$  is a normalizing constant and  $\alpha$  is a positive constant governing the shape of the density function. If  $\alpha \leq 1$ , then the density is monotonically decreasing, indicating that a sample typically consists of many small values and a few large values. If  $\alpha > 1$ , then the density is humped, but the mode is to the left of the mean. As  $\alpha$  approaches infinity, the density converges to a symmetrical normal density. Finally, if  $X$  is a unit-mean gamma-distributed random variable, then  $Y = XP_t$  is gamma distributed with the same value of  $\alpha$  and mean  $P_t$ .

The fraction of hosts that escape parasitism in equation (1) is thus given by

$$F(P_t) = \int_0^\infty g(\epsilon) e^{-aP_t\epsilon} d\epsilon, \quad (3)$$

in which  $a$  is the per capita searching efficiency of the parasitoid (see Hassell 1978). The term  $\exp(-aP_t\epsilon)$  is the zero term of a Poisson distribution with mean  $aP_t\epsilon$ . It gives the probability of a host's being attacked zero times by parasitoids that search randomly *within* a patch containing parasitoid density  $P_t\epsilon$ . Note that  $\epsilon$  may be viewed as a multiplicative residual in a (zero-slope) regression of local parasitoid on local host density (Chesson and Murdoch 1986).

Equation (3) reduces to

$$F(P_t) = [\alpha/(\alpha + aP_t)]^\alpha;$$

thus, the unique, nontrivial equilibrium of the models (1) and (3) is

$$P^* = \alpha (\lambda^{1/\alpha} - 1)/a \quad \text{and} \quad N^* = \alpha \lambda (\lambda^{1/\alpha} - 1)/a(\lambda - 1).$$

This equilibrium exists if  $\lambda > 1$ . Stability condition (2b) is always satisfied because  $\partial F/\partial N_t = 0$  and  $\partial F/\partial P_t < 0$ . Condition (2a) reduces to

$$\alpha (1 - 1/\lambda^{1/\alpha}) < 1 - 1/\lambda, \quad (4)$$

and condition (4) is true if the equilibrium exists and  $\alpha < 1$  (May 1978).

Because the variance in the density of parasitoids is

$$\int_0^\infty g(\epsilon)(P_t\epsilon - P_t)^2 = P_t^2/\alpha,$$

the CV<sup>2</sup> of parasitoid density is simply 1/α. Thus, the condition, CV<sup>2</sup> > 1, is identical to α < 1, which is the necessary and sufficient condition for local stability. Notice, incidentally, that this model is formally identical with the phenomenological model proposed by May (1978), in which parasitoid attacks are effectively distributed in a negative-binomial manner (cf. the above expression for F(P<sub>t</sub>) with May's k identified as α).

*Model II*

From the extreme of no correlation between parasitoid and host spatial distributions, we now turn to the opposite extreme of a perfect correlation between the two. We assume that local parasitoid density deterministically tracks patch-to-patch variation in host density (see the empirical examples in Pacala and Hassell 1991). Specifically, let us suppose that the local density of searching parasitoids is given by the regression function, aP<sub>t</sub>(N/N<sub>t</sub>)<sup>μ</sup>, in which N is the local host density and μ is a constant governing the degree to which parasitoids aggregate in patches with high host density. The function is identical, except for a normalization constant, to that in Hassell and May (1973). If local host density is a gamma-distributed random variable with mean N<sub>t</sub>, then the average density of hosts surviving parasitism is

$$\int_0^\infty g'(x)x \exp[-aP_t(x/N_t)^\mu] dx,$$

in which g'(x) is the gamma density with mean N<sub>t</sub>; the average fraction of hosts surviving parasitism is, therefore,

$$\int_0^\infty g'(x) \frac{x}{N_t} \exp\left[-aP_t\left(\frac{x}{N_t}\right)^\mu\right] dx.$$

Now let the relative local host density be n = N/N<sub>t</sub>. The random variable n is gamma distributed with the same value of α as N, but with unit mean. Again using g(X) for the unit-mean gamma density, we have

$$F(P_t) = \int_0^\infty g(x)x \exp(-aP_t x^\mu) dx. \tag{5}$$

The models (1) and (5) are not as tractable as Model I. Three facts simplify the necessary numerical work. First, it is straightforward to prove that the model has a single internal equilibrium that exists if λ > 1. Second, stability criterion (2b) is always true because ∂F/∂N<sub>t</sub> = 0 and ∂F/∂P<sub>t</sub> < 0. Third, the searching efficiency, a, does not affect stability (to see this, introduce new state variables, P'<sub>t</sub> = aP<sub>t</sub> and N'<sub>t</sub> = aN<sub>t</sub>). We are thus left with three parameters that affect stability (λ, μ, and α) and a single stability criterion (2a).

Results of a numerical examination of criterion (2a) are illustrated in figure 2

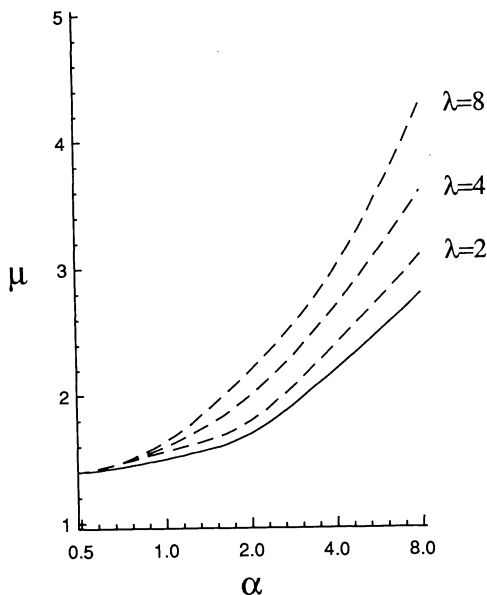


FIG. 2.—Stability criterion for Model II. The internal equilibrium is stable for values of  $\mu$  and  $\alpha$  above the appropriate dashed curve and unstable for values below. The solid curve shows values of  $\mu$  and  $\alpha$  at which  $CV^2 = 1$ .  $CV^2 > 1$  above the curve and  $CV^2 < 1$  below.

(*dashed curves*). For each of the three values of  $\lambda$  shown, the internal equilibrium is unstable for values of  $\mu$  and  $\alpha$  below the curve and stable for values above. The expression for  $CV^2$  is given by

$$\int_0^{\infty} g(x)x^{2\mu+1} dx / \left[ \int_0^{\infty} g(x)x^{\mu+1} dx \right]^2 - 1.$$

The solid line in figure 2 shows values of  $\mu$  and  $\alpha$  for which  $CV^2 = 1$ ;  $CV^2 < 1$  applies below the curve and  $CV^2 > 1$  above. Note that the  $CV^2 > 1$  rule is approximately the condition for stability in Model II. The approximation is best for values of  $\lambda$  near one and for highly aggregated host distributions (small values of  $\alpha$ ). Although the  $CV^2$  criterion is only approximate for this HDD model, there is a class of HDD models for which it is exact. These are the models discussed by Chesson and Murdoch (1986) in which host-density-dependent heterogeneity gives rise to a gamma distribution with constant parameters for the distribution of parasitoids among hosts.

### Model III

Models I and II represent opposite endpoints of the continuum between host-density-independent (HDI) heterogeneity and host-density-dependent (HDD) heterogeneity. They also include restrictive, though reasonable, assumptions about the different functional forms (e.g., gamma-distributed populations or power-law

dependence of local parasitoid on local host densities). We now consider a much more general model that removes these restrictive assumptions; spatial distributions are left unspecified and any degree of spatial covariance between parasitoid and host is allowed. We do, however, make two assumptions ensuring that stability criterion (2b) is always satisfied, as it is in Models I and II. Considerations of stability then remain with the dependence of the average fraction escaping parasitism on parasitoid density (criterion 2a).

We assume first of all that the distribution of relative numbers ( $n = N/N_i$ ) of hosts in patches does not change with host density but otherwise can be any distribution whatever. Second, we assume that the mean number of parasitoids in a patch, given host density, is expressible as  $P_i f(n)$ , in which  $f$  is an arbitrary function of relative host density ( $n$ ). These restrictions are unlikely to be met exactly in nature, but the available evidence (see Murdoch and Stewart-Oaten 1989) suggests that they are not too grossly in error.

The description of the model is complete once we define variation about the conditional mean parasitoid density. We consider a combination of multiplicative and additive variation about this mean, which we hope covers an adequate range of possibilities for variability in this system. From the basic underlying Nicholson-Bailey assumptions in these models, we know that parasitism depends not just on the number of parasitoids visiting a patch, but also on the amount of time they spend there (Hassell and May 1974). If the  $i$ th parasitoid to visit a patch spends  $T_i$  time units there, the probability that a particular host escapes parasitism is the zero term of the Poisson distribution and takes the form

$$\exp\left(-a \sum_{i=1}^P T_i\right). \tag{6}$$

We allow the  $T_i$  to have any distribution but assume that  $P$  is Poisson distributed, given local environmental conditions and host densities. This is a standard way of recognizing that  $P$  is a discrete variable (Chesson and Murdoch 1986), and it incorporates further additive variation. Multiplicative variation enters through the assumption that environmental factors alter the attractiveness of a locality to parasitoids, as in Model I. We then obtain a “patch-specific” mean parasitoid density equal to

$$Z = P_i f(n)U, \tag{7}$$

in which  $U$  is a random variable with mean 1, representing variation in environmental factors attracting parasitoids to patches. The mean density  $Z$  (which is really a conditional mean given  $n$  and  $U$ ) is called patch specific because it depends on the properties of the patch, such as the environment and the host density. It excludes chance variation in parasitoid visits to the patch that cannot be explained by  $n$  or  $U$ .

With these details, we can now specify the fraction of hosts surviving as

$$F(P_i) = E\left[n \exp\left(-1 \sum_{i=1}^P \right)\right], \tag{8}$$



in which  $E$  simply means the mathematical expected value of the expression in brackets. This can be defined by a set of integrals and sums over the joint probability distributions of  $N$ ,  $U$ ,  $P$ , and  $T_1, T_2, \dots$ , but it is much easier to analyze if left in the random-variable form.

If  $\psi(a)$  is the Laplace transform,  $E[\exp(-aT_i)]$ , of the times spent in patches, use of conditional expectations shows that equation (8) reduces to

$$F(P_i) = E(ne^{-Z[1-\psi(a)]}), \quad (9)$$

which is equivalent to a situation with no additive variation, but with  $a$  replaced by  $1 - \psi(a)$ . We should not be surprised, therefore, that additive variation plays no role in stability.

Expression (9) is analyzed in the Appendix under the assumption that  $\lambda$ , the host rate of increase, is near 1. It is shown that a  $CV^2 > 1$  rule does apply, but the  $CV^2$  is not for the actual number of parasitoids visiting a patch, nor is it for the actual total amount of time that parasitoids spend in a patch. Rather, it is the  $CV^2$  of  $Z$ , the patch-specific mean parasitoid density, equation (7), calculated on a per-host basis. This  $CV^2$  is independent of additive variation, as anticipated by expression (9). Indeed, on the basis of expression (9), which generalized the corresponding expressions in Models I and II, we must conclude that the  $CV^2$  of the patch-specific mean parasitoid density is also the quantity required in those models.

The variable  $Z$  is not directly observable, and so we face the empirical problem of how it can be estimated. It is thus instructive to see under what circumstances the required  $CV^2$  can be approximated by the  $CV^2$  of some more observable quantity. We consider just the total amount of time,  $T = \sum_i T_i$ , spent by parasitoids in a patch, because this is often closely related to the usual observation of percent parasitism in a patch.

Repeated application of the conditional-variance formula

$$V(Y) = E[V(Y|X)] + V[E(Y|X)] \quad (10)$$

shows that

$$CV_T^2 = CV_Z^2 + (1 + CV_T^2)/EZ, \quad (11)$$

where all means and  $CV^2$ s are calculated on a per-host basis. The second term on the right-hand side of equation (11) is the error caused by using  $CV_T^2$  as an approximation of  $CV_Z^2$ . The error is small if the mean number of parasitoids,  $EZ$ , visiting a patch containing a randomly chosen host is large. This is the sort of information that might be easily obtained in many settings, and if  $EZ$  is not large, then one might attempt to measure the error so that it can be subtracted.

Given that the error structure of this model is so important, how do we interpret it in relation to existing information on variation in host-parasitoid systems? The power-law relationship  $\sigma^2 = cx^s$ , relating the mean  $x$  and variance  $\sigma^2$  of distribution, with constants  $c$  and  $s$ , has been used to describe mean and variance relationships for local abundances of a variety of organisms including parasitoids (Taylor et al. 1978; Elliott 1983). The distribution of  $T$ , as defined here, does not

belong to this family, but equation (11) implies that it has a relationship of the form

$$\sigma^2 = ax + bx^2, \tag{12}$$

in which  $a$  and  $b$  are constants. This remains true when the distribution of  $T$  is assessed on a per-patch, rather than a per-host, basis.

Although equation (12) is not a power law, it approximates one with a value of  $s$  between 1 and 2. Indeed, as remarked by Murdoch and Stewart-Oaten (1989), the difference between equation (12) and a true power law is unlikely to be detectable empirically. Moreover, as Taylor et al. (1978) showed, values of  $s$  between 1 and 2, as required here, seem most realistic for insect counts. The same must be true for the related quantity  $T$ . In this context we can see that the error in using  $CV_T^2$  as an approximation to  $CV_Z^2$  will be small when  $x$  is large, reflecting a large value of EZ. This then means that the relationship between the mean and variance of  $T$  can be well described by a power law with  $s = 2$ .

*Model IV*

Godfray and Hassell (1991) explored a quite different case of heterogeneous parasitism, one in which host individuals vary in their ability to encapsulate the parasitoid progeny (eggs or larvae). Such variability has been well documented in *Drosophila* species and their parasitoids (Bouletreau 1986). Suppose that an individual host has probability  $R$  of encapsulating an egg of an endoparasitoid and that  $R$  varies randomly among hosts with probability density function  $q(r)$ . If the number of attacks per host is a Poisson random variable, if one egg is laid per attack, and if the probability that any one host successfully encapsulates  $n$  eggs is  $R_n$ , then we may write  $F(\cdot)$  in equation (1) as

$$F(P_i) = \int_0^1 q(r)e^{-aP_i(1-r)} dr.$$

Godfray and Hassell (1991) approximated Taylor's expression by expanding  $\exp[aP_i(1 - r)]$  about the mean,  $\bar{R}$ , and dropping terms of higher than second order. They then derived a local stability criterion for the resulting model (the approximation together with eq. [1]). If  $\lambda$  is close to one (roughly between 1 and 2.5), then the necessary and sufficient condition for local stability is approximately

$$\sigma_R^2/(1 - \bar{R})^2 > 1, \tag{13}$$

in which  $\sigma_R^2$  is the variance of  $R$ .

Because of interhost variation in  $R$ , there is interhost variation in the mean level of successful parasitism. We define the mean density of *effective* parasitoids experienced by a host with probability of encapsulation  $R$  as  $P_i(1 - R)$ . Thus, the mean density of effective parasitoids across all hosts is  $P_i(1 - \bar{R})$ , and the variance is

$$\int_0^1 q(r)[P_i(1 - r) - P_i(1 - \bar{R})]^2 dr = P_i^2 \sigma_R^2.$$

Thus, in this very different model, the stability criterion (13) is again the  $CV^2 > 1$  rule.

#### Model V

In the previous models all hosts and parasitoids redistributed themselves among the available patches in each generation. Although there are many natural examples of this, particularly from univoltine species, there are also many cases of less complete mixing, with some of the hosts and parasitoids tending to remain within the patch from which they originated. A general model allowing some hosts and/or parasitoids to stay in the patch from which they emerged, while the remainder enter a "pool" to be redistributed anew in the next generation has recently been discussed by Hassell and May (1988) and Reeve (1988). There is now a continuum from complete host mixing to no host mixing, and complete parasitoid mixing to no parasitoid mixing. Assuming, for simplicity, that the probability of leaving a patch is density independent and that there is no mortality associated with the movement, the hosts and adult parasitoids in the  $i$ th patch,  $N_i$  and  $P_i$  respectively, are now given by

$$N_i(t + 1) = \lambda \left[ S_i(1 - x_i) + \alpha_i \sum_{j=1}^n S_j x_j \right], \quad (14a)$$

$$P_i(t + 1) = N_{ai}(1 - y_i) + \beta_i \sum_{j=1}^n N_{aj} y_j. \quad (14b)$$

Here  $\alpha_i$  and  $\beta_i$  are the fractions of dispersing hosts and parasitoids, respectively, that enter the  $i$ th patch,  $S_i$  is the number of these hosts surviving from parasitism and  $N_{ai}$  the number of hosts parasitized  $\{N_i[1 - \exp(-aP_i)]\}$ . Finally,  $x_i$  and  $y_i$  are the fraction of host and parasitoid progeny, respectively, leaving the patch for subsequent redistribution in the next generation, and  $n$  is the total number of patches.

A full analysis of this model would require a separate treatment. Numerical studies, however, indicate that the  $CV^2$  rule is a good indicator of stability for at least some cases of the model (14). For example, suppose that there is complete host mixing in each generation ( $x_i = 1$ ) and that the fraction of parasitoids mixing varies from zero to one. We assume an even host distribution, and that those parasitoids that do disperse redistribute themselves according to a negative binomial distribution. The model is thus an HDI model, not dissimilar to Model I. Figure 3 shows a numerical example in terms of the  $CV^2$  of the parasitoid distribution at equilibrium as the fraction of parasitoid mixing is changed. Once again the  $CV^2 > 1$  rule is a good indicator of stability.

#### CONCLUSION

While it is widely appreciated that heterogeneous parasitism has the potential to regulate host-parasitoid interactions, there is no consensus on just what kinds

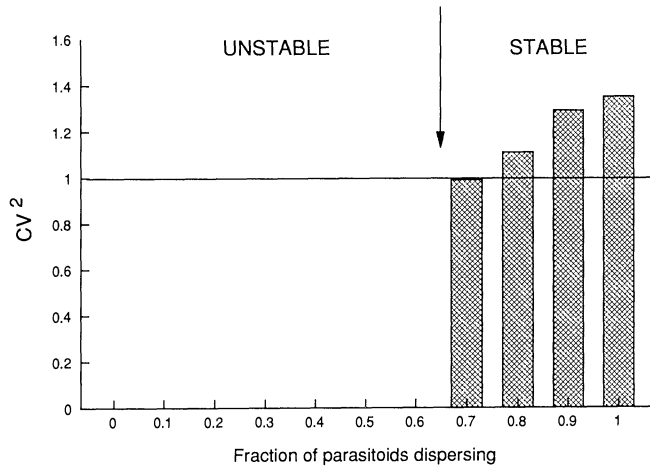


FIG. 3.—A numerical example from Model V. The histogram bars show the values of  $CV^2$  at equilibrium as a function of the fraction of parasitoids that disperse in each generation ( $y$  in eq. [14b]). The model is stable, with  $CV^2 \geq 1$ , provided that at least 70% of the parasitoids disperse in each generation. Below this value, the model shows limit cycles, and  $CV^2$  fluctuates with values less than one. Parameter values:  $\lambda = 2$ ,  $a = 0.01$ ,  $k$  (negative binomial) = 1,  $n = 20$ .

of heterogeneity do achieve such regulation. This article shows that, for associations of a single host and a single parasitoid in which the populations have discrete generations, the dynamic effects of any pattern of distribution of searching parasitoids can be assessed within a common framework: the populations are regulated if the  $CV^2$  of the distribution is greater than one.

We have also shown how this measure of variation has two components: (1) HDD heterogeneity (direct or inverse) and (2) HDI heterogeneity whereby the variation from host-to-host is independent of local host densities. Each of these components promotes population regulation in the same way, by contributing to the value of  $CV^2$ .

To see this more clearly, consider the fraction of hosts that escape parasitism [ $F(N_p, P_t)$ ] from a general pure HDD model,

$$F(N_p, P_t) = \int_0^\infty \phi f(N) (N/N_t) e^{-f(P_t, N)} dN, \tag{15}$$

in which  $\phi(N)$  is the host's spatial distribution. The corresponding fraction from a general pure HDI model is

$$F(N_p, P_t) = \int_0^\infty r(\epsilon) e^{-f(P_t, \epsilon)} d\epsilon, \tag{16}$$

in which  $r(\epsilon)$  is the distribution of the factor  $\epsilon$  that causes the host density-independent variation. Like  $\phi(N)$ , the quantity  $\phi'(N) = \phi(N)N/N_t$  is a probability density. Whereas  $\phi(N)$  governs the fraction of patches with host density  $N$ ,

$\phi'(N)$  governs the fraction of hosts that inhabit a patch with host density  $N$ . We may write equation (15), using  $\phi'(N)$ , as

$$F(N_p, P_t) = \int_0^{\infty} \phi'(N) e^{-f(P_t, N)} dN, \quad (17)$$

which has exactly the same form as equation (16). Dynamics are affected by the level, but not the source, of host-to-host variation in the probability of parasitism, as reflected in the structural equivalence of HDD and HDI models (17) and (16).

The five models discussed in this article show that the “ $CV^2 > 1$  rule” is likely to apply across a wide variety of host-parasitoid interactions. The analysis, however, makes several fundamental assumptions (listed below) about the biology of the interactions that certainly do not apply to all host-parasitoid model or field systems.

(1) *Coupled, synchronized interactions.*—This restricts our analysis to parasitoids that are effectively specialists on the one host species. The dynamics of generalist parasitoids and their hosts can be very different (Hassell and May 1986) and will require a separate treatment.

(2) *Discrete-host and parasitoid generations.*—Univoltine systems in temperate regions provide some of the best examples of discrete generations. Many other systems in which hosts and parasitoids are multivoltine, with some degree of generation overlap, are also likely to be adequately represented in discrete time (Godfray and Hassell 1989). Interactions in which host and parasitoid generations overlap more comprehensively are better represented in continuous time, and these systems are typically more stable than their discrete-time counterparts. Additional work is required to develop parallel results that apply to such systems with overlapping generations and continuous reproduction. The distribution of parasitoids in host-parasitoid models with discrete generations is sometimes described in terms of a single episode of parasitoid distribution among patches, which is then “fossilized” until the next generation. This, however, is not a necessary assumption: the models require only that a particular distribution of total searching time by parasitoids in the different patches be specified over the generation period; within any one patch, this can be the result of a single visit or many visits.

(3) *Random exploitation of hosts within patches.*—The extent to which the parasitoids encounter hosts at random within patches, and the importance of any deviations from this, depends in part on the size of the patches relative to the foraging area of the parasitoids. This introduces important questions of appropriate scales in host-parasitoid associations, which is discussed in more detail in the companion article (Pacala and Hassell 1991).

(4) *No interference between parasitoids or competition among hosts.*—The models in this article focus on situations in which interactions between host and parasitoid populations are of predominant importance for the overall dynamics. Any additional density-dependent and density-independent factors that markedly influence fecundity and/or survival of the hosts and parasitoids will also affect the dynamics and change the overall stability conditions. In neglecting these,

our emphasis is primarily on understanding the extent to which one factor—the distribution of parasitism among hosts—can contribute to population regulation.

A difficulty in applying the  $CV^2 > 1$  criterion to situations in the field is the scarcity of interactions in which it is practical to observe and quantify the distribution of searching time by adult female parasitoids (but see Waage 1983). The only data usually available from the field are those of percent parasitism in relation to host density per patch. The companion article (Pacala and Hassell 1991) shows how the  $CV^2 > 1$  rule may be applied directly to such data in order to evaluate the contributions of HDD and HDI to population stability.

Heterogeneity has often been regarded as a complicating factor in population models, and one that rapidly leads to analytical intractability. The present study emphasizes that this need not be so; the end product of our analysis of the dynamical effects of heterogeneity in host-parasitoid models with discrete generations is the simplest of criteria. It offers the hope that comparable, general rules can be found for assessing the role of heterogeneity on the dynamics of a much broader range of interactions among species.

#### ACKNOWLEDGMENTS

We are grateful to C. Godfray for his perceptive comments on the manuscript. This work was supported by a grant from the Natural Environment Research Council (to M.P.H.), by National Science Foundation grants BSR-8918616 (to S.W.P.) and BSN-8615031 (to P.L.C.), and by the National Environment Research Council Centre for Population Biology at Imperial College, Silwood Park. We also thank J. Reeve, A. R. Ives, and one anonymous reviewer for suggestions that markedly improved the paper.

#### APPENDIX

For Model III in the text define  $X = Z[1 - \psi(a)]P^*/P_t$ , and calculate all expected values on a per-host basis. Then

$$F(P_t) = E \exp(-XP_t/P^*). \quad (A1)$$

Using a prime for a derivative,

$$F'(P^*) = -E[(X/P^*)\exp(-X)]. \quad (A2)$$

The equation for equilibrium is

$$1/\lambda = F(P^*) = E \exp(-X). \quad (A3)$$

Substituting equations (A2) and (A3) into stability condition (2a), we obtain

$$E[X \exp(-X)] < E[\exp(-X)]E[1 - \exp(-X)]. \quad (A4)$$

Now if  $\lambda$  is near 1, equation (A3) implies that  $X$  must be small with high probability. From the definition of  $X$ , this is achieved by having  $P^*$  be small if no parameter other than  $\lambda$  is varied. Mild regulatory conditions on the distribution of  $X$  now permit the exponentials in (A4) to be expanded about zero to give

$$E[X(1 - X)] < E(1 - X + X^2/2) E(X - X^2/2) + O(P^{-3}),$$

which simplifies to

$$EX^2/(EX)^2 > 2 + O(P^*). \quad (A5)$$

Now, to order  $P^*$  (= order  $1 - 1/\lambda$ ), equation (A5) is the requirement that  $CV_{\frac{1}{2}}^2 > 1$ .

#### LITERATURE CITED

- Bouletreau, M. 1986. The genetic and coevolutionary interactions between parasitoids and their hosts. Pages 169–200 in J. K. Waage and D. Greathead, eds. *Insect parasitoids*. Academic Press, London.
- Brown, M. W., and E. A. Cameron. 1979. Effects of diapause and egg mass size on parasitism by the gypsy moth egg parasite, *Ooencyrtus kuwani*. *Environmental Entomology* 8:77–80.
- Chesson, P. L., and W. W. Murdoch. 1986. Aggregation of risk: relationships among host-parasitoid models. *American Naturalist* 127:696–715.
- Ehler, L. E. 1987. Patch-exploitation efficiency in a torymid parasite of a gall midge. *Environmental Entomology* 16:198–201.
- Elliott, J. M. 1983. The responses of the aquatic parasitoid *Agriotypus armatus* (Hymenoptera: Agriotypidae) to the spatial distribution and density of its caddis host *Silo pallipes* (Trichoptera: Goeridae). *Journal of Animal Ecology* 52:315–330.
- Free, C. A., J. R. Beddington, and J. H. Lawton. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. *Journal of Animal Ecology* 46:543–554.
- Godfray, H. C. J., and M. P. Hassell. 1989. Discrete and continuous insect populations in tropical environments. *Journal of Animal Ecology* 58:153–174.
- . 1991. Encapsulation and host-parasitoid population dynamics. In C. Toft, ed. *Parasitism: coexistence of conflict?* Oxford University Press, Oxford (in press).
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton.
- . 1984. Parasitism in patchy environments: inverse density dependence can be destabilizing. *Institute of Mathematics and Its Applications. Journal of Mathematics Applied in Medicine and Biology* 1:123–133.
- Hassell, M. P., and R. M. May. 1973. Stability in insect host-parasite models. *Journal of Animal Ecology* 42:693–726.
- . 1974. Aggregation in predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43:567–594.
- . 1986. Generalist and specialist natural enemies in insect predator-prey interactions. *Journal of Animal Ecology* 55:923–940.
- . 1988. Spatial heterogeneity and the dynamics of parasitoid-host systems. *Annales Zoologici Fennici* 25:55–61.
- Lessells, C. M. 1985. Parasitoid foraging: should parasitism be density dependent. *Journal of Animal Ecology* 54:27–41.
- May, R. M. 1978. Host-parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology* 47:833–843.
- McClure, M. S. 1977. Parasitism of the scale insect, *Fiorinia externa* (Homoptera: Diaspididae) by *Aspidiotiphagus citrinus* (Hymenoptera: Eulophidae), in a hemlock forest: density dependence. *Environmental Entomology* 6:551–555.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* 9:2–131.
- Murdoch, W. W., and A. Stewart-Oaten. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. *American Naturalist* 134:288–310.
- Pacala, S. W., and M. P. Hassell. 1991. The persistence of host-parasitoid associations in patchy environments. II. Evaluation of field data. *American Naturalist* 138:584–605.
- Pacala, S. W., M. P. Hassell, and R. M. May. 1990. Host-parasitoid associations in patchy environments. *Nature (London)* 344:150–153.

- Perry, J. N. 1987. Host-parasitoid models of intermediate complexity. *American Naturalist* 130: 955–957.
- Reeve, J. D. 1988. Environmental variability, migration, and persistence in host-parasitoid systems. *American Naturalist* 132:810–836.
- Stiling, P. D. 1987. The frequency of density dependence in insect host-parasitoid systems. *Ecology* 68:844–856.
- Taylor, L. R., I. P. Woiwod, and J. N. Perry. 1978. The density-dependence of spatial behaviour and the rarity of randomness. *Journal of Animal Ecology* 47:383–406.
- Waage, J. K. 1983. Aggregation in field parasitoid populations foraging time allocation by a population of *Diadegma* (Hymenoptera: Ichneumonidae). *Ecological Entomology* 8:447–453.
- Walde, S. J., and W. W. Murdoch. 1988. Spatial density dependence in parasitoids. *Annual Review of Entomology* 33:441–466.