Environmental heterogeneity and the stability of host–parasitoid interactions

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Summary

1. Spatial heterogeneity has long been recognized as a potentially powerful stabilizing force in host–parasitoid interactions. Most previous work has emphasized heterogeneity in the rate of attacks experienced by individual hosts. In contrast, we highlight the potential importance of spatial heterogeneity in demographic parameters other than the rate of parasitism.

2. Following the model structure explored by Hassell & May (1973) in which hosts and parasitoids are distributed across patches according to fixed distribution rules, we show that, in the absence of heterogeneity in the rate of parasitism, spatial variability in other demographic parameters has no effect on population stability.

3. Spatial heterogeneity in demographic parameters may, however, interact with heterogeneous attack rates to augment or, conversely, destroy stability. This is illustrated from a generalized proportional refuge model in which a fixed fraction of hosts escape parasitism each generation, and refuge hosts have a different growth rate from exposed hosts. We show that the system may be stable even if hosts have high average rates of increase, provided that those hosts with the higher rates of increase are differentially afflicted by parasitism.

4. The generality of this conclusion is assessed by numerical studies of a two-patch model in which the host and/or parasitoid show partial rather than complete mixing between patches in each generation. We show that such partially coupled refuges are most likely to be stabilizing if they are 'sinks', with relatively low host growth rates. Moreover, and a unique feature emerging from these partially coupled models, heterogeneity in the number of adult female parasitoids produced per parasitized host can be sufficient by itself to stabilize the system.

5. These theoretical results suggest that a fruitful direction for empirical work is to document the patterns of covariance among attack rates, host rates of increase and parasitoid emergence rates.

Key-words: parasitoids, refuges, spatial heterogeneity, stability.

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Introduction

The world is heterogeneous in many dimensions, and at many spatial and temporal scales. In recent years, considerable work has sought to elucidate the contribution heterogeneity makes to the persistence of host–parasitoid interactions. Much of this work has concentrated on one particular kind of spatial heterogeneity; namely, heterogeneity in the rate of

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attacks experienced by individual hosts (e.g. Hassell 1978; Chesson & Murdoch 1986; Murdoch & Stewart-Oaten 1989). Recently, Pacala, Hassell & May (1990), Hassell *et al.* (1991) and Pacala & Hassell (1991) have shown how the dynamical effects of such spatial patterns in coupled, discrete-generation host–parasitoid interactions can be assessed by a common criterion, the '$CV^2 > 1$ rule'. Specifically, this states that the overall population densities will be locally stable if the coefficient of variation squared (CV^2) of the density of searching parasitoids in the vicinity of each host exceeds approximately unity. This criterion synthesizes a large body of previous

work on the dynamical consequences of predator aggregation, prey refuges, and heterogeneous attack rates in general, into a common framework.

An important aspect of heterogeneity that has been neglected in these host–parasitoid studies has been any variability in demographic parameters other than the rate of parasitism. In this paper we will explore the influence on the persistence of host–parasitoid systems of environmental heterogeneity affecting such parameters as the patch-specific host reproductive rate. Consider for instance a scenario in which the host population is divided into discrete patches in which adult hosts distribute their eggs. A specialist parasitoid searches within these patches, and is effective enough that the host population is limited to levels well below that set by available resources. One dimension of heterogeneity in such a system certainly arises from variance in the abundance of parasitoids per patch, or in the rate of attack per parasitoid within patches. But there may also be variation among patches reflected in the other demographic parameters affecting the contribution of an individual host or parasitoid to its population, that overlays and interacts with any spatial heterogeneity in attacks. For instance, spatial variation in resource quality or microclimate might be reflected in spatially variable intrinsic growth rates for the host (e.g. Prestidge & McNeill 1983; Kidd *et al.* 1990). There are many different biological mechanisms that could generate such heterogeneity. For example, fecundity is often correlated with adult body size (e.g. Hanski 1987), so that any patch-specific environmental factors that influence body size could in turn generate patch-to-patch variance in host reproductive rates. Similarly, the fraction of parasitized hosts that on average produce viable parasitoid offspring could also vary among patches; for example, due to patch-specific bird predation on parasitized hosts (Hubbard 1972).

A BRIEF HISTORY

In principle, many different kinds of factors other than spatial heterogeneity can contribute to the persistence of a host–parasitoid interaction. These include competition for resources among hosts (Roughgarden & Feldman 1975; Hassell & Comins 1975), interference among parasitoids (Hassell 1978) and shifting parasitoid sex ratios (Hassell, Waage & May 1983; Comins & Wellings 1985). Interest in the dynamical role of spatial factors was sharpened by the recognition that many of these stabilizing mechanisms are unlikely to limit population sizes to the very low levels often seen in the field (Beddington *et al.* 1978). In contrast, refuges, parasitoid aggregation and any other causes of spatial heterogeneity can be effective even at very low host population sizes.

Theoretical studies of spatial heterogeneity in

host–parasitoid systems can be roughly divided into three stages. First, the effect of within-population spatial heterogeneity was explored (e.g. Bailey, Nicholson & Williams 1962; Hassell & May 1973, 1974). In each generation the populations of both the host and parasitoid were partitioned into patches where they would interact; the output of each patch would then mix in a single panmictic population before the start of the following generation. Except in special limiting cases, these models quickly become parameter-rich and difficult to treat analytically. The second stage was to seek useful approximations which would summarize this complexity in simple, phenomenological models (May 1978; Perry 1988). For example, May's model assumed a negative binomial distribution of attacks amongst hosts, the detailed interpretation of which has been well reviewed by Chesson & Murdoch (1986). The search for simple ways of describing the net affect of heterogeneity on host–parasitoid dynamics has led to the so-called '$CV^2 > 1$ rule' (Pacala, Hassell & May 1990; Hassell *et al.* 1991; Pacala & Hassell 1991) as a convenient guide to the magnitude of heterogeneity in parasitism between individual hosts that is required for stability. The third stage has been to imagine that the host and parasitoid are distributed in a metapopulation of local populations only partially coupled by dispersal (Reeve 1988, 1990; Hassell & May 1988). When such dispersal is by diffusion rather than global mixing, the interaction can persist, even in a spatially homogeneous environment (Hassell *et al.* 1991; Comins, Hassell & May 1992).

In this paper, we will retrace part of this route already taken in the literature on spatial heterogeneity, but now incorporating spatial variability in demographic parameters as well as in the rates of parasitism. We will first examine systems in which the spatial heterogeneity is manifested among patches within single panmictic populations. We will then consider systems in which patches are partially coupled by dispersal.

By itself, demographic heterogeneity is not stabilizing

Previous work on the stabilizing effect of spatial heterogeneity has, for simplicity, quite sensibly ignored the influence of components of spatial heterogeneity other than in the rate of attack. Indeed, in simple cases one can demonstrate that spatial variance in demographic rates is irrelevant to the stability of the system if parasitism is spatially homogeneous. Consider, for instance, the model explored by Hassell & May (1973), generalized to incorporate spatial heterogeneity among patches in host and parasitoid demographic rates, together with variation in attack rates and in the distribution of both the host and parasitoid. In each generation, a fraction α_i of the hosts and β_i of the parasitoids are

found in patch i (out of n patches). The hosts in patch i have a finite rate of increase, λ_i, and the number of adult female parasitoids produced per parasitized host in that patch is c_i. The fraction of hosts in patch i that escape parasitism is described by the usual Nicholson & Bailey (1935) form:

$$N_{t+1} = N_t \sum_{i=1}^{n} \lambda_i \alpha_i \exp(-a_i \beta_i P_t) \qquad \text{eqn 1a}$$

$$P_{t+1} = N_t \sum_{i=1}^{n} c_i \alpha_i [1 - \exp(-a_i \beta_i P_t)]. \qquad \text{eqn 1b}$$

Here a_i is the attack rate in patch i. Now assume that the parasitoid has a uniform distribution among patches, so that $\beta_i = 1/n$, and that the attack rates are spatially homogeneous, $a_i = a$. The above model simplifies to

$$N_{t+1} = N_t \left[\sum_{i=1}^{n} \lambda_i \alpha_i \right] \exp(-a' P_t) = N_t \bar{\lambda} \exp(-a_i \beta_i P_t) \atop \text{eqn 2a}$$

$$P_{t+1} = N_t \left[\sum_{i=1}^{n} c_i \alpha_i \right] [1 - \exp(-a' P_t)]$$

$$= N_t \bar{c} [1 - \exp(-a' P_t)] \qquad \text{eqn 2b}$$

in which $a' = a/n$, $\bar{\lambda}$ is the average host growth rate, and $\bar{c}$ is the average parasitoid emergence parameter. But this model is none other than the unstable Nicholson-Bailey model. In other words, spatial variance in host or parasitoid demographic parameters has no effect on the stability of the system if parasitism is spatially uniform. Although this result needs to be checked in a broader array of models, it does suggest that if environmental heterogeneity affecting demographic rates in host–parasitoid systems is to have any important effect it is likely to be in augmenting or diminishing the stabilizing effect of heterogeneous attack rates, rather than in providing of itself a mechanism for stabilizing the interaction.

A generalized proportional refuge model

To this end, we will first examine a limiting case of the above model that has come to be known as the 'proportional refuge model' (Hassell 1978). Assume that for each generation, a fraction of hosts are exposed to parasitism, and that the remaining fraction $1-\varepsilon$ reside in refuges, free of parasitism. Biologically, the factors that permit some hosts to escape parasitism may also influence their intrinsic rate of natural increase, for instance by affecting their developmental rate, or body size (and hence fecundity) as adults. If the refuge consists of a microhabitat that is not accessible to the parasitoid, it may contain a suite of mortality factors (e.g. generalist predators) different from those found in exposed microhabitats.

The proportional refuge model, generalized to allow a different host growth rate in the refuge from that outside, is as follows (the indices 1 and 2 denote hosts outside and within the refuge, respectively):

$$N_{t+1} = \varepsilon N_t \lambda_1 f(P_t) + (1 - \varepsilon) \lambda_2 N_t \qquad \text{eqn 3a}$$

$$P_{t+1} = c N_t \varepsilon [1 - f(P_t)]. \qquad \text{eqn 3b}$$

Here $f(P_t) = \exp(-a P_t)$ describes the fraction of hosts escaping attack outside the refuge; this expression assumes that parasitoid attacks on this component of the host population are distributed at random.

Hassell & May (1973) assumed that the host intrinsic growth rates inside and outside the refuge were equal. They found that a proportional refuge could indeed stabilize an otherwise unstable host–parasitoid interaction, but only for a rather limited range of parameters. For instance, if hosts are equally divided each generation between the refuge and non-refuge classes ($\varepsilon = 0.5$), the equilibrium is stable only if the host intrinsic growth rate is bounded between 1 and 2. By generalizing this model to incorporate spatial variance in host intrinsic growth rates, we show that proportional refuges are potentially stabilizing over a much wider range of average host intrinsic growth rates.

At equilibrium, the densities of the parasitoid and host are, respectively,

$$P^* = \ln \left[\frac{\varepsilon \lambda_1}{1 - (1 - \varepsilon) \lambda_2} \right] \qquad \text{eqn 4a}$$

$$N^* = \frac{1}{ac} \ln \left[\frac{\varepsilon \lambda_1}{1 - (1 - \varepsilon) \lambda_2} \right] \left(\frac{\lambda_1}{\bar{\lambda} - 1} \right) \qquad \text{eqn 4b}$$

where $\bar{\lambda} = \varepsilon \lambda_1 + (1 - \varepsilon) \lambda_2$ is the average host rate of increase. There are two conditions that must be satisfied for this equilibrium to exist. First, $\bar{\lambda} > 1$; otherwise, both the host and parasitoid populations go extinct. Second, $(1 - \varepsilon) \lambda_2 < 1$; otherwise, the subpopulation of hosts in the refuge will increase geometrically, regardless of the abundance of parasitoids outside. (Note that adding the refuge increases parasitoid density if $\lambda_2 > 1$, and decreases parasitoid density if $\lambda_2 < 1$.)

Proceeding with the usual linearized stability analysis, let $N_2 = N^*(1 + x_t)$, and $P_t = P^*(1 + y_t)$. Near the equilibrium, the dynamics of the system are described by

$$\begin{pmatrix} x_{t+1} \\ y_{t+1} \end{pmatrix} = \begin{pmatrix} 1 & -\mu_1 \varepsilon a P^* f(P^*) \\ 1 & c_i \varepsilon N^* a f(P^*) \end{pmatrix} \begin{pmatrix} x_t \\ y_t \end{pmatrix}.$$

Applying the Schur-Cohn criterion to the characteristic equation leads to the following stability condition

$$af(P^*)[c \varepsilon N^* + \lambda_1 \varepsilon P^*] < 1,$$

or

$$[1 - (1 - \varepsilon) \lambda_2] \left(\frac{\bar{\lambda}}{\bar{\lambda} - 1} \right) \ln \left(\frac{\varepsilon \lambda_1}{1 - (1 - \varepsilon) \lambda_2} \right) < 1. \qquad \text{eqn 5}$$

In the limit $(1 - \varepsilon) \lambda_2 \rightarrow 0$, this reduces to $\varepsilon \lambda_1 \ln(\varepsilon \lambda_1)$

$< \varepsilon\lambda_1 - 1$. Let $x = \varepsilon\lambda_1 - 1$; the condition then becomes $\ln(1 + x) < x/(1 + x)$. But a fundamental fact about logarithms is that $x/(1 + x) < \ln(1 + x)$. Hence, the above stability condition is violated if the realized growth rate in the refuge is too low; if the system persists at all, it will show limit cycles or chaotic dynamics.

Let $R_1 = \varepsilon\lambda_1$ and $R_2 = (1-\varepsilon)\lambda_2$, so that $\bar\lambda = R_1 + R_2$. The quantities R_1 and R_2 can be interpreted as the portions of the net intrinsic growth rate that can be ascribed to hosts outside and inside refuges, respectively. Figure 1 depicts the slice of parameter space permitting stability. A family of straight lines with slope $= -1$ describes hosts with given net finite rates of increase, $\bar\lambda = k$. If $\bar\lambda < 1$, the system goes to extinction. If $\bar\lambda > 1$, the proportional refuge may stabilize the interaction even if the host has a high intrinsic rate of increase, as long as the contribution of 'refuge hosts' to the average host rate of increase (i.e. their actual growth rate weighted by the fraction of the population found in the refuge) is less than unity.

If the contribution of refuge hosts to total population growth is too low, the system does not reach a stable point equilibrium, but instead fluctuates with limit cycles or chaotic dynamics. These oscillations increase in amplitude as R_2 decreases and, in the limit $R_2 \to 0$, approach the expanding oscillations of the classical Nicholson-Bailey model. Figure 2 shows this pattern of increasing oscillations as the contribution by the refuge toward the net growth of the host population declines. When exposed hosts have $\lambda = 3.8$ and refuge hosts have $\lambda = 0.2$, the system displays sustained, large-amplitude oscillations that appear to be chaotic. In the absence of the parasitoid, the refuge hosts account for just over 5% of the net growth rate of the host population and thus might seem to be unimportant for its dynamics. Yet it is the presence of these hosts that are responsible for the persistence of the host–parasitoid interaction.

Figure 3 shows another numerical example that displays this effect in an even more dramatic fashion. In Fig. 3a, the hosts divide equitably into exposed and refuge classes each generation, but because of the high growth rate of the exposed hosts the refuge hosts contribute less than 2% to the net growth rate of the host. These hosts nonetheless suffice to stabilize the host–parasitoid interaction. Increasing the contribution of refuge hosts to the growth of the host population weakens the stabilizing influence of the refuge (see Fig. 3b).

The important conceptual message of the generalized proportional refuge model is that hosts which provide a negligible contribution to the average intrinsic growth rate of the host population can nonetheless be critical in determining the stability of the host–parasitoid interaction. Moreover, this effect may be observed even in host populations with high intrinsic growth rates. Heterogeneity in host growth rates can thus augment the stabilizing influence of heterogeneity in parasitism, provided hosts with relatively high growth rates are those attacked.

This result stills holds, albeit with less force, if hosts in the refuge are not completely protected from parasitism. In the original treatment of model 1 by Hassell & May (1973), a parameter was used to describe the degree of aggregation by parasitoids in patches each generation. Figure 4 shows a numerical example for a moderately high (but not unrealistic) value of this aggregation parameter. In Fig. 4a, the host has a growth rate ($= 2$) that is the same in the two patches ($\bar\lambda = 2$), and the parasitoid aggregates sufficiently to keep the interaction persistent, but with sustained cycles. In Fig. 4b, we assume that the host in the refuge has a low growth rate relative to the host outside but the same net growth rate; in this case, the system is strongly stable. This example illustrates that the stabilizing effect of lowered host growth rates in the refuge is not highly sensitive to
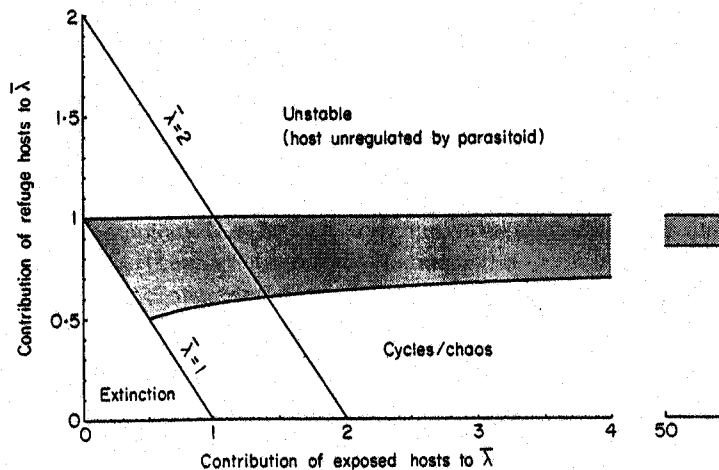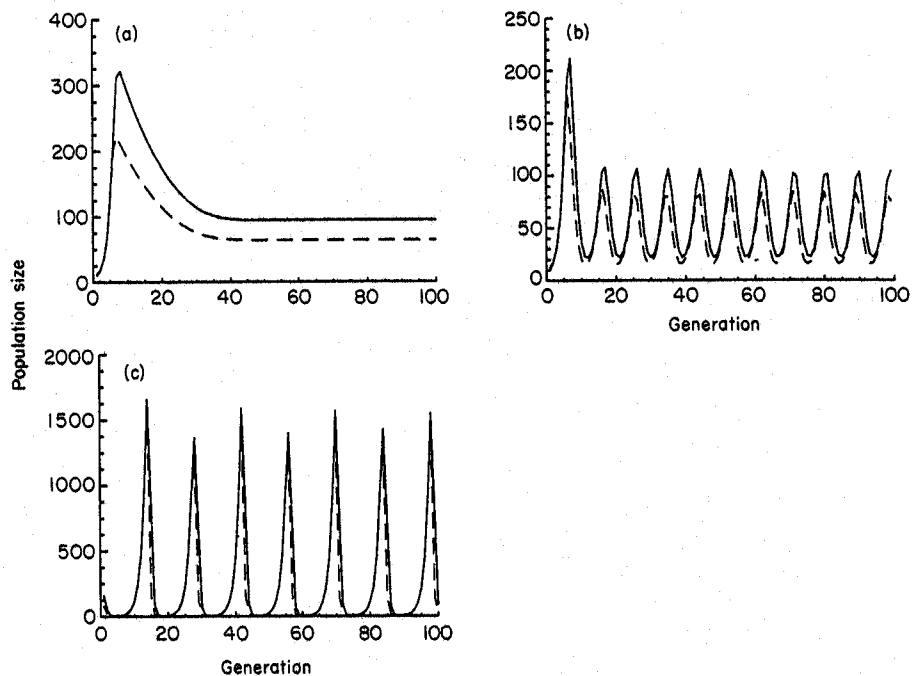

Fig. 1. The effect of spatial variance in host rate of increase on stability in the proportional refuge model. The abscissa and ordinate are, respectively, $R_1 = \varepsilon\lambda_1$, the contribution of hosts outside the refuge to the net intrinsic growth rate, $\bar\lambda$ and $R_2 = (1-\varepsilon)\lambda_2$, the contribution of hosts inside the refuge to $\bar\lambda$ (where $\bar\lambda = R_1 + R_2$). The shaded region demarcates parameter combinations that lead to local stability. For further details see text.

Fig. 2. The effect of decreasing hosts in the refuge, relative to exposed hosts, on the stability of the proportional refuge model. Host populations are denoted by solid lines and adult parasitoid populations by broken lines. For the examples shown, the mean host growth rate $\lambda = 2$, and there is an even division of hosts within and outside the refuge (i.e. $\varepsilon = 0.5$). (a) Low spatial variance in host λ (where $\lambda_1 = 2.1$ and $\lambda_2 = 1.9$, where 1 and 2 respectively denote exposed and refuge hosts) leads to highly stable interactions. (b) Moderate spatial variance in host λ ($\lambda_1 = 3$, $\lambda_1 = 1$) leads to stable limit cycles. (c) High spatial variance in host λ ($\lambda_1 = 3.8$, $\lambda_1 = 0.2$) generates chaotic dynamics. The amplitude of the oscillations tends to increase with decreasing host refuge growth rates.
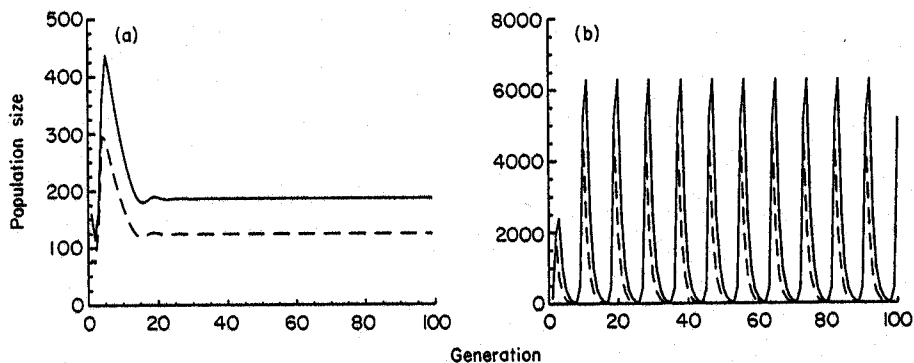

Fig. 3. Refuges with low host growth rates can stabilize host–parasitoid systems with very high overall host growth rates. (a) $\lambda_1 = 98.2$, $\lambda_2 = 1.8$, $\varepsilon = 0.5$; (b) $\lambda_1 = 98.2$, $\lambda_2 = 4.0$, $\varepsilon = 0.9$. The low-quality refuge in (a) stabilizes an otherwise unstable interaction, and an increase in the refuge growth rate can be destabilizing.

the assumption that hosts in the refuge completely escape parasitism. It further reinforces our theme that spatial heterogeneity in host growth rates can augment the stabilizing influence of spatial heterogeneity in parasitism, as long as parasitism is differentially inflicted on the hosts with relatively high growth rates.

Patches partially coupled by dispersal

The structure of the model given by equation 1a,b assumes that in each generation the population of both the host and the parasitoid are distributed among patches according to a deterministic rule. Recently, there has been increasing interest in the consequences of spatial heterogeneity in systems in which a number of populations are coupled by dispersal, but not so thoroughly that they can be considered to be one panmictic population (Comins, Hassell & May 1992; Hassell *et al.* 1991). In this section, we demonstrate that effects similar to those explored above for the proportional refuge model also emerge from models with partially coupled patches.

Consider a habitat with two patches, denoted 1 and 2, between which either or both the hosts and
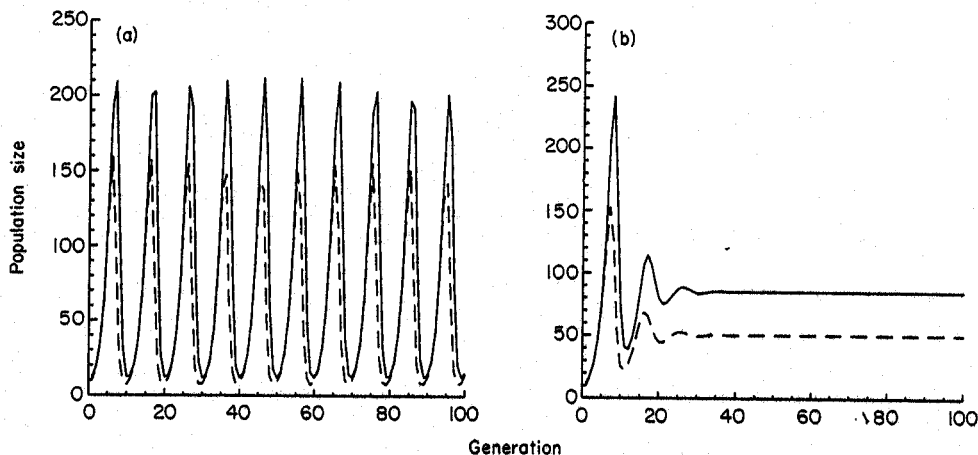
Fig. 4. The effect of heterogeneous host growth rates with incomplete refuges. Using model (1) in the text, let $n = 2$, $\alpha_1 = 0.6$, and thus $\alpha_2 = 0.4$. Following Hassell & May (1973), we assume that parasitoid aggregation in relation to host density is described by $\beta_i = q\alpha_i^\mu$, where q is a normalization constant and μ $(=5.4)$ describes the strength of aggregation. (a) $\lambda_1 = \lambda_2 = 2$, and $a_i = a_2 = 0.1$; the systems persists with large-amplitude oscillations. (b) $\lambda_1 = 3.5$, $\lambda_2 = 0.5$; the system rapidly moves to its stable equilibrium. Unlike the examples in previous figures, refuge hosts do not completely escape parasitism.

parasitoids can move. Patch i at the beginning of generation t has $N_i(t)$ hosts and $P_i(t)$ parasitoids. After parasitism, the number of unparasitized hosts remaining is $S_i(t) \leq N_i(t)$, and of these a fraction μ_h disperse to the other patch. The number of parasitoids that emerge from the parasitized hosts in patch i is given by $c_i[N_i(t) - S_i(t)]$, and of these a fraction μ_p disperse to the other patch and the remaining fraction $1 - \mu_h$ stay in their natal patch. The parasitoid recursion over a single generation (where we census following dispersal) can thus be described by

$$P_1(t + 1) = c_1(1 - \mu_p)[N_1(t) - S_1(t)] + c_2\mu_p[N_2(t) - S_2(t)] \qquad \text{eqn 6a}$$

$$P_2(t + 1) = c_1\mu_p[N_1(t) - S_1(t)] + c_2(1 - \mu_p)[N_2(t) - S_2(t)]. \qquad \text{eqn 6b}$$

A subtlety arises in developing the parallel recursion for the host. Let us say that a host born in patch i that escapes parasitism contributes λ_i to the next generation. The number of hosts found in each patch in generation $t + 1$ is then given by

$$N_1(t + 1) = \lambda_1 S_1(t)(1 - \mu_h) + \lambda_2 S_2(t)\mu_h \qquad \text{eqn 7a}$$

$$N_2(t + 1) = \lambda_1 S_1(t)\mu_h + \lambda_2 S_2(t)(1 - \mu_h). \qquad \text{eqn 7b}$$

This model structure assumes that the fitness of a host individual depends upon the patch it was born in, rather than the patch to which it disperses. This is a quite reasonable assumption in many circumstances; for instance, if adult fecundity depends upon the quantity or quality of resources available for larval growth.

An alternative model structure arises if one assumes that the fitness of a host individual depends upon the patch into which it disperses:

$$N_1(t + 1) = \lambda_1[S_1(t)(1 - \mu_h) + S_2(t)\mu_h] \qquad \text{eqn 8a}$$

$$N_2(t + 1) = \lambda_2[S_1(t)\mu_h + S_2(t)(1 - \mu_h)]. \qquad \text{eqn 8b}$$

This could occur if, for instance, habitats differ in the availability of the plant species required for larval growth, such that in a patch with low food-plant availability, adult hosts tend to have a low fecundity irrespective of whether that adult had dispersed there or not.

For simplicity, in the remainder of this paper we assume that the host population dynamics is described by equation 7a,b rather than equation 8a,b. Within each patch, we further assume that parasitism occurs at random, so that the number of hosts in patch i that escape parasitism is given by

$$S_i(t) = N_i(t)\exp(-a_iP_i(t)).$$

In general, it is impossible to find closed-form expressions for the equilibrial densities of the host and parasitoid in each patch, much less explicitly analyse the local stability conditions. We will therefore not attempt a full exploration of the dynamics of this model, but instead examine some special limiting cases that illustrate our general theme.

A REFUGE MODEL

Let $a_2 \to 0$ and $\mu_p \to 0$. Hence, no parasitoids disperse, and after a single generation no parasitoids remain in patch 2, so that $S_2(t) = N_2(t)$ and $P_2(t) = 0$. This limiting case is in a sense a generalization of the proportional refuge model considered in detail above, because the hosts in patch 2 are free from parasitism each generation; indeed, when $\mu_h = 0.5$, this model is equivalent to a proportional refuge with an equitable division of hosts between refuge and exposed classes. Now let

$$Q \equiv \lambda_1(1 - \mu_h) + \frac{\lambda_1 \lambda_2 \mu_h^2}{1 - (1 - \mu_h)\lambda_2}. \qquad \text{eqn 9}$$

The equilibrial densities of the parasitoid in patch 1 and hosts in both patches are:

$$P_1^* = \frac{\ln(Q)}{a_1}, \quad N_1^* = \frac{Q}{Q-1}\frac{\ln(Q)}{a_1},$$

$$N_2^* = \frac{\ln(Q)}{a_1(Q-1)}\frac{\lambda_1 \mu_h}{1 - (1 - \mu_h)\lambda_2}.$$

Two necessary and sufficient conditions for the existence of this point equilibrium are (i) that $\lambda_2(1 - \mu_h) < 1$, and (ii) that $Q > 1$. Condition 1 states that the refuge population by itself is not growing exponentially. Condition 2 is equivalent to stating that the host population in the absence of the parasitoid has an asymptotic net rate of increase greater than 1, and hence must hold for the host to persist on its own (see Appendix for proof).

These two conditions correspond in their interpretation to the necessary conditions for the existence of an equilibrium in the proportional refuge model (viz., as represented by the horizontal line and the line of slope −1 in Fig. 1). With partially coupled patches and with one patch a refuge from the parasitoid, it becomes more difficult for the parasitoid to regulate the host as the degree of coupling (measured by μ_h) becomes lower, and the host growth rate in the refuge becomes higher. If the refuge is a sink (i.e. $\lambda_2 < 1$), this necessary condition is always met; for $Q > 1$, this in turn requires that patch 2 be a source, with λ_1 sufficiently greater than 1.

The local stability of the above equilibrium is determined in the usual manner by evaluating the eigenvalues of a 3×3 Jacobian matrix. This procedure does not in the present instance simplify in a particularly useful manner. Numerical studies, however, show that refuges with low growth rates have a generically stabilizing effect in this model. Figure 5 shows the population fluctuation resulting from various levels of μ_h, the host dispersal rate. For the values of host growth rate used in this illustration, the system displays regular cycles for $\mu_h = 0.5$ (a case of the proportional refuge model). Because the refuge patch has a growth rate less than unity, it represents a sink for the host population. A modest decrease in the rate of host dispersal (from 0.5 to 0.2) if anything reduces the amplitudes of the population fluctuations. With further decreases in the rate of host dispersal (to 0.05, and then to 0.005), the system begins to show larger-amplitude oscillations, which eventually become so severe that the host–parasitoid interaction cannot persist. This figure thus emphasizes that even quite weak coupling between a low-quality sink population and source population can nonetheless stabilize the latter, provided that the sink population acts as a refuge from parasitism.

A typical example of results of our numerical studies of the effect of reduced host dispersal on stability is shown in Fig. 6. Figure 6a shows the range of host growth rates in the two patches consistent with stability for $\mu_h = 0.5$ (proportional refuge), and Fig. 6b shows the same for $\mu_h = 0.2$
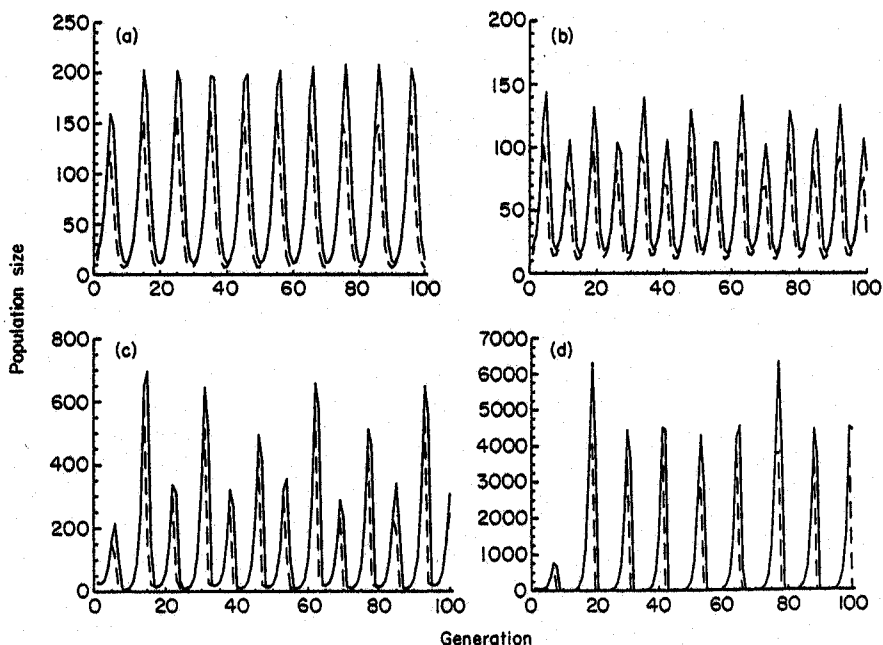

Fig. 5. Partially coupled patches. For each case shown, $\lambda_1 = 3$ (patch 1 is a source), $\lambda_2 = 0.75$ (patch 2 is a sink, and $a_1 = 0.1$, $a_2 = 0$. The parasitoids are thus restricted to patch 1, but the hosts can move between the two patches. (a) $\mu_h = 0.5$; a special case of the proportional refuge model, and the system shows limit cycle behaviour. (b) $\mu_h = 0.2$; the system still displays limit cycles. (c) $\mu_h = 0.05$ and (d) $\mu_h = 0.005$; in these cases the population fluctuations become increasingly severe with decreased coupling, but even weak coupling permits a sink refuge for the host, and thus allows the system to persist.
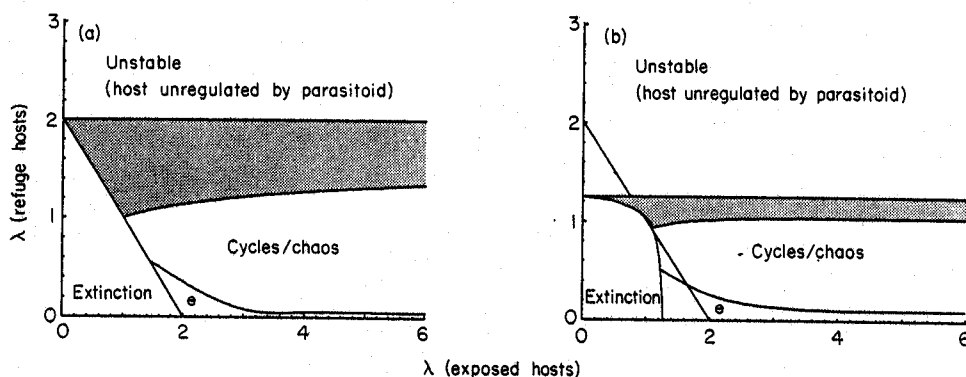
Fig. 6. The effect of spatial variance in host λ on stability in the partially coupled patch model. One patch is a refuge. The abscissa and ordinate are the host intrinsic growth rates outside and within the refuge, respectively. (a) Host migration rate of $\mu_h = 0.5$; this is a special case of the proportional refuge model. (b) Host migration rate of $\mu_h = 0.2$. Hatched regions denote local stability. The bowed line describes $Q > 1$. In the regions marked 'e', oscillations lead to extinction.

(partially coupled patches). The regions indicated by 'e' are those parameter combinations leading to extinction because of oscillatory instability. For both cases, if host growth rates are too low, the system crashes; if host growth rates are too high in the refuge, the parasitoid cannot regulate the host population. There is a range of moderate host growth rates inside the refuge for which the system is stable, more-or-less irrespective of the host growth rates outside the refuge. And finally, the system may persist (albeit with cycles or chaotic dynamics, as shown in Fig. 4) even if refuge hosts have quite low growth rates, and this effect becomes more pronounced when non-refuge hosts have high growth rates.

Our intuitive interpretation of the stabilizing effect of a partially coupled host refuge — a patch that 'in isolation' is a sink — runs along the following lines. Consider a sequence of generations during which host numbers are increasing because parasitism is low. Because of dispersal, host numbers in the sink increase together with those in the source. But parasitoid numbers are also increasing, and eventually the host population in the source will be depressed to low densities by increased parasitism. Yet this does not eliminate the host entirely, because of the build-up of host numbers in a patch where they are immune from parasitism. Even if every last host in the source is parasitized, some hosts will disperse from the sink; this supply of fresh hosts moderates the rate of decline in the parasitoid population, and does so for more generations if the decline of the sink population is slow. In effect, good years of recruitment in the host (i.e. when parasitoid numbers are low) get stored in the sink, which then acts later to buffer the rate of decline in both the host and parasitoid populations in the source patch.

SPATIAL VARIATION IN THE PARASITOID EMERGENCE PARAMETER, c_i

Certain kinds of spatial variation in parasitoid attack

rates eliminate the possibility of variation in host intrinsic growth rates influencing stability. If the parasitoids are very effective in attacking hosts in patch 1, so that to a reasonable approximation $a_1 \to \infty$ and hence $S_i(t) \to 0$, the model defined by equation 6a,b and equation 7a,b reduces to

$$N_1(t+1) = \lambda_2 \mu_h S_2(t) \qquad \text{eqn 10a}$$

$$N_2(t+1) = \lambda_2 (1 - \mu_h) S_2(t) \qquad \text{eqn 10b}$$

$$P_1(t+1) = c_1(1 - \mu_p)N_1(t) + c_2\mu_p(N_2(t) - S_2(t)) \qquad \text{eqn 10c}$$

$$P_2(t+1) = c_1\mu_p N_1(t) + c_2(1 - \mu_p)(N_2(t) - S_2(t)) \qquad \text{eqn 10d}$$

where $S_2(t) = N_2(t)\exp[-a_2 P_2(t)]$.

The persistence of the parasitoid in patch 1 depends on a continual flow of hosts from patch 2. When $\mu_h = 0$, the parasitoid in patch 1 becomes extinct after a single generation, and the host–parasitoid interaction in patch 2 is simply the unstable Nicholson-Bailey system. Patch 1 is manifestly a 'sink' for the host, because any host dispersing there is guaranteed to leave no descendants. Hence, spatial variation in the host intrinsic growth rates is irrelevant to stability. However, spatial variation in parasitoid emergence rates (c) may exist and this may influence the stability of the interaction, comparable to the effects explored in the refuge models.

Because the structure of the above limiting case incorporates substantial spatial variance in parasitism (with hosts in one patch experiencing much higher attack rates than hosts in the other patch, though the latter is not a refuge), it is not surprising that the two-patch system can be stable when the parasitoid emergence parameter is spatially invariant. Moreover, if both species disperse at slow rates, it is not surprising that the system is unstable; in the limit $\mu_h \to 0$, $\mu_p \to 0$, the model reduces to two uncoupled patches with unstable dynamics. Variation in c can influence the point at which one observes a transition from a stable to an unstable system. Figure 7 shows a numerical example. When the two patches are
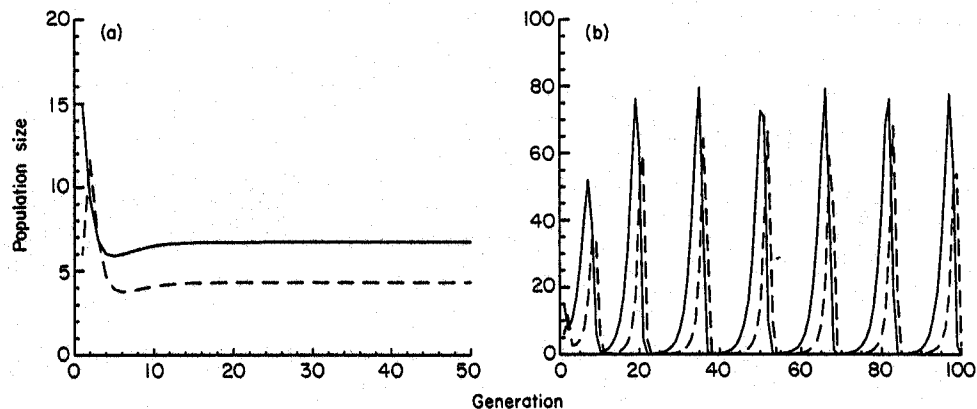
Fig. 7. Partially coupled patches. The attack rate in patch 1 is very high, so that all hosts are in effect attacked each generation, while $a_2 = 0.1$. The other demographic parameters are spatially homogeneous: $\lambda_1 = \lambda_2 = 2$, and $c = c_1 = 1$. (a) Strongly coupled patches ($\mu_h = \mu_p = 0.4$). (b) Weakly coupled patches ($\mu_h = \mu_p = 0.1$).

strongly coupled by dispersal (Fig. 7a, $\mu_h = \mu_p = 0.4$), the interaction is indeed quite stable. Reducing the rate of dispersal (Fig. 7b, $\mu_h = \mu_p = 0.1$) leads to a persistent, but strongly cyclic system. Further reductions in dispersal eventually preclude persistence altogether.

What is the effect of spatial variation in c? In Fig. 8a, we show how the dynamics of Fig. 7b are modified if we let $c_1 = 1$, $c_2 = 0.5$. This spatial variation in parasitoid demographic rates has the effect of enhancing the stabilizing influence of spatial variation in attack rates. In this example, variation in c_i is superimposed on variation in a_i. An interesting feature of the partially coupled patch model is that variation in c, if large enough, is sufficient to stabilize the host–parasitoid interaction. Figure 8b illustrates the dynamics of two coupled patches with equal host intrinsic growth rates ($=2$), equal attack rates ($=0.1$), and equal, low dispersal rates ($\mu_h = \mu_p = 0.1$). The only heterogeneity in the system is in parasitoid emergence rates ($c_1 = 1$, $c_2 = 0.04$), yet the system is quite stable.

We find this example to be particularly intriguing, because it represents a novel phenomenon emerging in the partially coupled patch model. When there is complete mixing each generation ($\mu_h = \mu_p = 0.5$), the model reduces to the original form explored by Hassell & May (1973), which is unstable with equal parasitism in each patch. In like manner, at low dispersal rates the system becomes unstable (two uncoupled Nicholson-Bailey patches). Our tentative interpretation of the stabilizing influence of variation in c_i is that it generates a 'source–sink' structure for the host and parasitoid populations, and that this is reflected in a kind of induced spatial variance in parasitism. Our numerical explorations have not uncovered a similar stabilizing influence of spatial variation in λ_i alone.

An understanding of the reasons for this difference, and indeed of the general role of environmental heterogeneity as a stabilizing factor in systems of partially coupled patches, awaits a more detailed treatment than we are attempting to provide here. However, the numerical examples presented above
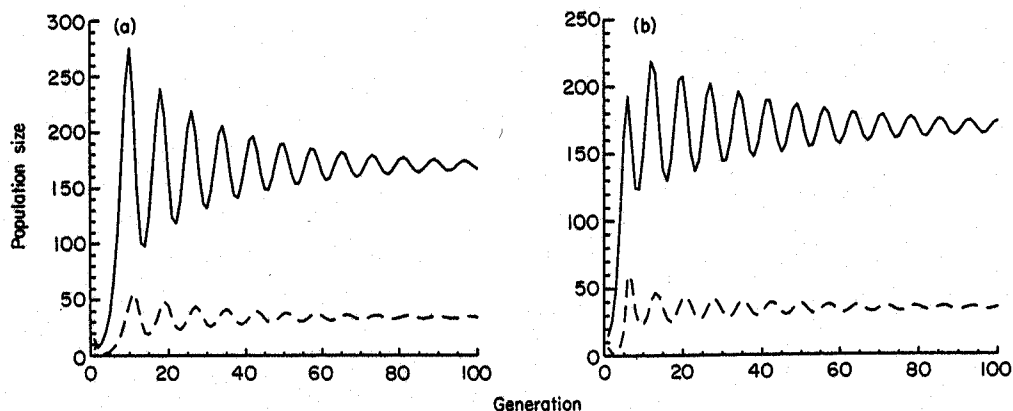

Fig. 8. Spatial heterogeneity in parasitoid emergence rates. The host parameters and dispersal rates are as in Fig. 7b. (a) $c_1 = 1$, $c_2 = 0.05$; introducing spatial heterogeneity in c dampens the oscillations shown in Fig. 7b. (b) Spatial homogeneity in all parameters except parasitoid emergence rates ($a_1 = a_2 = 0.1$, $\lambda_1 = \lambda_2 = 2$, $\mu_h = \mu_p = 0.1$, $c_1 = c_2 = 0.04$).

do suggest that the results of the proportional refuge model (encapsulated in Fig. 1) are not peculiar to the particular assumptions of that model, but may apply broadly to host—parasitoid interactions in patchy environments.

Discussion

COMPARISON WITH OVERLAPPING GENERATION SYSTEMS

It is useful to compare our results with theoretical investigations of the stabilizing influence of spatial heterogeneity in general predator—prey models. The continuous-time equivalent of the Nicholson-Bailey model is, of course, the classical Lotka-Volterra predator—prey model, which exhibits neutrally stable oscillations around its equilibrium (May 1974). Incorporating a proportional refuge into this model simply re-scales equilibrial densities without influencing the neutral stability of the system (Hassell 1978); the same is true with simultaneous heterogeneity in attack rates and prey intrinsic growth rates. Introducing spatial heterogeneity into partially coupled patches in this framework, however, does tend to stabilize the interaction. Holt (1984) explored a two-patch Lotka-Volterra model in which the prey were sedentary and predators moved between patches at constant, density-independent rates. If the two patches were homogeneous and dispersal rates uniform, the system was once again neutrally stable: dispersal by itself did not stabilize the system. However, introducing essentially any kind of difference between the patches — in prey intrinsic growth rates, predator mortality rates, attack rates, or asymmetries in predator dispersal — produced a locally stable interaction. Reminiscent of the generalized proportional refuge model discussed above, introducing partially coupled refuges into the Lotka-Volterra model can foster stability, and this effect is strongest when the intrinsic rate of increase of the prey in the refuge is low relative to that outside the refuge (Holt 1992).

One interpretation of the heterogeneous, two-patch, Lotka-Volterra model is that random predator dispersal in a spatially heterogeneous environment sets up a system of sources and sinks in the predator population; the time lag implicitly provided by dispersal in and out of sinks then tends to buffer fluctuations in the source populations (Holt 1984, Appendix II). McLaughlin & Roughgarden (1992) have recently examined a spatially continuous Lotka-Volterra model. They show that heterogeneity in prey growth rates and differential species mobility leads to stable population dynamics, and likewise interpret their results in terms of source—sink dynamics. The observation that spatial heterogeneity in prey growth rates alone can lead to stability is one intriguing difference between these continuous-time

systems and the partially coupled host—parasitoid system, where it appears that spatial variation in the host growth rate alone does not as a rule stabilize the interaction.

IMPLICATIONS FOR EMPIRICAL STUDIES

Theoretical work on the effects of heterogeneity in attack rates on host—parasitoid dynamics has stimulated considerable fieldwork on characterizing the rate of parasitism as a function of host density (e.g. Walde & Murdoch 1988), culminating recently in an assessment for published field data of the relative stabilizing potentials of density-dependent vs. density-independent components of parasitism (Hassell *et al.* 1991; Pacala & Hassell 1991). A qualitative, intuitively sensible conclusion of the work reported above is that the stabilizing potential of host refuges is enhanced if protected hosts have relatively low intrinsic growth rates compared to exposed hosts. This suggests that a fruitful avenue for future empirical investigation will be to document the patterns of covariance between attack rates and host intrinsic growth rates. The partially coupled patch model points to a similar importance for heterogeneity in parasitoid demographic rates. A full understanding of the role of heterogeneity in stabilizing host—parasitoid interactions will ultimately require a more refined understanding of how spatial patterns in attack rates and in basic demographic parameters interrelate than is yet available for any natural host—parasitoid system.

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Appendix

In the absence of the parasitoid, the dynamics of the host population are described by a model of geometric growth in two patches coupled by dispersal:

$$\begin{pmatrix} N_1(t+1) \\ N_2(t+1) \end{pmatrix} = \begin{pmatrix} \lambda_1(1-\mu_h) & \lambda_2\mu_h \\ \lambda_1\mu_h & \lambda_1(1-\mu_h) \end{pmatrix}$$
$$\begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix}. \qquad \text{eqn A1}$$

Because the entries in the transition matrix are constant, one knows, as with almost any transition matrix model (Caswell 1989), (i) that the host population eventually settles into a stable patch distribution, with a fixed proportion of hosts found in each patch, and (ii) that the population in this stable distribution grows at a constant per capita rate $\tilde{\lambda}$,

where $\tilde{\lambda}$ is the dominant eigenvalue of the above matrix. This asymptotic net growth rate is

$$\tilde{\lambda} = \frac{(\lambda_1 + \lambda_2)(1-\mu_h) + \sqrt{(\lambda_1 + \lambda_2)^2 - 4\lambda_1\lambda_2(1-2\mu_h)}}{2}$$
$$\text{eqn A2}$$

For the host population to persist without parasitism requires $\tilde{\lambda} > 1$. Manipulating the above expression shows that $\tilde{\lambda} > 1$ implies $Q > 1$ and, conversely, that $Q > 1$ implies $\tilde{\lambda} > 1$. Hence, $Q > 1$ in the text can be interpreted as a statement of a necessary condition for persistence of the host, and hence of the host—parasitoid interaction.

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