



Migration Frequency and the Persistence of Host-Parasitoid Interactions

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This paper analyses the effect of migration frequency on the stability and persistence of a host-parasitoid system in a two-patch environment. The hosts and parasitoids are allowed to move from one patch to the other a certain number of times within a generation. When this number is low, i.e. when the time-scales associated with migration and demography are of the same order, host-parasitoid interactions are usually not persistent. When this number is high, however, persistence is more likely. Moreover, in this situation, aggregation methods can be used to simplify the proposed initial model into an aggregated model describing the dynamics of both the total host and parasitoid populations. Analysis of the aggregated model shows that the system reaches a stable steady state for some regions of the parameter domain. Persistence occurs when the movement of the parasitoids is asymmetrical, i.e. they move preferentially to one of the two patches. We show that the growth rate of the host population is a key parameter in determining which migration strategies of the parasitoids lead to persistent host-parasitoid interactions.

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Introduction

Many theoretical studies of the dynamics of spatially distributed host-parasitoid systems have been conducted (for a review see Hassell & Wilson, 1997; Hassell, 2000a, b). A point of particular interest is whether non-persistent host-parasitoid interactions become persistent when they are considered in a spatial context. The example of the Nicholson–Bailey model is very demonstrative. This model does not allow for persistent host-parasitoid interactions (the number of hosts and parasitoids show diverging oscillations over time, leading to extinction). In a patchy environment, however, if the Nicholson–Bailey model acts on every patch and dispersal

occurs between the patches, host-parasitoid interactions may turn out to be persistent. The dispersal between the patches is global when the hosts and the parasitoids are redistributed among all the patches in each generation according to a given distribution (e.g. Hassell & May, 1973, 1974; Hassell *et al.*, 1991b). In this case, the persistence of host-parasitoid interactions is assured if the distribution for the parasitoids is sufficiently heterogeneous. More precisely, the square of the coefficient of variation of this distribution must be more than 1 (the ‘ $CV^2 > 1$ ’ rule, Pacala *et al.*, 1990; Hassell *et al.*, 1991b; Taylor, 1993). The dispersal between the patches is local when the hosts and the parasitoids move to adjacent patches in each generation. In this case, host-parasitoid interactions persist provided the number of patches is

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large enough (Hassell *et al.*, 1991a; Comins *et al.*, 1992; Rohani & Miramontes, 1995). In addition, the spatial dynamics of the system shows a variety of patterns (spirals, spatial chaos, crystal lattice), depending on the proportion of hosts and parasitoids that move to adjacent patches. Such complex patterns arising from simple rules have opened fresh perspectives in understanding some of the complexity of natural systems (Bascompte & Solé, 1995), particularly as they have turned out to be fairly realistic (Rohani *et al.*, 1997). The time hosts and parasitoids spend traveling from one patch to another also appears to have stabilizing effects, regardless of whether dispersal is global (Hassell & May, 1974; Weisser & Hassell, 1996) or local (Weisser *et al.*, 1997). Other potentially stabilizing factors apart from dispersal have also been investigated: spatial heterogeneity in the growth rates of the hosts (Reeve, 1988, 1990; Holt & Hassell, 1993), spatial heterogeneity in the initial number of hosts and parasitoids (Adler, 1993), within-generation redistribution of the parasitoids (Rohani *et al.*, 1994), spatial heterogeneity in the carrying capacity of the hosts (Allen *et al.*, 2001), and demographic stochasticity (Keeling *et al.*, 2002). These studies have been extended to more complex systems involving two parasitoids and one host (Hassell *et al.*, 1994), two hosts and one parasitoid (Comins & Hassell, 1996; Bonsall & Hassell, 2000), and host, parasitoid, and hyperparasitoid (Comins & Hassell, 1996). Another extension involves introducing evolutionarily stable migration strategies (ESS) into the models and investigating the consequences for ecological stability and persistence (van Baalen & Sabelis, 1993, 1999; Savill *et al.*, 1997; Schreiber *et al.*, 2000). The potentially destabilizing effect of dispersal has also been studied: persistent host-parasitoid interactions in each patch may cease to be persistent when there is dispersal among patches (Reeve, 1988; Rohani *et al.*, 1996; Rohani & Ruxton, 1999a, 1999b).

Most parasitoids are winged adults (e.g. wasps, flies, midges, see Godfray, 1994) as are some hosts (e.g. butterflies, flies). This enables them to move frequently from one patch to another. In a butterfly-wasp system, for example, the adult butterflies disperse and oviposit, and then the wasps disperse and attack the

caterpillars. There are several experimental studies indicating that adult parasitoids make several flights from patch to patch within a generation (Briggs & Latto, 2000; Tenhumberg *et al.*, 2001) and both parasitoids and hosts are able to fly long distances (Byrne, 1999; Altizer *et al.*, 2000; Hastings, 2000). The objective of the present paper is to analyse the conditions for persistence of host-parasitoid interactions with respect to migration frequency. We first present a general host-parasitoid model in a heterogeneous environment. The spatial heterogeneity is described by means of two patches. In each of them, changes in the local host and parasitoid densities follow either the Nicholson-Bailey or the May (1978) models. Host and parasitoid individuals can move from one patch to the other a certain number of times within a generation. When this number is high, i.e. when the time-scales associated with migration and demography are markedly different from each other, we take advantage of the two different time-scales to reduce the system. The study of the reduced system is carried out and the dynamics of the reduced and complete systems are compared. The model is finally extended to the situation where the migration of the parasitoids depends on host density.

Presentation and Reduction of the Model

The classical structure of a model describing the dynamics of a host-parasitoid system reads as follows:

$$\begin{aligned} N_{t+1} &= \lambda N_t f(P_t), \\ P_{t+1} &= c N_t [1 - f(P_t)]. \end{aligned} \quad (1)$$

The two state variables are the host population N_t and the parasitoid population P_t at generation t . Parameter λ is the growth rate of the host population. It is assumed that in the absence of the parasitoid, the host population grows, which implies that $\lambda > 1$. Parameter c is the average number of parasitoids that emerge from a single infected host. The function $f(P_t)$ is the proportion of hosts that are not infected between t and $t+1$. It is reasonable to assume that this proportion decreases with increasing values of P_t , that no host is infected when there is no

parasitoid and that all hosts are infected when the number of parasitoids tends to infinity, i.e.

$$\begin{aligned} f'(P_t) &< 0, \\ f(0) &= 1, \\ \lim_{P_t \rightarrow \infty} f(P_t) &= 0. \end{aligned} \tag{2}$$

More general host-parasitoid models allow the function f to depend on both N_t and P_t , i.e. $f(N_t, P_t)$.

A particular form of function f , $f(P_t) = \exp(-aP_t)$, corresponds to the classical Nicholson-Bailey model, with the positive parameter a representing the searching efficiency of the parasitoids. When $f(P_t) = (1 + aP_t/b)^{-b}$, the system (1) is the model of May (1978), b being a positive parameter defining the degree of aggregation of parasitoids. The Nicholson-Bailey model can be considered a limit case, where $b \rightarrow \infty$, of May's model. The Nicholson-Bailey model has two fixed points: a trivial one, the origin (0,0), and a non-trivial one, which is positive when $\lambda > 1$. It can be shown that the two fixed points are unstable for all parameter values (see, e.g. Edelstein-Keshet, 1988). Consequently, this model does not predict persistent host-parasitoid interactions. May's model also has two fixed points, the origin and a non-trivial one, which is positive when $\lambda > 1$. In this case, May (1978) showed that this fixed point is stable when $b < 1$. Otherwise, this model also predicts non-persistent host-parasitoid interactions (except immediately outside the domain of stability, where the system shows fluctuations ensuring persistence).

A GENERAL HOST-PARASITOID MODEL IN A TWO-PATCH ENVIRONMENT

We will now consider a system with two spatial patches. We define four state variables,

the host and the parasitoid population densities on each patch at generation t , denoted $(N_{1,t}, N_{2,t})$ and $(P_{1,t}, P_{2,t})$ respectively, with the first index indicating the patch number. We denote the population vector $V_t = (N_{1,t}, N_{2,t}, P_{1,t}, P_{2,t})$.

In the time elapsed between t and $t+1$, two processes are involved in the model: the migration of hosts and parasitoids between the two patches and the demography on each patch.

Let us describe first the migration part of the model. We assume constant migration proportions. We denote by f_{ij} the proportion of hosts migrating from patch i to patch j and by g_{ij} the corresponding proportion for the parasitoids. Then we define the migration matrix M as follows:

$$M = \begin{pmatrix} 1 - f_{12} & f_{21} & 0 & 0 \\ f_{12} & 1 - f_{21} & 0 & 0 \\ 0 & 0 & 1 - g_{12} & g_{21} \\ 0 & 0 & g_{12} & 1 - g_{21} \end{pmatrix}. \tag{3}$$

Secondly, we propose the general host-parasitoid model (1) for describing the demography on each patch:

$$\begin{aligned} N_{1,t+1} &= \lambda_1 N'_{1,t} f(P'_{1,t}), \\ N_{2,t+1} &= \lambda_2 N'_{2,t} f(P'_{2,t}), \\ P_{1,t+1} &= c N'_{1,t} [1 - f(P'_{1,t})], \\ P_{2,t+1} &= c N'_{2,t} [1 - f(P'_{2,t})], \end{aligned} \tag{4}$$

where $V'_t = (N'_{1,t}, N'_{2,t}, P'_{1,t}, P'_{2,t})$ denotes the population densities after migration. Parameters $\lambda_1 > 1$ and $\lambda_2 > 1$ are the host growth rates on each patch. We assume a patch-independent value of parameter c and of function f . We define the following density-dependent demography matrix:

$$D(V'_t) = \begin{pmatrix} \lambda_1 f(P'_{1,t}) & 0 & 0 & 0 \\ 0 & \lambda_2 f(P'_{2,t}) & 0 & 0 \\ 0 & 0 & c[1 - f(P'_{1,t})] \frac{N'_{1,t}}{P'_{1,t}} & 0 \\ 0 & 0 & 0 & c[1 - f(P'_{2,t})] \frac{N'_{1,t}}{P'_{2,t}} \end{pmatrix}. \tag{5}$$

Then, eqns (4) can be rewritten as

$$V_{t+1} = D(V'_t)V'_t. \quad (6)$$

Finally, the complete model combines migration and demography as follows:

$$V_{t+1} = D(M^k V_t)M^k V_t, \quad (7)$$

where k is an integer approximately describing the ratio between the time-scales associated with migration and demography (here we suppose that this ratio is the same for the parasitoids and the hosts). It is assumed that between t and $t+1$, the migration process occurs k times whereas the demography acts only once. In other words, it is assumed that before the demography starts, the hosts and the parasitoids explore the environment by a series of k migrations and then settle down.

When $k=1$, the model consists of one migration phase and one demography phase for each generation, which is an assumption made in most models with local dispersal. When $k \gg 1$, it is assumed that the migration process is very fast in comparison to the demography, which is the implicit assumption made in the models with global dispersal. We shall see in the next section that in the case $k \gg 1$, the complete model (7) can be simplified into a reduced model (the aggregated model) the properties of which are easier to analyse. We will also see that this reduced model is a good approximation of the complete model, even for moderate values of k .

THE AGGREGATED MODEL

The existence of two different time-scales allows us to apply aggregation methods. The idea is to consider the events occurring at the fastest scale as being instantaneous compared to the slower events. This means that fewer variables or parameters are needed to describe the evolution of the system. To carry out aggregation we choose a global variable (sometimes also called a macrovariable) for each subsystem and build up a reduced system for these global variables.

Aggregation methods were initially applied to ecology (Iwasa *et al.*, 1987). If the consistency between the dynamics of the global variables in

the original and the reduced (or aggregated) system is only approximate, it is referred to as an approximate aggregation (Iwasa *et al.*, 1989). Approximate aggregation has been developed extensively (Auger & Poggiale, 1998; Bravo de la Parra & Sánchez, 1998; Bravo de la Parra *et al.*, 1999; Sanz & Bravo de la Parra, 1999; Auger & Bravo de la Parra, 2000) for systems with two time-scales. This kind of aggregation has been used to study both continuous (Auger & Poggiale, 1996; Auger & Pontier, 1998; Bernstein *et al.*, 1999; Auger *et al.*, 2000a, b) and discrete (Charles *et al.*, 1998, 2000; Chaumot *et al.*, in press) models in ecology.

We now proceed to construct the aggregated model. In our case, the global variables are the total densities of the host and parasitoid populations N_t and P_t :

$$N_t = N_{1,t} + N_{2,t}, \quad (8)$$

$$P_t = P_{1,t} + P_{2,t}.$$

There are two properties of the fast part of the model, the migration process, which makes possible finding a reduced system for the chosen global variables: N_t and P_t are constants of motion, and, for fixed values of N_t and P_t , the state variables $N_{1,t}$, $N_{2,t}$, $P_{1,t}$ and $P_{2,t}$ reach an equilibrium. The first step in constructing the aggregated system consists in calculating this fast equilibrium in terms of the global variables. Then, assuming that between time t and time $t+1$ the fast system has reached its equilibrium, we can substitute the equilibrium values for the state variables. Finally, adding up the two host and the two parasitoid equations of the complete model (7) we obtain the following aggregated model (see Appendix A for the details of the calculation):

$$\begin{aligned} N_{t+1} &= N_t [\lambda_1 v_1^* f(\mu_1^* P_t) + \lambda_2 v_2^* f(\mu_2^* P_t)], \\ P_{t+1} &= c N_t [1 - v_1^* f(\mu_1^* P_t) - v_2^* f(\mu_2^* P_t)], \end{aligned} \quad (9)$$

where

$$v_1^* = \frac{f_{21}}{f_{12} + f_{21}}, \quad v_2^* = \frac{f_{12}}{f_{12} + f_{21}}, \quad (10)$$

$$\mu_1^* = \frac{g_{21}}{g_{12} + g_{21}}, \quad \mu_2^* = \frac{g_{12}}{g_{12} + g_{21}}. \quad (11)$$

In the particular case, $\lambda_1 = \lambda_2 = \lambda$, $v_1^* = v_2^* = 1/2$ and $\mu_1^* = \mu_2^* = 1/2$ the aggregated model simplifies to

$$\begin{aligned} N_{t+1} &= \lambda N_t f(P_t/2), \\ P_{t+1} &= c N_t [1 - f(P_t/2)] \end{aligned} \tag{12}$$

which is the general model (1) with $P_t/2$ instead of P_t . Model (12) is identical to the local model (4) on each patch and consequently exhibits the same dynamics. This means that when the local model is unstable on both patches, the aggregated model shows the same behavior, which is the case of the Nicholson–Bailey model.

A priori, it would be expected that in the case of frequent migrations, a system of two connected patches would merge as a single patch, so that the aggregated model would show the same dynamics as each of the local models. However, we shall now show that, for some values of the parameters, the aggregated model exhibits qualitatively different dynamics from the local models. In particular, we shall see that, although the local host-parasitoid systems are unstable, the aggregated model can have a fixed point that is asymptotically stable.

The analysis of the aggregated model (9) is carried out in Appendix B. In the case $\lambda_1 = \lambda_2 = \lambda$, there is one positive fixed point (N^*, P^*) defined by

$$\begin{aligned} v_1^* f(\mu_1^* P^*) + v_2^* f(\mu_2^* P^*) &= 1/\lambda, \\ N^* &= \frac{1}{c} \frac{\lambda}{\lambda - 1} P^*. \end{aligned} \tag{13}$$

This positive fixed point is stable when:

$$\begin{aligned} \text{Det}(J^*) &< 1 \\ \text{Det}(J^*) &= -[v_1^* \mu_1^* f'(\mu_1^* P^*) + v_2^* \mu_2^* f'(\mu_2^* P^*)] P^*. \end{aligned} \tag{14}$$

When condition (14) holds, the positive fixed point is stable and the system shows damped oscillations of N_t and P_t : host-parasitoid interactions are persistent. Henceforth we call domain of stability of the model the regions of the parameters domain where the condition of stability (14) holds. When $\text{Det}(J^*) > 1$, the positive fixed point is locally unstable and the

system shows amplified oscillations of N_t and P_t . The oscillations may not amplify indefinitely, but approach an invariant curve, leading to persistent host-parasitoid interactions. Consequently, the persistence of host-parasitoid interactions is not restricted to the domain of stability. Henceforth we call the regions of the parameters domain where persistence is assured the domain of persistence of the model. In the following sections, we will focus on the domain of stability, but we will also explore the domain of persistence.

HOST-DENSITY DEPENDENT MIGRATION OF THE PARASITIDS

We now extend the model to the situation where parasitoid migration depends on host density. More precisely, we assume that the proportion of parasitoids migrating from patch i to patch j , g_{ij} , decreases with increasing number of hosts in patch i , $N_{i,t}$. Here we choose

$$\begin{aligned} g_{12}(N_{1,t}) &= \frac{1}{1 + N_{1,t}^\alpha}, \\ g_{21}(N_{2,t}) &= \frac{1}{1 + N_{2,t}^\alpha}. \end{aligned} \tag{15}$$

The value of g_{ij} ranges from 1, for small values of $N_{i,t}$, to 0 for high values, and the function is steeper for high values of the parameter $\alpha > 0$.

The complete model is still given by eqn (7), but the migration matrix is now a function of the population vector, i.e. $M(V_t)$. Similarly, the aggregated model is still given by eqns (9), but the equilibrium patch frequencies for the parasitoids after migration are now functions of total host density, i.e. $\mu_1^*(N_t)$ and $\mu_2^*(N_t)$. Equations (10) still holds, whereas eqns (11) becomes (see Appendix C)

$$\begin{aligned} \mu_1^*(N_t) &= \frac{1 + (v_1^* N_t)^\alpha}{2 + (v_1^{*\alpha} + v_2^{*\alpha}) N_t^\alpha}, \\ \mu_2^*(N_t) &= \frac{1 + (v_2^* N_t)^\alpha}{2 + (v_1^{*\alpha} + v_2^{*\alpha}) N_t^\alpha}. \end{aligned} \tag{16}$$

For small values of host density, N_t , μ_1^* and μ_2^* are close to 1/2: the parasitoids show no preference for a particular patch. For

high values of N_t , $\mu_1^* \rightarrow v_1^{*\alpha}/(v_1^{*\alpha} + v_2^{*\alpha})$ and $\mu_2^* \rightarrow v_2^{*\alpha}/(v_1^{*\alpha} + v_2^{*\alpha})$. In the case $\alpha = 1$, $\mu_1^* \rightarrow v_1^*$ and $\mu_2^* \rightarrow v_2^*$: the distribution of the parasitoids is similar to that of the hosts. When $\alpha > 1$, the parasitoids are more aggregated than the hosts. The parameter α controls parasitoid aggregation at high host density, and has similarities with the parasite aggregation index defined in Hassell and May (1973). Here, however, the parasitoid distribution also depends on host density.

In the case $\lambda_1 = \lambda_2 = \lambda$, the aggregated model still has one positive fixed point (N^*, P^*) defined by eqns (13) with $\mu_1^*(N^*)$ and $\mu_2^*(N^*)$. However, it was not possible to derive a condition as simple as eqn (14) for the stability of this fixed point. This stability was therefore determined by calculating the trace and determinant of the Jacobian matrix.

Results

DOMAIN OF STABILITY OF HOST-PARASITOID INTERACTIONS IN THE COMPLETE MODEL

Extensive numerical stability analyses and simulations of the complete model show that increasing the value of k (the number of migrations performed by the hosts and parasitoids within a generation) generally promotes the stability of the host-parasitoid interactions. For example, for all sets of parameters $\{f_{12}, f_{21}, g_{12}, g_{21}\}$ with f_{12}, f_{21}, g_{12} and g_{21} taken in $\{0.1, 0.2, \dots, 0.9\}$, we found 156 sets that lead to a stable positive fixed point of the model with

$k = 1$ and 210 sets with $k = 5$ in the case $\lambda_1 = \lambda_2 = 2$, 40 sets with $k = 1$ and 102 sets with $k = 5$ in the case $\lambda_1 = \lambda_2 = 5$. These results were obtained with the Nicholson–Bailey function $f(P_t) = \exp(-aP_t)$ for the proportion of non-parasitized hosts, $a = 0.05$ and $c = 1$, but changing the values of a and c has no effect on the stability. For an illustrative particular case where $g_{12} = 0.1$ and $g_{21} = 0.8$ (proportions of the parasitoids migrating), Fig. 1 shows the values of f_{12} and f_{21} (proportions of the hosts migrating) that assure the stability of the interactions when $k = 1$ [Fig. 1(a)] and $k = 5$ [Fig. 1(b)]. Although the stability is possible with $k = 1$, it is more likely with $k = 5$.

SIMULATED DYNAMICS OF THE COMPLETE MODEL AND THE AGGREGATED MODEL

In the case of persistent host-parasitoid interactions, the dynamics of the aggregated model in the (N, P) space either shows spirals [Fig. 2(a) left], i.e. damped oscillations of N_t and P_t , or approaches an invariant curve [Fig. 2(a) right]. The aggregated model exhibits the same qualitative behavior as the complete model even for moderate values of k [Fig. 2(b)]. When k is large enough, the dynamics of the aggregated and complete models are indistinguishable [Fig. 2(a) and Fig. 2(c)].

We now focus on the dynamics of the aggregated model for three reasons: simulations show that the aggregated model provides a good approximation of the complete model even for

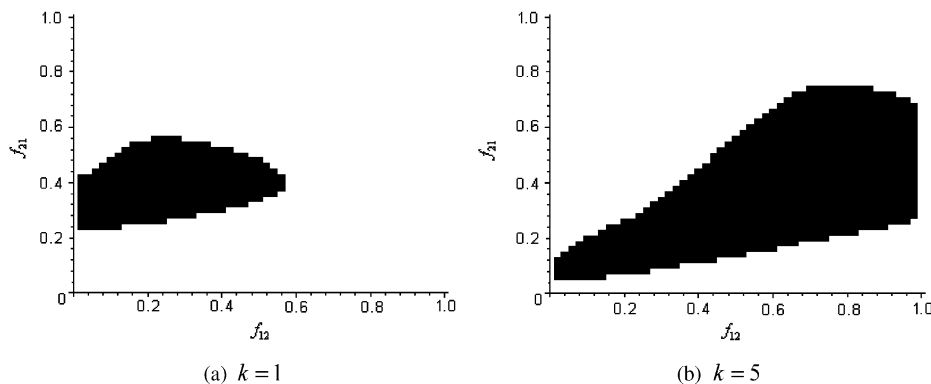


FIG. 1. Domain of stability (in black) of the complete model with Nicholson–Bailey local demography for different values of f_{ij} (proportion of hosts migrating from patch i to j) and k (number of migrations performed in each generation by hosts and parasitoids). The parameters are $\lambda_1 = \lambda_2 = 2$, $a = 0.05$, $c = 1$, $g_{12} = 0.1$, $g_{21} = 0.8$. The boundaries are obtained by simulation.

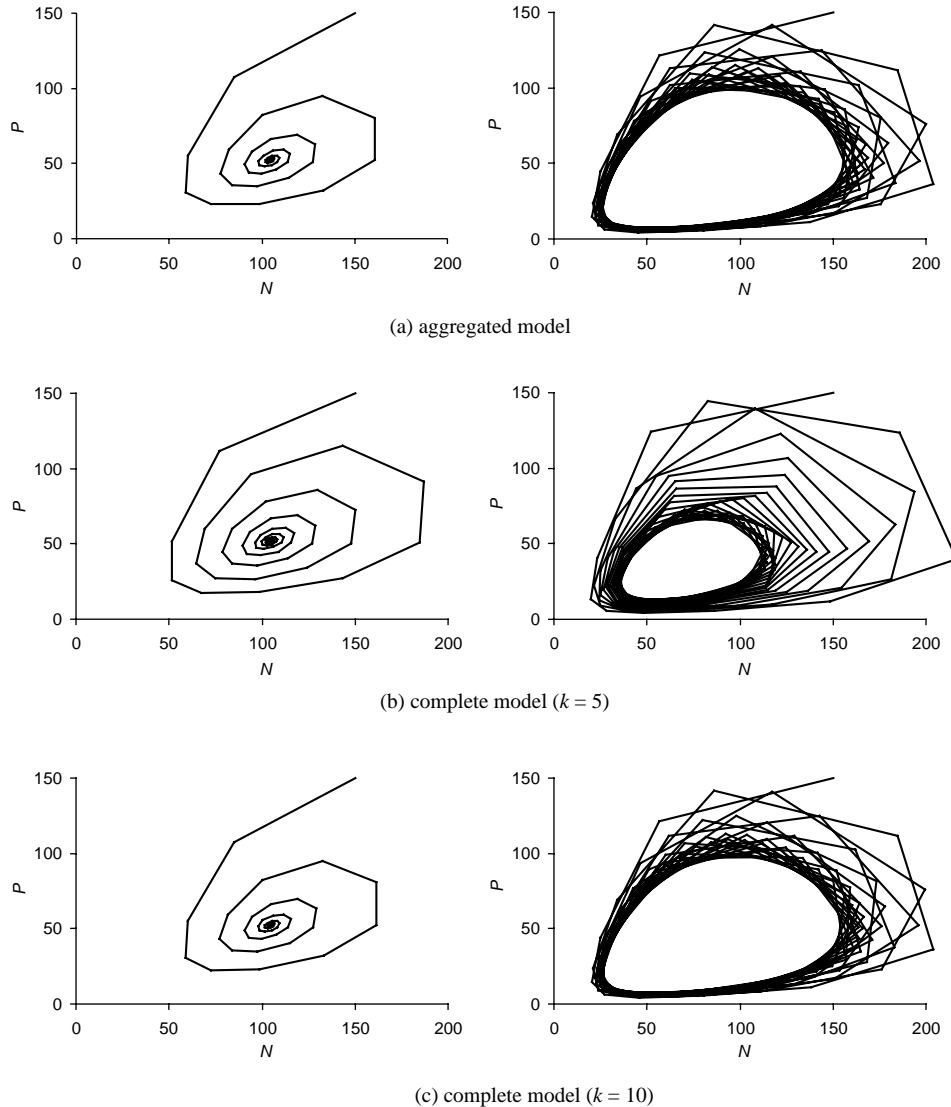


FIG. 2. Evolution of the global variables N (host density) and P (parasitoid density) in the aggregated model and in the complete model with Nicholson–Bailey local demography. The parameters are $\lambda_1 = \lambda_2 = \lambda = 2$, $a = 0.05$, $c = 1$, $f_{12} = 0.3$, $f_{21} = 0.2$ ($v_1^* = 0.4$, $v_2^* = 0.6$) and $g_{12} = 0.05$, $g_{21} = 0.45$ ($\mu_1^* = 0.9$, $\mu_2^* = 0.1$) (left side) or $g_{12} = 0.45$, $g_{21} = 0.05$ ($\mu_1^* = 0.1$, $\mu_2^* = 0.9$) (right side). The initial conditions are $N_{1,0} = N_{2,0} = P_{1,0} = P_{2,0} = 75$ in the complete model and $N_0 = P_0 = 150$ in the aggregated model.

moderate values of k ; numerical stability analyses of the complete model show that the stability of host-parasitoid interactions is more likely when k is high, i.e. when the complete model can be approximated by the aggregated model; the aggregated model is more tractable analytically than the complete model.

DOMAIN OF STABILITY OF HOST-PARASITOID INTERACTIONS IN THE AGGREGATED MODEL

If we use the Nicholson–Bailey function for the proportion of non-parasitized hosts, i.e.

$f(P_t) = \exp(-aP_t)$, eqns (13), which defines the positive fixed point (N^*, P^*) of the aggregated model, and eqn (14), which states the condition of stability of this point, become

$$v_1^* \exp(-a\mu_1^* P^*) + v_2^* \exp(-a\mu_2^* P^*) = 1/\lambda, \tag{17}$$

$$N^* = \frac{1}{c} \frac{\lambda}{\lambda - 1} P^*,$$

$$[v_1^* \mu_1^* \exp(-a\mu_1^* P^*) + v_2^* \mu_2^* \exp(-a\mu_2^* P^*)] a \frac{\lambda^2}{\lambda - 1} P^* < 1. \tag{18}$$

In this case, the aggregated model is equivalent to model D in Hassell & May (1973) except that now the host and parasitoid distributions (v_i^* and μ_i^*) are related to individual properties (the migrations parameters f_{ij} and g_{ij}) by eqns (10) and (11).

The first equation in eqn (17) and the definition of $v_2^* = 1 - v_1^*$ and $\mu_2^* = 1 - \mu_1^*$ show that eqn (18) actually depends just on three parameters: λ , v_1^* and μ_1^* . We have determined numerically the values of these parameters for which the condition of stability (18) holds. For four values of parameter λ , Fig. 3 shows the regions of the domain of the parameters v_1^* and μ_1^* that assure the stability of the fixed point given by eqns (17) and, therefore, the persistence of the host-parasitoid interactions.

For small values of the growth rate of the host population, λ , the persistence of the host-parasitoid interactions occurs for either high values of v_1^* and small values of μ_1^* or small values of v_1^* and high values of μ_1^* [Fig. 3(a)].

This means that the proportion of the migrant parasitoids that migrate to patch 1, μ_1^* , is negatively correlated to the proportion of the migrant hosts that migrate to patch 1, v_1^* (exactly the same can be said for patch 2).

Conversely, for high values of λ , the persistence of the host-parasitoid interactions occurs for either small values of v_1^* and μ_1^* or high values of v_1^* and μ_1^* [Fig. 3(d)]. The proportion of the migrant parasitoids that migrate to patch 1 is positively correlated to the proportion of the migrant hosts that migrate to patch 1.

For intermediate values of λ , the persistence of the host-parasitoid interactions occurs for intermediate values of v_1^* and either high values or small values of μ_1^* [Fig. 3(b) and (c)]. The proportion of the migrant parasitoids that migrate to patch 1 is not correlated to the proportion of the migrant hosts that migrate to patch 1.

Using May's model as local demography, i.e. $f(P_i) = (1 + aP_i/b)^{-b}$, eqns (13) and (14)

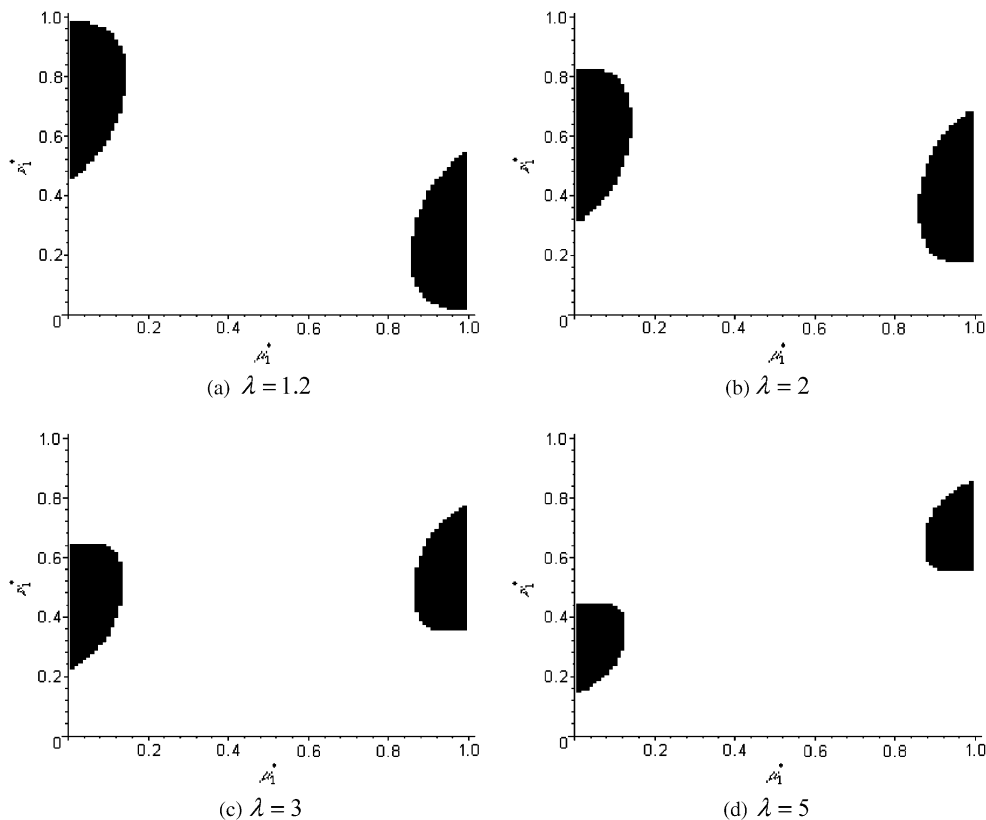


FIG. 3. Domain of stability (in black) of the aggregated model with Nicholson–Bailey local demography for different values of μ_1^* (proportion of migrant parasitoids migrating to patch 1), v_1^* (proportion of migrant hosts migrating to patch 1) and λ (growth rate of the host population). The boundaries are obtained by simulation.

become

$$v_1^*(1 + a\mu_1^*P^*/b)^{-b} + v_2^*(1 + a\mu_2^*P^*/b)^{-b} = 1/\lambda, \tag{19}$$

$$N^* = \frac{1}{c} \frac{\lambda}{\lambda - 1} P^*,$$

$$\left[v_1^*\mu_1^*(1 + a\mu_1^*P^*/b)^{-b-1} + v_2^*\mu_2^*(1 + a\mu_1^*P^*/b)^{-b-1} \right] \tag{20}$$

$$a \frac{\lambda^2}{\lambda - 1} P^* < 1.$$

Equation (20) now depends on four parameters: λ , v_1^* , μ_1^* and b . We have determined numerically the values of these parameters for which the condition of stability (20) holds. For $b < 1$, the system is stable whatever the values of the parameters λ , v_1^* and μ_1^* . For high values of b ($b > 10$), we get the same domains of stability as in Fig. 3. For $b = 1.5$ and for four values of the parameter λ , Fig. 4 shows the regions of the domain of the parameters v_1^* and μ_1^* that assure the stability of the fixed point given by eqns (19).

Figure 4 shows more clearly than Fig. 3 that the domain of stability of the aggregated model shrinks with increasing values of λ , i.e. stability of host-parasitoid interactions is promoted by small values of the growth rate of the host population.

DOMAIN OF PERSISTENCE OF HOST-PARASITOID INTERACTIONS IN THE AGGREGATED MODEL

We have explored the values of the parameters for which the condition of stability (18) does not hold, but the system eventually shows oscillations assuring the persistence of the host-parasitoid interactions (gray areas in Fig. 5).

DENSITY OF HOSTS AND PARASITIDS AT EQUILIBRIUM IN THE AGGREGATED MODEL

Host density N^* and parasitoid density P^* at equilibrium are given by eqns (13) for the aggregated model. Provided k is large enough, these numbers are approximately equal to the host density and the parasitoid density at

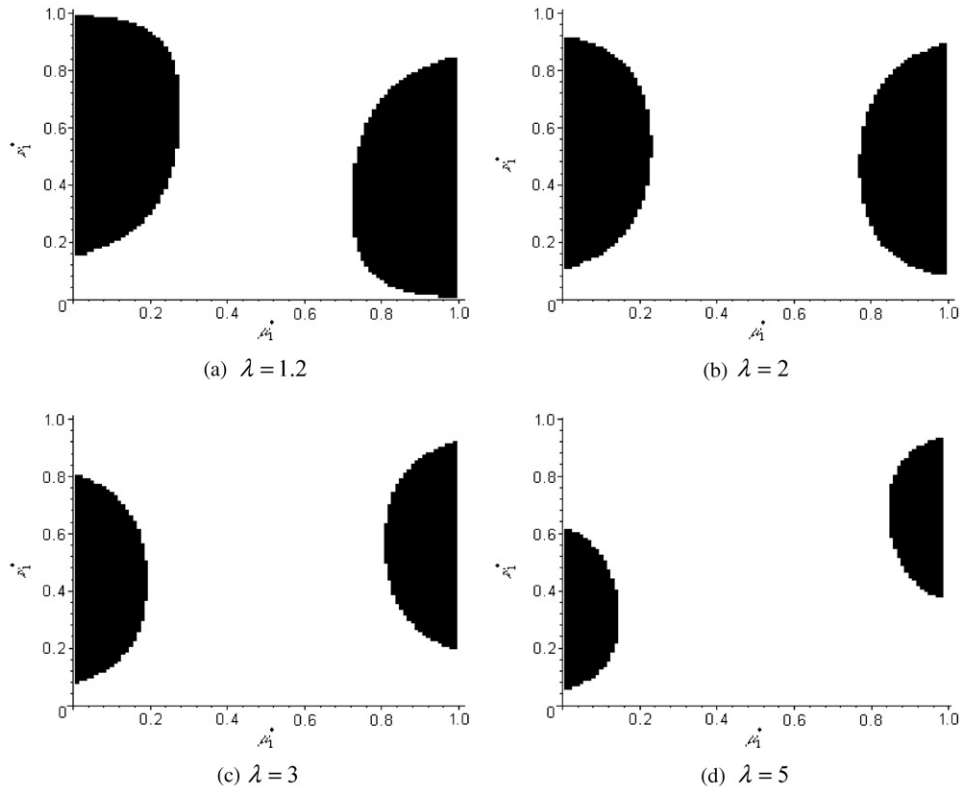


FIG. 4. Domain of stability (in black) of the aggregated model with May local demography and $b = 1.5$.

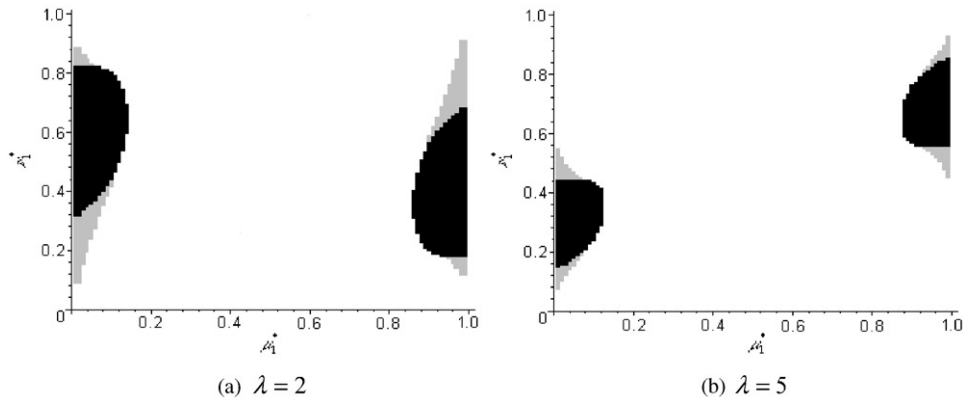


FIG. 5. Domain of stability (black) and domain of persistence (black and gray) of the aggregated model with Nicholson–Bailey local demography.

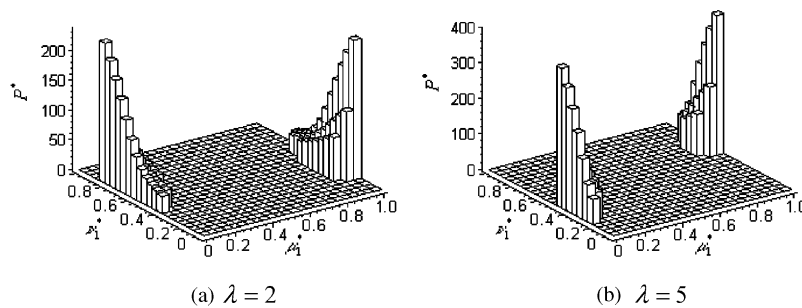


FIG. 6. Parasitoid density at equilibrium P^* . Nicholson–Bailey local demography with $a=0.05$ and $c=1$.

equilibrium for the complete model. P^* increases with either increasing values of v_1^* and decreasing values of μ_1^* or decreasing values of v_1^* and increasing values of μ_1^* (Figs 6 and 7). The same is true of N^* , as N^* is proportional to P^* , see the second equation in eqns (17).

HOST-DENSITY DEPENDENT MIGRATION OF THE PARASITIDS

If we use the Nicholson–Bailey function for the proportion of non-parasitized hosts, the stability of the positive fixed point (N^*, P^*) of the aggregated model extended to host-density dependent migration of the parasitoids depends on four parameters, λ , v_1^* , α and the product ac . For two values of the parameter λ , Fig. 8 shows the regions of the domain of the parameters v_1^* and α that assure the stability of the fixed point and, therefore, the persistence of host-parasitoid interactions. This figure was obtained with $a=0.05$ and $c=1$. It appears that the domain of stability shrinks slightly for increasing values of ac . For higher values of the growth rate of the

host population, λ , the persistence of the host-parasitoid interactions is assured for a wider range of values of the parasitoid aggregation index, α . The parasitoid density P^* at equilibrium is shown in Fig. 9. For fixed values of α , there are two symmetrical values of v_1^* which lead to a maximum value of P^* . These values also correspond to a maximum value of the host density N^* , because of the second equation in eqns (13). The values change little with α , but depend on λ . For $\lambda=3$, P^* is maximal for $v_1^* \approx 0.35$ and $v_1^* \approx 0.65$, whereas for $\lambda=5$, P^* is maximal for $v_1^* \approx 0.25$ and $v_1^* \approx 0.75$.

Discussion

Our study shows that non-persistent host-parasitoid interactions on two patches may become persistent when the hosts and parasitoids move between the two patches. Other authors (Hassell *et al.*, 1991a; Comins *et al.*, 1992) have suggested that the persistence of host-parasitoid interactions in a patchy environment with migration is assured when the number of

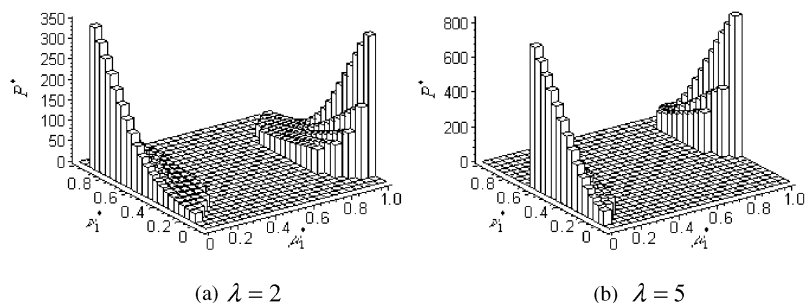


FIG. 7. Parasitoid density at equilibrium. May local demography with $a = 0.05$, $c = 1$ and $b = 1.5$.

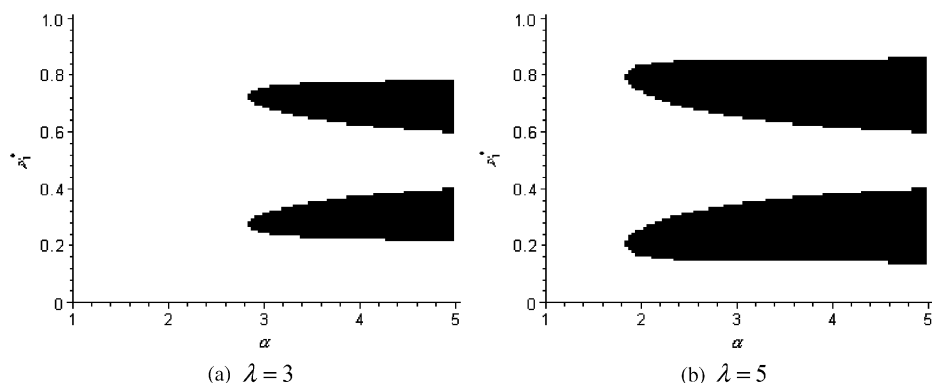


FIG. 8. Domain of stability (in black) of the aggregated model with host-density dependent migration of the parasitoids for different values of α (parasitoid aggregation index), v_1^* (proportion of migrant hosts migrating to patch 1) and λ (growth rate of the host population). Nicholson–Bailey local demography with $a = 0.05$ and $c = 1$.

patches is high (some hundreds of patches at least). In our work, persistence occurs even if there are only two patches, provided that the movement is asymmetrical, i.e. the parasitoids (and sometimes the hosts too) move preferentially to one of the two patches. This result is in line with those reported by Ives (1992), who showed that variability in dispersal rate promoted stability in a two-patch continuous-time host-parasitoid model. Comins & Blatt (1974) also established that biased diffusion had a stabilizing effect in prey–predator models. We also showed that when movement between the patches occurs several times within a generation, the interactions are generally more likely to be stable. This occurs when the movement is asymmetrical, which explains why Rohani & Miramontes (1995), who considered several symmetrical migrations within a generation in their model, found no stabilizing effect. It should be noticed that Adler (1993) did find persistent host-parasitoid interactions in a two-patch

environment even for symmetrical migrations, but in rather specific situations, where the initial value of each population was set very close to the unstable equilibrium point of the system. Unlike the systems studied by Rohani *et al.* (1996) and Rohani & Ruxton (1999a, b), our system did not show any destabilizing effect of migration: when the interactions were persistent on each patch in the absence of migration (May local demography with $b < 1$), they were also persistent in the two-patch environment with migration.

We found that the persistence of host-parasitoid interactions is facilitated for small values of the growth rate of the host population λ (Hassell *et al.*, 1973, 1974; Comins *et al.*, 1992 and Adler, 1993 got a similar result). For small values of λ , persistence is assured when most of the parasitoids migrate to one patch and most of the hosts to the other patch [Fig. 3(a)], i.e. hosts and parasitoids avoid each other. Such situations where hosts and parasitoids exhibit “contrary choices” are probably rare in the field.

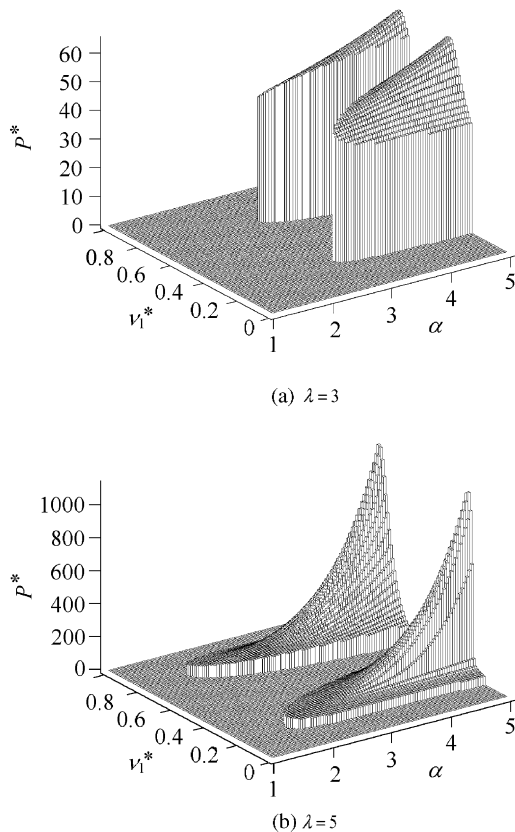


FIG. 9. Parasitoid density at equilibrium P^* . Host-density dependent migration of the parasitoids and Nicholson-Bailey local demography with $a=0.05$ and $c=1$.

However, Fox & Eisenbach (1992) have reported such a situation, and Schreiber *et al.* (2000) showed that contrary choices could be evolutionarily stable strategies and promote ecological stability. For high values of λ , persistence is assured when most of the parasitoids and most of the hosts migrate to the same patch [Fig. 3(d)], i.e. the hosts and parasitoids aggregate and display “congruent choices”. These findings suggest that the host and parasitoid strategies (avoidance or aggregation) that lead to a stable system depend considerably on the growth rate of the host population.

Furthermore, for a system with a stable fixed point, we can ask the following question: which migration strategies of the hosts and parasitoids maximize their biomass (i.e. maximize host density N^* and parasitoid density P^* at equilibrium)? For small values of λ , P^* (and N^*) are maximum for the most asymmetrical movements

of the hosts and parasitoids in different directions [Fig. 6(a)], i.e. when hosts and parasitoids avoid each other as much as possible. For high values of λ , P^* (and N^*) are maximum for the most symmetrical movements of the hosts and the most asymmetrical movements of the parasitoids in the direction where the hosts move preferentially [Fig. 6(b)], i.e. when the parasitoids aggregate as much as possible on the patch where most of the hosts are, whereas the hosts still avoid the parasitoids. Then, at a critical value, λ_c , of λ , the parasitoids “switch strategies”; they avoid hosts whose $\lambda < \lambda_c$, whereas they aggregate with hosts whose $\lambda > \lambda_c$. The value of λ_c can be defined: it is the value of λ for which P^* (and N^*) are maximum for symmetrical movements of the hosts (i.e. for $v_1^* = v_2^* = 0.5$). This value depends on the local demography of our model. For a Nicholson-Bailey local demography $\lambda_c \approx 4.3$, whereas for a May local demography, the value of λ_c depends on the parameter b : λ_c decreases when b increases, and with $b=1.5$ as in Figs. 4 and 7, $\lambda_c \approx 7.1$. When the migration of parasitoids is host-density dependent, P^* (and N^*) are not maximum for the most asymmetrical movements of the hosts or for the most symmetrical movements, but for some particular intermediate values. These values change little with the parasitoid aggregation index but, as before, they change considerably with the growth rate of the host population. For $\lambda=3$ the maximum is obtained when about 65% of the migrant hosts go to one patch and 35% to the other patch [Fig. 9(a)], whereas for $\lambda=5$ the maximum occurs when 75% go to one patch and 25% to the other patch [Fig. 9(b)].

We used aggregation methods to simplify the analysis of our model. Indeed, aggregation methods make it possible to obtain a global (aggregated) model involving a reduced number of variables and parameters, which is more tractable analytically or numerically (e.g. for a bifurcation analysis). These methods can be applied to the study of dynamical systems with two time-scales. The variables handled by the aggregated model (the aggregated variables) are chosen as variables that remain constant at the fast time-scale. In our model, the migration process is repeated several times within a

generation, whereas the demography is applied only once, i.e. migration operates on a fast time-scale and demography on a slow time-scale. Migration is conservative for the total host and parasitoid densities, and so these variables are chosen as aggregated variables. In our case the aggregated variables are simply the sum of the fast time-scale variables, but the global variables may be more complex functions of the fast time-scale variables (Auger & Poggiale, 1998). One should remember that the aggregated model is only an approximation of the complete model. There are few mathematical results that can be used to estimate the quantitative differences between the dynamics of the aggregated model and the complete model, and so this has to be checked numerically. In our model, we found that when k (the ratio between the fast time-scale and the slow time-scale) is of the order 10–100 there was a very good quantitative agreement between the dynamics of the two models.

In the aggregated model, it is easy to evaluate the consequences of changes in properties of individuals (such as the migration parameters) on the persistence of host-parasitoid interactions. Consequently, aggregation methods can be used to study how properties at the population level emerge from properties at the individual level. In this regard, our model shares some characteristics with the model of Schofield *et al.* (2002), who also explored the consequences of different within-generation search and flight strategies of individuals on the between-generation dynamics of the host and parasitoid populations. In the study reported here, we considered constant host and parasitoid migration rates and also host-density dependent migration of the parasitoids. In future work, we would like to investigate other types of migration behavior, such as parasitoid-density dependent migration of the hosts to model the avoidance by hosts of patches with many parasitoids. Both types of density-dependent migrations could also be considered together. The present study focuses on host-parasitoid interactions in two patches. It could be extended to interactions in a row or an array of patches. A condition for persistent interactions in the two-patches model is asymmetrical movements of the individuals. This condition is likely to be

preserved in a model with a row or an array of patches. Asymmetrical movements could generate spatial structures different from those generated by symmetrical movements (spirals, spatial chaos, crystal lattice). Aggregation methods are promising in their ability to relate such structures to individual properties.

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Appendix A

CONSTRUCTING THE AGGREGATED MODEL

The first step in constructing the aggregated model consists in studying the fast dynamics, in our case the migration process. We can observe that the migration matrix M (3) is a stochastic matrix. Migration is conservative, i.e. it keeps the total host and parasitoid densities constant. We denote these constants N and P , respectively. We must look for the existence of a stable equilibrium (N_1^* , N_2^*) and (P_1^* , P_2^*) solution of the equation $V_t' = MV_t'$:

$$\begin{aligned} N_1^* &= (1 - f_{12})N_1^* + f_{21}(N - N_1^*), \\ N_2^* &= N - N_1^*, \\ P_1^* &= (1 - g_{12})P_1^* + g_{21}(P - P_1^*), \\ P_2^* &= P - P_1^*. \end{aligned} \quad (\text{A.1})$$

The fast equilibrium for the hosts is

$$N_1^* = \frac{f_{21}}{f_{12} + f_{21}}N, \quad N_2^* = \frac{f_{12}}{f_{12} + f_{21}}N \quad (\text{A.2})$$

and that for the parasitoids

$$P_1^* = \frac{g_{21}}{g_{12} + g_{21}}P, \quad P_2^* = \frac{g_{12}}{g_{12} + g_{21}}P. \quad (\text{A.3})$$

We define equilibrium patch frequencies for the hosts and the parasitoids

$$v_1^* = \frac{f_{21}}{f_{12} + f_{21}}, \quad v_2^* = \frac{f_{12}}{f_{12} + f_{21}}, \quad (\text{A.4})$$

$$\mu_1^* = \frac{g_{21}}{g_{12} + g_{21}}, \quad \mu_2^* = \frac{g_{12}}{g_{12} + g_{21}}. \quad (\text{A.5})$$

Then, at the fast equilibrium, the densities on each patch and the total density for the hosts and the parasitoids are related by

$$\begin{aligned} N_1'^* &= v_1^*N, \quad N_2'^* = v_2^*N, \\ P_1'^* &= \mu_1^*P, \quad P_2'^* = \mu_2^*P. \end{aligned} \quad (\text{A.6})$$

In order to obtain the aggregated model, the second step consists in assuming that the fast system has reached its equilibrium between time t and time $t+1$. The aggregated model can then be obtained by adding the two host and the two parasitoid equations of the complete model (7) and substituting the fast equilibrium values (A.6). Simple calculations yield the following aggregated model:

$$\begin{aligned} N_{t+1} &= N_t [\lambda_1 v_1^* f(\mu_1^* P_t) + \lambda_2 v_2^* f(\mu_2^* P_t)], \\ P_{t+1} &= cN_t [1 - v_1^* f(\mu_1^* P_t) - v_2^* f(\mu_2^* P_t)]. \end{aligned} \quad (\text{A.7})$$

Appendix B

ANALYSIS OF THE AGGREGATED MODEL

We look for the existence of a positive fixed point (N^* , P^*) of the aggregated model (9). It is solution of the equations:

$$\begin{aligned} \lambda_1 v_1^* f(\mu_1^* P^*) + \lambda_2 v_2^* f(\mu_2^* P^*) &= 1, \\ P^* &= cN^* [1 - v_1^* f(\mu_1^* P^*) - v_2^* f(\mu_2^* P^*)]. \end{aligned} \quad (\text{B.1})$$

Because of the assumptions made about f , see eqns (2), the function on the left-hand side of the first equation monotonically decreases with P^* and takes the value $\lambda_1 v_1^* + \lambda_2 v_2^*$ for $P^* = 0$. Consequently, when $\lambda_1 v_1^* + \lambda_2 v_2^* > 1$ there is a unique positive value for P^* . The second equation then gives the corresponding value for N^* , which is also positive. To study the local

stability of the positive fixed point, let us calculate the Jacobian matrix

$$J^* = \begin{pmatrix} 1 & N^*[\lambda_1 v_1^* \mu_1^* f'(\mu_1^* P^*) + \lambda_2 v_2^* \mu_2^* f'(\mu_2^* P^*)] \\ \frac{P^*}{N^*} & cN^*[-v_1^* \mu_1^* f'(\mu_1^* P^*) - v_2^* \mu_2^* f'(\mu_2^* P^*)] \end{pmatrix}. \tag{B.2}$$

Because $f'(\mu_1^* P^*) < 0$ and $f'(\mu_2^* P^*) < 0$, both the trace and the determinant of J^* are positive. Consequently, local stability is assured when

$$Tr(J^*) < 1 + Det(J^*) < 2. \tag{B.3}$$

The first inequality is always satisfied. The condition for local stability of the positive fixed point (N^*, P^*) of the aggregated model is $Det(J^*) < 1$.

In the case $\lambda_1 = \lambda_2 = \lambda$, $\lambda_1 v_1^* + \lambda_2 v_2^* = \lambda > 1$ is satisfied and the equations above simplify. The positive fixed point (N^*, P^*) is defined by

$$v_1^* f(\mu_1^* P^*) + v_2^* f(\mu_2^* P^*) = 1/\lambda, \tag{B.4}$$

$$N^* = \frac{1}{c} \frac{\lambda}{\lambda - 1} P^*.$$

This positive fixed point is stable when

$$-[v_1^* \mu_1^* f'(\mu_1^* P^*) + v_2^* \mu_2^* f'(\mu_2^* P^*)] \frac{\lambda^2}{\lambda - 1} P^* < 1. \tag{B.5}$$

Appendix C

EQUILIBRIUM PATCH FREQUENCIES FOR HOST-DENSITY DEPENDENT MIGRATION OF THE PARASITIDS

Following Appendix A, equilibrium patch frequencies for the hosts are

$$v_1^* = \frac{f_{21}}{f_{12} + f_{21}}, \quad v_2^* = \frac{f_{12}}{f_{12} + f_{21}} \tag{C.1}$$

and those for the parasitoids

$$\mu_1^* = \frac{g_{21}}{g_{12} + g_{21}}, \quad \mu_2^* = \frac{g_{12}}{g_{12} + g_{21}} \tag{C.2}$$

with

$$g_{12} = \frac{1}{1 + N_1^{*\alpha}} = \frac{1}{1 + (v_1^* N)^{\alpha}},$$

$$g_{21} = \frac{1}{1 + N_2^{*\alpha}} = \frac{1}{1 + (v_2^* N)^{\alpha}}. \tag{C.3}$$

Substituting eqns (C.3) into eqns (C.2) gives

$$\mu_1^* = \frac{1 + (v_1^* N)^{\alpha}}{2 + (v_1^{*\alpha} + v_2^{*\alpha}) N^{\alpha}},$$

$$\mu_2^* = \frac{1 + (v_2^* N)^{\alpha}}{2 + (v_1^{*\alpha} + v_2^{*\alpha}) N^{\alpha}}. \tag{C.4}$$