Mathematical Modelling of Host–Parasitoid Systems: Effects of Chemically Mediated Parasitoid Foraging Strategies on Within- and Between-generation Spatio-temporal Dynamics

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In this paper we develop a novel discrete, individual-based mathematical model to investigate the effect of parasitoid foraging strategies on the spatial and temporal dynamics of host–parasitoid systems. The model is used to compare naïve or random search strategies with search strategies that depend on experience and sensitivity to semiochemicals in the environment. It focuses on simple mechanistic interactions between individual hosts, parasitoids, and an underlying field of a volatile semiochemical (emitted by the hosts during feeding) which acts as a chemotactrant for the parasitoids. The model addresses movement at different spatial scales, where scale of movement also depends on the internal state of an individual. Individual interactions between hosts and parasitoids are modelled at a discrete (micro-scale) level using probabilistic rules. The resulting within-generation dynamics produced by these interactions are then used to generate the population levels for successive generations. The model simulations examine the effect of various key parameters of the model on (i) the spatio-temporal patterns of hosts and parasitoids within generations; (ii) the population levels of the hosts and parasitoids between generations. Key results of the model simulations show that the following model parameters have an important effect on either the development of patchiness within generations or the stability/instability of the population levels between generations: (i) the rate of diffusion of the kairomones; (ii) the specific search strategy adopted by the parasitoids; (iii) the rate of host increase between successive generations. Finally, evolutionary aspects concerning competition between several parasitoid subpopulations adopting different search strategies are also examined.

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1. Introduction

Host–parasitoid systems have proved fruitful models for many experimental and theoretical investigations in ecology and there is a rich literature on parasitoid population dynamics. The book of Godfray (Godfray, 1994) and the references therein provide an excellent review.

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1993), and especially on the evolution of searching strategies in environments where resources are distributed heterogeneously in space. In particular, various mechanisms have been modelled that attempt to maximize the return from patchy environments, where a parasitoid has to balance the diminishing value of a known patch against the potential value of new patches that might be found by relocation and the risk and expense involved in relocation. How patches are located, how the value of the current patch is assessed and how that value is altered by evidence from host encounters during patch residence are the issues that have formed the core of most of these models.

It is our intention in this paper to focus on hitherto unexplored aspects of spatial modelling of host–parasitoid systems—the within-generation movement and interaction of hosts and parasitoids in a two-dimensional spatial domain where the movement of the parasitoids and their location of resource or host patches are controlled by chemicals (kairomones) (Vinson, 1976; Godfray, 1994). This biased, directed movement in response to the spatial gradients of the kairomones is known as chemotaxis. Kairomones can originate from various sources: those produced directly by the host, such as host frass, pheromones and other host semiochemicals (Ambroz et al., 1996; Colazza et al., 1999), or those produced indirectly, for example chemicals produced by plants under attack from herbivores (Turlings et al., 1990).

Although kairomone levels can direct parasitoids to locations where hosts are feeding, they may not provide an accurate picture of the quality of a patch. For example, hosts may continue to feed and emit kairomone after parasitism (as with koinobionts). A parasitoid that leaves a poor-quality patch quickly if rewards do not match expectations could be more efficient than a parasitoid that does not. A number of possible criteria have been suggested to enable this behaviour. Waage (1979) originally suggested an incremental system where the number of host encounters increases the time spent in the patch (i.e. decreases the likelihood of leaving). In contrast to this, Driessen and Bernstein (Driessen et al., 1995; Driessen & Bernstein, 1999) have suggested a “count-down” system where the number of host encounters will decrease the time spent in the patch (i.e. increase the likelihood of leaving). There is some evidence that the strategies adopted are not only species-dependent but also environment-dependent. Driessen & Bernstein (1999) found that V. canescens searching for hosts in granaries have a different strategy from V. canescens searching for hosts in fallen fruit.

There are many mathematical techniques which can be used to model spatial heterogeneity in ecological systems [see Dieckmann et al. (2000) and references therein for a comprehensive review]. A recent paper of Durrett & Levin (1994b) has drawn attention to the fact that the specific technique employed can qualitatively affect the outcome of the results of the modelling. For example, when individual contact and interaction is a central part of the system under study, important details can be lost if a continuous population density approach is used (e.g. reaction–diffusion system models). However, continuum partial differential equation (PDE) models are more amenable to some form of mathematical analysis and may therefore yield more complete results (S. Shigesada et al., 1979; Shigesada, 1980; Okubo, 1980; Murray, 1989).

At the other end of the modelling spectrum, discrete models can capture the important individual interactions in a system. Probabilistic automata have been used to model host–parasite dynamics (Keeling & Rand, 1995; Keeling, 2000), while coupled map lattice systems have been used to model meta-population systems (White et al., 1996, 1999; Rohani & Ruxton, 1999), host–parasitoid systems (Comins et al., 1992; Savill et al., 1997) and predator–prey systems (Sherratt et al., 1997). Excellent reviews of discrete techniques and their applications to ecological systems can be found in the papers of Durrett & Levin (1994a,b). However, the simplified spatial movement/transition rules can lack realism and are, in general, not amenable to mathematical analysis.

Durrett & Levin (1994b) recently noted that an ideal mathematical model of interacting species in an ecological habitat should incorporate the two key points of (i) using interacting particle systems that account for individual interactions in a realistic manner and (ii) modelling any spatial effects explicitly i.e. “the importance of being discrete (and spatial)”. In this paper we present
a novel mathematical model of host–parasitoid interaction that explicitly models the effects of space and spatial behaviour on the interactions and hence on the dynamics of a host–parasitoid system. We develop and extend a technique previously used for modelling nematode movement in soil (Anderson, 1996), and endothelial cell movement in angiogenesis (Anderson & Chaplain, 1998). This technique enables individuals moving on a discrete spatial grid to be distinguished and enables the modelling of individual interactions with local environments. Behaviour of individuals can then be based on experience rather than a mean field approach.

The structure of the remainder of the paper is as follows: in the next section we present in more detail the biological basis for our mathematical model which itself is presented in Section 3. In Section 4 we present the results of the model simulations before finally concluding with a discussion section.

2. The Biological Model

The ecological system considered in this model is a generic asexual, haplodiploid, solitary, koinobiont, larval parasitoid that searches for a relatively immobile concealed host. This might be in a small experimental arena with a bran substrate, or a larger granary environment. The hosts are concealed in and consume the substrate, and chemicals (kairomones) are produced by the hosts as a function of consuming the substrate. It is further assumed that the host and parasitoid populations have synchronized generations where the hosts are in a vulnerable larval stage for the whole of the adult parasitoid’s searching life. It is assumed that the chemical attracts the parasitoid to a patch of substrate but once within the patch the parasitoid must probe randomly for the hosts beneath the substrate. It is in this state that hosts are detected and parasitized. The model assumes that parasitoids have perfect discrimination and all parasitized hosts are rejected, but an egg is laid in all unparasitized hosts encountered. We assume that all hosts are of equal value and capable of supporting a parasitoid larva to enclosure.

(3) Refractory state: The parasitoid is stationary in this state which represents a handling time in a broad sense and not only includes host pacification, manipulation and oviposition time but also cleaning, resting and feeding time when active searching is not taking place.

(4) Flight state: In this state the parasitoid relocates to a new area. Movement is again either random or chemotactic, but the likelihood of remaining stationary is removed. During this, the parasitoid will switch to probing locally but must land and switch to walking first.

The selective pressures on parasitoids are likely to be very high in order to develop a more efficient foraging mechanism and it seems unlikely that a purely random searching could compete.
However, in the model we use a random strategy as a base for comparison. We model two contrasting mechanisms for each of the two main components of behaviour—movement and state switching.

Movement mechanisms. The movement decision mechanisms we model are random searching, where the parasitoid performs an unbiased random walk over the substrate, and chemotactic searching, where the parasitoid's random movement is biased by a propensity to respond to gradients of kairomone in directions of increasing concentration, i.e. to “follow its nose”. In the model stimulations, if a parasitoid finds that it cannot move in the direction it chooses since the new grid point is already at capacity, the parasitoid will switch to the flying state.

State-switching mechanisms. Although it is not necessarily the case that the attractant and the arrestant chemical need be the same we have chosen to model them this way. We examine two different mechanisms for forcing the parasitoid to switch to local probing. The parasitoid either switches randomly from walking over the substrate to local probing with a fixed probability or it uses chemical cues in the form of the local kairomone concentration to trigger the change in behaviour. A parasitoid that uses kairomone cues for switching is assumed to have a learning capacity (Vet & Groenewold, 1990; Turlings et al., 1992) and to start as a naïve individual and initially to probe randomly. However, it is assumed to possess a memory of the level of kairomone when hosts are encountered and bias the probability of subsequent switches by the ratio of the local level to the memory of the level in the patch that last produced host encounters. This memory is modified and updated when a patch produces a higher encounter rate than the previously memorized patch.

The mechanism for patch time allocation is related to the switching mechanism. A random switcher allocates a fixed amount of time within which the parasitoid would expect to make one encounter. A non-naïve kairomone-mediated switcher possesses a memory of the number of hosts encountered as well as the kairomone level in the last patch and will estimate the number of hosts it expects to find from the kairomone level and allocate time to encounter this estimated number. A naïve kairomone-mediated switcher is assumed to adopt the fixed time strategy until it has a host encounter. Both these strategies are used in an attempt to model the observation that the time spent in a patch may be influenced by the “quality” of the patch (Hubbard & Cook, 1978). The random switchers use an incremental strategy, while the kairomone-mediated switchers use a count-down strategy.

While searching locally we assume the probability of a host’s encounter is positively density-dependent on the number of hosts in the patch and negatively density-dependent on the number of searching conspecifics. Host encounters alter the probability of the parasitoid remaining in the patch. For random switchers and naïve kairomone switchers it increases it (van Alphen & Galis, 1983). For kairomone-mediated switchers it decreases it. The probability of staying in a patch reduces with time spent in the patch. After each encounter with a host there is a fixed refractory period after which the parasitoid will resume probing.

When the parasitoid leaves the patch, if it has encountered hosts it switches to the flight state for a fixed time, and if it has not encountered hosts it resumes walking. Flight is accomplished either by random or chemotactic movement, mirroring the walking strategy. During flight the parasitoid does not monitor the kairomone level for the purpose of switching to local probing. After the flight time has expired, the parasitoid lands if possible and returns to walking behaviour. If it cannot land due to overcrowding it will enter another period of flight.

It is assumed that a walking parasitoid will not leave the area. However, a parasitoid in flight can leave the area from any position, and at each time point of its flight there is an associated probability that the flying parasitoid will leave. This probability is related to the length of time since the last successful oviposition. Once a parasitoid has left the arena it is assumed never to return.

Permutations of the above mechanisms give the four strategies outlined in Table 1.

In summary, we consider within-generation encounters between individual parasitoids (using one of the above strategies) and individual hosts. In any given generation $t$ there will be a number $P^t$ of individual parasitoids and a number $H^t$ of
individual hosts. We assume that there is no host mortality other than parasitism and therefore at the end of generation $t$ a certain number of hosts $U^t$ will have escaped encounter and will remain unparasitized. These unparasitized hosts will then breed to produce the next generation $H^{t+1}$ of hosts. The number of parasitized hosts $H^t!$ will then give rise to the next generation of parasitoids $P^{t+1}$. In the next section, we describe the mathematical model we have developed to simulate and analyse the above host–parasitoid system.

3. The Mathematical Model and Method

The mathematical model that we will develop to analyse the movement and interactions of individuals in the host–parasitoid system described in the previous section is based initially on a system of partial differential equations. The equations describe the interactions between the three variables of the model, the hosts $(h)$, parasitoids $(w)$ and an underlying kairomone concentration field $(k)$. From a discretized version of these equations, we will then derive movement probabilities for individual hosts and parasitoids as well as incorporating rules for interactions between individuals. We first formulate the system of partial differential equations.

We assume that the kairomone is produced by the host at some prescribed rate, and then simply diffuses throughout the domain with a linear decay rate (cf. Sherratt & Murray, 1990; Anderson & Chaplain, 1998). Hence the equation for the kairomone concentration $k$ is

$$\frac{\partial k}{\partial t} = \delta_k \nabla^2 k + \mu h - \rho k,$$

where $\delta_k$ is the kairomone diffusion coefficient, $\mu$ is the production rate per host and $\rho$ is a decay constant.

Parasitoid movement is assumed to consist of a random and a chemotactic component. Since we are considering only within-generation dynamics (birth and death processes are handled elsewhere in the model), there are no birth or death terms and therefore the equation governing parasitoid movement is given by

$$\frac{\partial w}{\partial t} = \delta_w \nabla^2 w - \chi_w \frac{\partial}{\partial w} (w \nabla k),$$

where $\delta_w$ is the parasitoid random motility coefficient and $\chi_w$ the chemotaxis coefficient. In the case of a purely randomly searching parasitoid the chemotaxis coefficient $\chi_w$ is zero.

The hosts are assumed to move randomly only. Again since we are considering only within-generation dynamics and parasitism is not instantly fatal (we have assumed a koinobiont parasitoid) there are no birth or death terms in the host movement equation which is therefore given by

$$\frac{\partial h}{\partial t} = \delta_h \nabla^2 h,$$

where $\delta_h$ is the host random motility coefficient.

The equations are taken to hold on a two-dimensional square domain of length $L$ i.e. $[0, L] \times [0, L]$ with zero flux boundary conditions. Appropriate initial conditions $k(x, y, 0)$, $w(x, y, 0)$, $h(x, y, 0)$ are imposed to close the system. Before solving the system numerically, we non-dimensionalize the equations using appropriate scaling variables i.e. a length scale $L$ (the
size of the domain), time-scale $t_0$ (related to the length of one generation, see below) and reference variables $k_0$, $h_0$, $w_0$ for the kairomone, hosts and parasitoids, respectively (these may be taken, for example, as the initial concentration of kairomone and the initial density of hosts and parasitoids).

Using the following substitutions:

$$x = L\tilde{x}, \ t = t_0\tilde{t}, \ w = w_0\tilde{w}, \ h = h_0\tilde{h}, \ k = k_0\tilde{k},$$

in eqns (1)–(3) and dropping the tildes for clarity, we arrive at the following non-dimensional system:

$$\frac{\partial k}{\partial \tilde{t}} = \alpha_k \nabla^2 k + \beta h - \gamma k,$$  \hfill (4)

$$\frac{\partial w}{\partial \tilde{t}} = \alpha_w \nabla^2 w - \chi \nabla^2 (w \nabla k),$$  \hfill (5)

$$\frac{\partial h}{\partial \tilde{t}} = \alpha_h \nabla^2 h,$$  \hfill (6)

where $\alpha_k = t_0\delta_h/L^2$, $\alpha_w = t_0\delta_w/L^2$, $\alpha_h = t_0\delta_h/L^2$, $\beta = \mu h_0 t_0/k_0$, $\gamma = \rho t_0$ and $\chi = \chi_w t_0/k_0 L^2$ are all dimensionless parameters.

These equations now hold on the unit square $[0,1] \times [0,1]$ and zero flux boundary conditions are imposed. Varying the size of the scaling parameter $L$ permits the modelling of domains of different sizes. In the numerical simulations carried out, we investigate length scales ranging from $L = 1 \text{ m}$ (typical of laboratory-based experiments) through $L = 10 \text{ m}$ (typical of storage rooms) to $L = 100 \text{ m}$ (typical of field sizes). An estimated parasitoid lifespan is 20 days and we estimate that there is an average of 10 active hours per day, thus giving a total searching time of 200 hr per parasitoid lifetime (i.e. one generation). We therefore took as our time-scale $t_0 = 200 \text{ hr}$. Finally, the kairomone diffusion coefficient $\delta_h$ was taken to be $5 \times 10^{-4} \text{ m}^2 \text{s}^{-1}$ (Leyton, 1975) and the parasitoid diffusion coefficient $\delta_w$ taken to be $5 \times 10^{-3} \text{ m}^2 \text{s}^{-1}$ (Nicholson & Bailey, 1935). Since the systems that we are considering have the hosts in a larval stage and the larvae are much more immobile than the parasitoids, we took the host diffusion coefficient to be 100 times smaller than the parasitoid diffusion coefficient i.e. $\delta_h = \delta_w/100$.

In order to solve the equations numerically, we used a standard explicit five-point central difference (finite difference) scheme. In the usual way, the unit square was divided into a $25 \times 25$ point grid, giving a grid spacing of $\Delta x = 0.04$. We took a time step of $\Delta t = 0.0001$ which represents 72 s of searching time per numerical iteration (since our scaling $t_0 = 200 \text{ hr}$ and there are 10 000 numerical iterations per generation).

We assume an initial arbitrary non-zero distribution of hosts throughout the domain, with no parasitoids initially present and no kairomone present. Equations (4) and (6) are first of all solved numerically in order to generate a kairomone concentration field throughout the domain appropriate to the underlying distribution of hosts. Parasitoids are then introduced into the domain and can utilize the kairomone field in chemotactic search strategies. In order to calculate the movement of individuals, we develop a discrete, stochastic model using the discretized form of eqns (5) and (6).

**Individual movement rules.** The grid points of our discretized unit square are taken to represent patches in the environment, and each grid point can contain a number of individual hosts and parasitoids. The number of hosts and parasitoids that can occupy a grid point can vary from grid point to grid point as can the vulnerability of hosts to parasitoids. The kairomone concentration at each grid point is also known. The movement of individual hosts and parasitoids is achieved by calculating the probability of an individual moving from one grid point to another (or remaining stationary). These probabilities are calculated from the explicit discretization of the parasitoid and host equations.

For illustrative purposes we present the discrete form of eqn (5) for the parasitoids (a similar equation is obtained for the hosts):

$$w_{i,j}^{t+1} = P_0 w_{i,j}^t + P_1 w_{i+1,j}^t + P_2 w_{i-1,j}^t,$$

$$+ P_3 w_{i,j+1}^t + P_4 w_{i,j-1}^t,$$  \hfill (7)

where the subscript $i,j$ specify the location on the grid and the superscripts the time steps.
In a numerical simulation of the continuous model (5), the purpose of the discrete equation (7) is to determine the parasitoid density at grid position \((i,j)\), and time \(\tau + 1\), by averaging the density of the four surrounding neighbours at the previous time step \(\tau\). For our discrete model, we use the five coefficients \(P_0 \sim P_4\) from eqn (7) to generate the probability of motion of an individual parasitoid. These coefficients can be thought of as being proportional to the probabilities of the individual parasitoid being stationary \((P_0)\) or moving left \((P_1)\), right \((P_2)\), up \((P_3)\) or down \((P_4)\). The precise functional forms of these coefficients are given in Appendix A.

Each time step \(\Delta t\) of the simulation process involves solving the discrete form of the system numerically to generate the five coefficients \(P_0 \sim P_4\). Probability ranges are then computed by summing the coefficients to produce five ranges, \(R_0 = 0 \sim P_0\) and \(R_j = \sum_{i=0}^{j} \sum_{i=0}^{j} P_j - \sum_{i=0}^{j} P_i\), where \(j = 1 \sim 4\). We then generate a random number between 0 and 1, and depending on the range in which this number falls, the individual parasitoid currently under consideration will remain stationary \((R_0)\) or move left \((R_1)\), right \((R_2)\), up \((R_3)\) or down \((R_4)\). The larger a particular range, the greater is the probability that the corresponding coefficient will be selected. Each parasitoid is therefore restricted to move to one of its four orthogonal neighbouring grid points or remain stationary at each time step (we note that using a higher-order finite-difference discretization scheme would enable movement to next-nearest neighbours to be incorporated, cf. Mitchell & Griffiths, 1980). Individual hosts are moved in a similar manner [full details of this technique are given in Anderson & Chaplain (1998) where it was developed and used to model individual cell migration during tumour angiogenesis]. Thus, in this manner, we can generate the movement of individuals from grid point to grid point in a stochastic fashion. With the addition of interaction rules (detailed below) when parasitoids encounter hosts, we thus have a novel technique to examine the within-generation dynamics in a host–parasitoid system. By computing the simulation for a number of generations, then we can also examine generation-to-generation dynamics and overall population levels.

**Individual interaction rules.** Having described how we generate the movement of individuals using the discretized form of eqns (5) and (6), we now describe how we implement the individual interaction rules as the parasitoids move through the domain and search for the hosts. Initially, we will have a number of hosts and parasitoids distributed randomly throughout the domain, with an underlying kairomone concentration field. Hosts always move randomly [see eqn (6)]. The “searching-state” of a parasitoid will either be random or chemotactic (depending on whether \(\chi = 0\) or \(> 0\)). At each time-step of the simulation, once the movement event for each individual has been performed, we then implement individual-based rules that govern the interactions and state-changes of the individuals within the patches (described in detail in Section 2).

The first thing we note is that if, at any time, a searching-state move (for a parasitoid) is “blocked” because the destination grid point (as determined by the choice of movement coefficient \(P_i\)) already holds the maximum number of parasitoids, the parasitoid switches to its “flight-state”. If a flying parasitoid attempts to land but it cannot, as the grid point is similarly full, then the parasitoid remains in flight. Whilst in flight mode there is a probability \(P(L)\) that the parasitoid will leave the arena. This increases with time since the last oviposition \(t\) as follows:

\[
P(L) = 0.5 + 0.5 \tanh \left( \frac{2t}{t_p} - 3 \right),
\]  

where \(t_p\) is a positive parameter. See Fig. 1 for a graphical representation.

We assume that the probability of an individual parasitoid, probing at grid point \((i,j)\), encountering a host at that grid point increases with the number of hosts at that grid point and decreases with the number of other parasitoids at the grid point, due to interference. Therefore, the probability \(P(E)_{i,j}\) of a parasitoid encountering a host at grid point \((i,j)\), is given by

\[
P(E)_{i,j} = \frac{h_{i,j}}{h_{i,j}} \left[ 1 - \tanh \left( \frac{\omega_{i,j}}{w_{i,j}} \right) \right],
\]
FIG. 1. Graph of the leaving probability function \( P(t) \) from eqn (8) where \( t \) is the time in hours since last oviposition. The graph shows that as time increases the parasitoid is more likely to leave. The value of the parameter \( t_p \) is 10.

FIG. 2. Encounter probability function \( P(E) \) from eqn (9) where \( w \) is the number of parasitoids and \( h \) is the number of hosts in the cell. The parameter values are taken to be a maximum twenty hosts per grid point and maximum ten parasitoids per grid point, i.e. \( h^*_{i,j} = 20; \omega^*_{i,j} = 10. \)

where \( h_{i,j} \) is the number of hosts, \( w_{i,j} \) the number of parasitoids, \( h^*_{i,j} \) is the maximum number of hosts and \( \omega^*_{i,j} \) the maximum number of parasitoids at the grid point \((i, j)\). See Fig. 2 for a graphical representation of this function.

When a parasitoid is moved to a grid point which contains hosts, one host is chosen at random from the total number of hosts at that grid point and the parasitoid then encounters this particular host. If the host is unparasitized, the parasitoid will oviposit and enters a refractory state for a period of time \( R_p \); if the host has already been parasitized then the parasitoid enters a refractory state for a period of time \( R_n \). At the end of the generation each unparasitized host is assumed to be capable of laying \( 1 + H \) eggs. This number \( H \) is limited in a logistic manner so that the total number of eggs \( H_{\text{tot}} \) laid by a host to form the next generation is given by

\[
H_{\text{tot}} = 1 + H(1 - U_{i,j}/K_{i,j}), \tag{10}
\]

where \( K_{i,j} \) is the carrying capacity of the grid point, which can vary with spatial scale, and \( U_{i,j} \) the number of hosts at the grid point. The new hosts are distributed in clutches of up to four eggs in a neighbourhood of \( 10 \times 10 \) patches surrounding the grid point \( i, j \).

All the parasitized hosts are assumed to hatch into new parasitoids at the start of the next generation and therefore the number of parasitoids at the start of the next generation \( P_{t+1} \) is given by

\[
P_{t+1} = H' - U'. \tag{11}
\]

In the next generation the new hosts are randomly distributed in clutches across the grid. Parasitized hosts are hatched \textit{in situ} and the location used as the initial position for a new adult parasitoid in the next generation.

In order to commence the stimulation, we assumed that initially \((t = 0)\) there was a certain number of hosts distributed randomly throughout the domain. Each simulation was first of all run for a period representing 1 day with these hosts and no parasitoids in the domain to generate an initial kairomone concentration field. The parasitoids were then introduced once the kairomone field was set up. This process was also repeated at the start of each new generation.

This novel discrete modelling approach, combining individual movement and interaction rules, permits us to investigate both within- and between-generation dynamics when parasitoids adopt one of the four strategies listed in Section 2 concerning their mode of search/flight and their mode of switching/patch-time allocation.

4. Simulation Results

For each simulation run 100 hosts were initially distributed in clutches of ten throughout the domain and Fig. 3 shows one such initial random distribution of ten patches of hosts.
This initial distribution of hosts was used to generate the initial kairomone concentration field [cf. eqn (4)]. In simulation runs where we were comparing different searching strategies used by different parasitoid types, the same initial host distribution (i.e. at $t = 0$) was used for each parasitoid type. Figure 4(a) and (b) shows plots of the initial kairomone concentration field in two differently sized domains generated by the initial host distribution shown in Fig. 3. It is clear that the local maxima of kairomone concentration coincides with the grid points occupied by hosts and that in the smaller domain the kairomone has spread more uniformly throughout the domain, as is to be expected [cf. eqn (4)]. An initial population of 50 parasitoids were then introduced to the grid once the initial kairomone concentration field had been set up. These were distributed randomly throughout the domain. For all the simulations presented here the kairomone production rate parameter $\beta = 1$ and the decay rate $\gamma = 0.1$.

As has been described in the previous section, the novel method we have developed to model the host–parasitoid system provides us with information regarding: (i) the behaviour of individuals within generations; (ii) the population behaviour and dynamics from generation to generation. Below we present results illustrating these features.

### 4.1. WITHIN-GENERATION DYNAMICS

Figure 5(a)–(d) shows the proportion of time during one generation spent at each grid point by a single parasitoid searching in the domain with an initial host distribution shown in Fig. 4(b). The plots (a)–(d) correspond to a parasitoid with strategies (1)–(4), respectively. It can be seen from the figures that the parasitoids which adopt random movement search strategies (1) and (2) [subplots (a) and (b), respectively] cover larger areas of the domain whilst the parasitoids adopting chemotactic movement search strategies (3) and (4) [subplots (c) and (d), respectively] concentrate their search more in the areas of higher kairomone concentration. There is also a correlation between the length of time spent at a particular grid point and the strategy adopted. As can be seen from the results, the longest time spent at any particular grid point is 0.0939 time units for strategy (1) parasitoids, 0.1251 time units for strategy (2) parasitoids, 0.1338 time units for strategy (3) parasitoids and 0.1341 time units for strategy (4) parasitoids. This is what one would intuitively expect from the movement equations.

Figure 6 shows a sequence of snap shots of the spatial distribution of host kairomone concentration profiles at the start of the 10th, 20th, 30th and 40th generations of the parasitoid searching life for four different parasitoid searching strategies. These profiles reflect the underlying spatial distribution of hosts at the start of each of these generations [cf. eqn (4)]. The parameter values used were the same for each set of simulations [(a)–(d), (e)–(h), (i)–(l), (m)–(p)] and the only difference between the simulations is in the particular search strategy adopted by the parasitoids. The aim of these simulations was to investigate how different searching strategies adopted by parasitoids could affect the spatial distribution of hosts and kairomones. The initial distributions of hosts (ten random patches, cf. Fig. 3), kairomone concentration field (cf. Fig. 4) and parasitoids were the same in each case.

Figure 6(a)–(d) [random search, random switch; strategy (1), RR] shows a homogeneous distribution of kairomone (and hence underlying host distribution) throughout the domain at each generation. There are few patches in the domain where there is no kairomone concentration.
FIG. 7. Plots of the parasitism against time within a generation. Numbers of unparasitized hosts against time in one generation. The curves marked RR, RC, CR, CC correspond to parasitoids pursuing strategies (1), (2), (3), (4), respectively. The parameter values used were (a) $d_k = 5 \times 10^{-4} \text{m}^2 \text{s}^{-1}$, $d_w = 10^{-3} \text{m}^2 \text{s}^{-1}$ and $d_h = 0$; (b) $d_k = 5 \times 10^{-3} \text{m}^2 \text{s}^{-1}$, $d_w = 10^{-3} \text{m}^2 \text{s}^{-1}$ and $d_h = 0$. In both cases $\chi = 1$; $h_{n,i} = 20$ and $\omega_{n,i} = 10$ and the domain size $L = 1 \text{m}$. (---) RR; (···) RC; (■) CR; (--) CC.

The results of the above simulations show that any heterogeneity arising in the spatial distribution of hosts is maintained best by strategy 4 parasitoids (in our case, the patchiness is present through the initial distribution of hosts). These are more efficient in detecting and locating the hosts through the gradients in the kairomone concentration field and therefore confining them to spatial positions close to their initial position. As the hosts secrete more kairomone this remains relatively localized and this in turn reinforces the chemotactic searching. The parasitoids pursuing the other three search strategies are not as efficient in detecting the hosts and so once the hosts manage to move away from their initial positions the kairomone concentration field becomes more diffuse (contains shallower gradients) and less patches are maintained.

Using our novel modelling technique, we can also track the number of hosts parasitized during each generation by parasitoids adopting different strategies. In this way we can estimate and compare the “efficiency” of each strategy. The results presented in Fig. 7 show the number of unparasitized hosts against time within one generation (200 hr) for each of the four parasitoid search strategies when the diffusion rate for kairomone is varied. These results have been averaged over ten simulation runs. The simulations leading to Fig. 7(a) were carried out with a more slowly diffusing kairomone while those in Fig. 7(b) considered a faster diffusing kairomone. One would expect that (at any given time) the concentration field of the kairomone with the faster diffusion coefficient would be distributed more uniformly throughout the domain with less steep gradients created. This should impact on the searching efficiency of the parasitoids and therefore on the number of hosts parasitized.

The results of Fig. 7(a) show that parasitoids adopting strategy (1) (random search, random switch; RR) are least efficient (96 unparasitized hosts, four parasitized); parasitoids adopting strategy (2) (random search, kairomone-mediated switch; RC) and strategy (3) (chemotactic search, random switch; CR) are “moderately” efficient and comparable (87 unparasitized hosts, 13 parasitized); while parasitoids adopting strategy (4) (chemotactic search, kairomone-mediated switch; CC) are the most efficient (77 unparasitized hosts,
23 parasitized). These results show that there is an almost six-fold difference in the number of hosts parasitized by strategy (4) parasitoids (most efficient searchers) as compared with strategy (1) parasitoids (least efficient searchers).

The results of Fig. 7(b) are qualitatively similar i.e. parasitoids adopting strategy (1) are least efficient (96 unparasitized hosts, four parasitized); parasitoids adopting strategy (2) and strategy (3) are “moderately” efficient and comparable (92 unparasitized hosts, eight parasitized); while parasitoids adopting strategy (4) are the most efficient (90 unparasitized hosts, ten parasitized). However, there is now only a 2.5-fold difference in the number of hosts parasitized by strategy (4) parasitoids as compared with strategy (1) parasitoids. The searching efficiency of strategy (4) parasitoids has been greatly reduced only ten hosts are parasitized compared with 23 previously.

The results of these figures show that (i) in both cases, the relative efficiencies of parasitoids with each strategy stays the same; (ii) the situation with a more slowly diffusing kairomone leads to a greater efficiency in the chemically mediated searchers. This is due to the fact that in the case of the more slowly diffusing chemical there are steeper gradients in the concentration field which is to the advantage of strategy (4) parasitoids. The faster diffusing kairomone is distributed throughout the domain more quickly with shallower gradients throughout (cf. Fig. 4). This means there is less advantage to chemically mediated searchers.

### 4.2. POPULATION DYNAMICS

We now turn our attention to information at the population level (generation to generation) which can be obtained from our model. Figures 8 and 9 show plots of the total population numbers for hosts and parasitoids over 100 generations obtained from the simulations using various host increase rates. In each figure, the subfigures (a)–(d) correspond with parasitoids adopting strategies (1)–(4), respectively.

In these simulations the key parameter we focus on is the host egg load. For the simulations of Fig. 8 the maximum host increase rate was set to 16 eggs per surviving host, while in Fig. 9 this parameter was set to eight eggs per surviving host. This was the only parameter difference in the two sets of simulations. Figure 8(a)–(d) exhibits the oscillatory “boom and bust” dynamics expected with high host increase rates, similar to those of non-spatial models (see, for example, Nicholson & Bailey, 1935), where numbers of hosts escaping parasitism are initially high enough to allow the host numbers to build

![Fig. 8. Plots of the total numbers of hosts and parasitoids over a period of 100 generations. The plots in (a), (b), (c) and (d) correspond to parasitoids pursuing strategies (1), (2), (3) and (4). The parameter values used were $h = 1$; maximum host increase rate of 16 eggs per surviving host i.e. $H = 15$ in eqn (10); $\delta_h = 5 \times 10^{-5} \text{m}^2\text{s}^{-1}$, $\delta_w = 10^{-3} \text{m}^2\text{s}^{-1}$ and $\delta_h = \delta_w/100$; $h_{ij} = 20; \omega_{ij} = 10; L = 1 \text{m.}$](image-url)
up over the first few generations. However, along with the high reproduction, the spatial abundance of the hosts ("host ubiquity") mean parasitoid numbers subsequently increases; this continues to such an extent that the host numbers are driven down to very low levels, leading to correspondingly low levels of parasitoids in the next generation.

This effect (large-amplitude oscillations) is not present in the simulations which were carried out with the lower host increase rate. Figure 9(a)–(d) shows that the host numbers do not build up to high levels and the parasitoids are able to control the hosts. The oscillations now have a much smaller amplitude. Indeed one can envisage that both populations have reached some stable "quasi-steady state" or "pseudo-equilibrium" (due to the stochastic nature of the model and simulations).

Finally, we note that using a host egg-load of less than four eggs per host, the hosts were not able to increase sufficiently when numbers were low, thereby enabling the parasitoids to detect all hosts in the domain. This drove the number of hosts to zero (i.e. the hosts became extinct) and subsequently the parasitoids would become extinct at the end of the following generation. This would normally happen within the first ten generations.

In the following set of simulations we fix the egg load per host (at an intermediate value of 12 compared with Figs 8 and 9) and vary the chemotaxis coefficient. The same initial conditions were used in each case and all parameters except $\chi$ and the switching mechanism were the same. Figure 10(a)–(f) shows the time series dynamics of the parasitoid population from six simulations of the model.

The simulations in Fig. 10(a) and (b) are for the case $\chi = 0$. In Fig. 10(a) the parasitoids have random switching while in Fig. 10(b) they have chemically mediated switching. These results exhibit large-amplitude oscillatory dynamics.

The simulations in Fig. 10(c) and (d) are for the case $\chi = 1$. In Fig. 10(c) the parasitoids have random switching while in Fig. 10(d) they have chemically mediated switching. The results show that (on average) the amplitude of the oscillations is less than in Fig. 10(a) and (b), as may be expected since the parasitoids in these two cases have greater searching efficiency.

The simulations in Fig. 10(e) and (f) are for the case $\chi = 5$. In Fig. 10(e) the parasitoids have random switching while in Fig. 10(f) they have chemically mediated switching. These results show another increase in parasitoid searching efficiency with the amplitude of the

![Fig. 9. Plots of the total numbers of hosts and parasitoids over a period of 100 generations. The plots in (a), (b), (c) and (d) correspond to parasitoids pursuing strategies (1), (2), (3) and (4). The parameter values used were $\chi = 1$; maximum host increase rate of 8 eggs per surviving host i.e. $H = 7$ in eqn (10); $\delta_h = 5 \times 10^{-5} \text{m}^2 \text{s}^{-1}$, $\delta_w = 10^{-3} \text{m}^2 \text{s}^{-1}$ and $\delta_h = \delta_w / 100$; $h^*_{i,j} = 20, \omega^*_{i,j} = 10; L = 1 \text{m}.$]
oscillations reduced further. Indeed the results of Fig. 10(f) show small-scale oscillations around a pseudo-equilibrium.

The simulations show that as the chemotaxis parameter is increased the host numbers do not build up to high levels uniformly throughout the domain. The differences in the results are due to the different searching strategies adopted.

Finally, simulations were also performed for a “mixed population” of parasitoids with a proportion (25%) of the parasitoid population pursuing one of the four searching strategies. The results of these simulations are shown in Fig. 11(a) and (b). It can be seen that the proportion of the subpopulation of parasitoids adopting strategy (4) (chemotactic search, kairomone-mediated switch; CC) increases steadily over the 50 generations simulated, with a corresponding decrease in the proportions of the subpopulations adopting strategies (1)–(3), until eventually the populations consists of only parasitoids adopting search strategy (4). This demonstrates that in a competitive environment, the more efficient strategy (4) parasitoids find the hosts first. The other parasitoids adopting strategies (1)–(3) are then reduced in oviposition rate since they encounter more parasitized hosts. These results demonstrate how the model can be used to explore evolutionary issues.

5. Discussion

In this paper we have presented a novel mathematical model for investigating the spatio-temporal dynamics of host–parasitoid systems. The model incorporates space explicitly by initially using a system of partial differential equations (PDEs) which describes the movement (both random and directed) and interactions of parasitoids, hosts and kairomone concentration.
field (produced by the hosts). The tracking of individuals is then achieved through a discretization of the continuous PDEs. The modeling of the movement of individual parasitoids and hosts is then coupled to automata-based rules that handle state-dependent individual micro-scale interactions. The model is capable of investigating within-generation effects and then using these results to generate generation-to-generation macro-scale population dynamics.

The modeling of individuals permits the investigation of competition between parasitoids with different behavioral phenotypes. The inclusion of explicit spatial modeling has the advantage over traditional automata models in that aspects of behaviour which affect spatial distributions can be addressed. It also permits the modelling of state-dependent behaviour where an individual’s past experience can influence its current response to environmental cues. The use of a system of PDEs also permits realistic parameter values to be used (length scale, time-scale, diffusion coefficients). The simulations of the model focussed on two aspects: (i) how changes to key parameters affected the within-generation spatio-temporal dynamics; (ii) how changes to parameters affected the between-generation (temporal) population dynamics.

Concerning the former aspect we first of all examined how different search strategies affected the movement of an individual parasitoid. These results showed that parasitoids adopting a random search strategy covered the domain more widely and spent a relatively short period of time at any given spatial location with little correlation with the underlying host distribution. In contrast to this, parasitoids which adopted a chemically mediated strategy had a more localized search pattern spending more time at spatial locations where there was a high host density (see Fig. 5). These general trends were also manifested in the results shown in Fig. 6. In these simulations we examined how different parasitoid search strategies affected the spatial distribution of hosts over a number of generations (all simulations used the same initial patchy distribution of hosts, cf. Fig. 3). These results showed that parasitoids adopting a random strategy gave rise to homogeneous spatial distributions of hosts whereas parasitoids adopting chemically mediated strategies gave rise to spatial distributions of hosts where the initial patchiness was maintained.

The effect of underlying spatial structure on the searching efficiency of parasitoids was also examined in detail by performing simulations of the model where we varied the diffusion rate of the kairomone. The results shown in Fig. 7 examine the effect of a slow- and fast-diffusing kairomone on searching efficiency. These results (and others not shown) indicate a general trend that parasitoids with random search strategies are least efficient (in terms of the numbers of hosts parasitized within one generation) while parasitoids adopting chemotactic search strategies are most efficient. However, the searching efficiency of the chemically mediated parasitoids is greatly affected by the size of the diffusion coefficient of the kairomone. The chemically mediated searchers perform far better (in terms of the numbers of hosts parasitized) when the kairomone is
diffusing slowly. This effect can be explained by the fact that a slowly diffusing kairomone will create a concentration field with steeper gradients. The chemically mediated searchers will then be able to use the gradients to find the patches of hosts more efficiently than the random searchers. This is in contrast with a fast-diffusing kairomone which will be more homogeneously distributed throughout the domain with less-steep gradients. In this situation chemically mediated searchers have less of an advantage over the random searchers. Indeed in a situation where the kairomone concentration field has no gradients (i.e. it is constant throughout the domain) there is no advantage at all to the chemically mediated searchers. Finally, we note that similar results are obtained when one varies the size of the domain (keeping all other parameters constant). In this case, the chemically mediated searchers have an advantage in larger domains, while in smaller domains the advantage is lost. We note that this is in keeping with the scaling used in our model where $x_k = t_0 \delta_k / L^2$.

Turning our attention to our results which focus on the between-generation (population dynamic) level (Nicholson & Bailey, 1935) we note that our model produces cyclic dynamics in the host–parasitoid populations whereby the amplitude of the cycles is reduced by varying either the host egg load or the parasitoid chemotaxis coefficient. The simulations of Figs 8 and 9 compared the global dynamics when the egg load of the hosts are varied. For a high egg load (Fig. 8) the simulations produced large-amplitude oscillations which persisted indefinitely. By reducing the egg load of the hosts we were able to reduce the amplitude of the oscillations and “stabilize” the system until we obtain very low-amplitude oscillations giving the appearance of a pseudo-equilibrium (we note that oscillations were always present due to the stochastic nature of the model). By reducing the egg load still further it was possible to drive both populations to zero (extinction) within around ten generations (results not shown).

A second way to “stabilize” the oscillations was to change the chemotaxis parameter $\chi$ (related to the searching efficiency of the parasitoids). For $\chi = 0$ and low values, once again large-amplitude oscillations were observed. As the value of $\chi$ was increased (and hence the searching of the parasitoids becomes more sophisticated and directed) the amplitude of the oscillations decreased and the system again appeared to “stabilize” with small-amplitude oscillations around a pseudo-equilibrium (Fig. 10).

Finally, we used the individual-based nature of the model to briefly investigate evolutionary aspects of competition between different search strategies. Simulations were carried out with four equal populations of parasitoids, each adopting one of the four different searching strategies used in the modelling. These parasitoids were initially distributed randomly in a domain with an initial random distribution of hosts. The simulation was run over a number of generations and the change in each of the parasitoid populations from generation to generation was recorded. This showed that the more-efficient chemically mediated searchers dominated, driving the less-efficient parasitoid populations to zero (extinction). In the long term this led to coexistence of the chemically mediated searchers and the hosts.

The defining characteristic of the models presented in this paper is that they are based on a realistic description of small-scale individual–interactions. By addressing host–parasitoid associations at the level of the chemical mechanisms which actually determine the outcome of parasitoid searches, our model therefore represents a significant improvement in usefulness in applications, such as biological pest control, over more generic models based on Nicholson–Bailey formulations. Whilst not having been exhaustively investigated, the model appears to support the view that insects are likely to use chemicals with differing properties for different purposes during foraging. Highly volatile chemicals with fast diffusion rates are not of use at short range, but are useful for long-range attraction to patches of hosts. In contrast, slowly decaying chemicals with slower diffusion rates are more useful for local foraging for individual hosts.

It is our opinion that this type of model has much to add not only to investigations into parasitoid foraging mechanisms but also to an understanding of host–parasitoid population dynamics over much longer ecological time-scales.
REFERENCES


APPENDIX A

The equation which is used to generate the movement of individual parasitoids is given by (7)

\[ w_{i,j}^{t+1} = P_0 w_{i,j}^{t} + P_1 w_{i+1,j}^{t} + P_2 w_{i-1,j}^{t} + P_3 w_{i,j+1}^{t} + P_4 w_{i,j-1}^{t}, \] (A.1)
where the subscript \(i, j\) specify the location on the grid and the superscripts the time steps. This is derived by discretizing eqn (5) using explicit central finite differences. The precise functional forms of the coefficients are given as follows: the coefficient \(P_0\), proportional to the probability of remaining stationary, takes the form

\[
P_0 = 1 - \frac{4\alpha_w \Delta t}{(Ax)^2} - \frac{\chi \Delta t}{(Ax)^2} (k_{i+1,m}^r + k_{i-1,m}^l - 4k_{i,m}^l + k_{i,m+1}^l + k_{i,m-1}^l),
\]

and the coefficients \(P_1, P_2, P_3\) and \(P_4\), which are proportional to the probabilities of moving to grid points left, right, up and down, respectively, have the forms

\[
P_1 = \frac{\alpha_w \Delta t}{(Ax)^2} - \frac{\chi \Delta t}{4(Ax)^2} [(k_{i+1,m}^r - k_{i-1,m}^l)],
\]

\[
P_2 = \frac{\alpha_w \Delta t}{(Ax)^2} + \frac{\chi \Delta t}{4(Ax)^2} [(k_{i+1,m}^r - k_{i-1,m}^l)],
\]

\[
P_3 = \frac{\alpha_w \Delta t}{(Ax)^2} - \frac{\chi \Delta t}{4(Ax)^2} [(k_{i,m+1}^l - k_{i,m-1}^l)],
\]

\[
P_4 = \frac{\alpha_w \Delta t}{(Ax)^2} - \frac{\chi \Delta t}{4(Ax)^2} [(k_{i,m+1}^l - k_{i,m-1}^l)].
\]

When the chemotaxis coefficient \(\chi\) is non-zero all the coefficients are functions of the underlying kairomone concentration field generated by eqn (4). In this situation, therefore, we essentially have a biased random walk equation governing the motion of an individual parasitoid and its movement is affected by the local kairomone concentration field. When \(\chi = 0\) the coefficients do not depend on the kairomone field (since there is no chemotaxis), and the parasitoid undergoes an unbiased random walk, with no preferred direction. If higher-order finite-difference discretizations are used (e.g. 9-, 13- and 25-point stencils) then we can move individuals to the next-nearest neighbour grid points (Mitchell & Griffiths, 1980).

The discrete equation and coefficients governing the movement of an individual host can be derived in a similar manner and is in fact identical to the case \(\chi = 0\) above (with \(\alpha_h\) replacing \(\alpha_w\)).
FIG. 4. Plots of the initial spatial distributions of kairomone concentration for (a) domain size $L = 10\,\text{m}$; (b) domain size $L = 1\,\text{m}$.

FIG. 5. Plots (a)–(d) show the proportion of time spent foraging in each patch on an $L = 1\,\text{m}$ domain by a single parasitoid adopting strategies (1)–(4), respectively. The parameter values used were $\delta_k = 5 \times 10^{-3}\,\text{m}^2\text{s}^{-1}$, $\delta_w = 10^{-3}\,\text{m}^2\text{s}^{-1}$ and $\delta_b = 0; \chi = 1; h_{i,j} = 20$ and $\omega_{i,j} = 10$. 

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P. SCOFIELD ET AL.
FIG. 6. Sequence of plots of the spatial distributions of kairomone concentration in a domain of size $L = 10$ m at the start of the 10th, 20th, 30th and 40th generations for four different parasitoid search strategies (see text for details). The parameter values used were $\delta_k = 5 \times 10^{-3} \text{m}^2 \text{s}^{-1}$, $\delta_w = 10^{-3} \text{m}^2 \text{s}^{-1}$, $\theta_h = \delta_w/100$, $\chi = 1$; $h_{i,j}^* = 20$ and $\omega_{i,j}^* = 10$. 

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