A MATHEMATICAL MODEL FOR THE POPULATION DYNAMICS OF ARMY ANTS

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A stochastic cellular automata model for the population dynamics of the army ant *Eciton burchelli* on Barro Colorado Island in Panama was set up. It was simulated on the computer and shown to give good agreement with biological data. It was analysed using two approximations akin to the mean field approximation in statistical mechanics, and good agreement with the simulations was obtained. Finally, the role of distance between successive statary phase bivouacs is discussed with regard to the rate of colony growth.

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1. Introduction

Army ants are among the most spectacular of social animals, living in organised colonies that may contain over half a million individuals. In the tropical rain forest their foraging raids sustain diversity among the litter floor fauna by creating a patchwork of areas in different stages of ecological succession (Franks 1982c, Franks and Bossert 1983, Otis *et al.* 1986). Many species of birds, lizards and invertebrates also associate with them (Willis 1967, Ray and Andrews 1980). Army ants are therefore an important component of rain forest ecology.

The focus of the paper is a well-studied (Rettenmeyer 1963, Willis 1967, Schneirla 1971, Franks 1982a,b, 1989) population of about fifty colonies of the neotropical army ant *Eciton burchelli*, confined to Barro Colorado Island (BCI) in Gatun Lake, Panama. These colonies have a single queen, reproduce by fission and the female reproductives are flightless. They are therefore descendants of those marooned when the lake was formed in 1914 by the construction of the Panama canal, and there has been no opportunity for further natural colonisation. The population is not necessarily genetically isolated, since the males can fly.

It seems likely that the population is regulated by intraspecific competition between colonies for patches of social insect prey (not army ants) that take about 200 days to recover from army ant occupation on BCI (Franks 1982a). Although *E. burchelli* also preys on large, non-social arthropods such as cockroaches, the levels of these recover so rapidly after a raid by army ants (Franks 1982a) that we assume they have negligible impact on the competition between colonies.

Colonies of *E. burchelli* exhibit a 35 day activity cycle (Willis 1967, Schneirla 1971), consisting of a statary phase and a nomadic phase. During the statary phase of about three weeks the colony occupies a fixed bivouac from which raids are made into the surrounding forest on most days. A typical distance covered by such a raid is about 90 metres (Franks, 1982a). During the nomadic phase raids take place every day, and the whole bivouac or nest is moved to a new position near the end of the raid. The direction taken each day is correlated with that taken on the previous day (Franks and Fletcher, 1983). By the end of the nomadic phase the colony has arrived at a new statary phase bivouac which is typically about 530 metres from the old one (Willis, 1976). Patches currently occupied by another colony tend to be avoided (Franks and Bossert, 1983). This activity cycle is the basic time step in the model during which, for modelling purposes, colonies are assumed to exploit one patch of prey in the forest. Each patch represented an area of about 30,000 square metres, roughly the area thought to be affected by the raids produced during the statary phase of the activity cycle.

We develop a stochastic cellular automata model (Caswell and Etter, 1993) for the population of *E. burchelli* on BCI, structured by taking into account the size of the colonies, and including density-dependent mortality. The cells in the model represent patches of land on BCI, each of which may be in one of a finite, but unusually large, number of states (if unoccupied, its state represents its stage of recovery from the last army ant occupation, if occupied, the size of the colony in occupation). An important parameter in the model is the length of time a patch of habitat takes to recover after army ant occupation. By varying it the effect of habitats of differing quality is simulated, good quality habitat being defined to be that which recovers quickly.

The model is simulated on a computer. It is then analysed using a mean field approximation, which gives reasonably good results. This allows a derivation of equilibrium population size. An improvement to the mean field approximation is derived that takes into account the difference between the mean field in a neighbourhood of any given colony and that in the island as a whole. It gives slightly better agreement with the simulations, but its main advantage is in elucidating the role of the patch neighbourhood N. For an occupied patch this is composed of the patches to which the occupying colony may move at the next time step, and for any patch is composed of the patches from which an occupying colony may arrive at the next time step. The advantage of moving a reasonably large distance between successive statary phase bivouacs is demonstrated.

2. The computer simulations

We set up a discrete time stochastic cellular automata (CA) model for the system. A CA model is a set of cells, each of which at any given time can be in one of a finite number of states, together with a set of rules governing how the state of each cell changes with time. The time step models the activity cycle time, about 35 days for *E. burchelli*. The set of cells is a lattice of K points on the computer, modelling K patches of forest on the island that can be exploited by the ants, and we shall refer to the cells as patches. Define the *age* of a patch to be the number of time steps since it was last exploited; it is of age zero if it is currently occupied by a colony of ants. Let n (typically six) be the number of time steps taken for a patch to recover from army ant exploitation. A patch that has not yet recovered nor is on the verge of recovery at a time step is referred to as *young*; all other patches are *old*. (A patch of age n is on the verge of recovery at the time step, so is old.) We shall divide the ant colonies up into size classes, the smallest being of size one unit and the largest of size $2m-1$ (typically nine) units. The *state* of a patch is its age, if unoccupied, or the size of its occupying colony, if occupied. This would give an infinite number of states except that the age of an old patch is immaterial, so that all old patches are taken to be in the same state.

The colony size referred to above is its size at the *beginning* of the time step. At the end of the time step, a colony that has been occupying a patch that was old on arrival increases in size by one unit; a colony that has been occupying a patch that was young decreases in size by one unit. A colony that by this rule would reach a size of $2m$ units divides into two colonies of size m units; a colony that would reach a size of zero units ceases to exist. Maximum colony sizes in nature are roughly 650,000 workers (Franks, 1985); therefore one size unit corresponds to about 65,000 workers (assuming $m = 5$), a not unreasonable net change in colony size over a single activity cycle. At the next time step the colonies move to any one of the patches a fixed distance away with equal probability, and the process is repeated. On BCI the diameter of each patch is about 180 metres, whereas the distance between successive statary phase bivouac sites is about 530 metres. There are various ways in which this can be approximated on a square lattice; we chose to allow each colony to move to any of the 24 patches at the edge of a 7×7 square whose centre is the current position. We shall refer to these 24 patches as the *neighbourhood N* of the current position. To investigate the consequences of moving such a large distance, we also ran simulations in which each colony was only allowed to move to one of its eight nearest neighbours. We shall refer to these two models as the jumping CA (JCA) and stepping CA (SCA) models. There are problems in interpreting the neighbourhood near edges of the island. We use periodic boundary conditions, i.e. any colony that disappears off one side of the island simply reappears at the other. This is for simplicity in coding only; more realistic boundary conditions would make colonies turn back in some random or determinate direction when they reach the coast, but we do not expect the particular choice of boundary conditions within this class to affect the results unduly for islands of reasonable size. Similarly, we do not expect the shape of the island to be crucial, as long as it is not very convoluted. Since the area of BCI is about 500 times the area of a patch we took a lattice of 20×25 points to represent the island.

The simulation is allowed to run until the system reaches an asymptotic state, which might in general be a steady state, a periodic solution, or chaotic behaviour. Since our system is stochastic, we can only expect this state (if it is non-trivial) to be asymptotic in distribution, for example the numbers of colonies of various sizes averaged over many simulations may reach a steady state. For an island the size of BCI, our simulations resulted in an oscillation of small amplitude in the numbers of colonies and other variables of interest. The mean of the oscillation for various variables is given below in Table 1, and compared with the data that are available for BCI and with the mean field approximations that are to be discussed in the next two sections. The data are not good enough to decide whether the oscillation found in the simulations also occurs on the island, or whether it is an artefact of the model. The oscillation is weakened if a third type of patch is introduced which is intermediate in effect between young and old patches. This may be a more realistic model of the biological situation.

3. The mean field approximation

In this section we derive an approximation to the CA model of section 2 that is amenable to mathematical analysis, which we shall refer to as the mean field (MF) model. The variables of interest are the numbers of ant colonies of various sizes and the numbers of patches of forest of various ages. At each time step, the rules of colony death and size change as given in section 2 are followed. The colonies then move to *any patch on the island* with equal probability, subject to the constraint that no two colonies end up on the same patch, and the process is repeated. This constraint was not applied in the simulations, but was felt to be biologically realistic and simpler to analyse. In the real situation and in the simulation of section 2 the colonies may of course only move to patches in the neighbourhood N of the given patch. The MF approximation is not intended to be a realistic model of such a process, but it may nevertheless approximate its behaviour very closely. It will isolate the temporal features of the population dynamics from the spatial features and give some clues as to what behaviour to expect from the real system. It is akin to the mean field approximation of statistical mechanics, and its success depends on the typical distances that are moved at each time step; for distances that are biologically realistic in this application we expect to get reasonably good results (Durrett and Levin, 1994). It is crucial that the distance moved between successive statary phase bivouacs is much greater than the diameter of the patches.

Let the proportion of patches that are of age j be y_j^t; thus $\Sigma_{j=0}^{\infty} y_j^t = 1$. Let the proportion of young patches be $y^t = \Sigma_{j=0}^{n-1} y_j^t$. Let the proportion of patches that are occupied at time t by an ant colony of size i units be x_i^t. Then the proportion of patches that are occupied by an ant colony of any size is given by $x^t = \Sigma_{i=1}^{2m-1} x_i^t$. Clearly,

$$x^t = y_0^t \tag{3.1}$$

At any time step, the chance of a colony finding itself in a favourable environment (an old patch) is $1 - y^t$, and the chance of an unfavourable environment is y^t. Therefore the equations satisfied by the ant (x) variables are

$$x_1^{t+1} = x_2^t y^t$$

$$x_2^{t+1} = x_1^t(1 - y^t) + x_3^t y^t$$

$$\vdots$$

$$x_{m-1}^{t+1} = x_{m-2}^t(1 - y^t) + x_m^t y^t$$

$$x_m^{t+1} = x_{m-1}^t(1 - y^t) + x_{m+1}^t y^t + 2x_{2m-1}^t(1 - y^t) \tag{3.2}$$

$$x_{m+1}^{t+1} = x_m^t(1 - y^t) + x_{m+2}^t y^t$$

$$\vdots$$

$$x_{2m-2}^{t+1} = x_{2m-3}^t(1 - y^t) + x_{2m-1}^t y^t$$

$$x_{2m-1}^{t+1} = x_{2m-2}^t(1 - y^t)$$

At time t+1, the number of patches of age $j \geq 1$ is equal to the number of patches of age $j - 1$ at time t that are not occupied by an ant colony at time t+1, so that the equations satisfied by the patch (y) variables are

$$y_j^{t+1} = y_{j-1}^t(1 - x^{t+1}) \tag{3.3}$$

for each $j \geq 1$.

The equations (3.1), (3.2) and (3.3) comprise the system we must analyse, and we first derive some consequences that will be useful later. Adding together the equations (3.2),

$$x^{t+1} = (x^t + x_{2m-1}^t)(1 - y^t) + (x^t - x_1^t)y^t \tag{3.4}$$

Multiplying the i-th of equations (3.2) by i, for $i = 1, 2, \cdots, 2m-1$, and adding gives

$$z^{t+1} = (z^t + x^t)(1 - y^t) + (z^t - x^t)y^t = z^t + x^t(1 - 2y^t) \tag{3.5}$$

where we have defined $z^t = \Sigma_{i=0}^{2m-1} i x_i^t$. (Although this observation is not relevant to the analysis, we may note that $65{,}000Kz^t$ is a measure of the total number of individual ants on the island.)

Let us now find the steady state of this system; we represent the values of the variables at the steady state by stars. From (3.5),

$$z^* = z^* + x^*(1 - 2y^*)$$

so that for a steady state with $x^* \neq 0$,

$$y^* = \frac{1}{2} \tag{3.6}$$

Then from (3.4),

$$x^* = (x^* + x^*_{2m-1})(1 - y^*) + (x^* - x^*_1)y^*$$

so that $x^*_{2m-1}(1 - y^*) - x^*_1 y^* = 0$, or with $y^* = ½$, $x^*_{2m-1} = x^*_1$. Then, using the steady state versions of equations (3.2),

$$x^*_i = x^*_{2m-i} = ix^*_1 \tag{3.7}$$

for $i = 1, 2, \cdots, m$, and

$$x^* = \Sigma_{i=1}^{2m-1} x^*_i = m^2 x^*_1 \tag{3.8}$$

A testable prediction of the model is therefore that the size distribution of colonies is triangular.

From the steady state versions of (3.1) and (3.3),

$$y^*_j = x^*(1 - x^*)^j \tag{3.9}$$

for $j = 0, 1, \cdots$, and

$$y^* = \Sigma_{j=0}^{n-1} y^*_j = \Sigma_{j=0}^{n-1} x^*(1 - x^*)^j = 1 - (1 - x^*)^n$$

so that

$$x^* = 1 - (1 - y^*)^{\frac{1}{n}} = 1 - (\frac{1}{2})^{\frac{1}{n}} \tag{3.10}$$

Equations (3.6) to (3.10) give the values of the variables at the steady state.

The system (3.1), (3.2), (3.3) is an infinite system of difference equations. There is a decoupled subsystem of order $2m + n - 1$ consisting of (3.1), (3.2) and the first $n - 1$ equations of (3.3). With $m = 5$ and $n = 6$ this is a system of order 15, which can be analysed numerically. The numerical results indicate that the system is stable.

Numerical values of the steady state when $m = 5$, $n = 6$, and the total number of patches $K = 500$ are given by

$$Kx^* = K\left[1 - (\frac{1}{2})^{\frac{1}{n}}\right] \approx 54{\cdot}6 \tag{3.11}$$

$$Ky^* = \frac{1}{2}K = 250 \tag{3.12}$$

The mean colony size is given by

$$E(i) = \frac{\Sigma_{i=1}^{m} i x_i^*}{\Sigma_{i=1}^{m} x_i^*} = m = 5 \tag{3.13}$$

and the variance of this size by

$$V(i) = E(i^2) - (E(i))^2 = \frac{\Sigma_{i=1}^{m} i^2 x_i^*}{\Sigma_{i=1}^{m} x_i^*} - \left[\frac{\Sigma_{i=1}^{m} i x_i^*}{\Sigma_{i=1}^{m} x_i^*}\right]^2 = \frac{m^2 - 1}{6} = 4 \tag{3.14}$$

By defining the generating function

$$Y(s) = \Sigma_{j=0}^{\infty} y_j^* s^j = \Sigma_{j=0}^{\infty} x^*(1-x^*)^j s^j = \frac{x^*}{1 - (1 - x^*)s}$$

it is easy to show that the mean patch age is given by

$$E(j) = \Sigma_{j=0}^{\infty} j y_j^* = Y'(1) = \frac{1 - x^*}{x^*} \approx 8{\cdot}17 \tag{3.15}$$

and the variance of this age by

$$V(j) = E(j^2) - (E(j))^2 = \Sigma_{j=0}^{\infty} j^2 y_j^* - (\Sigma_{j=0}^{\infty} j y_j^*)^2$$

$$= Y''(1) + Y'(1) - (Y'(1))^2 = \frac{1 - x^*}{x^{*2}} \approx 74{\cdot}8 \tag{3.16}$$

The standard deviation is therefore $8{\cdot}65$, greater than the mean. This suggests that most patches are younger than eight units, (in agreement with the result that half the patches are young), but a few are much older.

The mean number of colony extinctions per unit time is equal to the mean number of fissions per unit time, since we are in a dynamic steady state, and is given by

$$Ky^* x_1^* = K(1 - y^*) x_{2m-1}^* = \frac{Kx^*}{2m^2} \approx 1{\cdot}09 \tag{3.17}$$

4. An improved mean field approximation

The model above takes no account at all of spatial effects. It therefore does not permit one to explore the consequences of moving longer or shorter distances in the nomadic phase, since the approximation is independent of these distances. The fact that a colony is more likely to return to a patch that it has recently exploited than one on the other side of the island, simply because the former patch is nearer, is not considered; we shall remedy this deficiency here.

Consider the situation at the beginning of the time step t, when colonies move to the patch that they will occupy for that time step. We have so far proposed that they move at random to any patch on the island with equal probability, so that the chance that any given colony has of landing on a good patch is equal to the proportion of good patches on the island, and the chance that any given patch has of being occupied is equal to the proportion of occupied patches at the next time step. That is, these chances depend on the two mean fields on the island, those of good patches and colonies. In fact, though, a colony lands somewhere in its neighbourhood N, and a patch can only be occupied by a colony from somewhere in N, and the idea of this section is to treat the mean fields in N separately from the mean fields in the rest of the island $I \backslash N$. The patch equation (3.1) is unaffected by this change, so we have

$$y_0^{t+1} = x^{t+1} \tag{4.1}$$

We first derive the ant equations. At each time step, each colony is taken to move to any point in its neighbourhood N with equal probability, again subject to the constraint that no two colonies end up on the same patch. We have to calculate the chance of a colony finding itself in a favourable patch, that is the mean field of good patches in the neighbourhood N. The colony came from somewhere in N on the previous time step, so we know that N has at least one young patch A in it. The standard mean field approximation is made in $N \backslash A$, the set of patches in the neighbourhood N that are not A, that the mean field there is the same as that in the rest of the island $I \backslash N$. This is only an approximation and will be justified by the fact that it gives reasonable results. Let the mean field proportion of young patches in N be y' and in $I \backslash P$ be y'', where I is the whole island. Then, by counting young patches on the island in three different ways,

$$1 + (K-1)y'' = |N|y' + (K-|N|)y'' = Ky$$

where $|N|$ is the number of patches in N. Eliminating y'' from these equations we obtain $y' = P + Qy$, or $1 - y' = Q(1-y)$, where $Q = \frac{K}{K-1}\,\frac{|N|-1}{|N|}$, $P = 1 - Q$. Hence the chance of a favourable patch is $Q(1-y^t)$ and that of an unfavourable one is $P + Qy^t$. The equations (3.2) become

$$\left.\begin{aligned}
x_1^{t+1} &= (P+Qy^t)x_2^t \\
x_2^{t+1} &= Q(1-y^t)x_1^t + (P+Qy^t)x_3^t \\
&\vdots \\
x_{m-1}^{t+1} &= Q(1-y^t)x_{m-2}^t + (P+Qy^t)x_m^t \\
x_m^{t+1} &= Q(1-y^t)x_{m-1}^t + (P+Qy^t)x_{m+1}^t + 2Q(1-y^t)x_{2m-1}^t \\
x_{m+1}^{t+1} &= Q(1-y^t)x_m^t + (P+Qy^t)x_{m+2}^t \\
&\vdots \\
x_{2m-2}^{t+1} &= Q(1-y^t)x_{2m-3}^t + (P+Qy^t)x_{2m-1}^t \\
x_{2m-1}^{t+1} &= Q(1-y^t)x_{2m-2}^t
\end{aligned}\right\} \tag{4.2}$$

Now let us consider the patch equations. Each of the equations (3.3) must be modified to take account of the adjusted mean fields of colonies in their neighbourhoods. It is important to note that these adjusted mean fields are different depending on the age of the patch. First consider a patch that is occupied (zero units old). Then we know nothing about N to distinguish it from the rest of the island, so that its mean field of colonies is simply x. Next consider a patch that is one unit old. Then there is definitely a colony at one point A of N, the colony that departed from the patch in question. Let the mean field proportion of colonies in N be x' and in $I \backslash P$ be x''. Counting the colonies on the island in three different ways,

$$1 + (K-1)x'' = |N|x' + (K-|N|)x'' = Kx$$

so that $x' = P + Qx$, $1 - x' = Q(1-x)$, with P and Q as before. Now let us consider a patch that is more than one unit old, and let x''' denote the mean field of colonies in N. Again counting colonies in different ways,

$$y_0 x + y_1 x' + (1 - y_0 - y_1)x''' = x \tag{4.3}$$

so that

$$1 - x''' = \frac{1 - y_0 - Qy_1}{1 - y_0 - y_1}(1 - x)$$

Equations (3.3) become

$$\left.\begin{aligned} y_1^{t+1} &= y_0^t(1 - x^{t+1}), \\ y_2^{t+1} &= Qy_1^t(1 - x^{t+1}), \\ y_j^{t+1} &= \frac{1 - y_0^t - Qy_1^t}{1 - y_0^t - y_1^t} y_{j-1}^t(1 - x^{t+1}), \end{aligned}\right\} \tag{4.4}$$

the last of these holding for all $j \geq 3$. Adding together equations (4.2),

$$x^{t+1} = Q(1 - y^t)(x^t + x_{2m-1}^t) + (P + Qy^t)(x^t - x_1^t) \tag{4.5}$$

Multiplying the i-th of equations (4.2) by i and adding gives

$$z^{t+1} = Q(1 - y^t)(z^t + x^t) + (P + Qy^t)(z^t - x^t) \tag{4.6}$$

Equation (4.5) at the steady state gives

$$Q(1 - y^*) = P + Qy^* = ½ \tag{4.7}$$

Equations (4.2) again lead to (3.7) and (3.8), and the patch equations give

$$\left.\begin{aligned} y_0^* &= x^* \\ y_1^* &= x^*(1 - x^*) \\ y_j^* &= Qx^*(1 - x^*)^2(1 - Qx^*)^{j-2} \end{aligned}\right\} \tag{4.8}$$

the last of these holding for all $j \geq 2$. Adding the first n of these,

$$y^* = 1 - (1 - x^*)^2(1 - Qx^*)^{n-2} \tag{4.9}$$

The equations (4.1), (4.2) and the first $n - 1$ of (4.4) comprise a system of order $2m + n - 1$ that we must analyse. Numerical results show that the steady state is stable for all biologically reasonable values of $|N|$.

The quantities of primary interest are therefore the steady state values of the number of colonies and their size distribution, the number of young patches and the age distribution of patches, and the rates of colony fission and extinction. These of course depend on the number $|N|$ of points in the neighbourhood, which depend on the model for the nomadic phase. As in the computer simulations we consider two possibilities, the jumping mean field (JMF) model in which each colony is assumed to move to one of the 24 patches a distance of three patch lengths away at the end of each time step, and the stepping mean field (SMF) model in which each colony is assumed to move to one of the eight patches adjacent to its current patch. The JMF model is more biologically realistic.

It is more difficult to obtain numerical values for the quantities of interest in the revised model of this section than in that of the previous section, since some of the equations whose counterparts gave explicit formulae in the last section no longer do so in this section; in particular (4.9) can no longer be solved to give an explicit formula for x^* as a function of y^*. However a good approximation can be obtained as a perturbation of the solution of the corresponding equation (3.10) in the last section, or the equation can be solved numerically. The difficulties do not apply to the mean of the colony size, where the calculations go through exactly as before, so that equations (3.13) and (3.14) still hold. Results for some other variables are given in section 5. Expressions for the mean and variance of the patch age may be found by a generating function approach, as in section 3.

5. Comparison of the models

The results of sections 2 to 4 are summarised in Table 1. All the models except the stepping models give results in reasonable agreement with biological data, although they underestimate the true value of the turnover rate by about 35%. The turnover rate is the rate of fission, or rate of death, since in a dynamic steady state the two quantities are equal, measured in colonies per time step. This may be improved by reducing the number of size classes, which is probably not biologically realistic, or by including senescence or some other form of density-independent mortality in the model.

The jumping simulation (JCA) model is assumed to reflect biological reality most closely, the mean field (MF) model is a simple approximation of it, and the jumping mean field (JMF) model an improved approximation. The stepping (SCA and SMF) models represent the effect of shorter distances being covered in the nomadic phase.

It is interesting to note how close the MF model is to the JCA model, vindicating the use of the mean field approximation in this case, and allowing very little room for improvement by the JMF model. However, the MF is not nearly such a good approximation to the SCA model, as expected from the general theory (Durrett and Levin, 1994), and the improvement given by the SMF model is much more necessary in this case. This is one reason for the development of the improved mean field approximations; another is that it allows us to compare the jumping and stepping strategies. We shall do this in the next section.

6. Competition between nomadic phase strategies

In this section we consider the advantage in moving a reasonably long distance in the nomadic phase. Let us consider a population with a particular nomadic phase strategy $\tilde{N}$ (represented by the neighbourhood to which it moves) invaded by a mutant population with a strategy $\hat{N}$. We shall denote variables and parameters associated with the wild type population by tildes, and those with the mutant population by hats. In particular we will label patches with a tilde or a hat according to whether they were last occupied by the wild type or the mutants; for example $\tilde{y}_j$ is the proportion of patches that were both (a) last occupied j time units ago and (b) last occupied by a colony of wild type. We define $\tilde{Y} = \Sigma_{j=0}^{\infty} \tilde{y}_j$, (the proportion of patches, young and old, that are occupied or were last occupied by a colony of wild type), and $\hat{Y} = \Sigma_{j=0}^{\infty} \hat{y}_j$, so that $\tilde{Y} + \hat{Y} = 1$. We also define $x = \tilde{x} + \hat{x}$, $y = \tilde{y} + \hat{y}$.

The patch equation (3.1) still holds for the total population and for each population separately, so we have

$$y_0^{t+1} = x^{t+1}\ , \quad \tilde{y}_0^{t+1} = \tilde{x}^{t+1}\ , \quad \hat{y}_0^{t+1} = \hat{x}^{t+1} \qquad (6.1)$$

For the wild type ant equations, we have to calculate the chance of a colony finding itself in an unfavourable patch, that is the mean field of bad patches in the neighbourhood $\tilde{N}$. The mean field of bad patches last occupied by a colony of wild type is calculated as in section 4, and the mean field of bad patches last occupied by a mutant colony is simply $\hat{y}$, so that we obtain

$$\tilde{x}_1^{t+1} = (\tilde{P} + \tilde{Q}\tilde{y}^t + \hat{y}^t)\tilde{x}_2^t$$

$$\tilde{x}_2^{t+1} = (\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_1^t + (\tilde{P} + \tilde{Q}\tilde{y}^t + \hat{y}^t)\tilde{x}_3^t$$

$$\vdots$$

$$\tilde{x}_{m-1}^{t+1} = (\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_{m-2}^t + (\tilde{P} + \tilde{Q}\tilde{y}^t + \hat{y}^t)\tilde{x}_m^t$$

$$\tilde{x}_m^{t+1} = (\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_{m-1}^t + (\tilde{P} + \tilde{Q}\tilde{y}^t + \hat{y}^t)\tilde{x}_{m+1}^t + 2(\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_{2m-1}^t \qquad (6.2)$$

$$\tilde{x}_{m+1}^{t+1} = (\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_m^t + (\tilde{P} + \tilde{Q}\tilde{y}^t + \hat{y}^t)\tilde{x}_{m+2}^t$$

$$\vdots$$

$$\tilde{x}_{2m-2}^{t+1} = (\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_{2m-3}^t + (\tilde{P} + \tilde{Q}\tilde{y}^t + \hat{y}^t)\tilde{x}_{2m-1}^t$$

$$\tilde{x}_{2m-1}^{t+1} = (\tilde{Q} - \tilde{Q}\tilde{y}^t - \hat{y}^t)\tilde{x}_{2m-2}^t$$

Similar equations hold for the mutant ant population with the tildes and hats transposed.

Similar equations hold for the mutant ant population with the tildes and hats transposed.

Now let us consider the patch equations. We need to calculate the mean fields of both kinds of colonies in the neighbourhood of each kind of patch. These adjusted mean fields are again different depending on the age of the patch, but also on the kind of colony that last occupied it. If a patch is occupied or was last occupied by colony of wild type, then we know nothing about the mean field of mutant colonies in its mutant neighbourhood to distinguish it from the rest of the island, so its mean field of mutants is $\hat{x}$. If a patch is occupied by colony of wild type, its mean field of colonies of wild type is simply $\tilde{x}$. Next consider a patch that is one unit old, and was last occupied by a colony of wild type. Then there is definitely a colony of wild type at one point P of $\tilde{N}$, the colony that departed from the patch in question. We may calculate the mean fields of colonies of wild type in $\tilde{N}$ in exactly the same way as in section 4, to obtain $\tilde{x}' = \tilde{P} + \tilde{Q}\tilde{x}$, $1 - \tilde{x}' = \tilde{Q}(1 - \tilde{x})$, with $\tilde{P}$ and $\tilde{Q}$ as before. Finally consider a patch that is more than one unit old and was last occupied by a colony of wild type. The argument of section 4 must be modified to take account of the fact that not all patches are of type $\tilde{Y}$, and (4.3) becomes

$$\tilde{y}_0 \tilde{x} + \tilde{y}_1 \tilde{x}' + (\tilde{Y} - \tilde{y}_0 - \tilde{y}_1)\tilde{x}''' + \hat{Y}\tilde{x} = \tilde{x}$$

leading to

$$1 - \tilde{x}''' = \frac{\tilde{Y} - \tilde{y}_0 - \tilde{Q}\tilde{y}_1}{\tilde{Y} - \tilde{y}_0 - \tilde{y}_1}(1 - \tilde{x})$$

Equations (4.4) become

$$\left.\begin{aligned} \tilde{y}_1^{t+1} &= \tilde{y}_0^t(1 - x^{t+1}), \\ \tilde{y}_2^{t+1} &= \tilde{y}_1^t\{\tilde{Q}(1 - \tilde{x}^{t+1}) - \hat{x}^{t+1}\}, \\ \tilde{y}_j^{t+1} &= \tilde{y}_{j-1}^t \left[\frac{\tilde{Y}^t - \tilde{y}_0^t - \tilde{Q}\tilde{y}_1^t}{\tilde{Y}^t - \tilde{y}_0^t - \tilde{y}_1^t}(1 - \tilde{x}^{t+1}) - \hat{x}^{t+1} \right], \end{aligned}\right\} \tag{6.3}$$

the last of these holding for all $j \geq 3$, and with similar equations holding with the tilde and the hat transposed.

The equations of this section reduce to those of section 4 if there is initially only one nomadic phase strategy, so the steady state analysis of that section leads to two steady states here. To determine the stability of these steady states we solved the equations numerically, taking initial conditions to be a small number of *J* strategists and a large number of *S* strategists. The results presented in Fig. 1 show that the *J* strategists successfully invade the *S* strategists, finally driving them to extinction.

7. Conclusions

We have shown that some aspects of the population dynamics of army ants may be successfully modelled by a cellular automata approach, and simulated on a computer. The mean field approximation represents a tractable alternative to simulation in modelling such populations whenever the distances moved in the nomadic phase are large compared to the statary phase patch diameter, as they are in *Eciton burchelli*. However it is much less successful when movements are small, that is, when interactions are more local. An improved approximation can then be made by treating the mean fields in the relevant neighbourhoods differently from those in the rest of the island. It will be important to have the mean field approximation available as a tractable alternative to simulation when we come to estimate expected times to extinction (Britton *et al.*, in preparation), since on large islands these times are very long and therefore impracticable to obtain by simulation.

Equilibrium population sizes given by the model were in good agreement with data, but model turnover rates under-estimated the data by about 35%. This suggests that density-dependent mortality is not the only cause of turnover, and that some kind of density-independent mortality may be important. A variant of the model including density-independent mortality does give higher turnover rates. For example, a model in which queens live on average six years and colonies die when their queen dies, and with m=5, n=6 as usual, gives with the mean field approximation an equilibrium population size of $Kx^* = 48.6$ and a turnover rate of about 1.3, an under-estimate of only about 20%. The alternative is that spending the statary phase in a bad patch has an even harsher effect, and/or spending it in a good patch an even more beneficial effect, than it does in our model. A value of m=4, equivalent to a net loss or gain of 25% more ants in these situations, and with n=6, gives an equilibrium population size of $Kx^* = 54.6$ and a turnover of about 1.7, exceeding the field data by about 5%.

We have also considered the importance of the large distances covered between successive statary phase bivouacs from a biological point of view. The analysis here suggests that the most important parameter in determining the effect that the nomadic phase strategy has on growth rate is the re-raid probability P, which, if we neglect boundary effects, depends only on $|N|$. In other words, the more patches there are in the neighbourhood N that is accessible in the nomadic phase, the higher is the growth rate of the individual colony concerned. We have not taken into account any costs associated with moving large distances, and we suggest that were these to be included there would be an optimum distance to move in the nomadic phase. It is interesting to note that if the colony does not always move the full distance possible, then more patches are available to it. A strategy that has some random variation in raid length and in the directions moved on successive days in the nomadic phase may therefore be better than one in which these quantities are always very similar (see Franks and Fletcher, 1983).

The behaviour of colonies near the coast was not modelled in this paper, and the simplest possible (periodic) boundary conditions were chosen. These were assumed to have effects similar to more realistic conditions, as long as the island was reasonably large and not too irregular. But for small or irregular islands it might be necessary to model the effect of the behaviour of the colonies near the coastline more carefully. In the cellular automata approach some kind of reflection might be adopted. In the mean field approach, one possibility might be to adapt the method of improved mean field approximation to take account of these effects. As mentioned above, this paper suggests that the number of neighbouring patches that can be reached from any given patch is the most important feature of the spatial organisation. This could be estimated for any given size and shape of island, and the corresponding equilibrium population size estimated. We would predict that an island with a very convoluted coastline would not be able to support such a large population as a rounder island of the same area.

Figure legends

Fig. 1. The improved mean field approximation was used to simulate the effect of introducing a single colony of mutant jumpers, that is colonies that move three patch diameters in the nomadic phase, into a population of wild type steppers, that is colonies that move one patch diameter. The mutants drive the wild type to extinction in 500 cycles, less than fifty years. The hump at the beginning of the graph of the wild type population occurs because the initial wild type population size was not at equilibrium.

Table 1. Summary of results of the various models compared with data from BCI.

Fig. 1. Mutant jumpers in a population of steppers

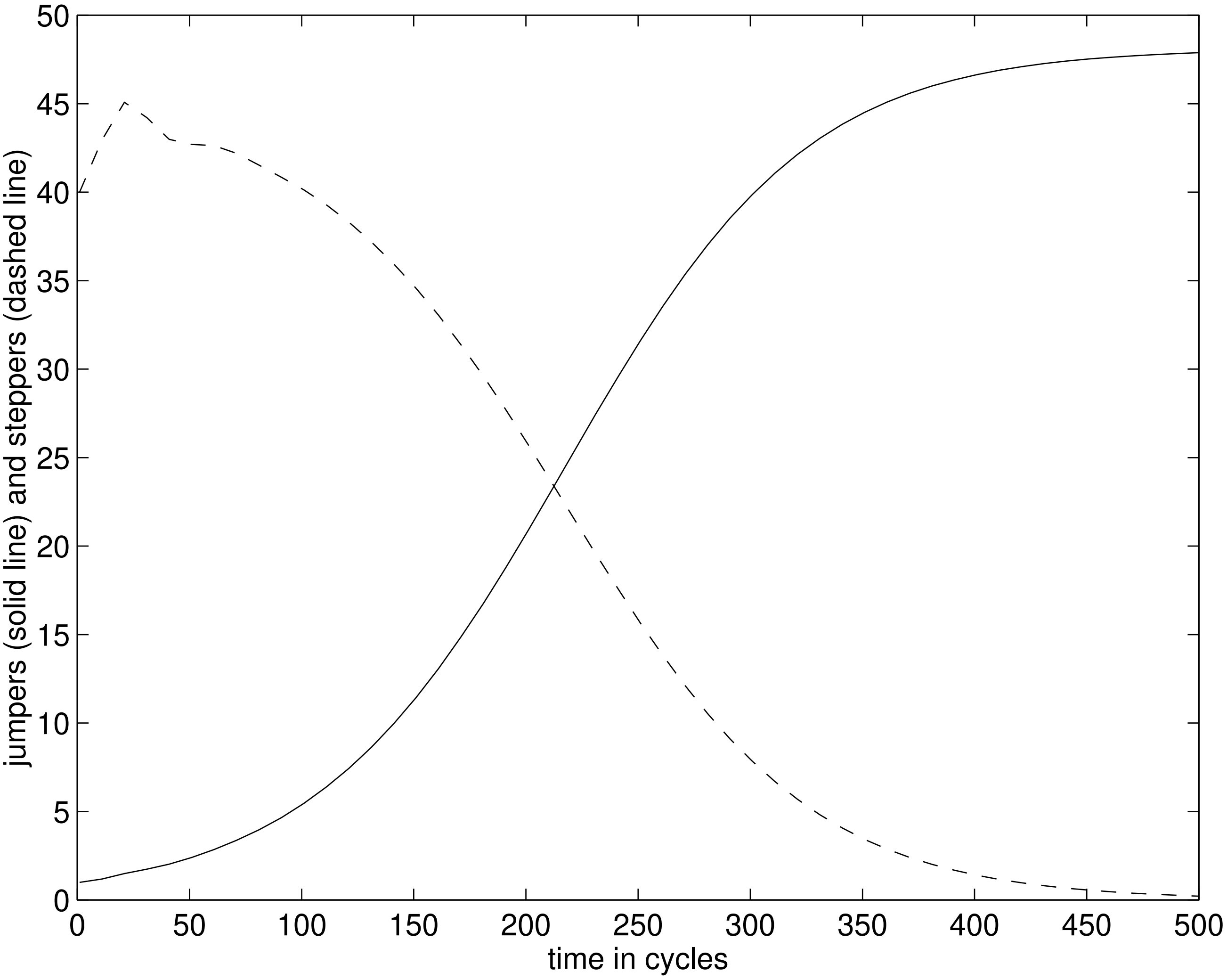

Table 1

	BCI	JCA	SCA	MF	JMF	SMF
Kx^*	45-55	54.5	40.8	54.5	52.9	48.7
Ky^*	?	233	174	250	240	215
$\mathbb{E}i$	?	5	5	5	5	5
$\mathbb{E}j$	?	9.17	15.45	8.17	8.76	10.4
turnover	1.6	1.22	1.16	1.09	1.06	0.97