

# Relating individual behaviour to population dynamics

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How do the behavioural interactions between individuals in an ecological system produce the global population dynamics of that system? We present a stochastic individual-based model of the reproductive cycle of the mite *Varroa jacobsoni*, a parasite of honeybees. The model has the interesting property in that its population level behaviour is approximated extremely accurately by the exponential logistic equation or Ricker map. We demonstrated how this approximation is obtained mathematically and how the parameters of the exponential logistic equation can be written in terms of the parameters of the individual-based model. Our procedure demonstrates, in at least one case, how study of animal ecology at an individual level can be used to derive global models which predict population change over time.

**Keywords:** population dynamics; *Varroa jacobsoni*; individual-based modelling; logistic equation

## 1. INTRODUCTION

Although there are many ways of approaching the modelling of ecological systems, they can usually be categorized as either ‘top-down’ or ‘bottom-up’. In top-down models, the relationships of interest are between variables that capture the global properties of a system, e.g. the relationship between the size of a honeybee colony and the number of parasites it contains. Nicholson (1954) was one of the first to describe how differential equations can be used as top-down models of the types of population change that can result from interactions between species and resources. Such models are derived both by reasoning phenomenologically about the interactions and by observing population changes overtime. Differential equations are now widely and successfully used in understanding and predicting population dynamics (Murray 1989; Schaffer & Kot 1996; Earn *et al.* 1998).

An area of top-down modelling that has attracted a lot of research interest is modelling density dependence in single-species populations using difference equations. Based on Nicholson’s (1954) concepts of resource competition, Hassell (1975) proposed a general model for single species density-dependent populations:

$$a_{t+1} = \gamma a_t (1 + \alpha a_t)^{-\beta}, \quad (1)$$

where  $a_t$  and  $a_{t+1}$  are populations in successive generations,  $\gamma \geq 0$  may be thought of as the low population density growth rate,  $\beta \geq 0$  is a constant defining the density dependent feedback term and  $\alpha \geq 0$  is a scaling. By fitting this model to population time-series for a variety of species, Hassell *et al.* (1976) attempted—albeit with limited success—to reconstruct the population dynamics of various laboratory studies. Recent work has produced better and more general methods for reconstructing these dynamics (Turchin & Taylor 1992; Zhou *et al.* 1997), and these methods have been widely applied in the analysis of yearly population census data (Cheke & Holt 1993; Turchin *et al.* 2000). This top-down approach is most often concerned with determining the relative

importance of density dependence—which can cause periodicity and chaos—and exogenous environmental factors, which are not represented in equation (1). It is not concerned with establishing how the individual interactions of the animals in the population produce the dynamics. Although Hassell (1978) gave an account of how some top-down models are related to Poisson-distributed encounters between individual predators and prey, in general top-down models are derived from reasoning about interactions at a population level.

In contrast, bottom-up models start from a description of local interactions. For example, how and when do parasites reproduce? What happens when two or more parasites compete for the same resource? The experimental data which answers these questions can then be built into an individual-based model (Kindlmann & Dixon 1996; Lomnicki 1999). Analysis and computer simulation of the model should produce, as emergent properties, the global relationships seen in the real world, without them being built explicitly into the model. By providing insight into the detailed interactions at the local level, bottom-up models allow the validity of the phenomenological assumptions made in global, top-down models to be tested directly. In theory, individual-based modelling is thus used to determine when a particular set of parameterized equations are applicable to modelling the population dynamics of a particular ecological system. In practice, however, individual-based models tend to be complicated and, while models should reflect the true complexity of the organisms they attempt to model, this complexity can actually obstruct understanding of the relationship between an individual and population.

An interesting and important question is therefore whether we can use individual-based models for making reliable and testable predictions about population dynamics. This question has received particular attention with regard to establishing the relationship between local interactions and the generation of spatially heterogeneous patterns (Durrett & Levin 1994; Czaran 1998; Rand 1999). In this paper, we look at a spatially well-mixed system produced by the interactions between the parasitic mite *Varroa* and its natural host the Asian honeybee. The

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link between individual and population is achieved by deriving a nonlinear mean-field approximation of a simple though realistic stochastic model of mite reproduction. We thus come to a complete understanding of how changes in the parameters which govern individual behaviour will affect the dynamics and equilibria of the population as a whole. The parameters of the population are no longer simply adjustable quantities used to obtain the best fit to time-series data. Rather, they are related to more fundamental parameters which can be obtained by examining the reproductive behaviour of individual organisms.

## 2. MODELLING VARROA MITE REPRODUCTION

### (a) *The mite's reproductive cycle*

The large mite *Varroa jacobsoni* (1 mm × 1.6 mm) is an ectoparasite which attaches itself to the bodies of worker (female) and drone (male) honeybees. The Asian honeybee *Apis cerana* F. has a balanced host–parasite relationship with the mite (Boecking & Ritter 1994); 63 out of 64 Asian bee colonies in South Thailand were found to contain low levels—usually less than 100 mites—of infestation (Rath & Drescher 1990). Parasitism may affect the vitality of some drone bees but does not greatly affect the performance or the survival of the colony. In contrast, infestation of a European honeybee *Apis mellifera* L. colony can lead to its collapse as populations grow to thousands of mites (Martin 1997*a*).

In the Asian bee, *Varroa* mites reproduce in brood cells containing immature drone pupae. A mature (or fertilized) female mite enters a cell containing a drone larva one to two days before it is capped by the worker bees. The female mite first produces a male offspring followed by an average of three to five female offspring (Donze & Guerin 1994; Boot *et al.* 1997). If only a single mite enters a cell then the bee will hatch with the mother mite and her female offspring attached to its body (the male mite dies in the cell). However, if two female mites attempt to reproduce in one cell then there is a high probability that the bee larva will die before developing, the cell will remain capped and the mites will become ‘entombed’ and die (Rath 1992). Drone cells are usually only produced once a year, for a period lasting around one month, and mite reproduction takes place almost exclusively during this time (Rath 1991). Throughout the other 11 months of the year, the mites remain attached to drone and worker bees. During this period there is a constant probability of death (Martin 1998).

### (b) *The individual-based model*

Let us make the above observations the basis of an individual-based model of mite reproduction. At generation  $t$ , each of  $A_t$  mites enters one of  $n$  cells, with the choice assumed to be made uniformly at random. There is strong evidence for this assumption, since between generations the mites move freely between the cells and the spatial distribution of mites in cells has been observed to be completely random (Salvy *et al.* 1999). If two or more mites choose the same cell then these mites die without reproducing, while single mites produce  $b$  offspring. Between breeding, mites have a probability  $p_d$  per month of dying. The  $A_{t+1}$  surviving mites become the next generation and again choose from  $n$  cells.  $n$  is

assumed constant over the generations, since Asian honeybee colony size is mainly unaffected by the mites.

We can use observational data for parameterizing this model. Martin (1998) estimated the probability of death per month for a mite attached to a bee for the 11 months when no drone brood is available as  $p_d = 0.1133$ . Donze & Guerin (1994) estimated that mites reproducing in a cell containing no other mites produce  $b = 3$  offspring on average. A typical small bee colony will produce  $n = 400$  drone cells once a year, while a large colony may produce around  $n = 800$  (Rath 1991).

The results of typical simulations for both small ( $n = 400$ ) and large ( $n = 800$ ) bee colonies are shown in figure 1. In simulations run for 300 years, directly after breeding the mite populations have a mean of 53.7 and a variance of 36.0 in the small colony, and a mean of 121.5 and a variance of 33.8 in the large colony. The gross feature of both these plots is the oscillatory form of the mite populations, showing a sharp increase annually during the breeding season followed by an exponential decay as the mites die at a constant rate throughout the rest of the year. The figure shows that the mite population is periodic for neither colony size and that peak heights are seen to vary over a time-scale of several years.

Rath & Drescher (1990) found in field experiments that colonies with drones (i.e. where mite breeding had already occurred) hosted more mites—mean  $92.5 (\pm 140.2)$  (pooled small and large colonies). In the field, colonies which did not contain drones had a mean mite population of 22.7, compared to 23.5 in the small simulated colony and 52.5 in the large simulated colony. Rath & Drescher (1990) also observed that, while most colonies contained less than 100 mites, infestations of more than 100 occurred in both small and large colonies. However, these observations did not control for the number of drone brood produced in the colonies studied and were taken at various stages in the annual cycle so, while consistent with our model, the current data cannot be used to validate it completely.

### (c) *The mean-field approximation*

It is possible to derive a simple mean-field approximation to the full stochastic individual-based model of mite reproduction. We let  $A_t$  be a random variable, representing the number of mites at time  $t$ . The conditional expectation of the population at the next generation, given that the current population is  $a_t$ , is the sum of the expected number of mites emerging from each cell multiplied by their probability of survival until the next year:

$$E(A_{t+1}|A_t = a_t) = (1 - p_d)^{11} \sum_{s=1}^n E(\text{number of mites emerging alive from cell } s | A_t = a_t). \quad (2)$$

If we now introduce the observation that only single mites can produce surviving offspring we obtain

$$E(A_{t+1}|A_t = a_t) = (1 - p_d)^{11} \sum_{s=1}^n (b + 1) P(\text{only one mite in cell } s | A_t = a_t). \quad (3)$$

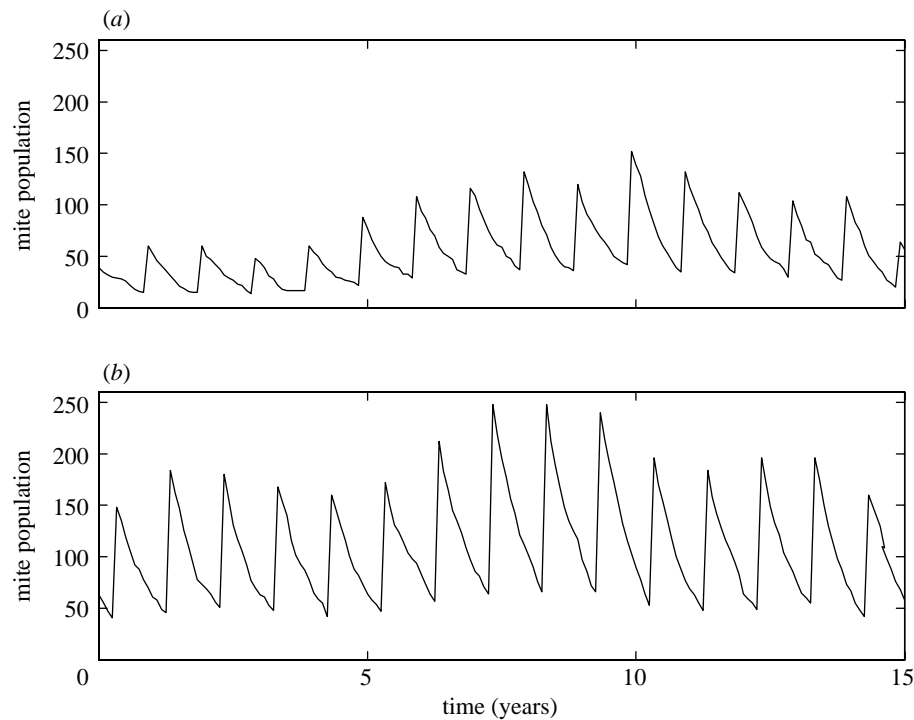


Figure 1. Typical simulated mite populations. (a) A small bee colony ( $n = 400$ ); (b) A large bee colony ( $n = 800$ ). The parameters for the simulation model are taken from the literature. Martin (1998) estimated the probability of death per month for a mite attached to a bee for the 11 months when no drone brood is available as  $p_d = 0.1133$ . Donze & Guerin (1994) estimated that mites reproducing in a cell containing no other mites produce  $b = 3$  offspring on average. A typical small bee colony will produce  $n = 400$  drone cells once a year, while a large colony may produce around  $n = 800$  (Rath 1991). The figure shows a simulation run for 15 years observed after the simulation had been running for 100 years.

We assume that the  $a_t$  mites are distributed uniformly at random between  $n$  cells. The probability that a particular mite enters cell  $s$  is  $1/n$  and the probability that out of the other  $a_t - 1$  mites none enters cell  $s$  is  $(1 - 1/n)^{a_t - 1}$ . The probability of only a single mite occupying a cell is therefore determined by a binomial coefficient:

$$\begin{aligned} E(A_{t+1}|A_t = a_t) &= \rho \sum_{s=1}^n \binom{a_t}{1} (1/n) (1 - 1/n)^{a_t - 1} \\ &= \rho a_t (1 - 1/n)^{a_t - 1}, \end{aligned} \quad (4)$$

where  $\rho = (b + 1)(1 - p_d)^{11}$  represents the density-independent reproductive gain per mite. Thus, we have the expected mite population at time  $t + 1$  as a function of the actual mite population at time  $t$ . We introduce a mean-field approximation by equating the actual mite population with the expected population  $a_{t+1} = E(A_{t+1}|A_t = a_t)$ . Hence,

$$a_{t+1} = f(a_t) = a_t \exp(r(1 - a_t/K)), \quad (5)$$

where

$$r = \ln \left( \frac{\rho}{1 - 1/n} \right) \quad (6)$$

and

$$K = \frac{\ln(\rho/(1 - 1/n))}{-\ln(1 - 1/n)} = \frac{r}{-\ln(1 - 1/n)}. \quad (7)$$

Equation (5) is the exponential logistic or Ricker map. It has a similar functional form to equation (1) and is often

applied in modelling the dynamics of density-dependent, non-overlapping populations (Cheke & Holt 1993; Sheeba & Joshi 1998).

Physically, it is only interesting to consider non-negative populations and, since non-negative populations remain non-negative under the exponential logistic map (i.e. non-negative reals are invariant under the map), we restrict our attention to these. Thus, we consider the map  $f: \mathbf{R}^+ \rightarrow \mathbf{R}^+$ , which is defined in equation (5), where  $a_t \geq 0$ . It is usual when studying this map to consider the bifurcations that can arise when changing the parameter  $r$  ( $e^r$  is, like  $\gamma$  in equation (1), a growth rate at low densities) while keeping the ‘carrying capacity’  $K$  fixed (May & Oster 1976). The map  $f$  has two  $r$ -independent fixed points at  $a_* = 0$  and  $a_* = K$ . If we take  $K > 0$  then a degenerate bifurcation occurs at  $r = 0$ , where these fixed points exchange stability. This bifurcation implies that certain parameter regions of the exponential logistic map are unphysical. In particular, we see that the fixed point  $a_* = K$  is repelling when  $r < 0$ . As a consequence, any initial population  $a_0 > K$  grows without bound, despite a growth rate  $e^r < 1$ . We note that this difficulty arises when the signs of  $r$  and  $K$  are different.

On the other hand, our derivation of the exponential logistic map gives  $r$  and  $K$  in terms of  $\rho$  and  $n$ , which specify the individual-based model. In particular, we note that  $r$  and  $K$  are constrained to have the same sign and, hence, the issue of divergent populations mentioned above does not arise. If, for example, we increase  $\rho$  at fixed  $n$ , we see that  $r$  increases with  $\rho$  and that  $K$  is proportional to  $r$ . When  $\rho$  is small enough,  $r < 0$  which

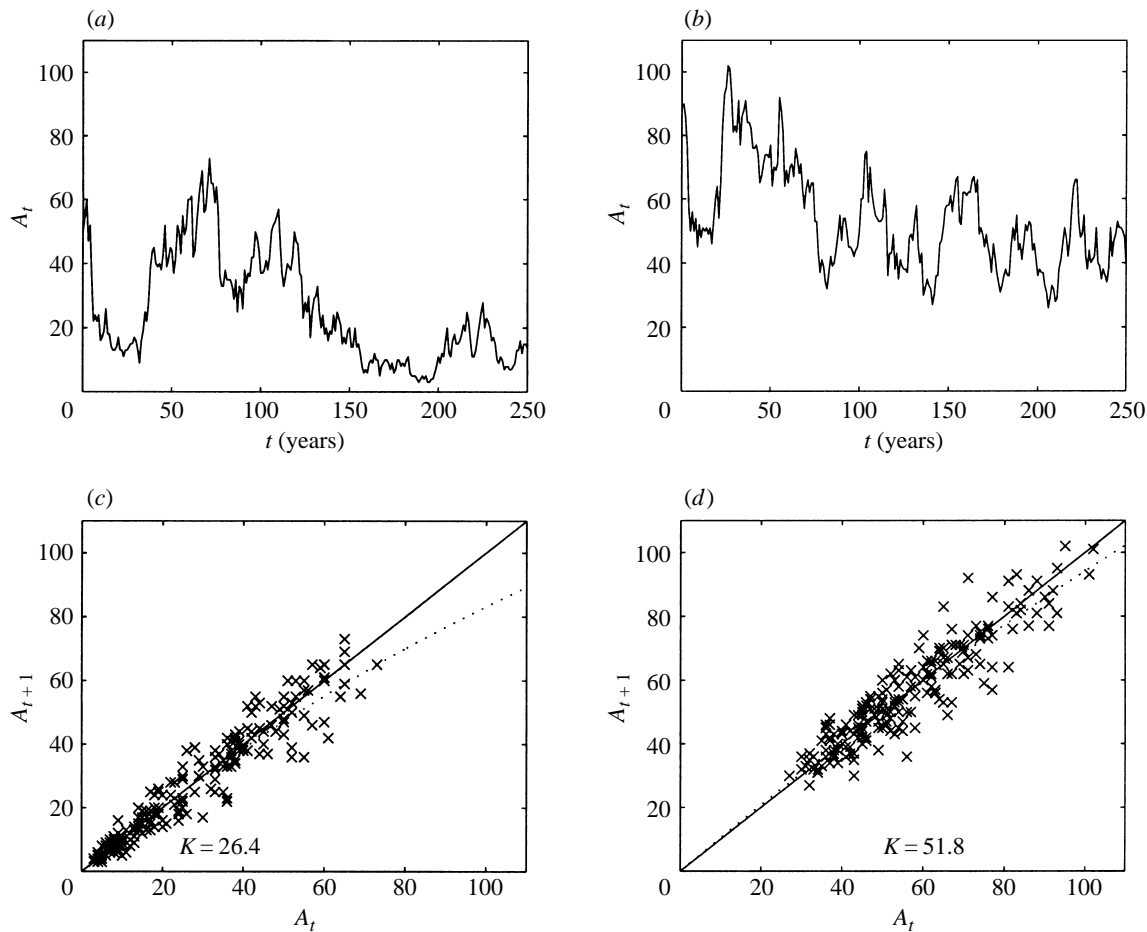


Figure 2. Simulated mite populations over 250 years for (a,c) a small bee colony ( $n = 400$ ) and (b,d) a large bee colony ( $n = 800$ ). (a,b) The mite populations before breeding for 250 simulated years of the individual-based model. (c,d) The change in populations from one year to the next in the individual-based model (crosses) and equation (5) (dotted line). The parameter values are identical to figure 1. The change in population  $A$  from year  $t$  to  $t + 1$  usually lies near equation (5). In particular, the population in the individual-based model fluctuates around the point where equation (5) crosses the line  $a_{t+1} = a_t$  (solid line).

implies  $K < 0$ . In this situation the only fixed point in  $\mathbf{R}^+$  is the origin and this a global attractor. Thus, for small enough  $\rho$  the mites become extinct. When  $\rho = 1 - 1/n$  then  $r = 0$  and the bifurcation occurs. As  $\rho$  increases from this value, a new attracting fixed point at  $a_* = K > 0$  moves away from the origin. The origin itself is now repelling and  $a_*$  is attracting. Having said this, it is clear that our naive discussion of this bifurcation has its own anomaly, since it suggests that the fixed point at the origin becomes unstable even when  $\rho < 1$ . This is not a problem with the mean-field approximation, which is exact for  $a_t = 0$  and  $a_t = 1$ . Rather the problem arises because we have interpreted  $a_t$  as a real variable, whereas it is clear that the number of mites should be an integer. In fact a better condition for local stability of the origin would be to test whether  $f(1) < 1$ . Note that  $f(1) = e^{r(1-1/K)} = \rho$ , so the stability condition is just  $\rho < 1$  as we might expect.

At the bifurcation the new fixed point  $a_* = K$ . If we now assume—with more justification—that  $a_*$  can be treated as a real variable we find that the fixed point is attracting as long as  $0 < r < 2$ , since

$$\left. \frac{df(a_t)}{da_t} \right|_{a_t=K} = 1 - r. \quad (8)$$

In terms of the individual-based parameters, provided  $\rho < e^2(1 - 1/n)$ , mite populations will approach the equilibrium value  $K$ . For a small bee colony ( $n = 400$ ), with the parameter values given in figure 1,  $K = 26.4$ , while for a large colony ( $n = 800$ )  $K = 51.8$ . The equivalent individual-based simulations have mean populations consistent with this prediction (23.5 and 52.5, respectively).

Figure 2 shows the results of simulations for small and large colonies as time-series of the population each year just before breeding (as opposed to figure 1 which shows monthly populations). The population appears to increase and decrease according to a bounded random walk for both colony sizes. Such behaviour may be explained in terms of the inherent randomness in the individual-based simulation and the parameterized form of equation (5)—populations fluctuate around  $a_* = K$  (see figure 2c,d). The large range of this random walk could explain the high variation in mite populations seen in the field (Rath & Drescher 1990; Rath 1999) with simulated populations growing as large as 408 directly after breeding. However, the maximum populations in the simulation do fall short of the 800 mites seen in some real colonies and predicted by some other models of mite reproduction (Fries *et al.* 1994; Martin 1997b). Such large populations of mites could be produced in our simulations if we increased  $b$ . For

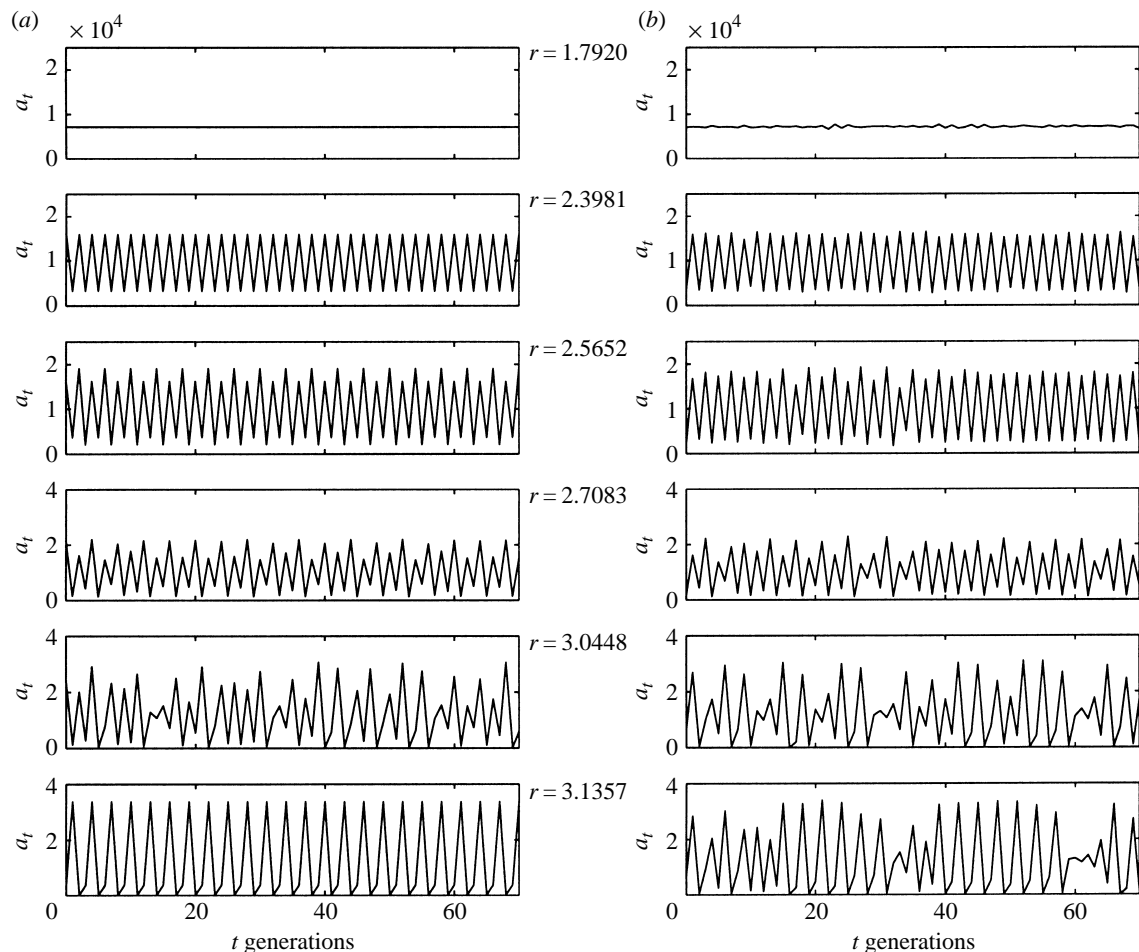


Figure 3. Time-series generated by  $a_{t+1} = f(a_t) = a_t e^{r(1-a_t/K)}$  (a) compared to the individual-based model (b) for various values of  $r$ . The parameter  $n = 4000$ , the number of available sites, is constant. The density-independent reproductive gains per mite  $\rho$  are, from top to bottom, 6, 11, 13, 15, 21 and 23. As  $\rho$  (and, therefore,  $r$ ) increases, the population dynamics go from stable ( $\rho = 6$ ) to period 2 oscillations ( $\rho = 10$ ) and period 4 oscillations ( $\rho = 13$ ) to oscillations which are aperiodic ( $\rho = 15$  and  $\rho = 21$ ). Periodic windows can also be seen, for example we see period 3 at  $\rho = 23$ .

example,  $b = 4$  has been observed as the successful reproduction rate of mites (Boot *et al.* 1997). This estimate for  $b$  would give  $K = 230.2$  in a large colony and, after breeding, populations of over 1000. In general, predictions of before and after breeding populations are given by  $K$  and  $bK$ , respectively.

#### (d) An individual-based route to chaos

At small values, the number of cells  $n$  plays an important role in determining the dynamics of equation (5). When  $n$  is small stochastic effects dominate individual-based simulations and the mean-field approximation has limited predictive power. However, for large but finite  $n$ , simulation of the individual-based model and iteration of equation (5) produce similar population dynamics for a wide range of parameter values (see figure 3 for the case where  $n = 4000$ ). Both undergo a series of period-doubling bifurcations as  $\rho$  is increased—the first of which occurs at  $\rho = e^2(1 - 1/n)$ —resulting in periodic and eventually chaotic dynamics. The match between the deterministic equation and stochastic simulation is remarkably good—figure 4 shows how closely equation (5) predicts the population in the next generation given the current population. The boundaries between regions

of parameter space characterized by a particular period are less well defined in the individual-based simulations than are the bifurcations of the exponential logistic map. For example, the period 4 oscillations when  $r = 2.3981$  often appear as period 2 oscillations in the corresponding individual-based simulation. Similarly, when  $r = 3.1357$  the individual-based simulation shows both period 3 and irregular oscillations. Such effects can be mathematically understood as resulting from the loss of structural stability of the model near to bifurcations.

### 3. FROM INDIVIDUAL TO POPULATION

The derivation of the exponential logistic map from an individual-based model is useful, not only because it helps us understand the properties of a simulation in terms of the behaviour of a simple dynamical system, but because it demonstrates, in terms of the behaviours of individuals, why the particular difference equation is applicable in modelling the dynamics of the population. In particular, it allows the assumptions which underlie the model parameters to be tested. For example, when applying the logistic map as a phenomenological model, the parameter  $K$  is said to relate to the ‘carrying capacity’ of the

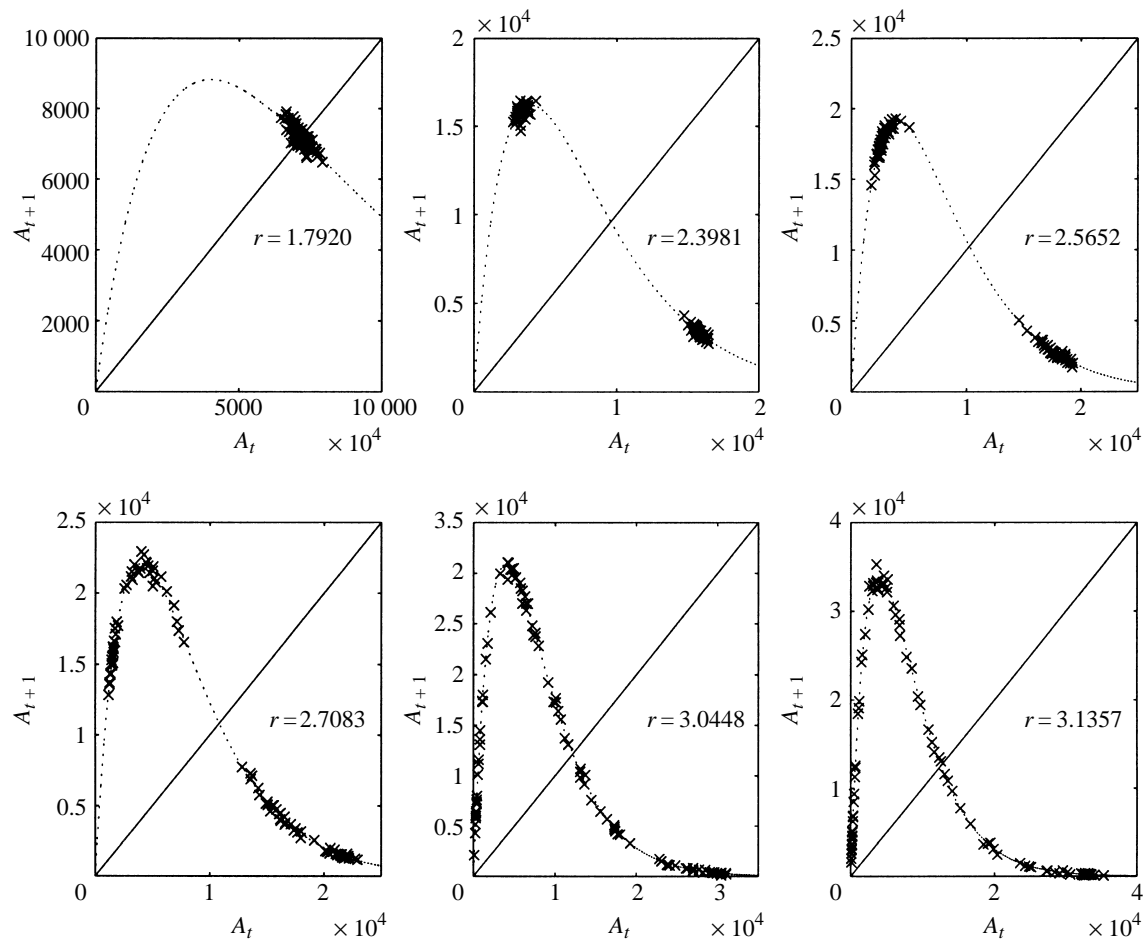


Figure 4. Plot of  $a_{t+1} = f(a_t) = a_t e^{r(1-a_t/K)}$  (dotted line) and the populations  $A_{t+1}$  resulting from various  $A_t$  in the individual-based model (crosses). The same values of  $r$  are used as in figure 3.

organism's environment. In fact  $K$  is a function of not only  $n$ —which can be correctly considered the capacity or breeding space of the environment—but also of  $\rho$ . Thus,  $K$  represents a balance between available space and the net gain in population per successful individual. This observation is important in a general ecological context, since reducing the breeding space of a particular organism may affect not only the equilibrium level of the population but, through the stability condition in equation (8), may also introduce periodic oscillations. Such oscillations would greatly increase the probability of species extinction.

The mathematical link between individual and population can also aid in the analysis of ecological time-series. Yearly population census data often consist of only 20–30 data points. This makes it difficult to fit top-down models accurately, which invariably require the estimation of large numbers of parameters (Turchin & Taylor 1992). An alternative approach would be to develop an individual-based model, the parameters of which may be measured by detailed observation of one or more reproductive cycles of the species of interest. The predictions of such a model and its mean-field approximation could then be compared with the known population data. Such a model may be useful for forecasting, for example, the chances of extinction of the species. As an observation of this general point, we note that the parameters of the *Varroa* reproduction model are density independent and, therefore, that

observation of only one reproductive cycle is necessary in order to parameterize the model.

#### (a) *Other applications of the model*

There are more complicated individual-based models of the reproduction of other organisms that simplify to the model we have discussed here. For example, Sole *et al.* (1999) described a model in which, at each generation, individuals are placed randomly on a lattice where they 'graze'—collecting energy from cells of the lattice. Individuals that collect enough energy reproduce while others die without reproducing. The energy in the cells is replenished every generation and the individuals are redistributed. This model has clear parallels with our mite model and it is therefore not surprising that simulating it produces dynamics which correspond to equation (5). We offer our simpler model as a mathematical explanation for this correspondence.

Kindlmann & Dixon (1996) used an individual-based model for studying within-year populations of tree-dwelling aphids and found that 'migration is the most important factor determining the [sometimes dramatic] summer decline in [aphid] abundance' (p. 28). Summer migration is thought to be caused by a combination of overcrowding and low host plant quality. This process can be modelled by dividing the host plant into  $n$  units, with each unit containing enough energy to support one aphid and then, in each generation, distributing the aphids

randomly amongst these units. The rule for migration is then made similar to that for survival in mites: if two or more aphids share the same unit then both migrate, while aphids with their own unit of energy reproduce. During the rest of the year populations evolve according to a simple linear law. The number of eggs laid in autumn depends linearly on the host-plant quality (Dixon 1990) and, thus, may be thought of as a linear function of  $n$  (with a constant of proportionality we will call  $\mu$ ) and in spring the number of aphids that hatch is proportional to the number of eggs laid in the previous autumn. This model is identical to the one we have described here for mites, with migration replacing death. Equation (5) is derived as before with  $\rho = p_w \mu n$ , where  $p_w$  is the probability that an egg survives from autumn to spring.

In this model, we have assumed that asexual reproduction, which takes place throughout the summer (Dixon 1985), is perfectly balanced by aphid death. We have also assumed that the host-plant quality is unaffected by the aphid population (see Dixon (1990) and Sequeira & Dixon (1997) for discussion of this). Accepting these simplifications, the model predicts that, depending on the values of  $\mu$ ,  $p_w$  and  $n$ , aphid population dynamics can be stable, periodic or even chaotic. Indeed, there is clear evidence of both stability and biennial oscillations in aphid populations (Dixon 1990) and a suggestion that certain species have shown chaotic oscillations (Turchin & Taylor 1992). Our model thus provides a simple mathematical explanation of how these 'see-saw' population dynamics may arise from the summer migration of aphids.

#### 4. DISCUSSION

We have presented an example of an individual-based model with population dynamics which can be approximated by a single difference equation. It is possible to generalize this approach using a formal mathematical framework for representing individual-based models. In this case, we used a process algebra known as weighted synchronous calculus of communicating systems (WSCCS) (Tofts 1994). This allowed us to determine the approximate mean-field dynamics of the model using well-defined mathematical techniques. Details of using WSCCS in modelling biological systems may be found in Tofts (1992) and Sumpter *et al.* (2001).

We have applied this generalized approach to other models of species interactions (Sumpter 2000). For example, consider a model with rules such that, if two or more individuals choose the same breeding site, then the conflict is resolved with exactly one individual breeding at the site, with others excluded and unable to reproduce that season. In nature this may correspond to the acquisition and protection of breeding space by territorial animals. An individual-based model describing this process can be shown to produce stable equilibrium dynamics, no matter how many offspring the individual can produce (details of this model may be found in Sumpter (2000)). The result shows that density dependence does not imply that increases in the net rate of population growth will lead from stable to periodic or chaotic population dynamics. In Hassell's (1975) general model (equation (1)) stable dynamics occur for all  $\gamma$  when

$0 < \beta < 1$ . A simple interpretation of such dynamics is that species with population dynamics which fit equation (1) with  $\beta < 1$  compete for breeding space using a mechanism comparable to exclusive acquisition and protection, while those with  $\beta > 1$  have competition for resources similar to the *Varroa* mites and the tree-dwelling aphids. Using Nicholson's (1954) definitions, our original individual-based model can be thought of as a generic model of a 'scramble' for resources, while the latter territorial model is a generic 'contest'.

Other individual-based models can be developed for modelling two or more species interactions—which can then be approximated with coupled difference equations—or spatially local interactions—which behave similarly to coupled map lattices of population densities. By expressing individual-based models in a formal framework, a mathematical link can be established between individual- and population-level behaviour. Such a link helps us provide causal explanations for population cycles. The study of such models produces counter-intuitive predictions about the effects of individual interactions on population dynamics and allows us to understand why certain models are better suited than others for capturing the population dynamics of particular species. We thus begin to bridge the gap between detailed and complicated models of individual interactions and simplified top-down models. Building this bridge is essential if we are to understand the complex interactions at work in real ecological systems.

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