

Allee effects and extinction in a lattice model

Alastair Windus, Henrik Jeldtoft Jensen*

Mathematics Department, Imperial College London, South Kensington Campus, London SW7 2AZ, UK

Received 30 November 2006
Available online 19 August 2007

Abstract

In the interest of conservation, the importance of having a large habitat available for a species is widely known. Here, we introduce a lattice-based model for a population and look at the importance of fluctuations as well as that of the population density, particularly with respect to Allee effects. We examine the model analytically and by Monte Carlo simulations and find that, while the size of the habitat is important, there exists a critical population density below which the probability of extinction is greatly increased. This has large consequences with respect to conservation, especially in the design of habitats and for populations whose density has become small. In particular, we find that the probability of survival for small populations can be increased by a reduction in the size of the habitat and show that there exists an optimal size reduction.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Extinction; Allee effects; Critical population density; Habitat size; Fluctuations; Mean field; Monte Carlo simulations

1. Introduction

Extinction is becoming a greater and greater issue all over the world and is a cause of extreme concern. It has been estimated that anthropogenic extinctions are resulting in the loss of a few percent of the current world's biosphere, which is of magnitude 3–4 times the natural background rate (May et al., 1995). The World Conservation Union (IUCN), through its Species Survival Commission (SCC) develops criteria to assess the extinction rate for plants and animals all over the world. This enables them to keep a so-called *Red List* (www.redlist.org) of species which are threatened with extinction in order to promote their conservation. The list currently shows over 16,000 threatened species around the world—a 45% increase in the figure from the year 2000.

It has been shown by examining both discrete (Escudero, 2005) and continuous (Skellam, 1951) populations that, at least analytically speaking, there exists a critical habitat size L_c above which survival of a population is assured. However, since individuals in a population are often reliant on each other for long-term survival, we intuitively expect

that, even for $L > L_c$, a sufficiently large population would be needed for growth.

In real populations, the positive correlation between size and per capita growth rate of a population is known as the Allee effect (Allee, 1931), which has recently received much interest (e.g. Dennis, 2002; Hurford et al., 2006; Johnson et al., 2006). If the Allee effect is strong enough, the per capita growth rate may even be negative for small population sizes and so the effect has been examined with respect to extinction (see for example Amarasekare, 1998; Courchamp et al., 1999; Stephens et al., 1999, and references therein). Often, the analytical approaches made, such as stochastic differential equations (e.g. Dennis, 1989), discrete-time Markov-chains (e.g. Allen et al., 2005) or diffusion processes (e.g. Dennis, 2002), take a macroscopic view of the population, examining population size or density. However, many ecological interactions, such as breeding, resource competition or predation, occur at scales much smaller than that of the entire population. Additional insight can therefore be gained by examining the many interactions of the *individuals* which result in the observed macroscopic behaviour. A method of taking the microscopic processes into account is through lattice models, which have been widely used in ecology (see for example Tainaka, 1988; Durrett and Levin, 1998; Itoh

*Corresponding author. Fax: +44 20 6594 8516.

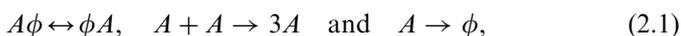
E-mail address: h.jensen@imperial.ac.uk (H.J. Jensen).

et al., 2004). In particular, space is explicitly defined as a variable and so much additional insight can be given, especially to the effects of the habitat size on the population.

Here, we introduce a simple lattice model, incorporating the processes of birth, death and diffusion, which display Allee effects. We attempt to keep the model as general as possible, not aiming to model a particular species, rather to show the general behaviour of species which rely on others for growth. After defining the model in the next section, we examine the fluctuations in the population density that are present in the Monte Carlo (MC) simulations in Section 3. The displayed Allee effects are studied in Section 4, particularly with respect to a sudden decrease in population. Finally, our conclusions are discussed in Section 5.

2. The model

We have a d -dimensional square lattice of linear length L where each site is either occupied by a single individual (1) or is empty (0). A site is chosen at random. If the site is occupied, the individual dies with probability p_d , leaving the site empty. If the individual does not die, a neighbouring site is randomly chosen. If this site is empty, the individual moves there. If occupied however, a second neighbouring site is chosen. If this second site is empty, reproduction occurs with probability p_b .¹ The parents remain at their original sites with the new individual occupying the second chosen site. If the second chosen site is occupied, no reproduction takes place in order to prevent over-crowding of the population. We therefore have the following reactions for an individual A :



where ϕ represents an empty site.

A time step is defined as the number of lattice sites and so is equal to approximately one update per site. This ensures that, in contrast to the total number of updates, the number of updates per site per time step remains independent of the lattice size. Despite an individual in the population being able to move, die or give birth in a single time step, simulations show that, as we would hope, the processes of birth and death occur with much less frequency than that of dispersal.

We use nearest neighbours and, throughout most of the paper, periodic boundary conditions. Although more unrealistic than, say, reflective, periodic boundary conditions allow for better comparison with analytical results, since periodic systems remain homogenous. We later, however, examine some results with reflective boundary conditions.

In order to justify some of the finer details of this modelling approach, we carried out tests, changing specific properties of the model. In particular, we investigated the consequences of the order in which the processes of birth,

death and diffusion were carried out and also the effect of the shape of the lattice sites and hence the number of neighbouring sites. The latter was examined by simply viewing next-nearest neighbour sites rather than just nearest neighbour sites. We expect neither detail to make any significant difference to the dynamics due to the coarse-grained level at which we view the system. This was indeed confirmed by simulations where, in both cases, the changes made to the model made no qualitative difference to the behaviour of the system.

Unlike other similar models such as the *contact process* (Harris, 1974), here, two individuals must meet in order to reproduce, whereas one individual can die by itself. The resulting density dependence of the population for survival leads to observed Allee effects which we examine in detail later.

We analytically examine our model by deriving the so-called mean field (MF) equation (e.g. Oppen and Saad, 2001) for the density of occupied sites $\rho(t)$. Assuming the particles are spaced homogeneously in an infinite system we have

$$\frac{\partial \rho(t)}{\partial t} = p_b(1 - p_d)\rho(t)^2(1 - \rho(t)) - p_d\rho(t). \quad (2.2)$$

The first term is the proliferation term and so is proportional to ρ^2 , the probability that the individual does not die, $(1 - p_d)$, the probability that the next randomly chosen site to give birth on is empty, $(1 - \rho)$ and finally the probability that it gives birth if this is the case, p_b . The second term represents annihilation of an individual and so is proportional to both ρ and p_d , the probability that the chosen individual dies.

Clearly the MF approach is limited in its applicability to real systems due to the false assumption of infinite lattice size and its neglect of spatial inhomogeneity. While MC simulation results of the model will clearly give us a more realistic insight into how a real system may behave, Eq. (2.2) does give us a good indication of what we may observe. In fact, we find very good qualitative agreement between the MF predictions and the MC results in subsequent sections.

When examining extinction through MC simulations, it is important to note that, in contrast to MF, extinction will always occur in a finite lattice. Survival probabilities in the infinite time limit are therefore zero for $p_d > 0$. With that in mind, when we discuss the probability of survival according to the MC results, we mean the probability of survival up to some $t = t_{\max}$.

2.1. Phase transition

Due to the conflict between the growth and decay processes in the model, we expect that, with certain values of p_b and p_d , extinction of the population would occur. Indeed, many models displaying such a conflict (see for example Vespignani et al., 2000; Dammer and Hinrichsen, 2003; Oborny et al., 2005; Peters and Neelin, 2006) show a

¹We note that the birth rate is actually given by $p_b(1 - p_d)$ and not p_b only.

critical parameter value separating an *active* state and an *inactive* or *absorbing* state that, once reached, the system cannot leave. As the rate of decay increases, the so-called *order parameter* (often the density of active sites) decreases, becoming zero at a critical point, marking a change in phase or *phase transition*. In our case, the absorbing state would represent an empty lattice and so extinction of the population.

Eq. (2.2) has three steady states,

$$\bar{\rho}_0 = 0, \quad \bar{\rho}_{\pm} = \frac{1}{2} \left(1 \pm \sqrt{1 - \frac{4p_d}{p_b(1-p_d)}} \right). \quad (2.3)$$

For $4p_d > p_b(1-p_d)$, $\bar{\rho}_{\pm}$ are imaginary, resulting in $\bar{\rho}_0$ being the only real stationary state. Keeping p_b constant from now on, we then have that our critical death rate is given by $p_{d_c} = p_b/(4 + p_b)$ which separates the active phase representing survival and the absorbing state of extinction.

As previously mentioned, we find at least good qualitative support for our MF analysis through numerical simulations. Fig. 1(a) shows the critical values of p_d and p_b separating the regions with one and three real stationary states according to both the MF equation and MC simulations for 1, 2 and 3 dimensions. We see convincing agreement between our analytical and numerical results, particularly in higher dimensions. The MC simulations were carried out on an initially fully occupied lattice with linear sizes $L = 1000, 32$ and 10 for each dimension, respectively, and we observed whether extinction occurred during 10^5 time steps. For each p_b , the simulation was repeated 500 times. If a single run survived, p_d was increased, whereas if extinction occurred in all runs, p_d was reduced. Using the same initial seed for the random number generator, an iterative procedure produced a critical value with accuracy $\pm 2^{-11}$. This iterative procedure was then repeated five times with different seeds and the average taken. Only a small number of repeats was needed since the largest variance of the values obtained was of the order of 10^{-8} . From the figure we find that to 3 d.p. for $p_b = 0.5$, $p_{d_c} = 0.073, 0.098$ and 0.105 in 1, 2 and 3 dimensions, respectively. Due to the finite size of the lattices and the finite time used for the above simulations, the actual critical death rates are likely to differ slightly from those given and more accurate techniques would have to be used to obtain them (see Hinrichsen, 2000, for examples of such techniques).

With $\rho(t=0) = 1$, as p_d is increased, the steady-state population density decreases, becoming zero at p_{d_c} as shown in Fig. 1(b), marking the phase transition. We see that the steady-state population density appears to change continuously in 1 dimension, whilst discontinuously in 2 and 3 dimensions in agreement with the MF results. We call such phase transitions *continuous* and *first-order*, respectively. In both cases, the phase transition is marked by a very rapid decrease in population density.

Aside from a decrease in population density, we expect to observe other phenomena that are highly significant to

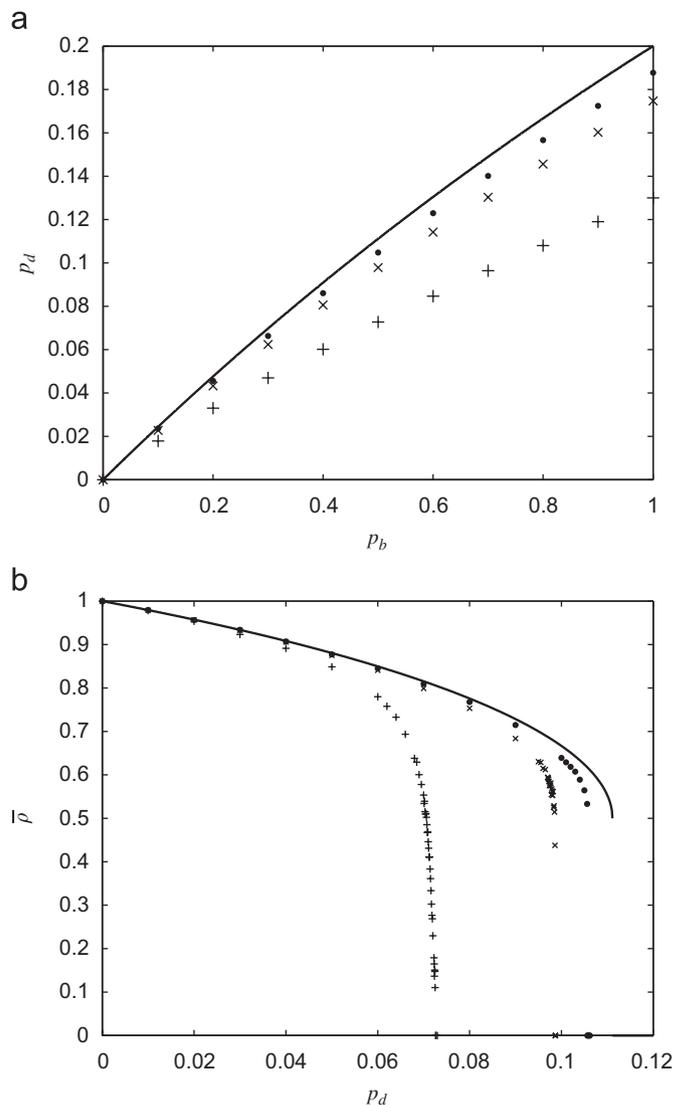


Fig. 1. (a) Values of p_{d_c} for different p_b and (b) the steady-state population densities with $p_b = 0.5$ according to the MF (line) and 1 (+), 2 (×) and 3 (●) dimensional MC simulations.

the population as p_{d_c} is approached. In particular, for continuous phase transitions, fluctuations in the population density $\Delta\rho$ are known to diverge as $p_d \rightarrow p_{d_c}$ according to

$$\Delta\rho \sim (p_{d_c} - p_d)^{-\gamma} \quad (2.4)$$

for some critical exponent γ (see again Hinrichsen, 2000). A population at risk from extinction due to a super-critical death rate will therefore display, not only a decrease in population density, but an increase in fluctuations (see also Oborny et al., 2005).

Many models displaying such a continuous absorbing phase transition are known to behave very similarly close to the critical point. This has allowed for the grouping together of those models which share the same properties into *universality classes*. Critical exponents such as γ , for example, will be identical for all models belonging to the same universality class. It has recently been shown that in 1

dimension, this model belongs to by far the largest universality class of models displaying absorbing phase transitions, called *directed percolation* (Windus and Jensen, 2007). Due to the size of this universality class, many other similar models will display the same behaviour close to criticality. These include models requiring different numbers of individuals for birth and death. The behaviour seen here in 1 dimension close to criticality is true then for a number of models different from our own, including the previously mentioned *contact process* or the *pair contact process with diffusion* (Carlon et al., 2001).

Extinction however may also occur for reasons other than having a super-critical death rate. We investigate the roles of fluctuations and that of Allee effects in the next two sections, where we examine simulations in the sub-critical or active phase and use the constant value $p_b = 0.5$.

3. Fluctuations

One of the main weaknesses of the MF approach is the absence of fluctuations in the population density. In reality, and indeed from MC results, we expect extinction due to fluctuations in the population density to occur when the order of the fluctuations approaches the mean population density. Empirically, demographic stochasticity (that is, chance events of mortality and reproduction) is known to be greater in smaller populations (Lande et al., 2003) than in larger ones. From our MC results, population and habitat size are positively correlated. This is true also, on average, in nature. We therefore expect extinction due to fluctuations to occur for smaller lattice (and therefore population) sizes as has been suggested (e.g. Pimm, 1991; Escudero et al., 2004) and indeed observed (e.g. Diamond, 1984).

We see in Fig. 2(a) that, numerically, the fluctuations in the population density $\Delta\rho$ decrease with the number of lattice sites N through a power law with exponent -0.50 in all dimensions, which is what we would expect from the *central limit theorem*. Simulations were carried out for fixed $p_d = 0.03$ and $p_b = 0.5$ and the standard deviation of the population density was obtained from 5×10^3 surviving runs for each lattice size. Fig. 2(b) shows how the size of the fluctuations also increase as the critical point is approached, as expected from Eq. (2.4). These larger fluctuations will also increase the probability of extinction as indicated in Fig. 3 where we examine the probability of survival P_s ; that is, the probability that extinction has not occurred up to some time t_{\max} . We examine the 1-dimensional case only using three different values of p_d with $t_{\max} = 10^3$ and repeat the simulation 5×10^4 times for each lattice size. The figure clearly shows how the probability of survival increases with L , yet decreases as p_d increases. Indeed, as p_{dc} is approached, population density decreases and fluctuation size increases, resulting in species with higher death rates being more susceptible to extinction. This is indeed observed in nature where long-lived species are known, in general, to have a higher chance

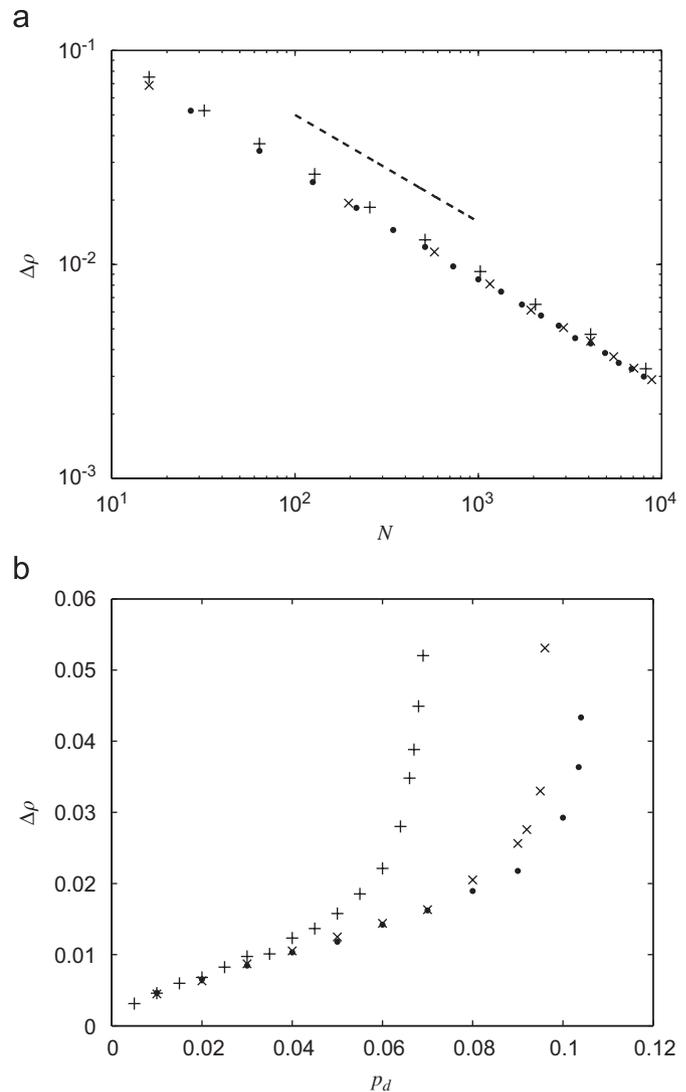


Fig. 2. (a) Log-log plot of the standard deviation of the population density $\Delta\rho$ versus the number of sites N in the 1 (+), 2 (x) and 3 (●) dimensional systems. The hashed line has gradient -0.5 for the eye and indicates the power law behaviour. (b) The fluctuations versus p_d for the same dimensions as in (a).

of survival than short-lived ones (Pimm, 1991; Stocklin and Fischer, 1999).

4. Allee effects

One reason we observe a decline in population growth at low densities is due to a decrease in mating successes at low densities. This is empirically known to occur in both plant (e.g. Aizen and Feinsinger, 1994) and animal (e.g. Birkhead, 1977; Robinson, 1988) populations. In our model, this aspect is incorporated by the fact that two individuals are required for reproduction whereas an individual can die by itself. As density decreases, each individual therefore finds it increasingly difficult to find another for reproduction before they die. To examine this, we return to our MF equation (2.2).

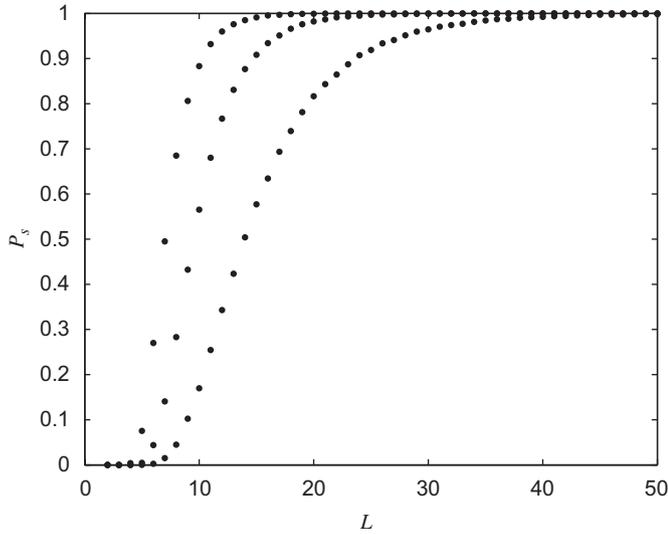


Fig. 3. How P_s varies with L for the 1-dimensional model with (from left to right), $p_d = 0.04, 0.05$ and 0.06 . Similar results are seen in 2 and 3 dimensions.

It is easy to show that whereas $\bar{\rho}_+$ and $\bar{\rho}_0$ are stable stationary points of Eq. (2.2), $\bar{\rho}_-$ is unstable. We may therefore treat $\bar{\rho}_-$ as a critical population density ρ_c since, from the MF, any population whose density $\rho(t) < \bar{\rho}_-$ will be driven to extinction by the dynamics of the system. In fact,

$$\rho(t) \rightarrow \begin{cases} 0 & \text{for } \rho(t) < \rho_c \\ \bar{\rho}_+ & \text{for } \rho(t) > \rho_c \end{cases} \text{ as } t \rightarrow \infty \quad (4.1)$$

for $p_d < p_{d_c}$.

We again wish to compare this MF prediction with the MC results in 1, 2 and 3 spatial dimensions. Due to the instability of $\bar{\rho}_-$, we instead use the initial population density $\rho(0)$ and find the value of p_d (or indeed vice versa) that separates the active and absorbing states. This then gives us an excellent way of finding $\bar{\rho}_- = \rho_c$ for different values of p_d . The MC simulations were carried out and the death rates found iteratively in the same fashion as in Section 2. The results are shown in Fig. 4 and clearly show the importance of the initial population density for survival. The density dependence appears to increase with dimensionality, which we expect, since two individuals meeting becomes progressively harder as the dimensionality of the system increases.

From Eq. (4.1) we expect that the population will survive only as long as $\rho(t) > \rho_c$. The MC results however in Fig. 5, show more of an increase in the probability of extinction as we approach ρ_c^+ rather than the definite extinction/survival cut-off that the MF predicts. We also see that as p_d , and therefore ρ_c , decreases, a greater increase in $\rho(0)$ is needed to increase P_s to 1.

The existence of this critical population density is highly significant to the conservation of species. It is clear from our model that a sufficiently small population will not grow, regardless of how much space and resources are available (see also Amarasekare, 1998). Such behaviour has been

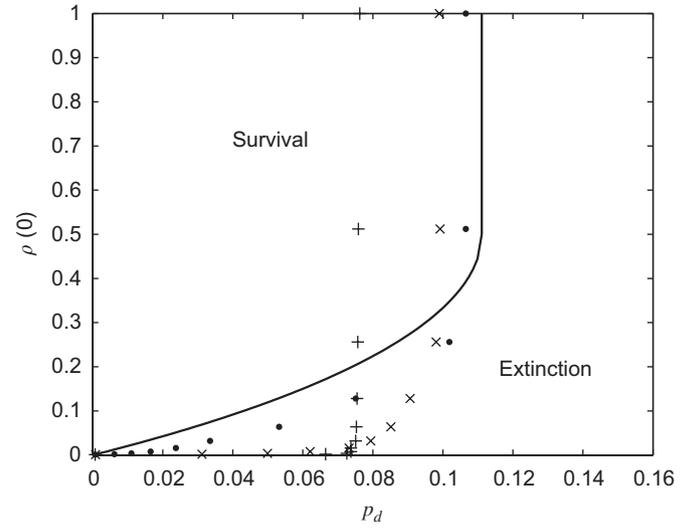


Fig. 4. Phase diagram showing the critical values of p_d separating the 2 long-term outcomes of the system for different initial population densities according to the MF (line) and the 1 (+), 2 (x) and 3 (•) dimensional MC simulations. We remind the reader that, from MF, extinction occurs in all cases for $p_d > p_{d_c}$.

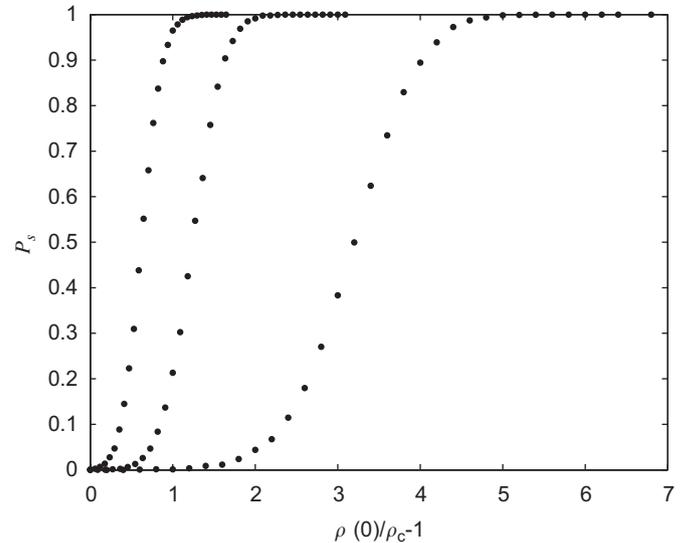


Fig. 5. Plot of P_s with $t_{\max} = 2000$ for different initial conditions. From left to right we have, $\rho_c = 0.17$ ($p_d = 0.94$), 0.11 ($p_d = 0.92$) and 0.05 ($p_d = 0.89$).

observed in nature. Populations of northern cod (*Gadus morhua*), for example, have failed to grow, despite having had seven years of moratorium (Shelton and Healey, 1999; Frank and Brickman, 2000). Similarly, when introducing bird populations to a new area, it has been found that repeated releases of large numbers of individuals are often needed before the introduction is successful (Long, 1981).

4.1. A decrease in population density

Apart from the initial conditions, it is certainly conceivable that the population density could fall below

the critical value due to a reduction in population size caused by disease or hunting, for example. We examine this through MC simulations by increasing p_d to 1 at some $t = t_k$ and then returning p_d to its original value once a density ρ_s has been reached. We examine this here in 2 dimensions with now reflective rather than the previously used periodic boundary conditions. Qualitatively, all previous results have been very similar when using reflective boundary conditions but here we want to increase this degree of realism in our model.

In 2 dimensions, for $p_d = 0.093$, ρ_c was found to be 0.140. So, from the MF, for $p_d = 0.093$, we would expect that if $\rho_s > 0.14$ the population will survive, with the population density returning to $\bar{\rho}_+$. However, for $\rho_s < 0.14$, extinction will occur. Using $\rho_s = 0.15 > \rho_c$ in Fig. 6, we see that for those runs that *did* survive, the population density does indeed return to what it once was. We also see, as suggested by Fig. 5, that most of the runs did result in extinction. In fact the survival probability was only 0.007.

From Fig. 6 we observe that there is a time delay between the start of the population decrease and when the probability of survival begins to fall. Assuming an individual that dies the n th time it is picked survives $n-1$ time steps, it is easy to show that the expected lifetime (in time steps) of an individual is given by $(1-p_d)/p_d$. Here, then, the observed time delay of approximately 40 time steps, with $p_d = 0.093$, corresponds to approximately four lifetimes. In general, the delay presents an opportunity to act in order to increase the probability of survival.

According to our model, in order to reduce the probability of extinction in such a case, the population density must be increased beyond ρ_c . This has important ecological implications since it shows that the probability of extinction can be decreased, not only by increasing the population (which is of course not always possible), but also by a *decrease* in habitat size for a fixed population.

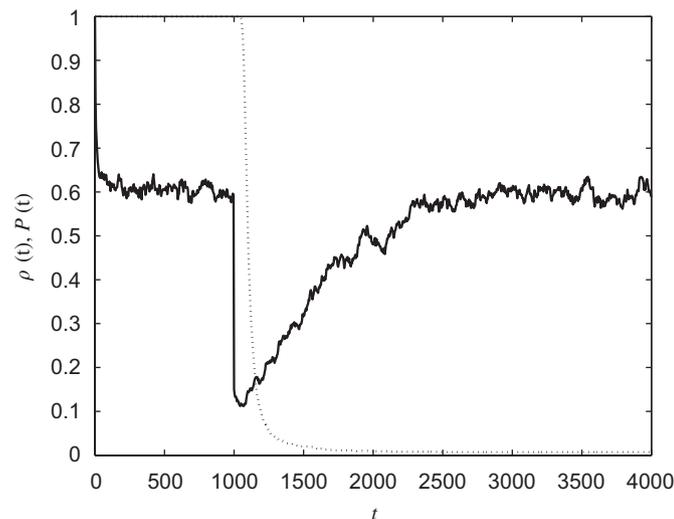


Fig. 6. The average population density of the surviving runs only with the survival probability $P(t)$ (hashed line), i.e. the probability that extinction has not occurred up to time t . A value of $L = 30$ was used with $t_k = 1000$.

To see whether this hypothesis holds, we simulate this again using $p_d = 0.093$ but with $\rho_s = \rho_c = 0.14$ so that the probability of survival is negligible. Now, however, once the population density has been reduced, the area covered by the lattice is halved. This is achieved by halving the linear length of the lattice in 1 dimension. The individuals in the half that is removed are randomly relocated in the remaining half therefore doubling the population density. Once the population has recovered and stabilized, the lattice is returned to its original size. Fig. 7 shows the recovery of the population once the lattice size has been reduced. With $t_{max} = 4000$, the probability of survival increased substantially from 0.004 to 0.278.

We expect there to be an optimal habitat reduction size — too large a reduction and the population will be in danger from the large fluctuations associated with smaller habitat or population sizes, whereas too small a reduction and the density will not be increased sufficiently. This is confirmed in Fig. 8 where we plot the probability of survival P_s up to some t_{max} against the proportional reduction in area $A = L^2$ for different values of ρ_c . We define this proportional reduction in area ΔA to be $\Delta A = 1 - A_{new}/A_{old}$. Again, a 2-dimensional lattice with an initial value $L = 30$ was used and P_s measured with $t_{max} = 4000$. An optimal value of ΔA clearly exists in each case.

From Fig. 8, we see that the greatest value of P_s is achieved with $\rho_s = 0.11$. Smaller values of ρ_s result in smaller populations, which, from Section 3, are at greater risk of extinction by fluctuations. Since in Fig. 8 $\rho_s = \rho_c$, larger values of ρ_s are associated with larger values of p_d . Again, from Section 3, these populations are also at a greater risk from extinction by fluctuations. We also observe that as $\rho_s = \rho_c$ increases, the value of ΔA giving

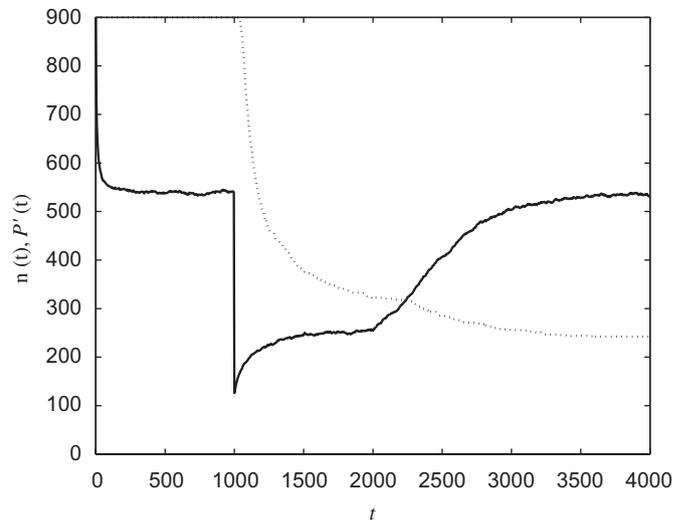


Fig. 7. Plot showing the surviving runs only (solid line) that recover, after a sudden decrease in population size at $t_k = 1000$, due to the re-sizing of the lattice. The lattice is returned to how it was originally at $t = 2000$ and the population recovers to its original value. The re-scaled probability of survival $P'(t)$ is also shown (hashed line).

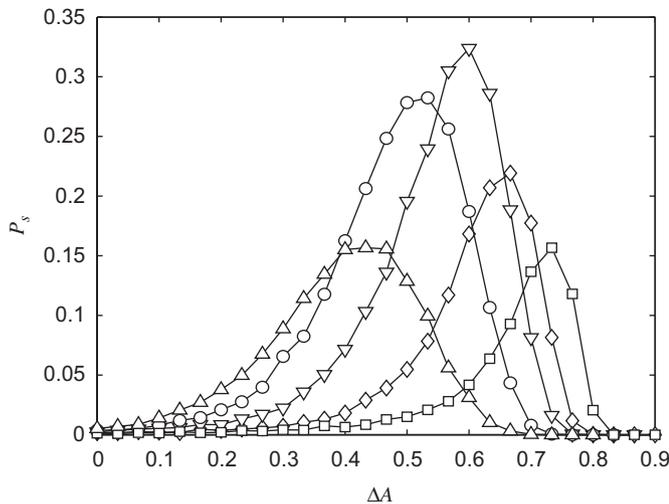


Fig. 8. How the probability of survival changes with different reductions in habitat area, ΔA for $\rho_s = \rho_c = 0.05$ (\square), 0.08 (\diamond), 0.11 (∇), 0.14 (\circ) and 0.17 (\triangle). The corresponding values of p_d were 0.089 , 0.091 , 0.092 , 0.093 and 0.094 , respectively.

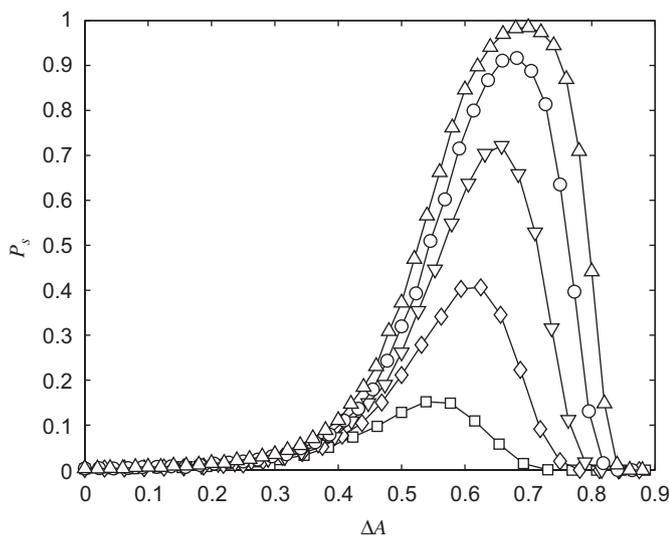


Fig. 9. How the probability of survival changes with reductions in habitat size, ΔA for different initial values $L = 26$ (\square), 32 (\diamond), 38 (∇), 44 (\circ) and 50 (\triangle) with $\rho_s = \rho_c = 0.11$.

the optimal value of P_s decreases. This is likely to be due to the fact that smaller values of ρ_c require a greater density increase to improve P_s as seen in Fig. 5.

We plot in Fig. 9 P_s against ΔA for a fixed $\rho_s = 0.11$, but with different initial values of A . We see that as L increases, P_s also increases for a fixed ΔA . This is likely to be due to the larger population sizes that remain after the reduction in habitat size which are less susceptible to extinction by fluctuations.

Whilst reflective boundary conditions were used here, very similar results were obtained using periodic boundary conditions. In fact, with periodic boundary conditions, the probability of survival increased more significantly due to

the population being able to grow in two directions rather than in just one after the lattice had been returned to its original size. This of course could be achieved in reality by reducing the habitat from more than one direction.

This model was proposed to represent how the area in which a population is found could be reduced in real life. The species could be driven towards one end of the habitat with a boundary placed to prevent them leaving the desired area. This boundary could then be removed once the population has recovered. Clearly this is easier for larger, land-based animals but in principle, at least, could be achieved for all non-plant species.

5. Conclusions

Allee effects are certainly observed in nature (Stephens and Sutherland, 1999; Pedersen et al., 2001; Gyllenberg et al., 1997) and have been studied with respect to extinction. Using a lattice model, we have observed Allee effects together with the role of fluctuations, with the advantage of being able to examine the effects of habitat size. Being able to model the population as a group of *individuals* which move, breed and die, rather than as a variable in an equation, has enabled us to gain a more realistic insight into how real populations behave. In particular, the MC results have taken into account the finite size of the habitats as well as fluctuations and clustering in the population. This has resulted in certain discrepancies between the MF and MC results. Most notably, we observed extinction occurring in the MC simulations where the MF predicted survival.

Rather than the clear-cut conclusions that deterministic models produce, conservationists often examine the *probability* that a population will maintain itself without significant demographic or genetic manipulation for the foreseeable ecological future (Soule, 1987). In this spirit, for a sufficiently large population density we have shown that the probability of survival does increase with habitat size due to the smaller fluctuations. However, far more important are the death rate and population density, since if these fall on the wrong side of their critical values, extinction is almost a certainty.

Our findings are certainly significant for the design of habitats. The idea of a critical habitat size, mentioned in the Introduction, is misleading since, according to our model, it is certainly not true that for a fixed population size the larger the habitat size the better. Regardless of the amount of space and resources available, a population will only grow if the density is above its critical value. We also proposed, in the last section, a method for greatly reducing the probability of extinction by reducing the habitat size once a species has become rare.

Our notion of density has been that of the number of individuals per unit area. While we assumed this to be constant in space when deriving our MF equation (2.2), clearly this will vary amongst real populations. In fact, for populations that are found in patches, the value of the

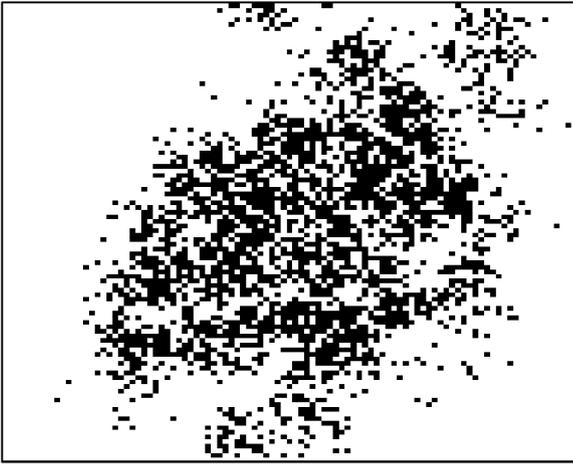


Fig. 10. Snapshot of the output from a 2-dimensional lattice with $L = 100$. A value of $p_d = 0.1$ was used and the picture was taken at $t = 600$ when $\rho = 0.2223$.

density will depend very much on the scales used. The same is true of the MC results as shown in Fig. 10, where we see clear examples of clustering. In nature, species will cluster to varying degrees and hence the value of the critical population density will also vary and would need to be estimated in each case.

So great is the variety of species on our planet that any attempt to create a general model that could accurately capture the behaviour of them all would be futile. Here, we have assumed a homogenous habitat, where all sites are equally accessible and habitable and have used the parameters p_b and p_d only to describe the species. Whilst our model may therefore not accurately describe any particular species, we believe that it shows the general behaviour of species which rely on others for growth and sustainability. Great care would certainly need to be taken in applying our findings to real situations since our findings are of more qualitative, rather than quantitative relevance. In particular, we think that our model would be most relevant for species where the individuals live alone yet sexually reproduce, rather than those which live in groups.

Acknowledgments

We would like to thank Beáta Oborny for very helpful discussions and references. Alastair Windus would also like to thank the Engineering and Physical Sciences Research Council (EPSRC) for his Ph.D. studentship.

References

Aizen, M., Feinsinger, P., 1994. Forrest fragmentation, pollination and plant reproduction in Chaco dry forrest, Argentina. *Ecology* 75 (2), 330–351.

Allee, W., 1931. *Animal Aggregation: A Study in General Sociology*. University of Chicago Press.

Allen, L., Fagan, J., Högnäs, G., Fagerholm, H., 2005. Population extinction in discrete-time stochastic population models with an Allee effect. *J. Differ. Equ. Appl.* 11 (4-5), 273–293.

Amarasekare, P., 1998. Allee effects in metapopulation dynamics. *Am. Nat.* 152 (2), 298–302.

Birkhead, T., 1977. The effect of habitat and density on the breeding success in the Common Guillemot (*Uria aagle*). *J. Anim. Ecol.* 46, 751–764.

Carlson, E., Henkel, M., Schollwock, U., 2001. Critical properties of the reaction-diffusion model $2A \rightarrow 3A$, $2A \rightarrow 0$. *Phys. Rev. E* 63 (3), 036101.

Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* 14 (10), 405–410.

Dammer, S., Hinrichsen, H., 2003. Epidemic spreading with immunization and mutations. *Phys. Rev. E* 68 (1), 016114.

Dennis, B., 1989. Allee effects: population growth, critical density, and the chance of extinction. *Nat. Res. Model.* 3, 481–538.

Dennis, B., 2002. Allee effects in stochastic populations. *OIKOS* 96 (3), 389–401.

Diamond, J., 1984. “Normal” extinctions in isolated populations. In: Nitecki, M. (Ed.), *Extinctions*. The University of Chicago Press, pp. 191–245.

Durrett, R., Levin, S., 1998. Spatial aspect of interspecific competition. *Theor. Popul. Biol.* 53 (1), 30–43.

Escudero, C., 2005. Particle statistics and population dynamics. *Physica A* 354, 371–380.

Escudero, C., Buceta, J., de la Rubia, F., Lindenberg, K., 2004. Extinction in population dynamics. *Phys. Rev. E* 69, 021908.

Frank, K., Brickman, D., 2000. Allee effects and compensatory population dynamics within a stock complex. *Can. J. Fish. Aquat. Sci.* 57 (3), 513–517.

Gyllenberg, M., Hanski, I., Hastings, A., 1997. Structured metapopulation models. In: Hanski, I., Gilpin, M. (Eds.), *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, London, pp. 93–122.

Harris, T.E., 1974. Contact interactions on a lattice. *Ann. Probab.* 2 (6), 969–988.

Hinrichsen, H., 2000. Non-equilibrium critical phenomena and phase transitions into absorbing states. *Adv. Phys.* 49 (7), 815–958.

Hurford, A., Hebblewhite, M., Lewis, M., 2006. A spatially explicit model for an Allee effect: why wolves recolonize so slowly in Greater Yellowstone. *Theor. Popul. Biol.* 70 (3), 244–254.

Itoh, Y., Tainaka, K., Sakata, T., Tao, T., Nakagiri, N., 2004. Spatial enhancement of population uncertainty near the extinction threshold. *Ecol. Model.* 174 (1-2), 191–201.

Johnson, D., Liebhold, A., Tobin, P., Bjørnstad, O., 2006. Allee effects and pulsed invasion by the gypsy moth. *Nature* 444 (7117), 361–363.

Lande, R., Engen, S., Saether, B., 2003. *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.

Long, J., 1981. *Introduced Birds of the World*. Universe, New York.

May, R., Lawton, J., Stork, N., 1995. Assessing extinction rates. In: Lawton, J., May, R. (Eds.), *Extinction Rates*. Oxford University Press, Oxford, pp. 1–24.

Oborny, B., Meszéna, G., Szabó, G., 2005. Dynamics of populations on the verge of extinction. *OIKOS* 109 (2), 291–296.

Opper, M., Saad, D. (Eds.), 2001. *Advanced Mean Field Methods: Theory and Practice*. MIT Press, Cambridge, MA.

Pedersen, B., Hanslin, H., Bakken, S., 2001. Testing for positive density-dependent performance in four Bryophyte species. *Ecology* 82 (1), 70–88.

Peters, O., Neelin, J., 2006. Critical phenomena in atmospheric precipitation. *Nat. Phys.* 2 (6), 393–396.

Pimm, S., 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. The University of Chicago Press.

Robinson, J., 1988. Group size in wedge-capped Capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. *Behaviour* 23 (3), 187–197.

Shelton, P., Healey, B., 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern

- cod (*gadus morhua*) stock? *Can. J. Fish. Aquat. Sci.* 56 (9), 1521–1524.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38 (1-2), 196–218.
- Soulé, M. (Ed.), 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Stephens, P., Sutherland, W., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* 14 (10), 401–405.
- Stephens, P., Sutherland, W., Freckleton, R., 1999. What is the Allee effect? *OIKOS* 87 (1), 185–190.
- Stocklin, J., Fischer, M., 1999. Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950–1985. *Oecologia* 120 (4), 539–543.
- Tainaka, K., 1988. Lattice model for the Lotka–Volterra system. *J. Phys. Soc. Jpn.* 57 (8), 2588–2590.
- Vespignani, A., Dickman, R., Munoz, M., Zapperi, S., 2000. Absorbing-state phase transitions in fixed-energy sand-piles. *Phys. Rev. E* 62 (4), 4564–4582.
- Windus, A., Jensen, H., 2007. Phase transitions in a lattice population model. *J. Phys. A: Math. Theor.* 40 (10), 2287–2297.