In search for the optimal strategy in population dynamics

K. Sznajd–Weron[a] and M. Wolański

Institute of Theoretical Physics, University of Wrocław, pl. Maxa Borna 9, 50-204 Wrocław, Poland

Abstract. A unification of recently proposed models describing population dynamics is presented. We study the effect of different factors, like environmental conditions, concentration of individuals in a given area and migration strategies, on population dynamics. Moreover, we show that a population occupying a smaller area is more susceptible to extinction, which is a well known biological fact. We solve the model using Monte Carlo simulations and the mean-field approach. Constructing flow diagrams we find the optimal strategy in population dynamics.

PACS. 87.10.+e General theory and mathematical aspects – 02.70.Rr General statistical methods

1 Introduction

Why individuals of one species are able to survive in a given habitat while in another environment they become extinct? This is probably the simplest ecological question one can ask. Although many factors can influence population viability, this paper focuses mainly on the role of population size. More specifically, we address the "minimum viable population (MVP)" question: As population size decreases, at what point does the risk of extinction become unacceptably high?

Beginning with Hooper [1], Shaffer [2], and Ginzburg *et al.* [3], conservation biologists have argued that the process of extinction is best viewed as stochastic, and that endangerment should therefore be defined probabilistically, that is, in terms of the probability of persistence over time. For example, MVP might be defined as the smallest isolated population size N at which probability of persistence over the next 1000 years is 99% [2].

To make the idea of MVP clearer, let us quote here a simple example. We toss N coins – representing N individuals – and say that the population becomes extinct in a given "year" if all N coins are tails. Is it possible that our "coin" population will die out? Yes, but only if we are very patient or our collection of coins is small. On average, this rare event will happen after 2^N "years". If we have 100 coins we will have to wait about a million "years", but if we take only 10 coins the population will, on average, become extinct already after a thousand "years"!

Extinction of natural populations is a much more frequent event than the coin example results suggest. However, a natural population is not just a set of non-interactive individuals. In 1931, Allee [4] proposed that

intraspecific cooperation might lead to inverse density dependence. After 70 years this idea is still attractive and there is widespread evidence for the Allee effect in mammals, birds and fish (for a review see [5]). Factors involved in generating inverse density dependence are numerous, but the difficulty of finding a partner to mate in a low density population is the most cited one. The major consequence of the Allee effect is the existence of the critical density below which a population is likely to become extinct.

Let us return to our coin example. This time we toss the coins on a large chessboard (in general – on a square lattice). If a coin (individual) is the only occupant of a given field on the chessboard or other occupants are tails we turn it to the tails side regardless of the actual outcome of the toss. Obviously, now we have to wait for population extinction much shorter then previously. For very low population densities, when all coins fall on different fields the population ceases to exist almost immediately, even if N is large.

It is not easy, if at all possible, to recognize which factor is involved in generating inverse density dependence in natural populations [6]: genetic inbreeding leading to decreased fitness, demographic stochasticity (*i.e.* individual probability of death in a given year) or shortage of receptive mate encounters when the population density is too low, etc. Moreover, some of these factors can be rather weak unless the population density is low. Probably for these reasons, in spite of numerous physical models describing biological evolution (for review see [7,8]), little attention has been paid to the idea of the minimum viable population or the Allee effect. However, the implications of the Allee effect are very important in most areas of ecology, evolution and population dynamics. Moreover, the existence of the critical concentration, below which the

[a] e-mail: `kweron@ift.uni.wroc.pl`

population will die out, is a very interesting phenomenon from the physical point of view.

In this paper we present a microscopic model of population dynamics in which the Allee effect appears very naturally and the minimum viable population can be determined. Furthermore, we ask and give possible answers to the question: "Is there something that a population can do to prevent extinction?" One strategy could be migration. Theoretical and empirical studies of seed dispersal have shown that whether a seed remains near the maternal plant or is dispersed from it influences the fitness of the seed (reviewed in [9]). In case of animals, migration strategies were mainly investigated on insects, because many insect species (*e.g.* pests) migrate from the parental area before reproduction [10]. On one hand, selection should favor migration because it allows finding new unsettled areas and giving more offspring. On the other hand, most of the migrants die. Thus, there is an open question: "is it better to stay or to go?". Quite recently it was found that in the case of an infinite population the optimal migration rate may not exist [11]. However, in case of small populations the migration strategy might be very important. For example, individuals staying near parental area can aggregate to high density clusters. It was shown recently that clustering prevents population extinction [12], which seems to be connected with the Allee effect. In such a case the MVP can be much lower than in the case of uniformly distributed population. In this paper we go even further and show in which environmental conditions it is better to stay then to go. To sum up, we look for the optimal strategy for population survival.

Numerous models of population dynamics with the Allee effect have been proposed (for a review see [5]) and different survival strategies investigated (*e.g.* [13–15]) by biologists and mathematicians. However, those models were mostly based on differential equations for global variables. For such mean-field type models usually some analytic results can be found, but they neglect many details which may be crucial. Physicists know that it is a good policy to start from a microscopic model and establish which details are essential to understanding macroscopic regularities, even if such a model can be solved only by computer simulations.

Extinction of small populations in small habitats using the Penna model (see *e.g.* [7]) was investigated through Monte Carlo simulations by Pál [16]. He found that the average time until the population dies out grows with the size of the habitat and survival chances hardly depend on the population size. It is a well known biological fact [17] that small area decreases the chances of survival, but it is also known that the size of the population is one of the most important factors influencing population extinction at small sizes (or at low densities) [5].

Another microscopic model that allows investigating the behavior of small populations in a given area was proposed few years earlier. In that paper [18] we studied the influence of environmental conditions on population dynamics. We showed, using Monte Carlo (MC) simulations, that there was some critical adaptation below which the

population could not survive in a given area. To separate spatial from genetic effects, we also investigated the same model without selection pressure [19]. In this case we were able to solve the model for an infinite system *via* the mean-field approach (MFA). Using MFA we constructed flow diagrams for one and two dimensions and showed the existence of the critical adaptation, as well as, of the carrying capacity and the minimum viable population. In presence of MFA results, no Monte Carlo simulations were conducted. Quite recently we presented a similar model of population dynamics, applying new rules for moving and mating [20]. We solved this model using both mean-field (for an infinite system) and Monte Carlo (for finite systems) approaches. We showed, through MC simulations, that a larger area increases the survival chances of a population. In that paper we also introduced two migration strategies – "to stay" and "to go", *i.e.* migrate from the parental area before reproduction. Unfortunately, we were not able to give a clear-cut answer which strategy should be preferred by a population. We investigated our model in two cases – with and without selection, and we showed that natural selection increases the survival chances of a population.

In the present paper we propose a unification of the models proposed earlier (reviewed in Sect. 2). We separate spatial from genetic effects to study influence of different factors on population dynamics. In Section 3 we present MFA results for finite lattices in those cases for which the approach is reasonable. The results for finite lattices (previously results only for infinite lattices were presented [19,20]) allow us to show analytically that survival probability increases in a larger area. This result is in agreement with biological [17] and simulation [20] observations. In Section 4 we present Monte Carlo results and construct flow diagrams, which allow us to give a clear-cut answer which of the analyzed migration strategies should be preferred by a population. We would like to point out that in the earlier papers we did not calculate flow diagrams using MC simulations. In the conclusions (Sect. 5) we show that the obtained results agree very well with ecological observations and choose the optimal survival strategy.

2 The general model

We consider a square $L \times L$ lattice with hard boundary conditions. No more than one individual may occupy a lattice site. Each individual is characterized by its genotype G_i, which in our model is represented as a double string (two *gametes*) of L_G loci. At each locus there might be either a zero or a one. Zeros correspond to recessive and ones to dominant allele. We assume total domination of an allele denoted by 1; thus the phenotype $F_i = \{F_i^1, F_i^2, \ldots, F_i^{L_G}\}$ of ith individual is constructed in the following way [18,20]. If at a given locus there are two zeros (recessive *homozygote*) then we put zero at the corresponding phenotype site. Otherwise (*heterozygote* or dominant homozygote) we put 1.

The selection pressure is realized by calculating the survival probability p_i as a correlation of an individual phenotype with the environmental optimum [18, 20]. Such an idea of an individual's survival probability has been already used in the literature and called adaptation or fitness. In reference [20] we have found that selection pressure increases the survival chances of a population. In this paper we investigate precisely the role of spatial factors and will not consider natural selection. In this case no rules for the construction of an offspring's genotype are needed, since each individual has the same survival probability p [20]. In the previous papers [18, 20] an offspring's genotype was constructed in two different ways. In reference [18] particular features were inherited independently, whereas in reference [20] an offspring's genotype was constructed using recombination.

In our model we consider the sexual reproduction of hermaphrodities. In order to procreate the initiating individual must first of all stay alive, which is realized with probability p, then move to an adjacent empty site and find a partner in the nearest neighborhood (nn) of the new site. The condition that only the individual which moved could mate represents all acts necessary to breed in real life [18]. Moreover, this procedure permits us to avoid invoking the Verhulst factor, which usually must be used to account for the limited resources of the habitat [7, 21]. Once the partner is found, the pair produces three offspring and the parents die. This is not as unrealistic as it may sound; there are well documented [7] examples of species that behave in this way (*e.g.* pacific salmon, bamboo plants). Alternatively we could say that the parents stay alive and produce only one offspring. This would probably be more natural but inconsistent with our earlier model [18]. Moreover, to avoid immortality the model would require the inclusion of an aging mechanism (like in [21]). In our model only a non-reproducing individual may live forever. This seems to be quite an extreme feature, but may be (at least to some extent) explained by the trade-off between longevity and fecundity [7, 22].

Two different rules for the moves and search have been proposed. In references [18, 19] some simulations and the mean field approach for the model with the "myopic ant" rule was presented. In the "myopic ant" rule the choice of the direction to move is made randomly from the free nn sites. Analogously, the partner is chosen randomly from the occupied nn sites. Recently [20] some results for the "blind ant" were also presented. In this case the choice of the direction is made randomly from all nn sites. If the attempt is unsuccessful there is no second choice. Thus the "blind ant" represents a population with less active individuals. In this paper we construct the general model, which includes both "ant's" rules. We present new results and show differences between these two rules.

We will also discuss two migration strategies. The first migration strategy ("to stay") is realized by putting two offspring on the dead parents' sites and the third one in the site occupied by the initiating individual before he moved. In the second one ("to go") the sites for the offspring are chosen randomly in the whole lattice. One of the aims of this paper is to show which migration strategy should be preferred by the population.

We can now formulate the general algorithm describing our model:

1. Put randomly N individuals on $L \times L$ square lattice with hard boundary conditions.
2. Select randomly one individual.
3. Select randomly a real number $r \in [0, 1]$. If adaptation p is greater than r the individual will stay alive. Otherwise it will die ($N = N - 1$) – go to 2.
4. Try to move the individual to an adjacent empty site. If the move cannot be done then go to 2.
5. Try to find the partner to mate from nn of the new site. If the partner was not found go to 2.
6. Parents die and 3 offspring are born ($N = N + 1$). Go to 2.

One Monte Carlo step MCS consists of repeating N times steps 2–6 of the algorithm. In the following sections we will investigate this general model using two rules ("blind ant" and "myopic ant") in steps 4–5 and two strategies ("to stay" and "to go") in step 6.

3 Mean field approach

In papers [19, 20] some analytical (mean field type) results for the "myopic" and "blind ants" in the case of an infinite lattice ($L = \infty$) were presented. However, Monte Carlo simulations and real population dynamics take place always in finite regions. It is well known by biologists that survival chances decrease for smaller areas [17]. For this reason the lattice size is taken into account in our analytical calculations.

Let us first recall the mean-field approach for the infinite lattice [19, 20]. In the model we have two processes that can change the population size:

(a) death of an individual with probability $1 - p$ (*i.e.* $N \to N - 1$);

(b) birth of three offspring and death of their parents with probability pR_1R_2 (*i.e.* $N \to N + 1$) because an individual will survive with probability p, then move with probability R_1, and then find a partner to mate with probability R_2.

Hence, the evolution equation is the following:

$$c(t + 1) = c(t) + c(t)\left[pR_1R_2 - (1 - p)\right]. \qquad (1)$$

In the mean field approach for the "blind ant" $R_1 = 1 - c(t)$ and $R_2 = \frac{3}{4}c(t)$, while in the case of the "myopic ant" $R_1 = 1 - c(t)^4$ and $R_2 = 1 - (1 - c(t))^3$.

From equation (1) we can calculate (analytically for the "blind ant" and numerically for the "myopic ant") the critical probability p^* below which the population is convicted to extinction. Above this critical value of p^* we can find fixed points of equation (1) *i.e.* the minimum viable population MVP (unstable) and the carrying capacity K (stable). These calculations and respective flow diagrams were presented in references [19, 20].

To include lattice size dependence in our calculations we divide the lattice into four regions with different probability for movement and mating. For example, an individual from the corner of a lattice has only two neighboring sites to make a move, while an individual from the middle has four neighbors. Each of the four regions has a different size. The ratio between region and lattice size gives us the probability that an individual from a given region will be chosen:
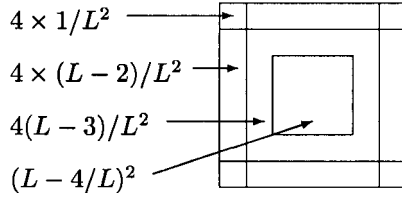
We can modify the evolution equation (1) both for the "myopic ant" and the "blind ant" and calculate the critical survival probability $p^*(L)$, as well as fixed points K and MVP. Since all these calculations are very simple we will not present them in detail. For the "blind ant", after simple algebraic transformations, we can rewrite the evolution equation (1) in the following way:

$$\frac{c' - c}{c} = \frac{4}{L^2}\left[\frac{2}{3}p(1-c)c - (1-p)\right]$$
$$+ \frac{4(L-2)}{L^2}\left[\frac{25}{36}p(1-c)c - (1-p)\right]$$
$$+ \frac{4(L-3)}{L^2}\left[\frac{35}{48}p(1-c)c - (1-p)\right]$$
$$+ \frac{(L-4)^2}{L^2}\left[\frac{3}{4}p(1-c)c - (1-p)\right]$$
$$= -Apc^2 + Apc + B(p-1), \qquad (2)$$

where

$$A = \frac{27L^2 - 11L + 13}{36L^2}, \qquad B = \frac{L^2 + 12}{L^2}. \qquad (3)$$

There is one stable fixed point $c = 0$ of equation (2), which exists for all p. Two other fixed points are solutions of the following equation:

$$c' - c = -Apc^2 + Apc + B(p-1) = 0 \qquad (4)$$

and exist only for $p \geq p^*(L)$, where p^* is the solution of $(Ap)^2 + 4ABp(p-1) = 0$. For the survival probability p smaller then $p^*(L)$ the only solution of equation (2) is $c = 0$. This means that below a certain critical value of $p = p^*(L)$, the population will become extinct independently of its initial concentration. If we plot the critical survival probability p^* *versus* lattice size L (Fig. 1) we can see that it is more difficult to survive on a smaller area. This fact is well known to biologists [17] and agrees with simulation results presented in [16,20].
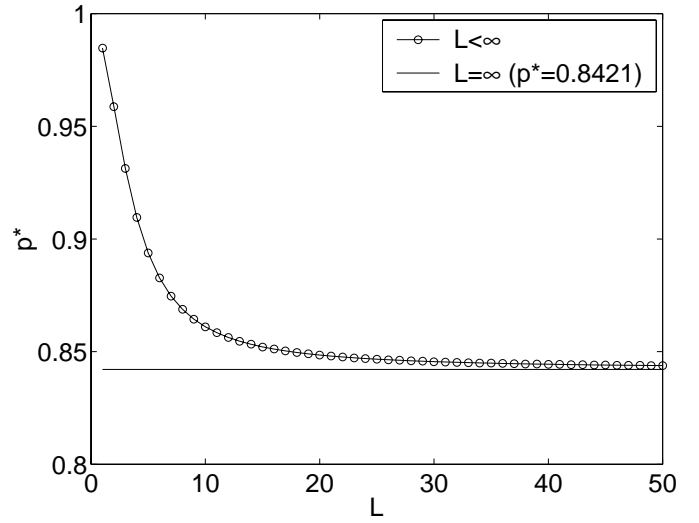

Fig. 1. Analytical dependence between lattice size L and critical survival probability p^* for the "blind ant".
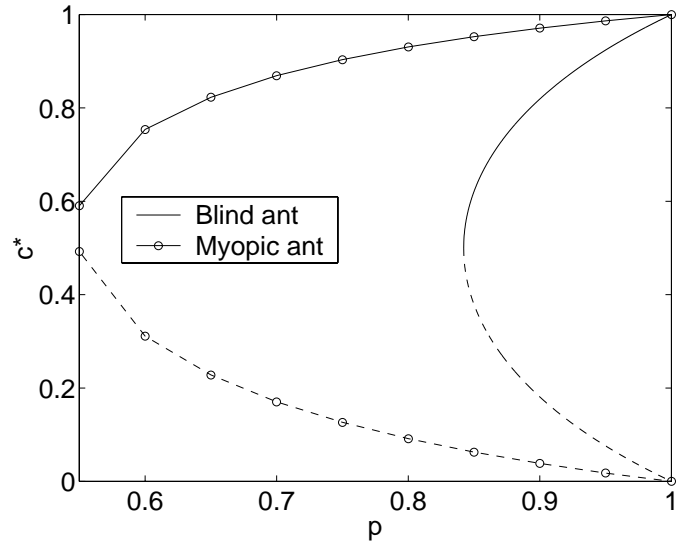

Fig. 2. Flow diagram for the "blind" and the "myopic ant" ($L = 100$). Dashed line represents the unstable steady state, *i.e. MVP*, and the solid line represents the stable steady state, *i.e. K*.

In order to construct a flow diagram for the "blind ant" we just have to find zeros of a polynomial of order 2. Unfortunately, for the "myopic ant" we have a polynomial of order 7. Since we cannot solve it analytically, we solve it numerically. In this case we have also found that the critical survival probability is larger for smaller territories, which means that it is harder to survive there. Flow diagrams for the "blind" and the "myopic ant" are presented in Figure 2. In both cases we have found existence of the critical survival probability p^*, the minimum viable population MVP and the carrying capacity K. In both cases p^* decreases with L. Thus both "ant" rules are proper to model population dynamics. However, as we can see in Figure 2 the more active population ("myopic ants") has higher chances for survival, which is quite obvious.
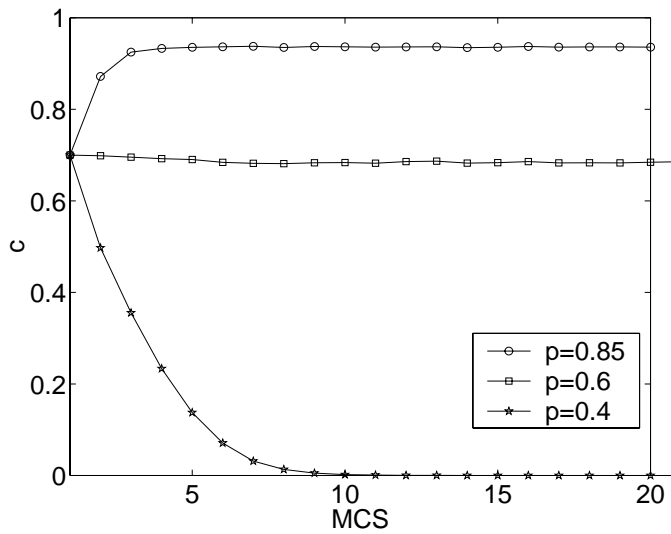
Fig. 3. Evolution of the "myopic ant" population for $L = 100$, initial concentration $c(0) = 0.7$ and different values of p.
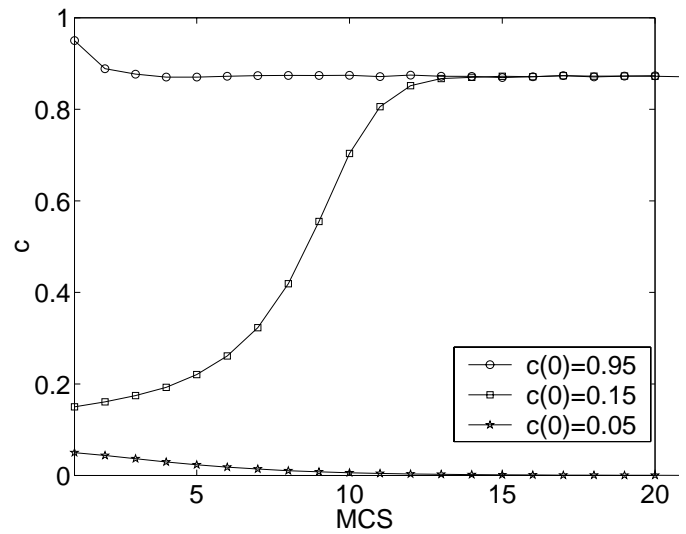

Fig. 4. Evolution of the "myopic ant" population for $L = 100$, survival probability $p = 0.75$ for different values of initial the concentration.

It is worth noticing here that the same model with asexual reproduction will not produce the existence of the MVP. For such a case the mean field approach yields the critical survival probability $p^* = 0.5$ (for $p > p^*$ the population will always reach the carrying capacity). This result suggests that in our model the Allee effect is generated mainly by difficulties with finding a partner to breed, which is treated as the main cause of the inverse density dependence [5].

4 Monte Carlo simulations

Until now we have investigated our model using only the mean field approach. We have seen that larger territories are preferred by populations since it is easier to survive in such environments. We have also shown, what was expected, that individuals should try to behave like "myopic ants" to increase the survival probability of the population. However, a question concerning the migration strategy remained that we could not answer using MFA: is it profitable for individuals to stay at the parental area or not? In reference [20] the problem "to stay or to go" was touched for the case of the "blind ant", but no clear-cut answer was given.

Let us start with the "myopic ant", since this rule gives higher chances for survival. In Figure 3 we present simulation results for the square lattice 100×100 and initial concentration $c(0) = 0.7$. It can be seen that for this value of $c(0)$ the survival probability $p = 0.6$ is enough for the population to survive. For $p = 0.4$ the population becomes extinct already after 10 MCS. Moreover, if p is large enough for the population to survive, the population reaches a certain carrying capacity $K(p)$. Analogous behavior we can found for all values of $c(0)$.
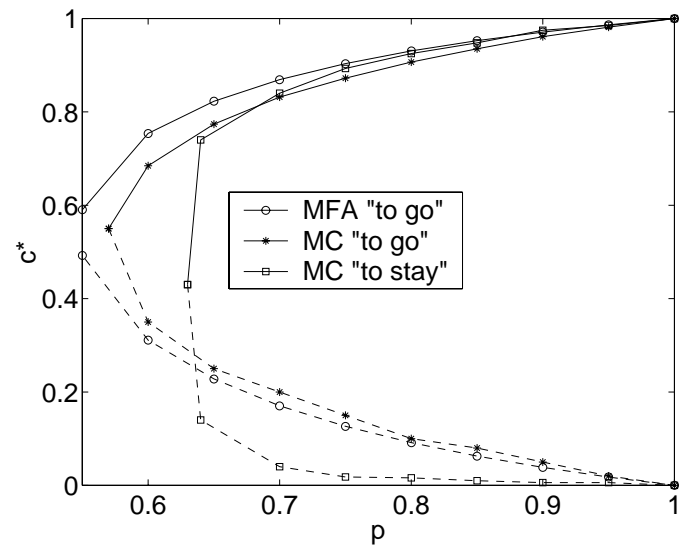

Fig. 5. Flow diagram for the "myopic ant". Dashed line represents the unstable steady state, *i.e. MVP*, and the solid line represents the stable steady state, *i.e. K*.

Let us now keep the survival probability constant *e.g.* $p = 0.75$ (Fig. 4) and start from different values of $c(0)$. It can be seen that independently of the initial concentration population reaches the same carrying capacity if only $c(0) > MVP$. For the initial concentration below MVP the population dies out. These observations are in agreement with MFA results. Similar results for the "blind ant" were already presented in [20]. Repeating simulations for different $c(0)$ and p we can construct flow diagrams (see Fig. 5). As can be seen, simulations agree very well with MFA results.

One very important issue should be mentioned here. In simulations (like in the real life) it can happen that
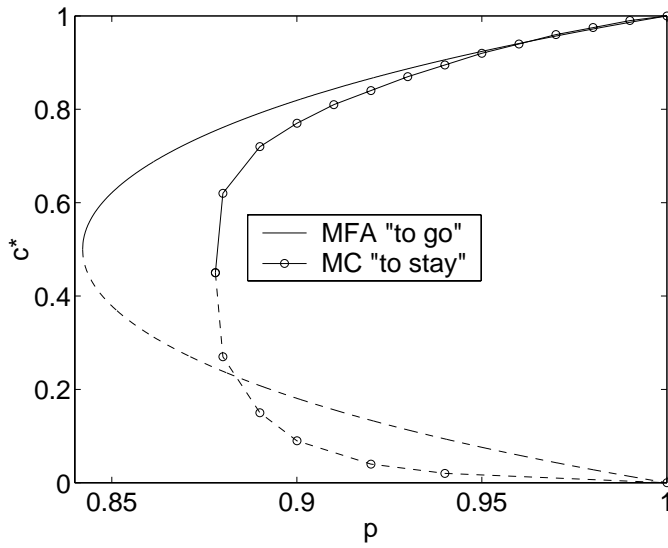
Fig. 6. Analytical ("to go") and Monte Carlo ("to stay") flow diagrams for the "blind ant" . Dashed lines represent the unstable steady states, *i.e.* MVP, and solid lines represent the stable steady states, *i.e.* K.
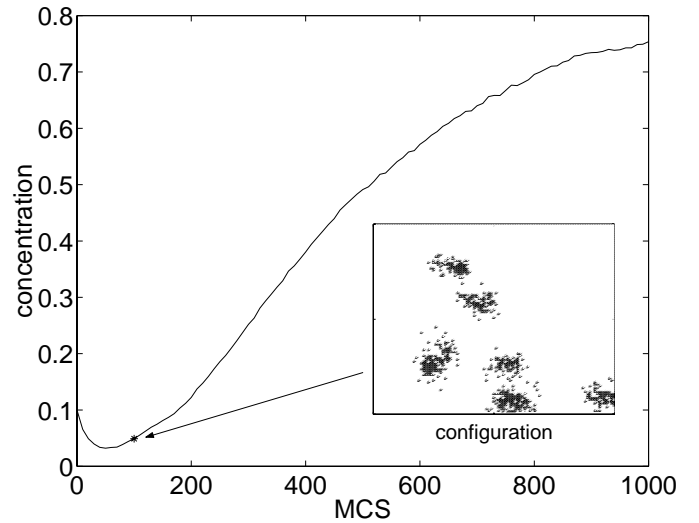

Fig. 7. Evolution of concentration for the "to stay" strategy and the "blind ant" for $p = 0.9$ and c(0)=0.1. In the inset spatial configuration after 100 MCS is presented.

even if the initial concentration $c(0)$ and fitness p are theoretically large enough to survive, the population extinct. For example, consider the "myopic ant" population with $c = 0.2$ and $p = 0.7$ (see Fig. 5). Looking at MFA results we see that the population should stay alive, but in MC simulations 10 out of 100 populations become extinct. So, how should we define MVP in Monte Carlo simulations? We used the simplest definition: MVP is such a concentration, that for a given p 100% (in our case 100 out of 100) of populations survive. This seems to be a very natural definition, but if we increase precision of calculations to 1000 populations this definition will give us different MVP. This is one of the reasons for which it is very difficult to precisely define the critical concentration for the real living population. For example Shaffer defined MVP as a concentration below which a population has 99% chances to survive for a period of 1000 years [2]. This definition is very tentative, but still no better one has been found. At this point we can see that MC simulations are much closer to real life than MFA, in which MVP is just an unstable fixed point of the evolution equation.

Now we will investigate the migration strategies. The first analyzed strategy ("to stay") is realized by putting two offspring in the sites of their parents and the third one in the place from which the initiating individual came. In the second strategy ("to go") offspring are distributed randomly on the lattice. Flow diagrams for the first strategy are presented in Figure 5 (for the "myopic ant") and in Figure 6 (for the "blind ant"). In both cases the "to stay" strategy increases probability p^*, *i.e.* the population has to be better adapted in order to survive. However, if it is better adapted its MVP is lower. For example, the "myopic ant" with $p = 0.8$ has $MVP("to go") = 0.1$, while $MVP("to stay") = 0.016$. This means that the population with the "to go" strategy needs 6 times more in-

dividuals to survive than the population with "to stay" strategy. This results suggest the following optimal strategy: if the environmental conditions are hard it is better to migrate from the parental area, but if the population is well adapted it is better to stay. This result is in agreement with biological observations [10]. Moreover, for all obtained results there are only quantitative differences between the "blind ant" and the "myopic ant".

In Figures 5 and 6 we presented MFA results only for the "to go" strategy. This is not a coincidence. The mean-field approach cannot be used for the "to stay" strategy, see Figure 7 where the time evolution of concentration for the "blind ant" with the "to stay" strategy is presented. We can see that initially the population decreases, like in the "to go" case, but after some time it starts to increase. This is very different from the results for the "to go" strategy (see Figs. 3 and 4), where only monotonic curves were observed. In the inset of Figure 7 the configuration after 100 MCS is presented. Clusters that have formed are clearly visible. It is worth noticing that if the survival probability p is constant in our model (as in this paper; we do not study environmental changes) then once a cluster is formed it will eventually spread to the whole lattice. A similar clustering effect was observed in [12], however, in their model the clusters grew in size despite the variable survival probability. The cluster growth in our model is quite easy to explain: even if the global concentration is very low, the local density is very high and prevents the Allee effect. The same non-monotonic behavior and clustering in spatial configuration was observed for the "myopic ant" with the "to stay" strategy. Due to the fact that local concentration in the "to stay" case is different from global one the MFA cannot be used.

5 Conclusions

We have presented the generalized model describing population dynamics without selection pressure. We have compared four subcases of the model: "blind ant" with migration strategy "to go", "blind ant" with migration strategy "to stay", "myopic ant" with migration strategy "to go", and "myopic ant" with migration strategy "to stay". Wherever it was possible we derived analytical (MFA) results, which agreed very well with those obtained from our computer simulations. On the basis of results presented in Sections 3–4 we have found the optimal strategy for the population which agrees with ecological data (for review see [10]).

Analytical flow diagrams as well as those obtained from Monte Carlo simulations show that in order to increase population survival chances individuals should behave like "myopic ants".

Moreover, if the population is well adapted to the environment, *i.e.* $p > p^*$("to stay"), individuals should stay in the parental area. However if $p < p^*$("to stay"), the population should migrate. Such a behavior was indeed observed in real biological systems.

We have also found analytically the dependence between the area size and the critical survival probability and showed that it is easier to survive in a larger region. This phenomenon is well known in biology and was described by MacArthur and Wilson already in 1967 [17].

After defining the *MVP* in a Monte Carlo simulation we have argued that the MFA cannot describe reality as good as a Monte Carlo simulation. This is well known by physicists, and proves the need for microscopic models in theoretical biology.

References

1. M.D. Hooper, in *The scientific management of animal and plant communities for conservation,* edited by E. Duffey, A.S. Watt (Blackwell Scientific Publications, Oxford, 1971), p. 555.
2. M.L. Shaffer, BioScience **31**, 131 (1981).
3. L.R. Ginzburg, L.B. Slobodkin, K. Johnson, A.G. Bindman, Risk Anal. **2**, 171 (1982).
4. W.C. Allee, *Animal Aggregations. A study in General Sociology* (University of Chicago Press, Chicago 1931).
5. F. Courchamp, T. Clutton-Brock, B. Grenfell, Trends Ecol. Evol. **14**, 405 (1999).
6. R. Lande, Oikos **83**, 353 (1998).
7. S.M. de Oliveira, P.M.C. de Oliveira, D. Stauffer, *Evolution, Money, war and Computers* (Teubner, Stuttgart, 1999).
8. B. Drossel, Adv. Phys. **50**, 209 (2001).
9. H.F. Howe, J. Smallwood, Annu. Rev. Ecol. Syst. **7**, 469 (1982).
10. Ch.J. Krebs, *Ecology. The Experimental Analysis of Distribution and Abundance*, 4th edn. (Harper-Collins, New York, 1994).
11. M. Lemire, S. Lessard, J. Math. Biol. **35**, 657 (1997).
12. N.M. Shnerb, Y. Louzoun, E. Bettelheim, S. Solomon, P. Natl. Acad. Sci. USA **97**, 10322 (2000).
13. R. Lande, Am. Nat. **142**, 911 (1993).
14. R. Gormulkiewicz, R.D. Holt, Evolution (Lawrence, Kans) **49**, 201 (1995).
15. S.A. Levin, B. Grenfell, A. Hastings, A.S. Perelson, Science **275**, 334 (1997).
16. K.F. Pal, Int. J. Mod. Phys. C **7**, 899 (1996).
17. R.H. MacArthur, E.O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ, 1967).
18. I. Mróz, A. Pękalski, K. Sznajd-Weron, Phys. Rev. Lett. **76**, 3025 (1996).
19. K. Sznajd-Weron, Eur. Phys. J. B **16**, 183 (2000).
20. A. Pękalski, K. Sznajd-Weron, Phys. Rev. E **63**, 031903 (2001).
21. A. Pękalski, Eur. Phys. J. B **13**, 791 (2000).
22. K. Schmidt-Nielsen, *Scaling. Why is animal size so important?* (Cambridge University Press, 1991).