Influence of habitat size on the viability of spatially structured populations of the landsnail *Trochoidea geyeri*

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Synopsis

We simulated the relative influence of the habitat size on the survival probability of a spatially structured population of a small landsnail, *Trochoidea geyeri*. The results indicate that the average survival time of the population is independent from the habitat size and rather a function of the population density. We explain this with the properties of the neighbourhood population structure, that is caused by the low dispersal ability of the snails.

population structure, landsnail, population viability, habitat size, Trochoidea geyeri

1 Introduction

In species conservation attempts, it is necessary to know vital requirements of the species in question. Many parameters can be estimated directly from field-observations, whereas other factors must be estimated from models. The habitat size requirement for a minimum viable population, in particular, is typically estimated from a computer based population viability analysis (PVA) (GILPIN & SOULÉ 1986, GILPIN 1987).

In cases where the area of continuous distribution of a population by far exceeds the dispersal ability of individuals, random mating can not be assumed for the whole population. The population structure can then be dominated by the interaction of population density and dispersal. Each individual in such a population has only a limited number of potential mates, the 'neighbourhood'. This measurement of the effective population size is a concept that was introduced by WRIGHT (1946). The expected genetic population structure can be calculated from the neighbourhood size and can be described as 'isolation by distance' within the population (SLATKIN 1993).

In this study we tackled the question of how this population structure affects the population dynamics in dependence of the habitat size. The issue of the viability of a population is often addressed in conservation studies, but the aspect of substantial within-population-structure has been neglected. A spatially structured, but continuous population can obviously not be regarded as a single reproductive unit. A metapopulation concept is not appropriate for the description of the population dynamics, because there is no exchange of individuals between identifiable subunits as in a stepping-stone model, but rather a range-limited free floating of individuals within the same entity.

In this study, we focused on a small annual gastropod, *Trochoidea geyeri* (SOÓS 1926). It could be shown by direct (field observations) and indirect (molecular genetic) methods that *T. geyeri* is a poor disperser with a pronounced neighbourhood population structure (PFENNINGER & BAHL 1995, PFENNINGER & al.1996).

We employed a computer simulation to investigate spatially structured, continuous populations of *T. geyeri*. The aim of the study was to evaluate the relative influence of the habitat size on viability of the population in dependence of the observed population structure.

2 Materials and Methods

Basic data

The data that were necessary to use realistic parameters in the simulation were obtained during field experiments on an abandoned vineyard close to Schlüchtern (Hessen/Central Germany). Details of the experimentation are published in PFENNINGER & al. (1996). We will recapitulate shortly the results that relate to this simulation study:

The population density was estimated to be 6.89 ± 3.89 individuals/m^2. The spatial distribution of *T. geyeri* was random. The average dispersal distance for the reproductive lifetime of 120 to 150 days ranged from 2.94 m to 3.22 m. The snails preferred no particular direction of movement, the direction of consecutive moves was independent from previous moves and the frequency distribution of dispersal distances fitted a function with exponential decay. These findings allowed us to employ a random walk model for the simulation of the snail dispersal (PIELOU 1969). Estimates of neighbourhood size according to WRIGHT (1946) range from 70 to 208 individuals. The area associated with a neighbourhood is 13 m^3 to 21 m^2.

The Model

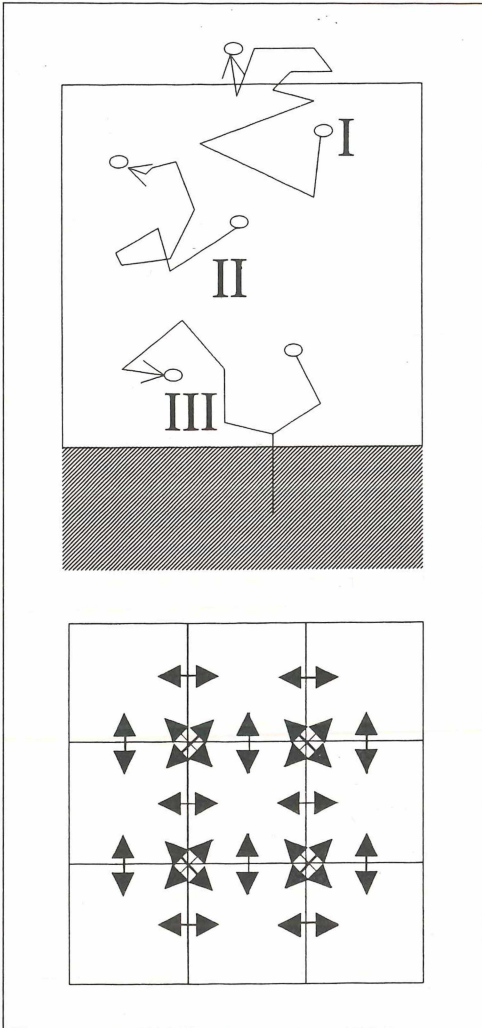To model the continuous population, it was divided into squares of 5 x 5 m². Such a square encloses a

circle of 21 m², the maximum estimate for the area of a neighbourhood. The relations between neighbouring squares was represented by the number of individuals migrating in either direction. To obtain realistic rates of exchange and their standard deviations, we applied an individual based model. A virtual 'snail' was placed on a randomly chosen spot within the square. To move the snail, a random variate for the dispersal distance was drawn from the dispersal function for 15 days obtained from the field data and assigned to a random direction. By repeating this procedure 10 times, a dispersal over 150 days was simulated. After the simulation of the movement for 1000 snails, the proportion of snails was determined that i) stayed within the square of their origin, ii) moved to the 4 squares sharing a side and iii) moved to the 4 squares neighbouring only in a corner (Figure 1). To obtain standard deviations, the procedure was repeated 10 times. Because it was known that *T. geyeri* does not leave the preferred habitat type (PFENNINGER & BAHL 1995), it was necessary to adopt this model to habitat patches bordered by unsuitable habitat on one or more sides. It was assumed that a snail, finding itself an unsuitable area after a move, returns directly with the next move of equal length, but inverted direction and moves on as described above (Figure 2). The exchange over the neighbouring squares was neglected, because it proved to be far below 1‰.

Each neighbourhood was treated as a separate reproductive unit. The following equation, taken from BEGON & al. (1990) was used to calculate the reproduction of the neighbourhoods:

$$N_{t+1} = \frac{NR}{1 + \frac{(R-1)N_t}{K}}$$

The variable R represents the intrinsic rate of increase, N the number of individuals within a neighbourhood at the time t, and K the carrying capacity. Initial neighbourhood sizes of 90, 130 and 200 individuals were used as start values. The value for the intrinsic rate of increase was set arbitrarily to 1.01, varying randomly about ± 10 % for each neighbourhood separately. The carrying capacity was set to 150 individuals, varying randomly about ± 5 % for all neighbourhoods alike. This stochastic fluctuations in the conditions from year to year can be viewed as representation of the weather in the model, affecting the whole area. The values for R and K are not known from the field – this would require long-term studies – but were chosen to keep computation time low. Nevertheless, they do not conflict with the observations made within 2 years of field studies.

Emigration and immigration into each neighbourhood took place before the reproduction. The number of migrants towards each neighbouring square was determined for each direction separately
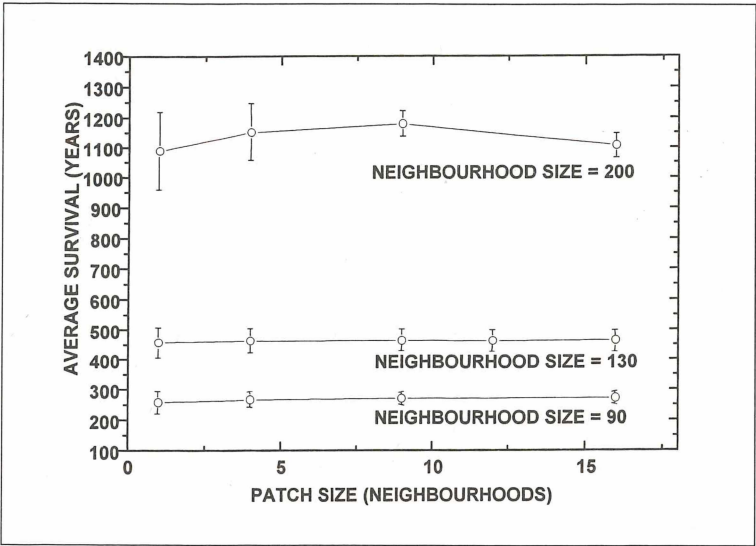
Fig. 2
Plot of the average survival time in years against the patch size in neighbourhood units for initial neighbourhood sizes of 90, 130 and 200 individuals. Each simulation was run 1000 times. The error bars indicate the standard deviation of the data.
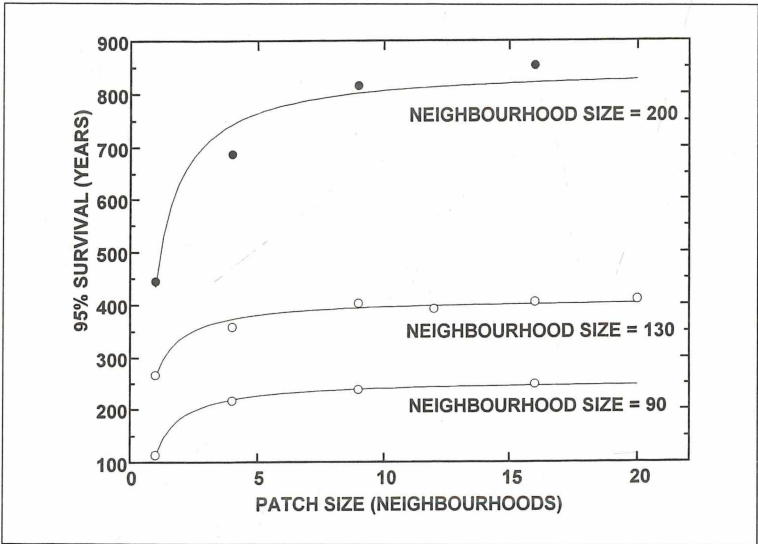

Fig. 3
Plot of the 95 % survival time in years against the patch size in neighbourhood units for initial neighbourhood sizes of 90, 130 and 200 individuals.

by multiplying the actual number present in the area with the rate estimated in the first model. This rate varied randomly within the bounds set by the standard deviation.

The simulations were run for habitat patches varying in size from 1 to 20 squares. Each simulation was run until the total population was extinct and was repeated 1000 times.

We obtained two measurements for the influence of the habitat size on the viability: (i) the average time it took for all the runs to become extinct and (ii) the time when 95 % of the runs were not extinct.

3   Results

The average time until extinction was not dependent on the habitat size in all simulations, but on the population density (Figure 2). This dependence follows a exponential function, as can be seen in figure 4. The 95 % survival time on the other hand was, for each population density on a different level, dependent on the habitat size for small values, whereas it approached a saturation value for larger habitat sizes, (Figure 3).
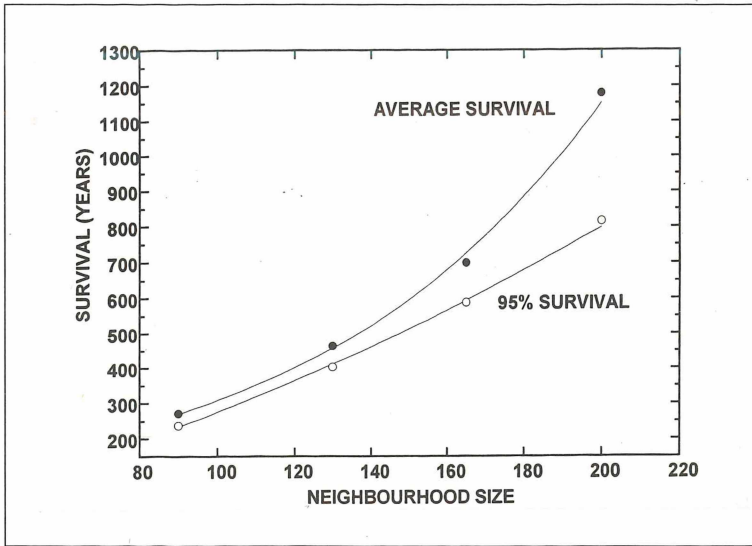
Fig. 4
Plot of average survival (filled circles) and 95 % survival (open circles) for a patch size of 9 neighbourhoods against the initial neighbourhood size.

4   Discussion

The finding that the average survival time is independent from the habitat size is at first sight counterintuitive. But the analysis of the simulation shows that, averaged over time, as many snails migrate out of each neighbourhood as do immigrate. The individual neighbourhoods therefore stay essentially isolated, but only as far as the number of individuals relevant for the reproduction is concerned. The average survival time remains accordingly a function of the initial neighbourhood size.

Larger demographic fluctuation, caused by stochastic effects, within the individual neighbourhoods are buffered by the surrounding neighbourhoods, which profit either from the high number of immigrants or support a neighbourhood with their own emigrants that experienced a drop in population size. This property of the neighbourhood model is reflected by the increase of the 95 % survival time which reaches its saturation-value when the habitat size takes on a value that allows the maximum number of directly neighbouring squares for all neighbourhoods. In case of a basically rectangular order, this point is reached in a 3 x 3 square, equalling a habitat size of 9 neighbourhoods.

The results show that the survival of a population, strongly structured due to restricted dispersal ability, is not so much a question of the available habitat-size, but rather of its quality as can be seen by the exponential dependence of the average survival time of the population density.

Due to their low dispersal ability, snail populations are frequently structured according to the neighbourhood model (*i.e.* CAIN & CURREY 1968, GREENWOOD 1974; COWIE 1984, BAUR 1993; JOHNSTON & BLACK 1995). These findings and the similar observations from our own study on the population structure of *Candidula unifasciata* (unpublished data) indicate that the results of this study can be transferred to other, equally structured populations of snail species.

The findings of this study are relevant for the praxis of species conservation insofar as the main attention should be focused on the maintenance of habitat quality and the connection of suitable habitat patches rather than on the habitat size, when organisms of low vagility like snails are concerned.

Acknowledgements

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