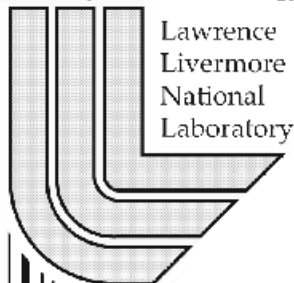


The Effect of Habitat Inhomogeneities and Fragmentation on Population Density and Time to Extinction

Tanya Kostova
Tina Carlsen

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The Effect of Habitat Inhomogeneities and Fragmentation on Population Density and Time to Extinction

Tanya Kostova
Lawrence Livermore National Laboratory
L-561, Livermore, CA 94550, USA
and Tina Carlsen
Lawrence Livermore National Laboratory
L-528, Livermore, CA 94550, USA

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Running Head : Inhomogeneities, Fragmentation and Time to Extinction

Author to whom correspondence should be sent:
Tanya Kostova
L-561 Lawrence Livermore National Laboratory
7000 East Avenue,
Livermore, CA 94550, USA

Abstract

We present a study, based on simulations with SERDYCA, a spatially-explicit individual based model of rodent dynamics, on the connection between population persistence and the presence of inhomogeneities in the habitat. We are specifically interested on the effect that inhomogeneities that do not fragment the environment, have on population persistence. Our results suggest that a certain percentage of inhomogeneities can increase the average time to extinction of the population. Inhomogeneities decrease the population density and can increase the ratio of juveniles in the population thus providing a better chance for the population to restore itself after a severe period with critically low population density. We call this the "inhomogeneity localization effect".

Keywords: *fragmentation, habitat, persistence, time to extinction*

1 Introduction

The role of habitat loss and fragmentation on species survival has been the topic of a fast increasing volume of scientific literature, both from the applied ecologist's and modeler's point of view (see [1, 10, 5, 6, 2], among many others). Habitat loss is widely accepted as the leading cause of local population extinctions, [3, 8, 9]. Habitat fragmentation is defined as the process of subdividing a continuous habitat into smaller, isolated pieces [1]. As a result of this process, animal movements between the patches are either impossible or impeded and local populations on the patches become isolated.

Human activities disrupt species habitats in various ways. For example, oil exploration and development activities fragment natural environments through the building of roads and pipelines which are impenetrable to smaller species but can also modify or disrupt habitats through oil and brine spills of various sizes. These polluted areas are avoided by some species [7]. Thus, for them the geometry of the habitat changes from an intact landscape to a landscape with "holes" or "spills". The occurrence of spill disruptions clearly creates a loss of habitat and possibly, fragmentation, and is expected to have a negative effect on the population persistence. However, even if the habitat has not been fragmented and even if additional habitat is added to compensate for the loss due to spills, the very presence of spills could have a certain effect on population viability.

Evaluation of the effect of the introduction of inhomogeneities such as spills, on population persistence has not been done. In this paper we compare the effect of various percentages of spill inhomogeneities in landscapes with equal habitat area on population persistence. We perform a study based on simulations with SERDYCA, a spatially-explicit, data-driven individual-based model of rodent dynamics [12], customized for prairie vole (*Microtus Ochrogaster*) populations. SERDYCA is a virtual ecological environment in which we perform *in silico* ecological experiments and observations. As it is with any modeling approach, our conclusions should not be treated as predictions or absolute truth but rather as scientific hypotheses that need further testing *in vivo*. Through simulations we establish that inhomogeneities up to a certain level exert a positive effect on the persistence of prairie vole populations. We offer an explanation for this counterintuitive result. The problem, the results and the interpretations obtained from them are, to the best of our knowledge, new and unique.

2 Statement of problem

2.1 Definitions

We use a routine representation of a landscape as a collection of square cells [5, 10]. Each cell has the size of the home range of the considered species. Each cell is of one of two types: *inhabitable* or *uninhabitable*. The inhabitable cells are assumed to contain varying amounts (that could be also zero) of vegetation consumed by the modeled species. The collection of inhabitable cells represents the *habitat*. The number of inhabitable cells is called the *habitat size*. The uninhabitable cells are either *penetrable* or *impenetrable*. We call the impenetrable uninhabitable cells "*spills*" referring to the original motivation of our study. Thus, in this study each spill is of the size of a home range. A *path* is defined as a set of cells, such that each one has a neighbor belonging to the set. Two inhabitable cells are called *connected habitat cells* if they belong to a path, containing only inhabitable cells. The habitat is *connected* if all inhabitable cells are connected. If a habitat is not connected, each connected subset of it is called a *patch*.

We keep the number A_h of inhabitable cells fixed and choose increasing numbers A_n of non-inhabitable cells, so that $A_h + A_n$ is an exact square. For a fixed A_h and given A_n we consider a square of $\sqrt{A_h + A_n} \times \sqrt{A_h + A_n}$ cells with random spatial distributions of the spills among the set of inhabitable cells. Each such square is called a *landscape of size $A_h + A_n$* . There are many landscapes with the same size and having different spatial distributions of habitat and spill cells. We denote each of the various spatial patterns as D_α , where α varies between 1 and the maximum number of possible different spatial patterns, $N(A_h, A_n)$.

Further, the simulation model is initialized by creating an initial animal distribution of model animals distributed over the landscape at the initial time 0. Initially, each spatial cell contains a certain, randomly generated number of animals with randomly generated characteristics (age, size, etc.).

For a given pattern D_α and initial animal distribution $P(0)$, we perform a simulation for a fixed time T_{max} and denote by $T[A_h, A_n, D_\alpha]$ the time for which the population with the given initial distribution dies out (the total number of individuals becomes 0). It is implicitly assumed that $T < T_{max}$ but if the population persists up to time T_{max} , then we set $T[A_h, A_n, D_\alpha] = T_{max}$.

We define the average time of extinction of the population depending on the landscape size $A_h + A_n$, as

$$ATE(A_h + A_n) = \frac{\sum T[A_h, A_n, D_\alpha]}{N(A_h, A_n)} \quad (2.1)$$

where the sum is taken over all possible spatial patterns.

Further, if $P_\beta(0), \beta = 1, \dots, M(A_h, A_n)$ are all possible initial spatial animal distributions for a landscape of size $A_h + A_n$, we define the *average time to extinction associated with landscape size $A_h + A_n$* as

$$\hat{ATE}(A_h + A_n) = \frac{\sum T[A_h, A_n, D_\alpha, P_\beta(0)]}{N(A_h, A_n) \cdot M(A_h, A_n)} \quad (2.2)$$

where the sum is taken over all possible spatial patterns and all possible animal distributions.

Finding the exact value of \hat{ATE} is theoretically possible, because all the possible initial animal and spill distributions are finite. In practice however, it is impossible in reasonable time to perform even a comparable number of simulations covering the variety of initializations because their number is enormous. For example, for a fixed animal distribution, the number of possible spill distributions is $\frac{(A_h + A_n)!}{A_h! A_n!}$. This number has to be multiplied by the number of possible animal distributions which is at least 2^{A_h} . Even for very small-scale landscapes with $A_h \approx 500$ habitat cells this number is obviously huge. Keeping in mind that the larger the landscape, the longer the time for a single simulation (with SERDYCA for a 100x100 landscapes the calculation time is 1 min/simulation but for a 250x250 landscape it is 13 minutes/simulation), in practice, we can perform only a very small amount of simulations and calculate average times which represent approximations to the ATE and \hat{ATE} .

2.2 Effect of landscape inhomogeneities on the ATE

Results from simulations with SERDYCA on homogeneous landscapes (no spills or fragmentation), reported in [12], showed that the population persistence, expressed by the $\hat{ATE}(A_h)$, is positively correlated with the habitat size A_h . For a large amount of simulations with different homogeneous habitat areas and various values of predation levels, the \hat{ATE} was a strictly increasing function of area.

When landscapes with spills are considered, two separate effects may occur. First, the presence of spills may fragment the landscape. If the positive correlation between habitat size and \hat{ATE} is universally true, any fragmentation leading to the formation of patches between which the individuals from a given species do not or rarely migrate, would lead to the reduction of the \hat{ATE} of this species because the considered population becomes subdivided into smaller local populations with smaller habitat sizes and each of them has a shorter \hat{ATE} .

Second, it is possible that spills are distributed among the inhabitable cells so that the habitat remains connected and the habitat size is preserved. This is the case of interest in this study. It is unclear whether the very presence of spills has an effect on the persistence. If the size of the habitat is the only factor affecting the ATE of any population then for a fixed A_h , the relations $ATE(A_h) = ATE(A_h + A_n)$ and $\hat{ATE}(A_h) = \hat{ATE}(A_h + A_n)$ should hold true for all A_n .

The probability that the first or second case will occur is higher when the ratio $\frac{A_n}{A_h}$ is, respectively, relatively large or small. To illustrate, Figure 1 represents three landscapes of 50x50 inhabitable square cells each and an increasing number of uninhabitable cells representing, respectively, 14%, 52% and 70% of

the total landscape. While the first habitat is connected, the second has a small amount of small isolated patches, but most of the remaining habitat is connected, and the third consists only of numerous small isolated patches.

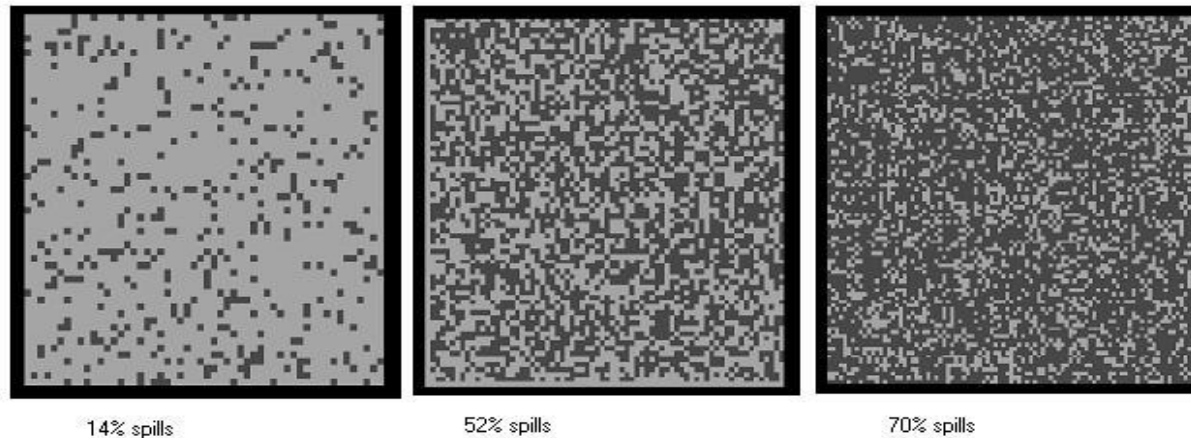


Figure 1: Landscapes of 50x50 inhabitable cells (grey) each and an increasing number of un-inhabitable and impenetrable cells (dark gray) representing, respectively, 14%, 52% and 70% of the total landscape. The black boundary consists of penetrable uninhabitable cells.

In this paper our objective is to study the relation between $ATE(A_h + A_n)$ and $ATE(A_h)$ for given A_h and initial animal distribution and for increasing values of A_n . While we expect that for values of A_n above a certain threshold, $ATE(A_h + A_n)$ will become considerably smaller than $ATE(A_h)$ (because of fragmentation), we do not have any initial hypothesis for the behavior of this relation for $ATE(A_h)$ below the threshold.

2.3 Complexity issues

Most of the modeling studies of fragmentation and habitat loss have been done with simple abstract models that take into consideration a small amount of spatially dependent factors (for a review see [4]). We find such an approach restrictive and the conclusion drawn unreliable.

The dependence of the persistence of a species on the geometry of the space it occupies is based on the action of numerous space-related factors. For example, persistence is strongly dependent on the availability of food (vegetation) which is usually distributed unevenly in space. When food resource is low, animals move from location to location in search of forage. These movements are determined by the geometry of the available space and by the bioenergetic status of the animal. The animal's bioenergetic status determines how long it will survive while searching for food in an environment with a specific pattern determined by the specific distribution of habitat and non-habitat areas. On the other hand the bioenergetic status depends on the energy the animal spends and on whether the animal's metabolic needs have been met, both of which depend on the specific pattern of the landscape. Similarly, the mating and offspring production process depend on the availability and geometry of the habitat. The life span of each individual thus depends on the characteristics of the space it occupies through a variety of factors. The persistence of the population is an emerging property of the livelihoods of the individual animals.

Expressed in mathematical form, if μ is a measure of population persistence and if persistence depends on factors Φ_1, \dots, Φ_k , each of which depend on some spatial characteristic σ (like, for example, the percentage of spills on the landscape), then the dependence of μ on σ is conditioned by the dependencies of $\Phi_i, i = 1, \dots, k$.

$$\mu(\sigma) = \mu(\Phi_1(\sigma), \dots, \Phi_k(\sigma))$$

Some of the factors in this equation might be especially sensitive to spatial patterns. Omitting to consider such factors will produce incorrect estimates.

Thus, a true assessment of the dependence of population persistence on spatial characteristics requires to consider the complexity of interwoven factors that act upon the population and depend on spatial patterns (to the extent of our knowledge of these). For example, such factors include, but are not limited to, vegetation availability, metabolic requirements of the species, mating mechanism, predation, movement patterns, etc. Such an effort requires a spatially-explicit approach. Persistence should be quantified in a suitable manner allowing comparison between various cases. One way to quantify persistence is by measuring the time to extinction of the model population. Continuous models are not suitable for this purpose because they do not produce finite times of extinction. Thus, a discrete complex spatially-explicit individual-based model is best suited for studying the persistence of a population.

With these considerations in mind, we studied the effect of habitat heterogeneity created by various quantities of randomly distributed spills in landscapes of constant habitat sizes on population persistence by performing simulations with SERDYCA, described shortly below.

3 Short overview of SERDYCA

3.1 Model description

A detailed description of SERDYCA (Spatially-Explicit Rodent DYNAMics Computation and Analysis) is provided in [12]. SERDYCA models the availability of the vegetation the rodent forages on and the growth and decline of the rodent population over a given landscape, represented as a collection of square cells. Spatial cells can be of the following types: a) habitat cells, having the type of vegetation the modeled species consumes, b) penetrable non-habitat cells, having vegetation the modeled species would not consume and c) impenetrable, barrier cells, avoided by the modeled species.

The rate of change of the amount of vegetation in each cell is calculated as the sum of two quantities: the rate determined by climatic factors and the rate of grazing determined by the metabolic needs of the animals present in the cell. The first was calculated in advance by using temperature and precipitation data and the package CENTURY 4, [13] and is used as caloric equivalent input, while the second one is obtained by calculating the caloric equivalent of the metabolic needs of the animals per day and is subtracted from the first.

The metabolic need of each animal is calculated as a power function of its weight which depends on the status (pregnant, lactating, other) of the animal. The weight of each animal is calculated using a rule that takes into consideration whether its metabolic need can be met by the vegetation available in the cell and also takes into consideration the animal's age and the maximum possible weight of the species. In the case of insufficient amount of vegetation in the cell, animals lose weight and leave the cell in search of a new one.

An animal can have the status of a resident or a floater. Floaters change their cells each day until they become residents. A resident becomes a floater if it has to leave the cell because of lack of forage or when it reaches adulthood. A male floater becomes a resident if he finds a cell with no male residents but having a female resident and having enough vegetation to meet its need. A female floater becomes a resident if it finds a cell with no female residents that meets its needs. Adult (over the maturation age) male and female residents produce offspring. Pregnancies last an amount of time called the generation time and can occur only in the months February-November. Births produce offspring equal to the litter size and the offspring is 50% male and 50% female.

Death occurs if an animal has been starving for a certain maximum amount of days or if it has lost too much weight, if it has become a victim of predation or when it reaches the maximum age for the species.

Predation is density-dependent: a certain percentage of animals is removed from the population each day. The percentage is proportional to the current density of animals and the constant of proportionality is different for adult and juvenile animals, currently being twice larger for juveniles.

The manner in which floaters choose a new cell is, what we call, "conditionally random". Floaters prioritize the quality of cells giving highest preference to habitat cells with no residents and availability of forage, second preference to habitat cells with no residents, even if forage is insufficient, third preference to penetrable non-habitat cells and last preference to cells having residents. Floaters move in a randomly chosen cell of the highest available preference.

Thus, if a floater is located in a cell that has a neighboring non-habitat penetrable cell and if all other neighboring habitat cells have residents, the floater will move into the non-habitat cell. In the cases when the non-habitat penetrable cell is on the boundary of the modeled region the animal leaves the region forever. This mechanism accounts for dispersion due to population pressure and territorial competition. If the boundary of the region has several layers of penetrable non-habitat cells, the floater might wander on the boundary with the possibility of returning to the habitat by finding an empty habitat cell or might disperse out of the region.

The model uses discrete time steps of one day. At time 0 it starts with a random spatial distribution of animals of randomly generated age, weight and gender.

3.2 The Graphical User Interface

The model uses metabolic and other data for the prairie vole obtained from a vast literature study and is based on published observations on the life histories of prairie voles. It was implemented in C++ with a Python graphic user interface (GUI) shown on Figure 2. The GUI is a new feature of the model. A short tour through it helps with the understanding how the model works.

The GUI maintains the input-output definitions. The upper left window on the GUI shows a part of the values used in the initialization of the model: the caloric digestible value of grass, the maximum life span, the average litter size, the average generation time, some weight and age characteristics of the prairie vole, the predation coefficients used in the definition of the density-dependent predation. The middle window on the left allows identification of the vegetation input file, while the bottom one serves as a place to define the parameters of the initial population spatial distribution. The bottom right part serves for maintaining the output.

The GUI is a convenient tool to define landscapes with spills or structures creating fragmentation. Given the coordinates of a certain region on the landscape and the desired number of spills, the GUI sets the configuration of the simulation so that the given amount of spills is distributed in the predefined region in a random manner for each simulation experiment. The GUI also has a landscape editor (one of the buttons on the right) that allows the modification of an already loaded landscape, for example making it fragmented, redefining the vegetation types of cells, etc. The editing can be done graphically by drawing on the screen curves, rectangles and circles.

3.3 Calibration and validation

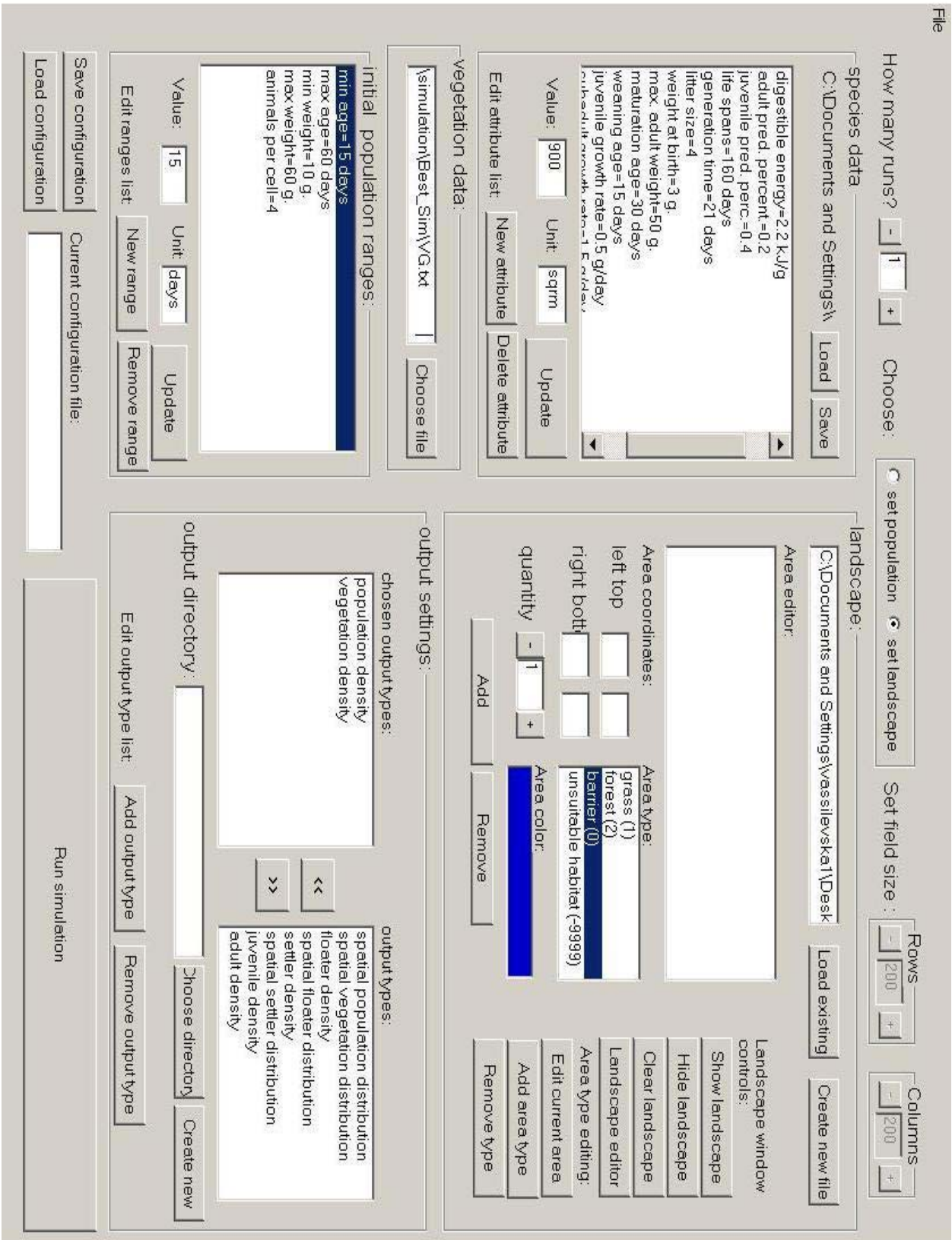
Most of the parameters used in SERDYCA for the prairie vole simulations are well established values. The coefficients modeling the density dependent predation are the only completely hypothetical parameters. The prairie vole maximum population density decreased with increasing the predation coefficients while the ATE first increased, reaching a maximum and then decreased when predation increased. We established values for the predation coefficients by assuming that the adult predation coefficient is twice larger than the juvenile coefficient and then calibrating the model by fitting a value for the adult coefficient for which the maximum density was in the experimentally reported bounds for tallgrass prairie. Interestingly, the calibrated predation was such that it resulted in a ATE close to the maximal. We named this predation level "optimal predation". The model predicts correctly prairie vole population fluctuations, both the annual locations of minima and maxima and the periodicity of the multiannual fluctuations, [11]. These results give a reasonable validation to the model.

4 Description of the simulations

The vegetation daily growth rates of tallgrass vegetation used in SERDYCA were calculated from a file containing a simulation data set for the daily dry mass quantities per m^2 for a 30 year period. The latter are obtained by using weather data for the years 1960-1990 from the Tulsa, Oklahoma airport weather station and a Konza Prairie vegetation parameter set used to initialize the model of grassland dynamics CENTURY 4 [13]. The plot of the vegetation density obtained is presented on Figure 3.

The simulations are carried out for time $T_{max} = 30$ years (limited by the scale of the vegetation data set). Since the prairie vole life span is less than half a year, this period represents 60 generations.

Figure 2: The graphic user interface of SERDYCA



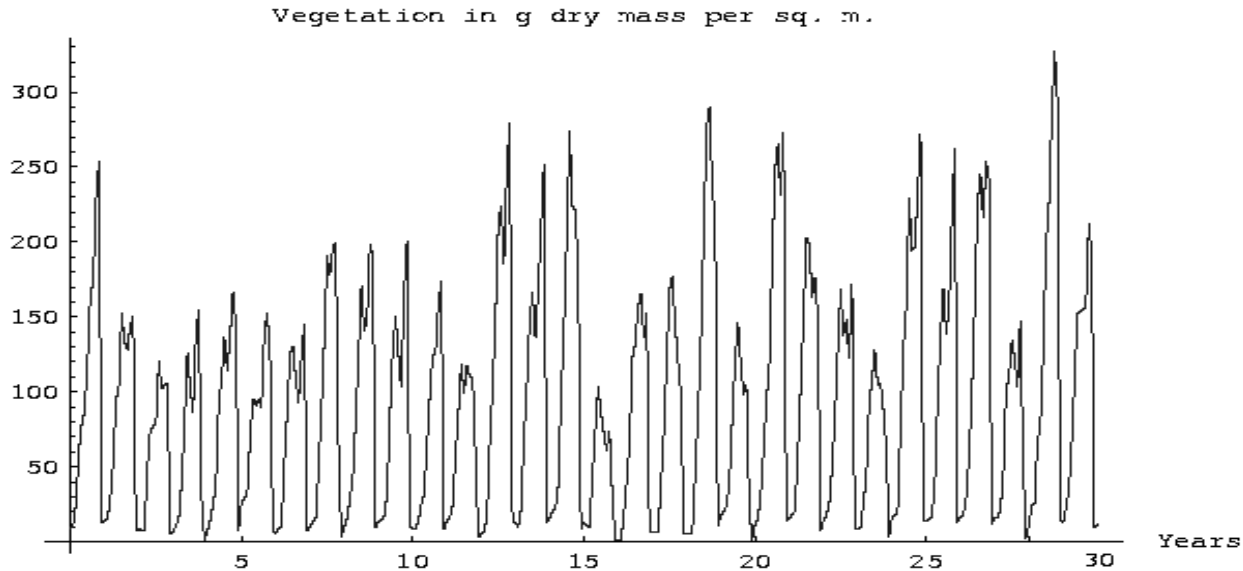


Figure 3: Estimated daily dry vegetation biomass (g/m^2) used as input for the model and calculated from temperature and precipitation data. See text for further explanation. (Publishing of this figure may need permission)

The landscape is a square region whose boundary consists of 4 layers of penetrable uninhabitable cells. The landscapes represented on Figure 1 are of this type. This structure was used to ensure that animals that are at the boundary of the habitat do not disappear forever if forced to leave by population pressure. Animals might wander on the boundary and possibly find an empty cell to enter the region again. However, if this does not happen for a certain amount of time (the starvation limit) the animal perishes.

The simulations are initialized by generating random initial animal and spill distributions. Initially the landscape inside the boundary consists of $K = A_h + A_n$ inhabitable cells. The boundary then consists of $(\sqrt{K} + 8)^2 - K$ cells. The inhabitable cells inside the boundary are initially populated with a random number (between 0 and 2) of floaters with randomly generated initial age, weight and gender in each cell. A_n of these cells are randomly chosen, redefined as non-penetrable (spills) and their vegetation quantity is set to zero. Various landscapes are produced following this procedure, keeping A_h constant and varying A_n so that K is an exact square.

The vegetation simulation data starts in January 1960 and has peaks in the summers of each year as well as minima in December or January of each year. The model assumes that the growth rates of vegetation are the same in all habitat cells; it is the different rates of grazing that produce different vegetation densities. At the initial time of the simulation all cells have the same initial vegetation density. Taking a closer look at Figure 3 we observe that some of the minima are very close to zero (they are positive, although this is not quite clear from the figure). Such amounts of vegetation in each cell can support very low numbers of animals and in these months most of the animals die of starvation. The time periods following these minima serve as bottlenecks for the persistence of the population.

Depending on the distribution of spills, the same population (starting with the same initial spatial distribution) persists (i.e. the total population number is not 0) for different amounts of time. The average of these times over all possible spill distributions is the ATE, (2.1).

We carried out 200 simulations for landscapes of 100×100 , 75×75 and 50×50 inhabitable cells and various amounts of spills, while using the same initial spatial population distribution for each landscape. For each set of 200 simulations we calculated the average time to extinction and the density of the total population per hectare as well as of the densities of the adults, juveniles, floaters and settled animals. Table 1 summarizes the types of landscapes simulated.

Table 1: Types of landscapes with constant habitat size for which simulations were carried out.

Habitat size (number of inhabitable cells)	Percentage of spills from the total landscape size
50x50	0, 14, 28, 35, 44, 52, 58, 63, 70
75x75	14, 24, 34, 41, 54, 62, 72
100x100	5, 10, 13, 18, 24, 28, 33, 38, 44, 50, 55, 60, 64, 67

All experiments were done for the "optimal" predation coefficients from [12] calibrating the model for Tallgrass prairie population densities.

5 Results and interpretation

Keeping the same initial animal distribution over a landscape and performing simulations with different arrangements of equal amounts of spills yields a wide variety of times to extinction across the simulations. However, calculating the ATE shows definite trends.

Figure 4 summarizes the simulation results on the effect of spill inhomogeneities on the ATE. Keeping in mind that all simulations were done for the same initial spatial population distribution, let TE_0 be the time to extinction in the case with no spills for the fixed initial animal distribution. Spills do not have any substantial negative effect until they become at least 50% of the total area for all the three considered habitat sizes. The ATE is slightly higher than TE_0 for the 75x75 habitat size and is substantially larger than TE_0 for the largest 100x100 habitat size. The ATE is larger than TE_0 for high spill percentages (30-50%) for the smallest habitat. Thus, the larger the habitat, the stronger the effect of spill inhomogeneities.

Though additional study is necessary to connect the percentage of spills with the probability that a landscape is fragmented, most probably at 50%-60% the reduction of ATE is due to the effect of fragmentation. At very small spill percentages the probability of occurring fragmentation is negligible, the habitat size remains the same and therefore the effect on the ATE is credited to the change in the shape of the habitat due to the spill inhomogeneities. At "intermediate" spill percentages, the probability of occurring fragmentation increases and we would expect the ATE to decrease. The expected negative effect from fragmentation seems to be compensated by a positive effect of spill homogeneities for the two larger habitats.

Taking into account only the ATE is not sufficiently informative. If N is the number of simulations (out of all performed) for which $TE \geq TE_0$, let us denote these TE by $TE_i^>, i = 1, \dots, N$. If M is the number of simulations for which $TE < TE_0$, let us denote these TE with $TE_i^<, i = 1, \dots, M$. Then, the ATE approximation calculated from these simulations can be written as

$$ATE = \frac{\sum_i ATE_i^>}{N} \frac{N}{N+M} + \frac{\sum_j ATE_j^<}{M} \frac{M}{N+M}.$$

Thus, the ATE is determined by the ratios $\frac{N}{N+M}$ and $\frac{M}{N+M}$ as well as by the means $ATE^> = \frac{\sum_i ATE_i^>}{N}$ and $ATE^< = \frac{\sum_i ATE_i^<}{M}$. So, the ATE might be slightly lower than the TE_0 (as it is for the 50x50 habitat, Figure 4) but still for a certain amount of simulations $TE \geq TE_0$.

Figure 5 represents the percentage of simulations (out of the performed 200) for each spill level for which the TE was larger than the TE_0 for the landscapes with 100x100 and 50x50 habitat cells. It shows that for up to 60% spills a certain part of the simulations demonstrate higher population persistence than in the case without spills. This percentage is higher in the larger landscape. An interesting tendency is the existence of an interval of spill percentages higher than 30% for which the cases with TE higher than TE_0 increases.

Trying to explain these observations, we study the effect of spills on population density. The population density measured as the total density divided by the area (in hectares) is a quantity that turns out to be affected by the percentage of spill inhomogeneities. Specifically, the maximum and minimum densities seem to be determined by the percentage of spill inhomogeneities and not affected by the specific spatial arrangements of the spills.

It is somewhat surprising that although the two-dimensional time series of the spatial population density patterns are different between simulations with different spatial arrangements of spills, the one-dimensional time series of the total population densities have similar patterns and the maximum and minimum densities

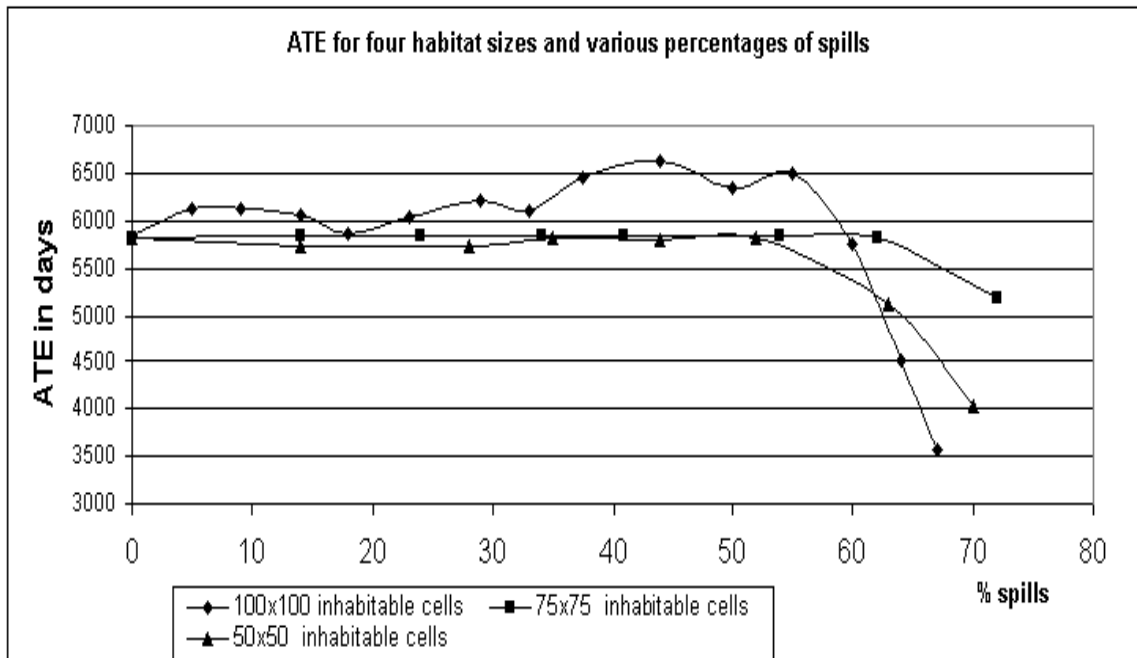


Figure 4: The dependence of the ATE on various percentages of spills in landscapes with the same amount of habitat. See text.

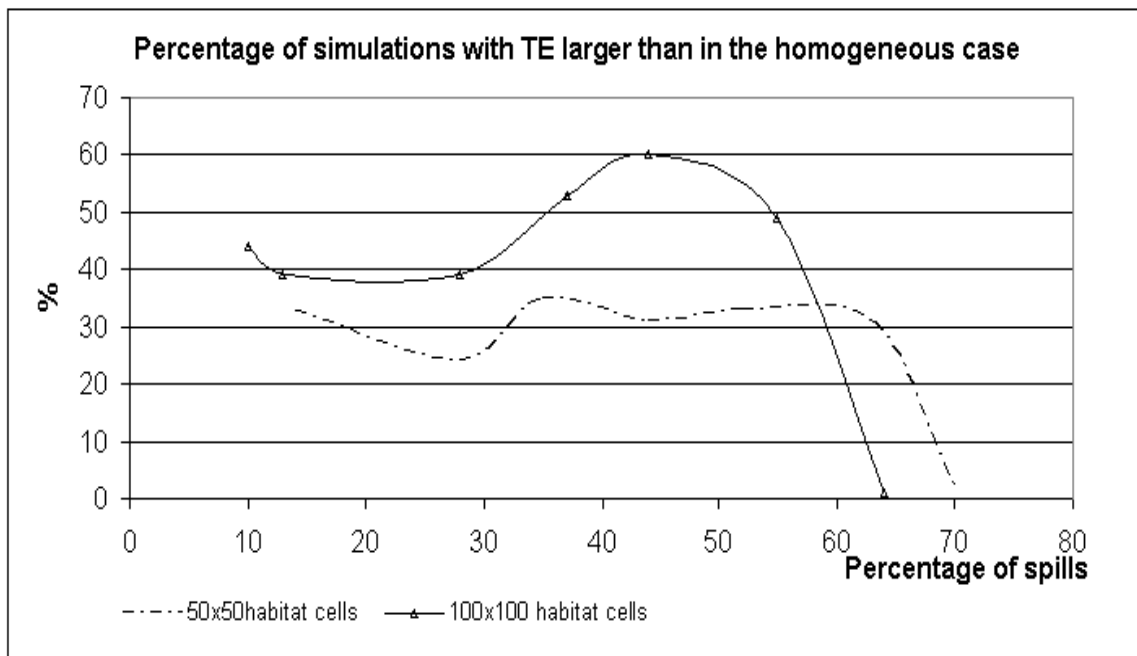


Figure 5: Percentage of simulations on landscapes with spills for which the TE was higher than TE_0 .

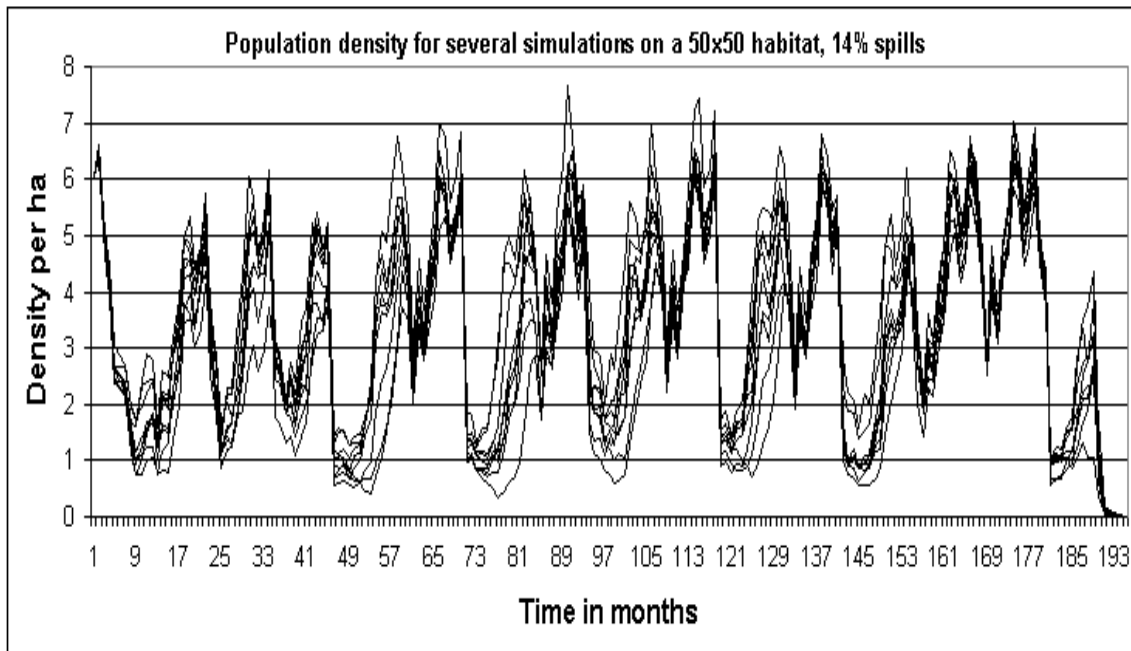


Figure 6: Total population density for a set of simulations on 50x50 habitat cells with 14% spills

are in the same range for a fixed percentage of spills. This is demonstrated on Figure 6 for 50x50 habitat cells and 14% spills but occurs in all simulations we performed. The different density curves correspond to different spill distributions. The spatial distributions of the animals for the same time moments are completely different across the cases (we do not present illustrations for lack of space) but the density time series have a very similar shape. The maximum and minimum densities occur at the same times and have close values.

These values change when the percentage of spills changes. The maximum population densities decrease with increasing percentage of spills. To illustrate, we present a plot of the density on the 50x50 homogeneous landscape, Figure 7. The maximum density in the homogeneous landscape case is between 8 and 9 per ha, while in the case with 14% spills it is between 6 and 7.5. When the spill percentage increases further up to 70%, the maximum density falls to 2 per ha. This monotonicity tendency was observed in all other simulations.

Why does the density decrease when the percentage of spills increases? Why does the ATE increase, although the density decreases? We give the following explanation, which we call the "inhomogeneity localization effect".

After a period of low vegetation density, only scattered groups or single animals survive. These become sources for gradually growing in size and expanding in space local populations. As floaters search for unoccupied space, a local population spreads by enlarging the space it occupies. The floaters in cells having neighbor spill cells have less choice of a cell to move to than in the case where all neighboring cells are habitat cells. The restrictions of movement lead to a slower speed of spatial spread of the population. Consequently, local populations occupy smaller spaces and are smaller in number, contributing to lower total population densities.

The simulated juvenile densities become zero in the end of January each year because of the assumed lack of pregnancies in December and January. (The last born animals in the end of December each year reach maturity in the end of January while the first newborns arrive in the end of February.) Extremely low population numbers in the winter's end are characteristic not just for voles, but for many species. The relative success in producing offspring in the end of the severe period is a crucial factor for population

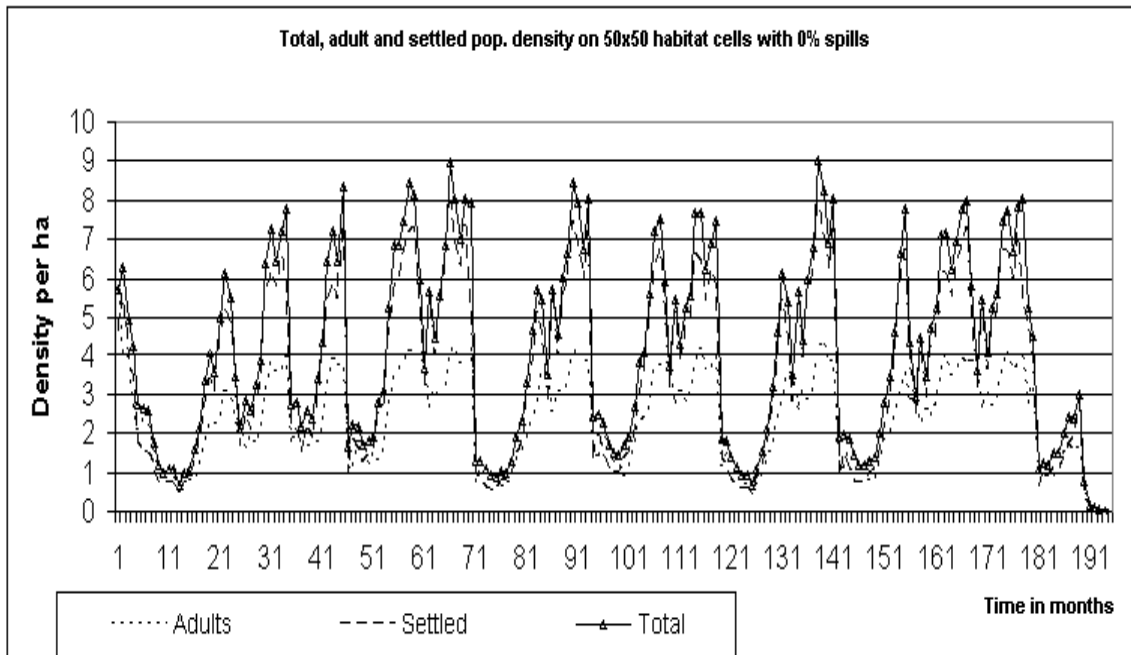


Figure 7: Total, adult and settled population density for a set of simulations on 50x50 habitat cells with 0% spills

persistence. Environmental conditions that contribute to this success should lead to a longer TE. The presence of inhomogeneities acts in this direction. Because of the restricted localization of the populations on landscapes with spills, floaters should be more successful in becoming residents and mating. In the homogeneous case floaters spread much farther and have lower probability to end up in a cell that has a resident of the opposite gender because the floaters have a priority to move into unoccupied cells. In the inhomogeneous case floaters are more often forced to move into occupied cells and thus end up forming pairs and producing offspring. Thus, at the end of severe (low-vegetation, no offspring production) periods, populations in the inhomogeneous environments should produce offspring at a higher per capita rate. This effect should be more visible after periods when the population has fallen to very low densities.

To check this conjecture, we calculated the monthly ratios of the juveniles to the total population in all 200 simulations and then took the averages for each month. We did these calculations for three landscapes with 50x50 habitat cells and a) without spills; b) with 14% spills and c) with 44% spills. The results are presented on Figure 8. The populations on the landscapes with 0% and 14% spills persisted no longer than 194 months while some populations on the 44% spills landscape persisted for the whole 30 year period. It is visible (Figure 8) that especially after periods of low population density (after months 71, 121, 145, 181: compare with Figures 7 and 6) the percentage of the juveniles from the total population increases fastest from zero for the 44% spills landscape, followed by the 14% spills landscape. It is notable that in the last year before the populations on the 0% and 14% spill landscapes crashed, the populations on the 44% spills landscape had a much higher average juveniles per capita ratio which contributed to their persistence.

One would also expect that for higher percentage of spills for which no habitat fragmentation has occurred the "inhomogeneity localization effect" will be more pronounced and the time to extinction will be longer. For even higher spill percentages the probability that the habitat gets fragmented will increase and the cases with TE higher than the one in the homogeneous case will become less and less frequent. This prediction is supported by the hunch-shaped curve on Figure 5.

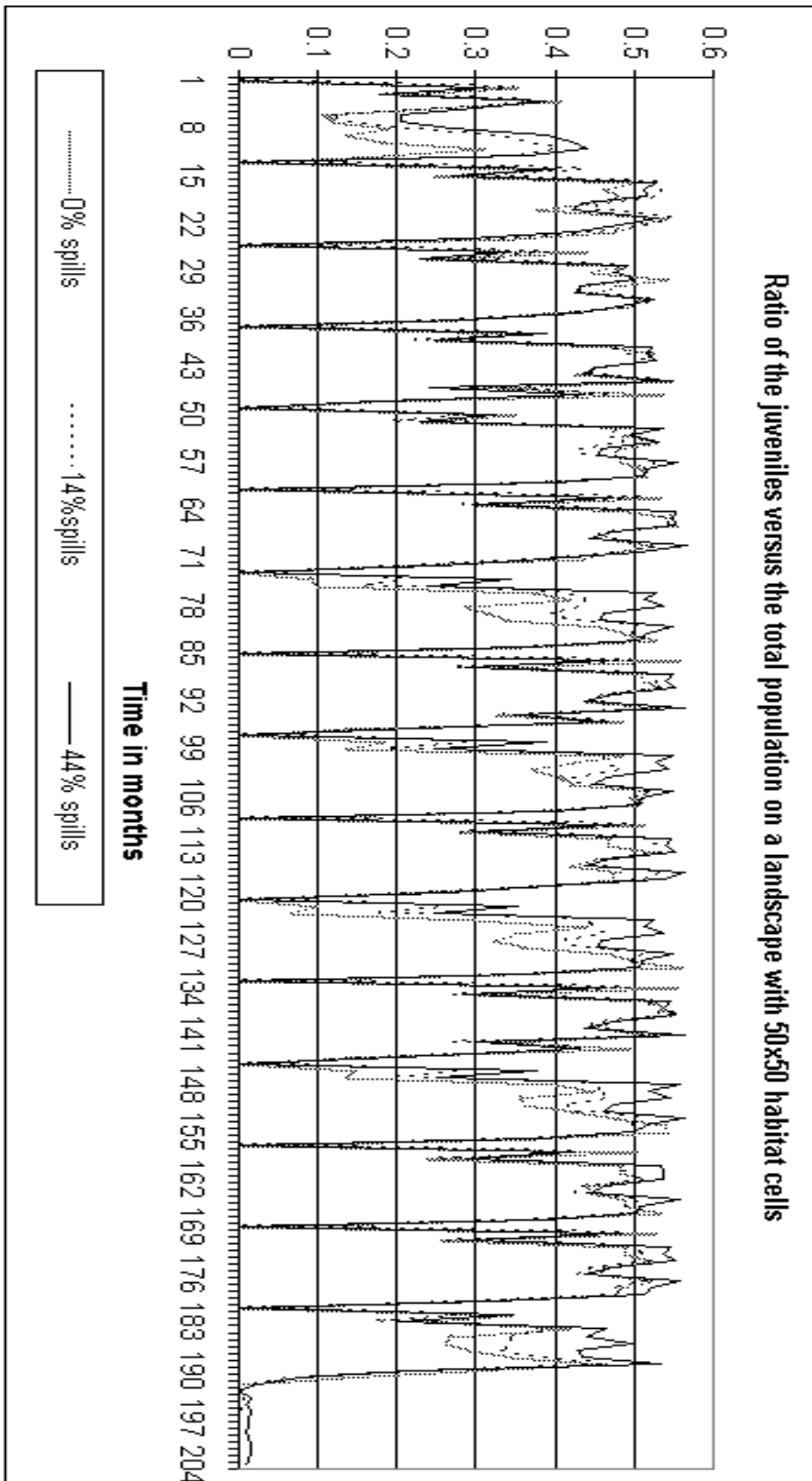


Figure 8: Ratios of the juveniles versus the total population on a landscape with 50x50 habitat cells and three levels of spill inhomogeneities.

6 Discussion

SERDYCA is a complex model of rodent dynamics that, for the current study, uses data for the prairie vole species. Thus, our results hold for this species but might as well be of more general validity.

Simulation models serve as "virtual environment" experimental tools. As other types of models, they serve to provide insight and help to formulate hypotheses and theories. The current simulations suggest that habitat inhomogeneities can enhance population persistence by enforcing the localization of subpopulations, thus improving the reproductive performance of the population. The "inhomogeneity localization effect" is a purely spatial effect. Its possible existence underlines the importance of taking space into consideration in population dynamics studies.

Of course, the model can be criticized for the bias put on territoriality. In our assumptions, it has a heavier weight than mating because floaters give priority to empty territories to territories with representatives of the opposite gender. The other alternative would be interesting to explore as well.

Another important theoretical problem is the connection between the percentage of spills and fragmentation. Obviously, there is a lower bound for the percentage that would make possible a habitat to be fragmented and, on the other hand, for each given percentage of spills there is the example when all the spills are clumped together so that the habitat is not fragmented. The problem is, given a certain percentage of spills, what is the probability that the habitat will remain connected. Addressing this problem will facilitate the understanding of the simulation results we presented in this paper.

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