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November 24, 2003

Ecological Complexity

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The effect of area size and predation on the time to extinction of  
prairie vole populations. simulation studies via SERDYCA: a  
Spatially-Explicit Individual-Based Model of Rodent Dynamics

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November 24, 2003

UCRL-JRNL-201153

## Abstract

We present a spatially-explicit individual-based computational model of rodent dynamics, customized for the prairie vole species, *M. Ochrogaster*. The model is based on trophic relationships and represents important features such as territorial competition, mating behavior, density-dependent predation and dispersal out of the modeled spatial region. Vegetation growth and vole fecundity are dependent on climatic components. The results of simulations show that the model correctly predicts the overall temporal dynamics of the population density. Time-series analysis shows a very good match between the periods corresponding to the peak population density frequencies predicted by the model and the ones reported in the literature. The model is used to study the relation between persistence, landscape area and predation. We introduce the notions of average time to extinction (ATE) and persistence frequency to quantify persistence. While the ATE decreases with decrease of area, it is a bell-shaped function of the predation level: increasing for "small" and decreasing for "large" predation levels.

**Keywords:** *individual based, spatially explicit, M. Ochrogaster, patch size, population persistence, multiannual fluctuations*

# 1 Introduction

As part of a project to determine the impact of habitat loss and fragmentation as a result of oil exploration and production on natural ecosystems, Efroymson et al. (in press), we are developing a model that can be used for monogamous rodent species exhibiting territorial behavior and can also be adapted for polygamous species. As small rodent species are a food resource for a large variety of carnivorous species, evaluation of their risk for extinction under habitat fragmentation and habitat loss conditions is important for determining the status of the full ecosystem. Creating a "virtual rodent dynamics laboratory" also permits us to study via virtual experiments various scientific questions related to rodent dynamics.

In a previous paper we presented an individual-based simulation model customized for the prairie vole (*Microtus Ochrogaster*) species, Kostova et al. (in press). The model had several shortcomings. It did not take into consideration important mechanisms of population density regulation such as predation and dispersal out of the patch and thus was only comparable to experimental cases where the patch was enclosed and predator-free. The population densities the model generated were unrealistically high for natural conditions, although corresponded well to populations in enclosures. Additionally, bioenergetic assumptions were taken into consideration but were weakly supported by existing data. This also contributed to unrealistic population density results.

In the present paper we introduce a new version of the model which is a substantial improvement over the previous one. The new model version includes mechanisms accounting for the dispersal of animals out of the region and for population losses due to predation. Additionally, we refined the model by incorporating accurate relationships between the metabolic need, body size and caloric uptake of each individual animal and generated vegetation growth rates based on actual temperature and precipitation data. Since during the winter period of certain years the estimated vegetation density becomes very low, these specific periods are crucial for the survival of the vole populations and serve as "bottlenecks" causing extinction under certain conditions. These climatic bottlenecks act together with other factors such as area loss, predation level and habitat fragmentation to affect vole population persistence. Our population persistence study focuses on the relationships between these factors and the average time to extinction (*ATE*) of the modeled population.

This paper is devoted to presenting the revised model and selected simulation results.

The form of presenting an individual-based model is an important issue of general concern. It is known that changing the order of execution of discrete rules may change the result. Therefore it is imperative that when a simulation is described, the exact order and interdependencies of functions are transparently presented. The format of the current paper is intended to serve as a standard for such presentations.

We propose a robust mathematical form of representing individual based models as nonlinear discrete maps. The usual form of IBM representation is a wordy description of each of the elements of the model accompanied by a formula where needed. The exact order of executing the rules is often omitted and it is usually unclear what values of the variables are used. This makes it difficult to understand the whole structure of the code and to reconstruct it if desired. In this paper for the convenience of the reader, we also describe each of the code's functions (maps) with words and formulae. But we accompany this description by a representation of the exact order in which the separate maps are executed as well as what arguments each map uses and what values it generates. A completely rigorous representation would also describe the exact form of the maps, as we did for the previous version Kostova et al. (in press) but we have omitted it in this publication for the sake of readability.

This paper presents the results of model simulations on the dependence of population density and time to extinction on a) area size and b) level of predation. The simulations are carried out on artificial landscapes without fragmentation. Simulation results on artificial landscapes with fragmentation and simulations using landscape geospatial data from a real study site will be presented in a subsequent paper.

## 2 General Properties and Structure of the Model

### 2.1 General properties

In our model, space is represented by a collection of square cells, each with an area equal to the average home range area of the modeled species. The amount of vegetation in the cell is determined by growth and grazing rates. The rodent population is substructured into classes of floaters and settled, males and females, juveniles, subadults and adults. The *settled* class represents animals that remain in the same cell until some

conditions occur that transforms them into *floaters* (e.g. a settled adult becomes a floater if the vegetation in the cell is not enough to meet its metabolic needs). The floater class represents animals that move to a new cell each day until certain conditions occur that transform them into settled (e.g. if a floater male finds a cell occupied by a settled single female, he becomes settled). The *juveniles* are below weaning age, the *subadults* are below maturation age and the *adults* are the mature animals.

Survival depends on reaching the lifespan limit and availability of forage. Birthrate occurs seasonally.

The model incorporates three important features: a) detailed metabolic relationships; b) a predation mechanism; c) dispersal of animals out of the modeled landscape. These features were added to more accurately model the trophic interactions between the herbivores and the vegetation.

The present state of knowledge on rodents bioenergetics allows for a credible model based on the trophic approach. The diet of most species of *Microtus* is comprised of green vegetation (Tamarin (1985), “Habitats” by L. Getz, “Nutrition” by G. Batzli). Caloric estimates for various types of forage exist in the literature, Klass (1998); Griffin et al. (1980). The digestible energy of forage is a certain percentage of its total energy, which depends on the specific animal species Boisen and Verstegen (2000), and estimates for this percentage are available for a vast amount of vegetation types. The metabolic needs of herbivores are met by obtaining the necessary amount of digestible energy by feeding. If the daily metabolic needs of an individual vole are estimated (in kcals), the amount of vegetation necessary to cover its needs can be calculated. Thus, the vegetation depletion caused by herbivores residing in a certain region (in our model, in a spatial cell) can be calculated. Grazing is compensated by vegetation growth. Knowing the rates of growth and grazing allows us to calculate the caloric quantity of vegetation in the cell. In the model this is done for convenience in kilocalories:

$$veget(n) = veget(n - 1) + AreaOfCell \times \text{digestive energy in kcals/gram dry mass} \times W_n - \sum_i MetNeed_i, \quad (2.1)$$

where  $veget(n)$  is the vegetation energy content in a spatial cell on day  $n$ , the area of the cell  $AreaOfCell$  is in square meters,  $W_n$  is the daily rate of vegetation growth on day  $n$  in grams per day per square meter,  $MetNeed_i$  denotes the current metabolic need of a given animal (numbered  $i$ ) and the summation is done for all the animals in a spatial cell.

When the total metabolic needs of the animals in a cell exceed the caloric equivalent of the vegetation present in the cell, the vegetation cover is “overgrazed” and the animals do not gain weight. Starvation for over a certain amount of days leads to death. On the other hand, if the metabolic needs are met, the herbivores gain weight until they reach the maximum weight for the species and can also successfully reproduce.

In the model we first construct an input file of the daily vegetation growth rates by using real temperature and precipitation data. Next, to evaluate the vegetation quantity grazed by the individual herbivores present in the spatial cell, we establish the specific metabolic needs of each animal based on its weight and physiological condition (taking into consideration whether the animal is in the weaning age, pregnant or lactating). We introduce the weight of an animal as a dynamic variable which changes depending onto whether its metabolic needs are met. Thus, interrelations between the weight of an animal, its metabolic needs, its physiological status and age and the food availability in the environment are incorporated in our model.

Modeled relationships were constructed to be trophically related. The survival of an herbivore is dependent on the time of starvation (if any). The way a floater animal chooses a new location to move to depends onto whether the vegetation quantity there will meet its metabolic needs. If more than one floater wants to stay in the same location, the one with the largest weight wins. Both juveniles and subadults are not considered able to relocate; juveniles do not graze.

Finally, predation and dispersal out of the region have been incorporated into the model. In previous work, the absence of these features led to high population densities and subsequent overgrazing of the modeled closed regions. In order to adequately evaluate the effect of fragmentation and area reduction, however, it is important to model naturally occurring densities.

## 2.2 General structure

Time is represented as discrete units  $0, 1, \dots, k, \dots$  and all variables of the model are updated at each time increment. The time unit represents one day and all rates in the model are daily rates. The general structure

of the model can be represented as

Input and Initialization → Time Loop → Output.

The time loop is executed until the population goes extinct (i.e. the number of rodents in each cell becomes zero) is or until the input vegetation data is exhausted, whichever comes first. The input vegetation data has been constructed for 30 years of real time. Figure 1 demonstrates the time loop in the order in which it is executed.

HERE PLACE FIGURE 1

The individual-based ideology is best represented computationally by the object-oriented approach. The spatial cells and the individual animals are formulated as *objects* which possess constant and variable attributes. The values of the variable attributes are calculated at each time increment via the object functions.

### 3 Input and Initialization

The first input parameter read is the number of consecutive runs of a model with the same parameter values but with varying initial distributions of animals in space. The next input are the dimensions of the spatial grid: *NRows* – number of rows, *NCols* – number of columns and the area of a cell, *AreaOfCell*, in square meters. All cells are assumed to be the same and their area to be equal to the home range of the rodent.

The home range size of a mammal species has been demonstrated to be related to its energetic needs McNab (1963) as well as to population density, Abramsky and Tracy (1980); Gaines and Johnson (1982). It is measured either as the longest distance covered by an individual animal or in quadratic units (area covered). The estimates of the prairie vole home range size, given by different authors and obtained by different methods, vary significantly. Swihart and Slade Swihart and Slade (1989) estimate the prairie vole home range length as about 30 m for reproductive males. Gaulin and FitzGerald Gaulin and FitzGerald (1988) used radiotracking to estimate the daily home range to be between 210-340 sq. m for males but report that the daily home range is about 3-4 times smaller than the total home range. For the purpose of the model we have accepted the home range area to be approximately  $30m \times 30m$ .

Next, an input file containing the spatial information for the modeled region is opened. The modeled region may have any shape but is enclosed in a rectangle. Thus, some of the cells of the rectangle may not actually belong to the modeled region. For each cell, an integer number encodes whether the cell belongs to the region, what type of vegetation (if any) grows in the cell and whether the cell is at all penetrable (see further sections 3.2 and 3.3 for more detail).

Further, an input file containing simulated rates of vegetation growth is open for reading. The first value of the file is the initial quantity of vegetation per  $m^2$ . This quantity is the same for all spatial cells which have that vegetation cover. The construction of this file is described next.

Finally, the constant object attributes are read from an input file, while the variable attributes values are *initialized*. The constant and variable attributes as well as their units, values, source and initialization details are described in the following sections.

#### 3.1 Vegetation growth rates

Vegetation is assumed to grow with rates depending only on environmental conditions such as temperature and precipitation and not on the rate of grazing or on other factors. We used weather data for the years 1960-1990 from the Tulsa, Oklahoma airport weather station, which we considered to be similar to the weather data for the Tallgrass Prairie Preserve as these locations are about 70 miles away. A parameter set developed for the Konza Prairie Research Natural Area, was used for vegetation-type dependent parameters.

The calculations were carried out by using the CENTURY version 4.0 model Parton et al. (2000) of grassland dynamics. CENTURY is a general model of plant-soil nutrient cycling and computes the flow of carbon and other elements through the model's compartments. Using the model, a 30-year simulation data set for the average production of carbon in aboveground monthly standing crop of tall grass prairie vegetation

(in grams per square meter) for the Tallgrass Prairie Preserve was produced. The data set contains monthly quantities of carbon per square meter. The conversion formula

$$\frac{1 \text{ gram } C/m^2}{0.475} = 1 \text{ gram dry biomass}/m^2$$

is then used to obtain the monthly dry vegetation mass per square meter. Further, the monthly data are interpolated linearly to obtain daily dry mass quantities per  $m^2$  for the 30 year period (Figure 2). Each month is considered to have 30 days.

A file containing the initial dry mass quantity (for the first simulation day, designated as  $V_0$ ) and the differences between the consecutive days, i.e. the daily growth rates was then created. This is the input vegetation growth rate data file, which contains the values  $W_n$  from (2.1).

HERE PUT FIGURE 2

### 3.2 Constant attributes

#### *Constant cell attributes*

Two types of spatial cell constant attributes are the coordinates of the cell (row and column) and its area *AreaOfCell*.

For each cell object, an attribute called *presence* denotes the type of the cell. A value equal to -9999 has the meaning that the cell is not suitable for habitation but still “penetrable”, if forced by territorial competition, animals could enter such cells. For example, these may be spatial cells that have vegetation not foraged by the species or that have been degraded by oil or brine spills. Value of *presence* = 0 denotes “barrier” cells such as rivers, buildings, fences, pipelines, etc. impenetrable by the animals. Other values can be codes for vegetation types, such as *VegetationCode* (Table 1). In the current simulations, this attribute is treated as constant, i.e. the types of the spatial cells are predetermined from the beginning and remain such to the end of the simulation. A dynamically changing environment with appearing and gradually healing pollution spots will imply the use of this attribute as a variable.

#### *Constant animal attributes*

The constant attributes relating to the rodent species are presented on Table 1. Some of these attributes require additional clarification.

The natural life span of *M. Ochrogaster* can reach up to 450 days, Getz et al. (2000), but the average life expectancy of small microtines is reported to be much shorter. The average life span used in our model is a fixed value above which no animal survives.

There is very scarce data on the length of the period a microtine can endure without food. Voltura and Wunder, Voltura and Wunder (1998), carried out experiments where prairie voles on restricted access to food (3 hours morning and 3 hours evening feeding) at 5 degrees C appeared very exhausted on the 7th day. Full starvation was described by Mosin Mosin (1982, 1984) who finds that voles of the species *Clethrionomys rutilus* and *Clethrionomys rufocanus* died after 24-26 hours of full starvation due to hypoglycemia. We have tentatively assumed a starvation period of 4 days.

There may be more than one type of vegetation in the modeled region. Each type of vegetation is thus encoded by an integer. The code of foraged vegetation defines the type of vegetation foraged by the modeled species (*M.Ochrogaster*).

Digestible energy is the digestible caloric value *DigEnergy* of the vegetation foraged by the modeled species. The caloric value of grasses is in the range of 4.4 kcal/g, Klass (1998). Studies on the nutrition of the prairie vole reveal that this species digests roughly 50% of the dry matter and energy in bluegrass Cole and Batzli (1979), which we assume to be in a similar range for tallgrass species. We conclude that the digestible energy caloric content of tallgrass is  $\approx 2.2$  kcal/g.

HERE PLACE TABLE 1

### 3.3 Variable attributes

*Variable animal attributes.*

The variable animal attributes are represented on Table 2. The meaning of most variable attributes is self-evident, but some clarifications are due. The time of starvation is the number of consecutive days the herbivore has been deprived of food. When this time surpasses *StarveLimit*, the animal is declared dead by changing the value of the variable *remove* to 1. The default value of *remove* is 0. Each animal belongs to either the resident or the floater class. A floater changes its location at each time increment (day) until it becomes a resident. A resident stays at the same cell location until the cell becomes uninhabitable, i.e. when the vegetation is insufficient to meet its metabolic needs. The *status* variable takes character values "s" (resident) or "f" (floater). The birth index takes the value 1 if the time has come the (female) animal to produce offspring. Otherwise it is set to 0.

HERE PLACE TABLE 2

Next, the code constructs initial distribution of animals in the cells. They are generated in a random manner as follows. For each spatial cell, a random number between 0 and a predefined number (usually between 3 and 5) is generated. This gives the initial number of animals present in the cell. Next, for all generated animal objects, the following initial values at time 0 are set:  $starvation(0) = 0, remove(0) = 0, status(0) = "f", TimeSinceBirth(0) = 0, TimeSincePregn(0) = 0, birth(0) = 0$ . The other variable attributes are initialized as follows. For half of the generated animal objects  $gender(0) = "m"$ , for the rest  $gender(0) = "f"$ . The row and column of the cell define the initial values of  $r(0)$  and  $c(0)$  for each generated animal object belonging to the cell. For each animal,  $age(0)$  is generated as a random number between *MaturationAge* and *LifeSpan*.  $Weight(0)$  is random number between the approximate weight at maturity (30 grams for the prairie vole) and *MaxAdultWeight(0)*.  $MetNeed(0)$  is calculated using the formula described below in Section 4.2.

*Variable cell attributes.*

The variable cell attributes are shown on Table 3. The initial mass of vegetation per  $m^2$  in each cell is the initial number  $V_0$  supplied by the vegetation data input file described in section 3.1. Thus, initially we assume uniform vegetation density over the whole simulated area. The variables *veget* and *vegdeplet* are initialized for time 0 as

$$veget(0) = V_0 \times DigEnergy \times AreaOfCell. \quad (3.1)$$

and  $vegdeplet(0) = 0$ .

The initialization of the population numbers and animal weights in the cells is carried out by traversing the already generated initial list of rodents and finding the number of male and female animals generated for each cell,  $malpop(0), fempop(0)$  as well as  $malmaxweight(0), femmaxweight(0)$ . As all animals have been initially defined as floaters, the initial values  $settlmalpop(0) = 0$  and  $settlefempop(0) = 0$ .

HERE PLACE TABLE 3

## 4 The Time Loop

After obtaining the constant cell and animal values and initializing the variable ones, the simulation model proceeds to calculating the values of the variable cell and animal attributes at consecutive time points. This is done by executing a time loop with increments of 1 day. In the course of the day, the model assumes that events like aging, satisfying metabolic needs, weight gain, vegetation grazing, predation and survival, pregnancies, births and deaths and spatial relocation happen. These occur in the order outlined on Figure 1. Because the input vegetation data is generated for 30 years (the period of available weather data), or 10800 days, each simulation has a time loop from day 1 to 10800 or is terminated in case that there are no surviving animals.

Mathematically, the procedure can be described as a nonlinear map transforming the cell and animal variable attributes at each time step of the loop, Kostova et al. (in press). By arranging the attributes of each cell and each animal object in column vectors and grouping the cell and animal columns we obtain matrices  $\mathcal{C}(n)$  and  $\mathcal{A}(n)$ .

For each time increment  $n$ , the cell matrix  $\mathcal{C}(n)$  has the form

$$\mathcal{C}(n) = (\vec{c}_1(n), \dots, \vec{c}_K(n)) \quad (4.1)$$

where

$$\vec{c}_i(n) = (\text{veget}_i(n), \text{vegdeplet}_i(n), \text{malpop}_i(n), \text{fempop}_i(n), \text{setlmalpop}_i(n), \text{setlfempop}_i(n), \text{setlpop}_i(n), \text{pop}_i(n), \text{malmaxweight}_i(n), \text{femmaxweight}_i(n))^T, i = 1, \dots, K \quad (4.2)$$

is a vector comprised of the variable attributes at time  $n$  of the  $i$ -th cell and  $i$  runs from 1 to  $K = NRows \times NCols$ . As usual, the superindex  $T$  denotes transposition, i.e.  $\vec{c}_i$  is the column vector obtained from the row vector in (4.2) above.

Similarly, the animal matrix  $\mathcal{A}(n)$  has the form

$$\mathcal{A}(n) = (\vec{a}_1(n), \dots, \vec{a}_{N(n)}(n)) \quad (4.3)$$

where  $\vec{a}_j(n), j = 1, \dots, N(n)$  is a vector comprised of the variable attributes at time  $n$  of the  $j$ -th animal,  $N(n)$  is the number of “alive” animal objects (i.e. such that the attribute *remove* is not 1) and  $j$  runs from 1 to  $N(n)$ .

$$\vec{a}_j(n) = (\text{starvation}_j(n), \text{remove}_j(n), r_j(n), c_j(n), \text{gender}_j(n), \text{status}_j(n), \text{weight}_j(n), \text{MetNeed}_j(n), \text{age}_j(n), \text{TimeSinceBirth}_j(n), \text{TimeSincePregn}_j(n), \text{birth}_j(n))^T. \quad (4.4)$$

Proceeding from time  $n$  to time increment  $n + 1$ , the matrices  $\mathcal{C}(n + 1)$  and  $\mathcal{A}(n + 1)$  are calculated iteratively by using the values  $\mathcal{C}(n)$  and  $\mathcal{A}(n)$ . The combination of rules defining how the new values at time  $n + 1$  are obtained from the old ones at time  $n$  represent the map  $\Phi(n)$ .

## 4.1 Time loop rules

Here we describe how the new variable attribute values at time  $n + 1$  are obtained from the old ones at time  $n$ . We use the following notation:  $k_j$  is the number of the spatial cell that has row  $r_j$  and column  $c_j$  in the list of cells. At each iteration  $n$  the following rules are executed in the order they are described. For each rule we use a formula to identify the values used (to the left of the arrow) and the values obtained (to the right of the arrow).

**Step I.** This step is a loop that traverses all cells from 1 to  $K$  and executes the rule  $\phi_0$ .

$\phi_0 : PopInit$  This rule nullifies the values of all variable cell attributes (described in Table 3) for all spatial cells.

$$\phi_0^k = PopInit \rightarrow (0, \dots, 0), k = 1, \dots, K.$$

**Step II.** This step is a loop that traverses all animals in the list from 1 to  $N(n)$  and consecutively executes the rules  $\phi_1$  to  $\phi_{11}$ .

$\phi_1 : IncreaseCellPop$  This rule updates the total number of animals, male and female adult animals and resident male and female adult animals in the animal’s spatial cell by exhausting the list of animals. This is done in the following way. If the number of the animal in the list is  $j$ , the variable  $pop_{k_j}$  is increased by 1,  $malpop_{k_j}, fempop_{k_j}$  are increased by 1 if the animal object in the list has gender “m” or “f” respectively,  $setlmalpop_{k_j}, setlfempop_{k_j}$  is increased by 1 if it has status “r” and has gender “m” or “f” respectively.

$$\phi_1^j = IncreaseCellPop(\text{age}_j(n), r_j(n), c_j(n), \text{gender}_j(n), \text{status}_j(n)) \rightarrow (\text{pop}_{k_j}(n + 1), \text{malpop}_{k_j}(n + 1), \text{fempop}_{k_j}(n + 1), \text{setlmalpop}_{k_j}(n + 1), \text{setlfempop}_{k_j}(n + 1)). \quad (4.5)$$

$\phi_2$  : GetOld This rule increases the age of each animal by 1 (day):  $age_j(n+1) = age_j(n) + 1$ .

$$\phi_2^j = GetOld(age_j(n)) \rightarrow age_j(n+1)$$

$\phi_3$  : GetVeg This rule calculates the per capita caloric value of the vegetation available in the j-th animal's cell:  $eveg_j = veget_{k_j}/pop_{k_j}$ .

$$\phi_3^j = GetVeg(veget_{k_j}(n), pop_{k_j}(n)) \rightarrow eveg_j(n+1)$$

$\phi_4$  : MetabolicNeed This rule calculates the daily metabolic need of each animal. The daily requirement of an animal for energy is defined as its field metabolic rate (FMR). It is utilized for maintenance, basal metabolism, thermoregulation and activity. There are several well known studies on the relationship between the metabolic need and weight of mammalian species that conclude that the FMR is proportional to the weight to the power of  $\approx \frac{3}{4}$ , Peters (1993), Nagy (1994). This relationship is empirically postulated and supported by a large variety of data. According to Nagy (1994), the average

$$FMR = 4.63W^{0.756} \text{ ( in } kJ/day) \approx 1.1W^{0.756} \text{ ( in } kcal/day),$$

where the weight  $W$  is in grams.

Lactating mammals more than double their food intake Gross et al. (1985), while pregnancy leads to energy need increase of about 30%, Tamarin (1985), p. 835. Thus, we calculate the metabolic need of an animal  $j$  using the formula

$$MetNeed_j = A \times weight_j^{0.75}$$

where  $A=1.1$  for non-pregnant ( $TimeSincePregn = 0$ ) and non-lactating voles ( $TimeSinceBirth = 0$ );  $A=2.2$  for lactating voles ( $TimeSinceBirth > 0$ ) and  $A=1.5$  for pregnant voles ( $TimeSincePregn > 0$ ). Juvenile animals depend entirely on the lactating parent. The metabolic need of a juvenile is included in the lactating parent's need, thus  $A = 0$ , if  $age_j < WeaningAge$ .

$$\phi_4^j = MetabolicNeed(age_j(n+1), gender_j(n), weight_j(n), TimeSinceBirth_j(n), TimeSincePregn_j(n)) \rightarrow MetNeed_j(n+1). \quad (4.6)$$

$\phi_5$  : Weight This rule calculates the weight of each animal, depending on the quantity of available vegetation in its current spatial cell. It also calculates the index *starvation*.

The weight gain and loss of a specific animal depends on whether the per capita caloric content of the vegetation in the cell,  $eveg$ , meets the metabolic need of the animal. Weight gain is modeled in a way specific to the age status of an animal. A juvenile animal gains weight with a daily rate equal to  $JuvenileGrowthRate$ . Unless they die due to the absence of the lactating parent, all juvenile voles have the same weight at weaning age. If the animal is above weaning age but below maturation age (subadult), then  $eveg_j$  is compared to the metabolic need,  $MetNeed_j(n)$  of the animal. The animal loses/gains weight with a rate equal to the  $SubadultGrowthRate$ . The values of  $JuvenileGrowthRate$  and  $SubadultGrowthRate$  (Table 1) are well established for *Microtus* species, Tamarin (1985).

When an animal reaches adult age and size, its growth continues up to a maximum value for the species,  $MaxAdultRate$ . We assume that if the animal's metabolic needs are met, its weight grows proportionally to the difference between the current weight and the maximum,  $MaxAdultRate - weight_j$ :

$$weight_j(n+1) = weight_j(n) + \alpha(MaxAdultRate - weight_j(n)).$$

If the animal's needs are not met, the animal loses weight. The energy content of tissue  $E$  is assumed to be  $70 \text{ kJ/g} = 16.8 \text{ kcal/g}$ , Peters (1993). During full starvation the amount of lost weight per day would be equal to  $MetNeed/E$ . Therefore weight loss is described as

$$weight_j(n+1) = weight_j(n) - A \cdot weight_j(n)^{0.75} / E.$$

The value of  $A$  is the same as the one used when determining the metabolic need (see rule  $\phi_4$ ). The value of the index *starvation* for each animal is calculated daily. It is increased with 1 if the animal's metabolic need is not met and set to 0 otherwise.

$$\begin{aligned} \phi_5^j = & \text{Weight}(\text{eveg}_j(n+1), \text{age}_j(n+1), \text{weight}_j(n), \text{MetNeed}_j(n+1)) \\ & \rightarrow (\text{weight}_j(n+1), \text{starvation}_j(n+1)). \end{aligned} \quad (4.7)$$

$\phi_6$  : VegDeplet This rule calculates the quantity of vegetation consumed by each animal and adds this quantity to the variable *vegdeplet* of the respective cell the animal resides at present. This function calculates the quantity of vegetation (expressed as caloric value) that would be grazed by all animal objects in each cell according to their metabolic needs. The sum of the metabolic needs of all animals in the cell (numbered  $k$ ) is calculated and this defines the value of the variable *vegdeplet*.

$$\text{vegdeplet}_k = \sum_{j=1,N} \text{MetNeed}_{k_j} \delta_k(k_j),$$

where  $\delta_k(k_j) = 1$  if  $k_j = k$  and 0 otherwise.

This function also calculates the maximum weights of the male and female floaters, *malmaxweight*, *femmaxweight*, currently present in the cell. These values are later used in the function *ChangeStatus*.

$$\begin{aligned} \phi_6^j = & \text{VegDeplet}(r_j(n), c_j(n), \text{MetNeed}_j(n+1), \text{vegdeplet}_{k_j}(n), \text{malmaxweight}_{k_j}(n), \text{femmaxweight}_{k_j}(n)) \\ & \rightarrow (\text{vegdeplet}_{k_j}(n+1), \text{malmaxweight}_{k_j}(n+1), \text{femmaxweight}_{k_j}(n+1)). \end{aligned} \quad (4.8)$$

$\phi_7$  : Survive This rule calculates the value of the variable *remove* for each animal. If it takes the value 1, the animal object is removed from the list.

The survival of an individual vole depends on many factors. In our model we assume that the most important ones are age, starvation, predation and dispersal out of the region. This function controls the value of parameter *remove<sub>j</sub>* based on its dependence on the first three factors. The dependence of survival on dispersal is controlled by the function *ChangeLocationRandomly* (see rule  $\phi_{11}$  below).

Voies are heavily predated by a large number of midsize mammals, raptors and avians, Lin and Batzli (1995), Tamarin (1985). Predation is an important factor in sustaining vole populations. Predation is modeled in the following way. Certain fractions of adult and immature animal objects are taken away from the list at each time increment (day). These fractions depend on the mean animal density for the whole region and differ for mature and immature animals. The fraction of predated immature animals (juveniles and subadults) is larger than the fraction of adults (as supported by experimental data, Lin and Batzli (1995)). Denoting the fraction of predated adults by  $P_A$ , and of juveniles by  $P_J$ , these quantities are expressed as

$$P_A = \text{AdultPredationCoefficient} \frac{\sum_{k=1, l=1}^{NCols, NRows} \text{pop}_{k,l}}{\text{TotalUsableArea}}$$

where  $\text{pop}_{k,l}$  is the population of cell in row  $k$  and column  $l$ , the total usable area is the total area in *ha* of all inhabitable cells, and similarly:

$$P_J = \text{JuvenilePredationCoefficient} \frac{\sum_{k=1, l=1}^{NCols, NRows} \text{pop}_{k,l}}{\text{TotalUsableArea}}.$$

Thus, we have incorporated density-dependent predation in the model (the denser the vole population is, the larger fraction of it is being predated). The rationale behind this assumption is that denser prey populations are easier to detect and catch. Predation is realized in the code by removing each  $1/P_A$ -th adult and each  $1/P_J$ -th juvenile in the list each day.

It is accepted that starvation leads to death if an animal has reached half of the average weight for its age, Peters (1993). Starvation can be full or occasional. During occasional starvation, an animal may not be able to maintain a healthy weight and would eventually die. We implement this by removing

from the list the adult animal objects whose weight is less than half the weight of a fully grown subadult ( $SubadultGrowthRate * MaturationAge$ ) and the subadult objects whose weight is less than half the weight of a fully grown juvenile ( $JuvenileGrowthRate * WeaningAge$ ). A juvenile animal is removed from the list if there is no female resident in the cell (presumably, the lactating parent has left the cell due to insufficient vegetation, see rule  $\phi_{10}$ , or has been predated).

On the other hand, full starvation (starvation for several consecutive days) may not lead to losing substantial weight, but the animal would die because of not being able to produce energy. As pointed out in the beginning of section 3.2, voles (smaller in size than *M. Ochrogaster*) have been observed to die after one day of full starvation due to hypoglycemia without really losing substantial weight. In our code, an animal object gets removed from the list if the value of the index *Starvation* has reached *StarveLimit*.

Finally, an animal object gets removed from the list also if its age is above the value *LifeSpan*.

$$\phi_7^j = Survive(age_j(n+1), starvation_j(n), weight_j(n+1)) \rightarrow remove(n+1).$$

$\phi_8$  : Pregnancy This rule sets the variable *TimeSincePregn<sub>j</sub>* to 1 if certain conditions are met. Setting the value to 1 denotes the occurrence of a pregnancy. This variable is set to zero originally (see Section 3.3). *TimeSincePregn<sub>j</sub>* takes the value 1 only if

$$\begin{aligned} &remove_j = 0, gender_j = 'f', age_j > MaturationAge, status_j = 's', TimeSincePregn_j = 0 \\ &\text{and } malpop_{k_j} > 0. \end{aligned} \quad (4.9)$$

That is, pregnancy occurs only if the animal is a non-pregnant adult resident female, and if there is a male occupant of the cell.

If the remainder of  $n$  (the time in days), divided by 360 is less than 30 or larger than 330 (that is, in the “months of December and January”), this map is not applied, i.e. pregnancies are not allowed to occur in the winter months, which corresponds to observations Tamarin (1985).

$$\begin{aligned} \phi_8^j &= Pregnancy(remove_j(n+1), gender_j(n), age_j(n+1), status_j(n), TimeSincePregn_j(n), malpop_{k_j}(n+1)) \\ &\rightarrow TimeSincePregn(n+1). \end{aligned} \quad (4.10)$$

$\phi_9$  : GiveBirth This rule controls the values of the variables *TimeSinceBirth*, *TimeSincePregn* and *birth*. *birth<sub>j</sub>* takes the value 1 only if  $status_j = 's'$  and  $TimeSincePregn_j = GestPeriod$ . When this happens, the animal gives birth to 4 new animals; i.e. 4 new animal objects are created, 2 of male, 2 of female gender.

The variable *TimeSincePregn<sub>j</sub>* increases with 1 daily only if it is positive until it reaches the value *GestPeriod*. In the latter case the index *birth<sub>j</sub>* is given the value 1 (birth occurs), *TimeSincePregn<sub>j</sub>* is set to 0 and the value of *TimeSinceBirth<sub>j</sub>* is set to 1. The variable *TimeSinceBirth* defines whether an animal is lactating or not. Once it gets the value 1, it gets increased until it reaches *WeaningAge* when it is set to 0.

$$\begin{aligned} \phi_9^j &= GiveBirth(age_j(n+1), remove_j(n+1), gender_j(n), status_j(n), TimeSinceBirth_j(n), \\ &\quad TimeSincePregn_j(n+1), malpop_{k_j}(n+1)) \\ &\rightarrow (TimeSinceBirth_j(n+1), TimeSincePregn_j(n+1), birth(n+1)). \end{aligned} \quad (4.11)$$

$\phi_{10}$  : ChangeStatus This rule determines which vole changes its residency status between ‘s’ (resident) and ‘f’ (floaters). Voles strive to become residents of a cell and to form heterosexual pairs. Unless their strategy is successful, they do not generate offspring. The survival and persistence of the population is dependent on the successful spatial settlement of vole couples.

At the initialization of the code, all voles are generated to be floaters. Then they start attempts to become residents of a cell. The rules encoded in this function are described as follows. Before reaching maturity, voles are residents of their parents’ cell. Upon reaching adulthood, a vole becomes a floater. A resident vole becomes a floater if the per capita quantity of vegetation, *evveg* is less than its metabolic need. An adult female floater vole becomes resident if there is no settled vole in the cell of the same gender and

if it has the largest weight among all floaters of the same gender in the cell. These conditions have to be fulfilled for a male floater to become a resident but in addition, there must be a female animal present in the cell. These rules reflect experimental findings that female voles prefer to settle in unoccupied territories, while male voles would seek for a female in addition.

The maximum weight assumption models a situation where the strongest prevail in competition for space. The imposed conditions ensure that only one couple is formed in an empty cell. As only one couple (with its immature offspring ) occupies a cell with the size of a vole's homerange, our rules also reflect territorial behavior.

$$\begin{aligned} \phi_{10}^j = & \text{ChangeStatus}(\text{age}_j(n+1), \text{remove}_j(n+1), r_j(n), c_j(n), \text{gender}_j(n), \text{status}_j(n), \text{weight}_j(n+1), \\ & \text{MetNeed}_j(n+1), \text{settlmalpop}_{k_j}(n+1), \text{settlfempop}_{k_j}(n+1), \text{settlpop}_{k_j}(n+1), \\ & \text{malmaxweight}_{k_j}(n+1), \text{femmaxweight}_{k_j}(n+1)) \rightarrow (\text{status}_j(n+1)). \end{aligned} \quad (4.12)$$

$\phi_{11}$  : *ChangeCellRandomly* This rule defines the rules of movement of floater voles between cells. They combine food resource and population pressure considerations and also model the possibility of perishing by entering non-inhabitable cells or leaving the region under population density pressure.

Each floater animal "considers" the cells belonging to the region and surrounding the one it is currently in, and makes a list of those that have vegetation of the suitable kind ( $\text{presence} = \text{VegetationCode}$ ). This list is split into two sublists: a) "first-rate" cells that have no occupants ( $\text{pop} = 0$ ) and have vegetation quantity satisfying its metabolic need ( $\text{veget} > \text{MetNeed}$ ) and b) "second rate" ones that have insufficient vegetation at that time but are also not populated.

If the first-rate list is not empty, the floater chooses a cell to move in randomly from among the list's members. Otherwise, a random choice is made from the members of the second-rate list. If this one is empty too (i.e. all inhabitable cells have been populated) the floater would be forced to move into a cell that is not inhabitable, i.e. such that  $\text{presence} \neq \text{VegetationCode}$  but penetrable (i.e.  $\text{presence} \neq 0$ ). Such cells might be inside the spatial region. But if the current cell is on the region's boundary and there are no inhabitable neighboring cells in the region, the floater is forced to leave the region. In this case the value of  $\text{remove}_j$  becomes equal to 1.

However, if such a movement is not possible because of lack of uninhabitable neighborhood, the animal chooses randomly among the inhabitable but populated cells. Finally, if there are no inhabitable and populated cells, then this means that all neighboring cells are impenetrable. Obviously then the animal would stay in the cell.

$$\phi_{11}^j = \text{ChangeCellRandomly}(r_j(n), c_j(n), \text{veget}_{k_j}(n)) \rightarrow (\text{remove}_j(n+1), r_j(n+1), c_j(n+1)),$$

**Step III.** This step is a loop that traverses the list of cells and executes the rule  $\phi_{12}$ .

$\phi_{12}$  : *Veg* This rule calculates the caloric content of the vegetation present in a specific cell  $C_k$ . Its increase resulting from vegetation growth is

$$\text{DigEnergy} \times W_n \times \text{AreaOfCell}$$

(for  $W_n$  see section 2.1). The decrease resulting from grazing is just  $\text{vegdeplet}_K$ . It is subtracted from the increase and the result is added to  $\text{veget}_K(n)$  to obtain  $\text{veget}_K(n+1)$ .

$$\phi_{12}^k = \text{Veg}(\text{vegdeplet}_k(n+1), \text{veget}_k(n)) \rightarrow \text{veget}_k(n+1), \quad k = 1, \dots, K.$$

**Step IV.** Finally, the list of animals is updated in order to proceed to the next iteration  $n+1$ .

$\phi_{13}$  : *UpdateListOfAnimals* This rule acts as follows. The list of animal objects  $\vec{a}_j, j = 1, \dots, N(n)$  is traversed. If  $\text{remove}_j(n+1) = 1$  for some  $j$ , this object is removed from the list. If  $\text{birth}_j(n+1) = 1$ , 4 new animal objects are created. These have age 0, 2 are male and 2 are female, all are residents, have weight equal to  $\text{WeightAtBirth}$  and inherit from the parent the cell coordinates. These objects are added to the end of the list.

## 4.2 Representation of $\Phi(n)$

The map  $\Phi$  is a product of the elementary maps  $\phi_i$  and can be written as

$$\Phi(n) = \phi_{13} \prod_{k=1}^K \phi_{12}^k \prod_{j=1}^{N(n)} \phi_{11} \phi_{10} \phi_9 \phi_8 \phi_7 \dots \phi_1 \prod_{k=1}^K \phi_0^k.$$

This representation holds for values of  $n$  whose remainder modulo 360 is greater than 30 and less than 330, i.e. in the "non-winter period". As mentioned before, the map  $\phi_8$  is not executed otherwise, so then

$$\Phi(n) = \phi_{13} \prod_{k=1}^K \phi_{12}^k \prod_{j=1}^{N(n)} \phi_{11} \phi_{10} \phi_9 \phi_7 \dots \phi_1 \prod_{k=1}^K \phi_0^k.$$

The product notation has the following meaning. A map on the right of another is executed first. That is, first are applied  $\phi_0^k$  for all  $k$  (that is the cell information is updated), then, for each  $j$  (from 1 to  $N(n)$ ) the maps  $\phi_1, \dots, \phi_{11}$  are executed (i.e. for the first animal in the list of  $N(n)$  animals the maps  $\phi_1^1, \dots, \phi_{11}^1(n)$  are applied in that order, next the same is done for the second animal and so on until the list is exhausted). Further,  $\phi_{12}^k$  are applied (i.e. the vegetation remaining in the cell at the end of the day is calculated) and finally the list of animals is updated by adding newborn animals and removing "dead" ones, which is the meaning of  $\phi_{13}$ .

Writing down a simulation in such a precise mathematical form represents an attempt to create a common form of presentation which facilitates the understanding of the model structure, lays a foundation for development of a theoretical framework as well as a common computational framework.

## 5 Results of Exploratory Simulations with Artificial Landscapes

A C++ code which we named SERDYCA (Spatially-Explicit Rodent DYNAMics Computation and Analysis) implements the above described model and is available for use by request to the authors. The code is supplemented with a graphic user interface and can be used in both Linux and Windows environment.

In this section we describe the results of simulations using the model on artificial landscapes. These landscapes represent square regions of various areas. Initially the landscape has the same density of vegetation over the entire region. 200 simulations were carried out for each area and predation level (PL). The simulation time depends on the size of the landscape as well as on the PL. For large areas and small predation, the model generated very high population numbers which required respectively a larger amount of calculations.

We conducted a series of simulation experiments on landscapes of 25x25, 50x50, 100x100, 150x150, 200x200 and 250x250 homeranges and for several sets of values of the parameters  $APC = \text{Adult Predation Coefficient}$ ,  $JPC = \text{Juvenile Predation Coefficient}$ , where we varied  $APC$  and kept  $JPC = 2APC$ . Each simulation was initialized by generating an initial animal population in every cell consisting of 0, 1 or 2 (a random number) of randomly generated animals (see Section 3.3).

### 5.1 Population density: the role of area and predation

Although the initial spatial animal distributions varied in each simulation instance, the total numbers (for the whole landscape) of generated animals did not vary much and approached the number of cells,  $K$ , for large  $K$ . This is not surprising because the initialization of animals is equivalent to conducting  $K$  independent experiments with three outcomes: 0,1,2. For any  $K$ , the probability that  $n_1$  cells contain one animal,  $n_2$  - two animals and  $K - n_1 - n_2$  - zero animals is

$$\frac{K!}{3^K n_1! n_2! (K - n_1 - n_2)!},$$

and the expectation of the number of generated animals is

$$\sum_{n_1=0, \dots, K; n_2=0, \dots, K-n_1} \frac{K!}{3^K n_1! n_2! (K - n_1 - n_2)!} (n_1 + 2n_2) = K$$

i.e. one per cell. One would expect that for large  $K$  the initially generated density per cell would be close to 1.

For landscapes of 25x25 cells the initial number of animals in the 200 experiments was between 280 and 320, i.e. on average 0.48 per cell and 5.3/ha, for landscapes of 50x50 cells these numbers were respectively between 1700 and 1850, 0.7/cell and 8/ha. The numbers per cell and ha increased with the increase of landscape size, approaching 1. For landscapes of 250x250 cells the respective numbers were between 58000 and 59000 with 0.92 animals per cell and 10.4/ha.

The initially generated animal distributions obviously did not depend on the level of predation. However, when the calculations were carried out, for each fixed PL, the density of animals had the same maximum amplitudes, which were characteristic for the PL and did not depend on the size of the landscape (Figure 3) or on the initial density distribution. For example, the maximum density corresponding to  $APC = 0.02, 0.2, 0.4$  was approximately the same for all six landscape sizes and was about 45/ha, 9/ha and 4/ha respectively. We note that Figure 3 shows densities starting from month 1 and thus the initial densities (month 0) are not visible.

We carried out simulations by gradually increasing the PL (i.e. increasing  $APC$ ). In all cases the maximum density was independent of the landscape area but decreased with the increase of the PL. This is illustrated on Figure 3, where we show results for the three mentioned above predation levels, which we denote as "low" ( $APC=0.02$ ), "optimal" ( $APC=0.2$ ) and "high" ( $APC=0.4$ ) PL.

HERE PLACE FIGURE 3

## 5.2 Calibration of the model

The maximum and average population densities of *M. Ochrogaster* vary in different environments. For example, a 25 year study of the population dynamics of prairie voles in three different types of habitats, Getz et al. (2001), show that the maximum density can reach more than 50/ha in alfalfa, 20/ha in bluegrass and 8/ha in tallgrass covered habitats.

As the only non-established parameter values of our model are the PL coefficients, and as the maximum densities in our model appear to be area-independent but monotonous with respect to the values of  $APC, JPC$ , we calibrated the model by finding values of  $APC, JPC$  for which the maximum population density is between 7 and 9/ha (shown on Figure 3, middle row). The calibrated values are  $APC = 0.2, JPC = 0.4$ . We will see further why these values are named "optimal".

## 5.3 Average time to extinction

If we observe the vegetation input (Figure 2), we note the existence of "bottlenecks" of very low amounts of vegetation in the end of the 4-th, 16-th, 20-th and 28-th years of the simulation. In the simulations these specific times are extinction-sensitive points. When varying the initial animal distributions, in certain cases the population dies out shortly after these specific times. Figure 3 illustrates these observations. Starting from the top left plot and going down, we see that on the smallest landscape consisting of 25x25 homeranges the vole populations perish before reaching even half of the simulated time period of 30 years and that there is a high variability in the population persistence in the various simulations. Moving to the right on Figure 3, we observe that the larger the area size, the more persistent the populations become and the more alike the population density patterns are.

We performed 200 simulations with randomly-varied initial animal distributions for each experimental setting (fixed landscape area or PL). The time for which the vole population persists (is non-zero) in the simulation is called its time to extinction (TE). The average value of TE for each set of 200 simulations is called the average time to extinction (ATE).

We compared the ATE for the various landscape sizes and PLs. The results are summarized on Figure 4.

We found that unlike the maximum vole population density, the ATE is sensitive to both area and predation. Increasing area in all tested cases led to increase in the ATE (Figure 4, middle).

The relation between ATE and predation was not straightforward. ATE increased when predation is small but decreased for high PLs. Our calculations showed that for the calibrated PL (the one generating densities characteristic of tallgrass prairie,  $a_A = 0.2, a_J = 0.4$ ) the ATE was the largest compared to all other PLs for which we performed simulations (including what we call "low" and "high" PLs) (Figure 4, bottom). This is the reason we call it "optimal" PL.

Besides comparing the ATE, it is informative to consider the *persistence frequency* depending on area and predation. This is defined as the percentage of the simulations in which the population did not go extinct (until year 30). Figure 4 (top) shows that for the "low" PL and all landscape sizes populations do not persist in 100% of the simulations. This is explained in the following way. Since "low" predation results in high population density, a leading cause of this low persistence is the higher mortality in the winter months as a result of severe overgrazing of the scarce vegetation cover.

However, Figure 4 also shows that populations do not persist in 100% of the simulations also for areas smaller than or equal to 50x50 cells independently of the predation level. Thus, there is a threshold of area size below which the population persistence frequency is zero.

Maximum population density was shown to be not sensitive to area. Thus, when reducing landscape size, persistence decreases due to factors not related to the value of the maximum population density. Rather, reduced persistence is caused by the low (late winter) total *numbers* of surviving voles in the small landscapes. Smaller landscapes provide a smaller number of surviving individuals to restore the population after a period of insufficient vegetation and no births (winter months). A part of these individuals are unable to find a mate and create offspring. The larger the landscape the bigger the number of cases when clusters of individual survive and successfully restore the local population.

The persistence frequency grows rapidly with increasing the landscape size for higher PLs (Fig. 4, top). Thus, the combination of increased predation and larger landscape sizes contributes to prolonged persistence.

HERE PLACE FIGURE 4

## 5.4 Population density fluctuations

It is known that the population densities of many microtine rodents (and in particular of the prairie vole) exhibit annual and multiannual fluctuations, Getz et al. (2001). The annual cycles are clearly connected with seasonal factors, but the multiannual ones have not been explained. Getz et al. (2001) mention that spectral analysis of tallgrass prairie population densities reveals multiyear fluctuations with frequency peaks of similar magnitude at 4.3 and 2.4 years.

As seen on Figures 3 and 5, our simulations produce population densities with clear annual fluctuations. The maxima of the densities occur in the "November-December" of each year while the minima are observed in "March"- "April", which corresponds to observations in natural populations. Groups of multiannual fluctuations are clearly visible.

Figure 3 shows that the fluctuations have a similar character (the peaks are around the same time moments) for different area sizes. This result associates with the observed *synchronized fluctuations* of vole populations on various spatially disparate habitats Getz et al. (2001). Especially for large areas and higher PLs, the time series show very low variability. These time series were generated for varying initial spatial animal distributions. As noted in the beginning of this section, the larger the area, the smaller the variability between the density of initially generated animals. The similarity between the patterns of the time series increased with the increase of area obviously because the initial densities became closer to each other. For similar initial population densities the time series had similar shape, although the spatial distributions of the initial populations are quite different. Thus, the fact that the model is spatial did not affect the population density fluctuation pattern.

Trying to understand this, an association with the properties of the wave  $W_t = W_{xx}$  equation comes to mind. The latter equation has separable solutions,  $W(x, t) = W_1(t)W_2(x)$ , and thus,  $\int W dx$  is the same function in time independently of the initial distribution.

Thus, even though the spatial movements of voles take into consideration factors such as mating opportunity and vegetation availability, the model is similar to a diffusion model in the sense that it generates

population density distributions that are "separable" into time and space components so that the time component determines the fluctuation patterns of the total density.

Varying the values of the PL did have some initial effect on the fluctuation pattern but for larger times and on larger areas the fluctuations synchronized (observe Figure 3, rightmost plots, from top to bottom).

Figure 5 shows a plot of the simulated population densities for 6 landscape areas and "optimal" PL, generated by the simulation for a 250x250 cells landscape and "optimal" PL.

HERE PLACE FIGURE 5

One method to get some understanding of the features of the observed fluctuations, is to perform time series spectral analysis. We performed Fourier analysis of the mean population density time series obtained by summing up the population density time series for the simulations in which the population persisted for the whole 30 year period and dividing by the number of simulations. These were simulations for the "optimal" PL and size of the artificial landscape 250x250 cells.

We obtained the highest frequency to correspond to a period of 12 months, which reflects the annual fluctuations. The next dominant frequencies corresponded to periods of 2.5 years and 4 years. These results are remarkably close to the ones observed by Getz et al. (2001), mentioned above. However, the 4.3 peak reported by Getz et al. was slightly higher than the 2.4 year peak; the peak corresponding to 2.5 years in our time series was higher than the one for 4 years, but both peaks were comparable.

Additional work is needed to understand whether the striking similarity between these values is not coincidental.

We also performed spectral analysis of the vegetation time series to see if there is similarity to the density time series. The vegetation density time series for each fixed PL were almost identical across various area sizes. The periods corresponding to the peak frequencies were 1 year (annual fluctuations), 1 year 11 months and 3 years 8 months. There were periods corresponding to seasonal fluctuations at 3, 4 and 6 months.

## 6 Validation

The problems accompanying the validation of an ecological model are well elucidated in Rykiel (1996). According to the classification given there, our model satisfies the requirements of conceptual and predictive validation. It is conceptually valid because it was built upon credible scientific hypotheses and data. As the model predicts the population density fluctuations very well we conclude that at this stage, it has good predictive validity.

## 7 Discussion and summary

The conclusions drawn from the behavior of simulation models are based on a restricted number of observations. This is in contrast with continuous deterministic models that sometimes allow the derivation of conclusions valid for a continuum of parameter sets. However, in both cases the results have only the value of conjectures, or of idea-generators, because in both cases we are dealing with models. A model can reject a conjecture but not confirm it, and it can lead to a conjecture but not to a real prediction. A new conjecture is good no matter how it was conceived; thus the discussion whether a mathematical or a simulation model "gives a better prediction" has no ground. Mathematical models that can be treated analytically to produce

general conclusions are necessarily restricted to the form for which theory can be applied. A simulation model as the one we described can be constructed using a great amount of well established information. Such a model can incorporate a much more complete set of the factors determining the properties of the modeled phenomenon. Thus, a complex model has more chances to produce new ideas even if they were inspired by a limited number of model observations.

Thus, all conclusions from the model we presented should be regarded as conjectures and not as absolute knowledge. We summarize them below.

Our results indicate that the maximum vole population densities are not sensitive to the size of the landscape but are sensitive and negatively correlated to the level of predation, while the average time to extinction is sensitive to both. The ATE is positively correlated with landscape area. If the maximum population density was the definitive factor for population persistence, then changes in area size should not affect persistence. Thus, when evaluating the effect of loss of habitat on population persistence, the important factor is not the maximum population density. The low persistence at small landscapes is explained by decreased probability of restoring the population after severe (winter) periods due to the small size of the population and thus, the small number of clusters of remaining individuals that can form couples and create offspring. The smaller the area of the habitat, the smaller the number of the surviving clusters of individuals to restore the population. The model shows the existence of a threshold prairie vole habitat area greater than 50x50 homeranges. More analysis is needed to understand well the low persistence in small landscapes.

The ATE's dependence on predation is more complex. There seems to be an "optimal" predation level (*PL*) maximizing the ATE: for lower and higher PL, the ATE decreases. At lower PLs, the rodent population can go extinct because of overpopulation and overgrazing; at higher PLs the rodent population becomes too small and cannot be sustained (Allee effect).

The persistence frequency also increases with area size. However, there is a threshold area value, larger than 50x50 homeranges below which the persistence frequency is 0, i.e. in none of the simulated cases did the population persist until the end of the simulated time period, even in the case of optimal predation.

The model is calibrated by adjusting the PL so that the population density varies in bounds that are characteristic for tallgrass prairie. It turns out that the calibrated PL coincides with the "optimal PL". This interesting observation leads to a conjecture from the realm of evolutionary adaptation: the herbivore-predatorial relationship has evolved in the specific environment so that the herbivore's TE is maximized. We can conjecture that a predator-herbivore system in a certain environment consisting of climatic and vegetation-type elements, adjusts in such a way that the rate at which the herbivore is predated ensures its maximum persistence.

The simulated population densities exhibit annual and multiannual fluctuations with a dominating frequency corresponding to a period of 2.5 years and a secondary one of 4 years. These are very close to the ones reported by Getz et al, Getz et al. (2001) in a 25 year study of vole populations in natural conditions. If this result is not a mere coincidence, it means that the elements of the vole population dynamics we have assembled into a model, are sufficient to explain the multiyear fluctuations. Thus, one way to establish the cause(s) for these specific fluctuations in the model is to study the sensitivity of the dominating frequencies with respect to the elements.

## 8 Acknowledgements

We would like to thank Nancy Comstock, U.S. Department of Energy National Petroleum Technology Office, for funding support.

The authors express gratitude to James Kercher from Energy and Environment Division, LLNL, who performed the calculation of the vegetation growth rates and to Henriette Jager, Oakridge National Laboratory who supplied the weather data from Tulsa airport.

This work was performed under the auspices of the U.S. Department of Energy at the University of California Lawrence Livermore National Laboratory under contract No. W-7405-Eng-48.

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## FIGURE CAPTIONS

**Figure 1.** A schematic representation of the time loop of the model. The arrows denote the order of events.

**Figure 2.** Estimated daily dry vegetation biomass ( $\text{g}/\text{m}^2$ ) used as input for the model and calculated from temperature and precipitation data. See text for further explanation.

**Figure 3.** Population densities for various initial animal distributions and three PLs, denoted as "low" ( $APC=0.02$ ), "optimal" ( $APC=0.2$ ) and "high" ( $APC=0.4$ ) PL, on landscapes with different sizes. Different curves represent different runs. Maximum density is sensitive to predation but not to area.  $y$ -axis represents total number of voles per ha.

**Figure 4** Different representations of the dependence of the ATE on area and predation. Top: percentage of simulations with extinction; middle: dependence of ATE on area for three PLs ( $AA = a_A, AJ = a_J$ ); bottom: dependence of ATE on PL for various areas; the x-axis corresponds to  $a_A$ .

**Figure 5** Simulated population densities for 6 landscape areas in numbers of voles per ha.

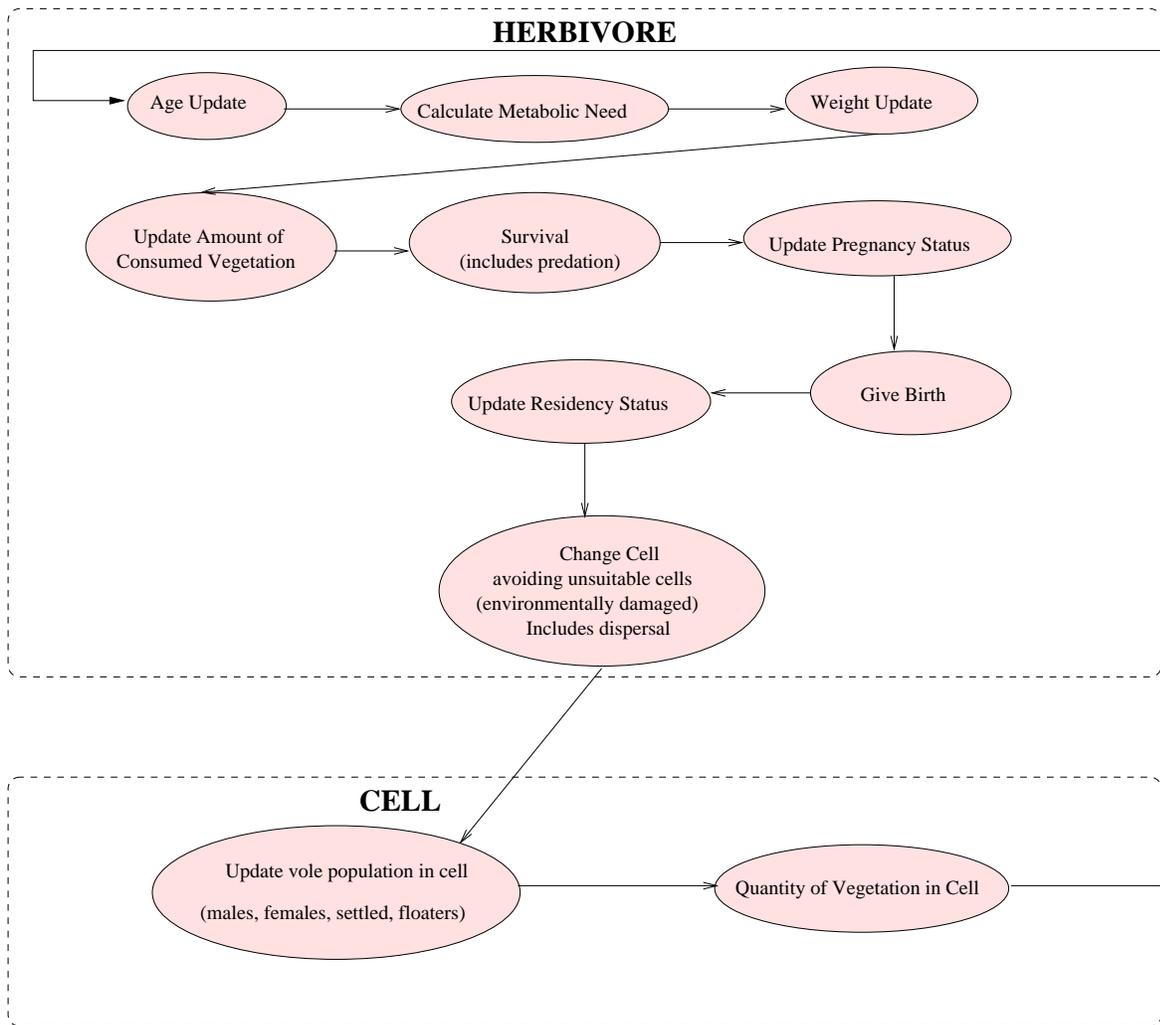


Figure 1

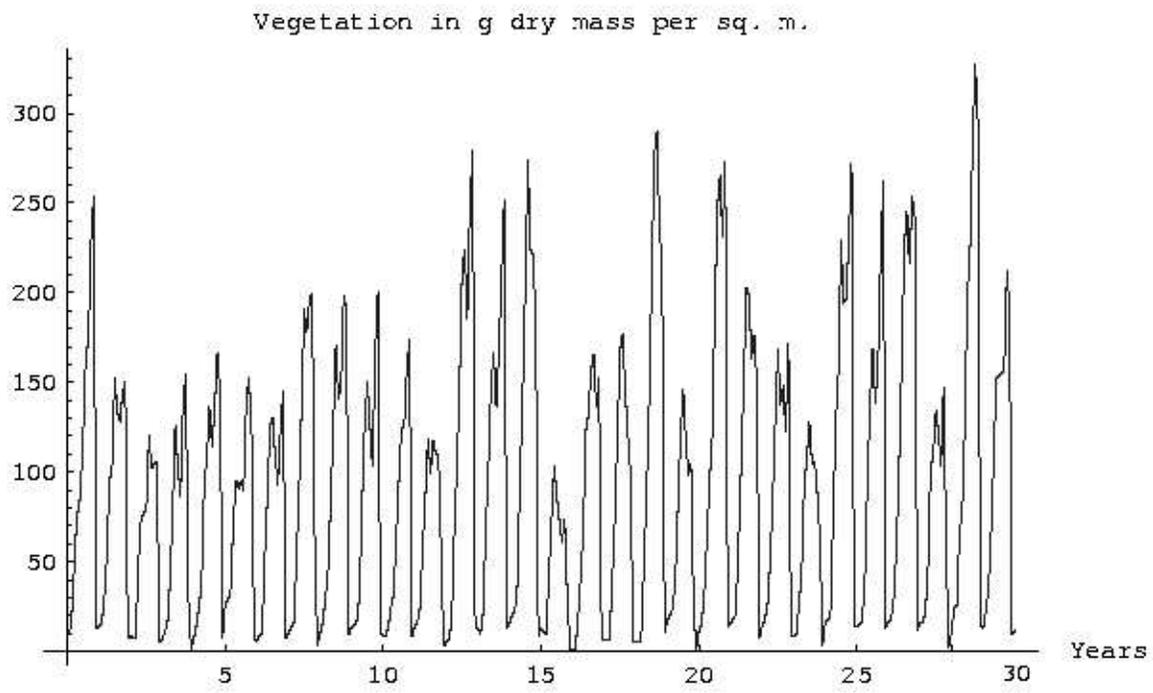


Figure 2

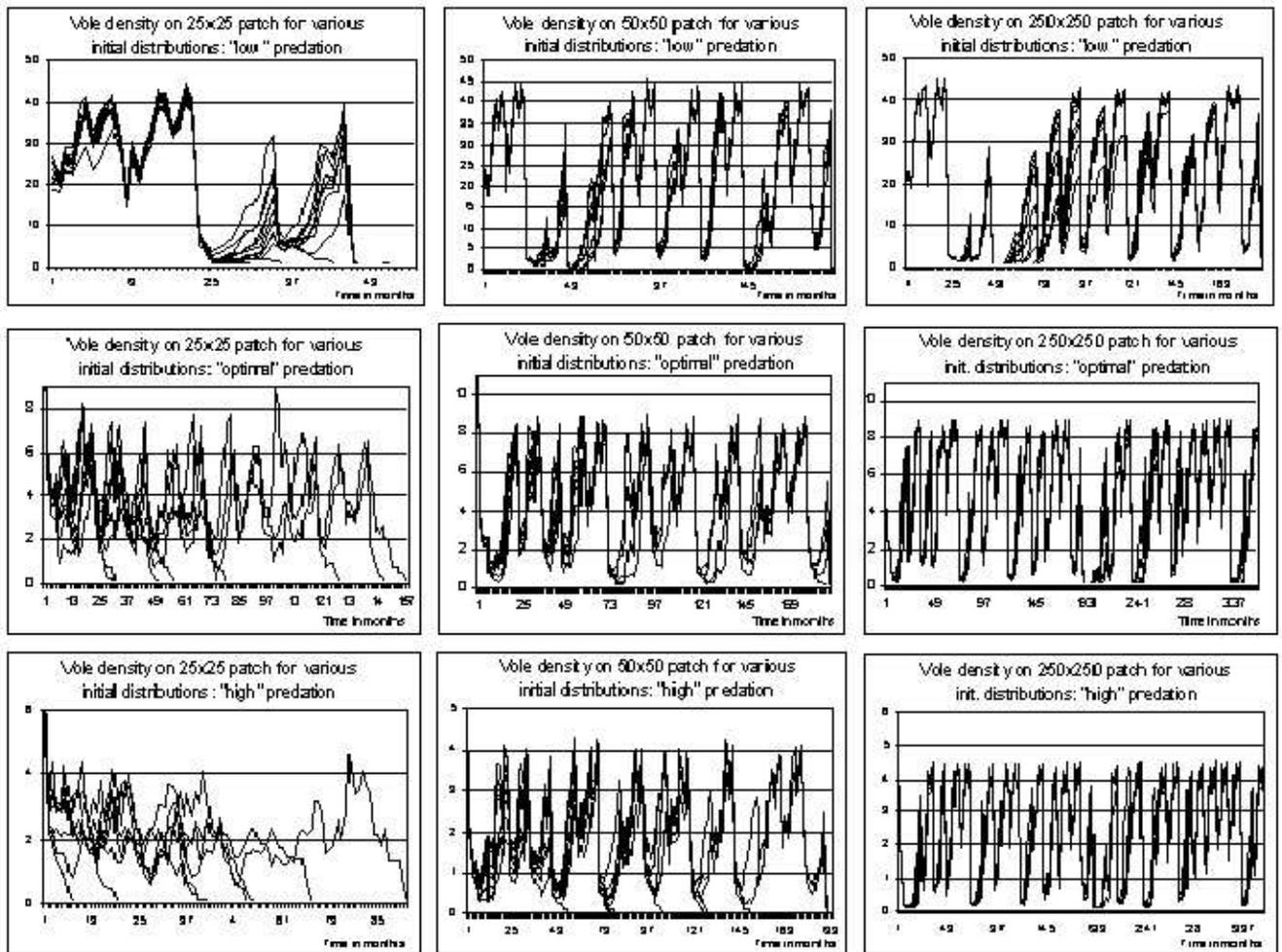


Figure 3

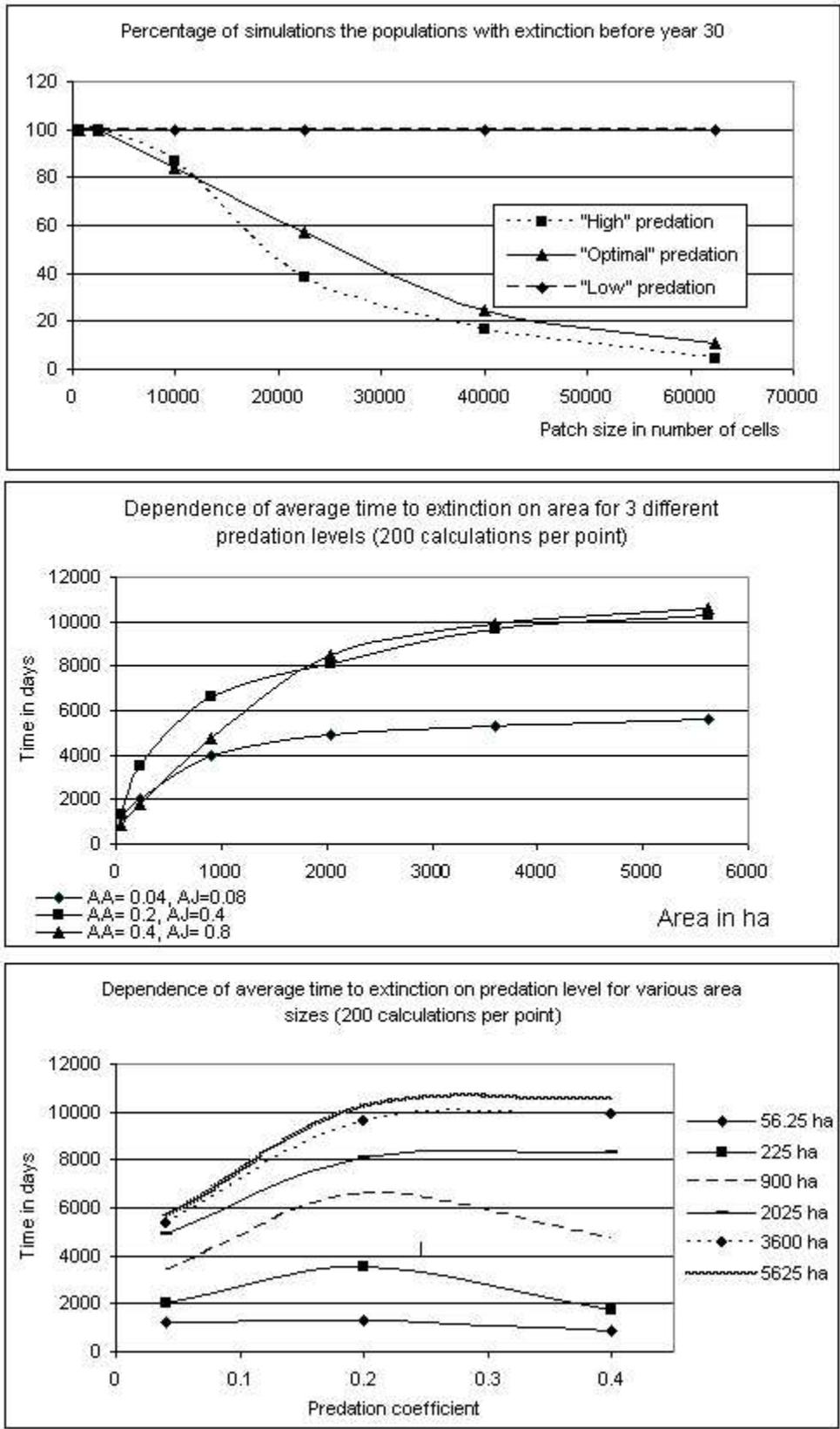


Figure 4

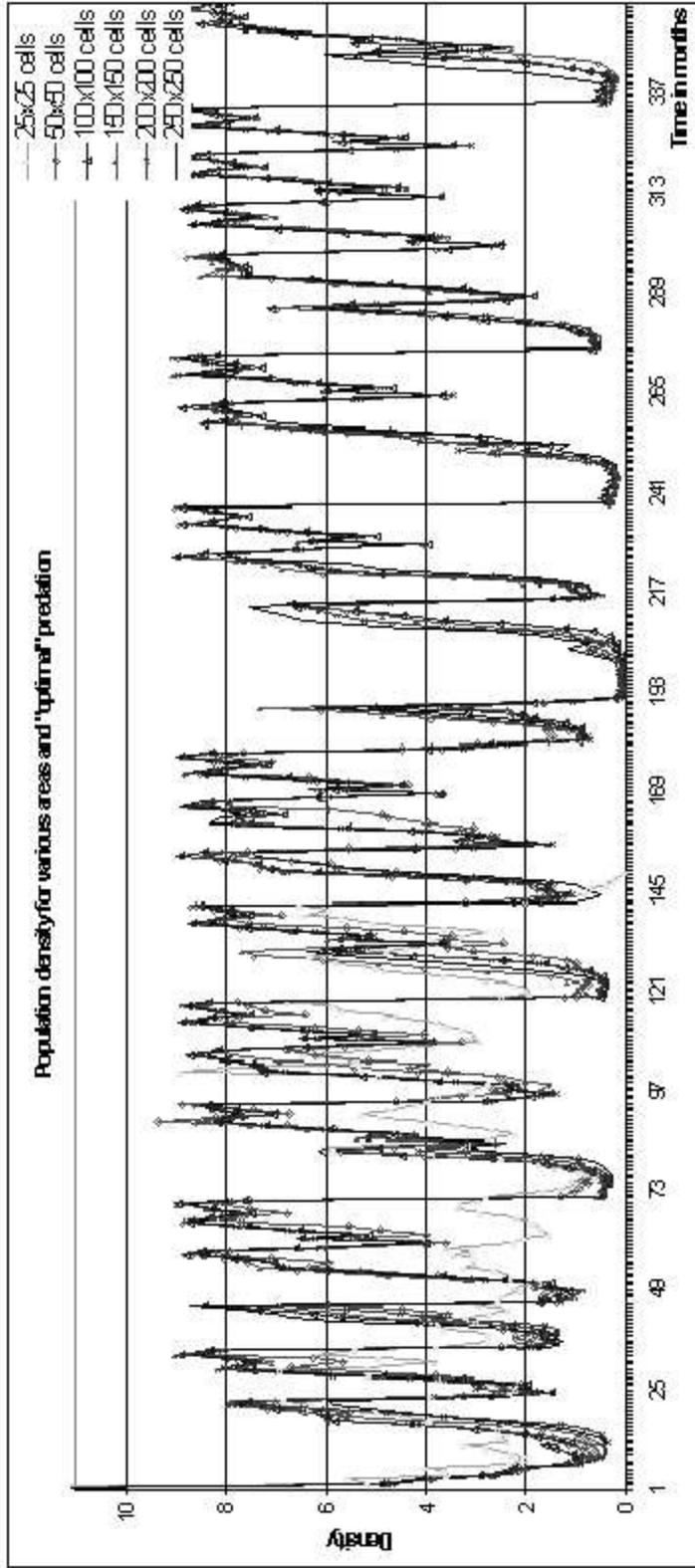


Figure 5

**Table 1.**

Description	Notation	Current Value	Source
average life span	<i>LifeSpan</i>	90 - 300 days	(a),(b)
maturation age	<i>MaturationAge</i>	30 days	(c)
age of weaning	<i>WeaningAge</i>	15 days	(c)
maximum adult weight	<i>MaxAdultWeight</i>	50 grams	(c), (d), (e)
weight at birth	<i>WeightAtBirth</i>	3 grams	
subadult rate of weight growth	<i>SubAdultGrowthRate</i>	1.5 grams/day	(c)
juvenile rate of weight growth	<i>JuvenileGrowthRate</i>	0.5 grams/day	(c)
gestation period	<i>GestPeriod</i>	21 days	(f), (g)
average length of starvation period	<i>StarveLimit</i>	4 days	
average litter size	<i>LitterSize</i>	4	(c)
adult predation coefficient	<i>AdultPredationCoefficient</i>	see section 4.2	
juvenile predation coefficient	<i>JuvenilePredationCoefficient</i>	see section 4.2	
code of vegetation foraged	<i>VegetationCode</i>	1	
digestible energy	<i>DigEnergy</i>	2.2 kcal/g	(h), (i), (g)

**Constant animal objects' attributes.**

In column 3 (a)=Getz et al. (2000), (b)=Rose and Dueser (1980), (c)=Tamarin (1985), (d)=Gaulin and Fitzgerald (1988), (e)=Desy and Batzli (1989), (f)=Getz and McGuire (1993), (g)=Rose and Gaines (1978), (h)=Klass (1998), (i)=Cole and Batzli (1979), (g)=Altman and Dittmer (1968).

**Table 2.**

Description	Notation	Units or values
time of starvation	<i>starvation</i>	days
death index if =1, animal is removed from list	<i>remove</i>	
row of animal's cell	<i>r</i>	
column of animal's cell	<i>c</i>	
gender of animal	<i>gender</i>	"m" or "f"
resident or floater status	<i>status</i>	"s", "f"
weight of animal	<i>weight</i>	grams
metabolic need of animal	<i>MetNeed</i>	kcal
available vegetation per capita in animal's cell	<i>veg</i>	kcal
age of animal	<i>age</i>	days
time since animal gave birth	<i>TimeSinceBirth</i>	days
time since start of pregnancy	<i>TimeSincePregn</i>	days
index of birth	<i>birth</i>	1, 0

**Variable animal attributes**

**Table 3**

Description	Notation	Units
caloric value of total vegetation in cell	<i>veget</i>	kcal
caloric value of vegetation grazed during 1 day	<i>vegdeplet</i>	kcal
total male/female population in the cell	<i>malpop/fempop</i>	
resident male/female population in the cell	<i>settlmalpop/settlefempop</i>	
resident/total population in cell	<i>settlpop/pop</i>	
weight of largest male/female floater animal in cell	<i>malmaxweight/femmaxweight</i>	grams

**Variable cell objects' attributes**