

== CONTROL IN SOCIAL ECONOMIC SYSTEMS, MEDICINE, AND BIOLOGY ==

A Complex Mathematical Modeling Method for Biological Objects. Modeling the Tundra Community

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Abstract—We consider a method for mathematical modeling of ecologo–biological systems based on computational studies that unites formal and informal, analytic and imitational approaches. The method is based on complex studies that include a complete set of operations, from filtering biological information to constructing a set of interrelated models, including simplified ones, that admit an analytic (parametric) study. This lets us overcome the disadvantages of purely imitational approaches: they are restricted by numerical experiments and often have huge models. The proposed approach has been used to analyze animal population fluctuations with the tundra community model “vegetation–lemmings–arctic foxes.” As a result of our studies, we formulate hypotheses on leading mechanisms that determine the fluctuations of tundra animal populations.

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1. INTRODUCTION

Fundamentals of quantitative ecology were first outlined in the pre-computer (analytic) era [1–5]. The first mathematical models of ecological systems, despite their internal perfection (in the mathematical and biophysical senses of the word), have attracted the attention of ecologists only after experimental works of G.F. Gauze [6]. The utmost importance of interdisciplinary interactions was, of course, understood in the classical (analytic) period but researchers did not have a method that could take them into account. The appearance of J. Forrester’s “system dynamics” [7] made such an interdisciplinary toolbox available; it was based on the method of creating imitational models in a dialogue with experts. This approach lets one take into account virtually all proposals of the experts in either quantitative or qualitative form, and the relative simplicity of the resulting models lets one perform comparative analysis for different sets of original assumptions, data, and hypotheses.

Efficiency of purely imitational technologies is held back by limitations of numerical computations and the high detail level of the description that grows into “boundless” models. These drawbacks can be alleviated through a symbiosis of imitational and analytic methods with complex studies (COST) that include the entire sequence of operations:

- collection, filtering, analysis, and processing of input (biological) information; justification and construction of imitational models and analysis of their properties;
- formulation of an imitational system, i.e., a set of interrelated models on different detalization levels; the set includes simplified models that admit an analytic (portrait) study;
- formulation of hypotheses on leading mechanisms in the phenomenon under consideration.

One can create simplified (analytic) models by joint analysis of ecologo–biological information and results of computational experiments based on reductions of basic imitational models.

The COST approach was created in order to model the tundra community. Based on expert estimates of the relationships, researchers have created the “vegetation–lemmings–arctic foxes” (VLF) imitational model that takes into account seasonal changes in the parameters (see Appendix). Interdisciplinary possibilities provided by computer technologies have been employed, and this has led to the idea of an “ecological constructor” in the primary formulation of the model and its subsequent modifications.

Final stages of the COST method resulted from the deficiencies of traditional final stages of imitational modeling studies, namely forecasts of dynamic model characteristics under various scenarios of external influences [6, 8–10], and the need to get closer to understanding the mechanisms that form the dynamics of tundra animal populations. We have created a model of lemming population that determines the character of fluctuations in the number of tundra community animals, which has led to justifying the use of a one-dimensional difference equation as a simplified model that relates lemming population size (leading unit in the VLF model) in two consecutive years [6, 11]. Such difference equations have let us find in the original imitational model the regions of parameters that ensure dynamic modes of changes in population sizes that are close to those observed in nature and formulate hypotheses on leading mechanisms that determine these fluctuations in tundra animal populations. The special role this simplified model plays in studying population fluctuations for tundra animals has led us to search for a closer connection between the Poincaré function and the original (imitational) VLF model. Based on the joint analysis of ecologo–biological information and results of computational experiments, we have been able to formulate and solve the “inverse imitational problem” (see Appendix). The problem is to introduce such additional assumptions that would let us get formulas relating the original community model parameters with parameters of the difference equation.

2. THE “VEGETATION–LEMMINGS–ARCTIC FOXES” MODEL

Disagreeing with Forrester on his “world dynamics” model [7], N.N. Moiseev and coauthors have proposed to consider the “human–environment” problem first of all as the problem of biological envelope stability. Based on this idea, studies were initiated at the Computational Center of the USSR Academy of Sciences that strived to adapt system dynamics to model biological envelope processes (which later gave rise to “nuclear winter” modeling [12]). These approaches were then transformed to more local ecological objects [6]. In this work, we consider the tundra as our modeling object.

Despite lack of study, tundra is in many ways an attractive object for modeling. It is a relatively simple ecosystem with few species, food chains are strained, and animals live on the verge of survival. To create a meaningful mathematical model, we need some striking phenomenon to explain which we would recreate in the model. Accounting for the fluctuations in animal population sizes was one of the motives for creating the most popular “predator–prey” model. The main advantage of this object is the existence of pronounced regular fluctuations in animal populations, in particular, arctic foxes and their primary prey, lemmings (tundra rodents widely known for their migrations), which produces a reliable testing effect in studying the dynamics of animal populations. Regular peaks in animal populations have been noted: approximately once per three–four years [6, 13–15], once per three years on the Taymyr peninsula [11].

Our choice of the modeling object and the structure of its mathematical description is done as a compromise between mathematical and ecological requirements. In constructing the model, we have used the following principles:

—*minimality principle*—using the minimal possible mathematical structure necessary to imitate the phenomenon in question;

—*system approach*—taking into account the entire variety of relations, both internal and external, for the object of study;

—*compatibility (ecological compatibility)*—using assumptions that do not contradict available ecological data.

Biophysical analysis of the structure of pasture (above-ground) part of the tundra biocenoses has indicated the possibility to consider the VLF community separately (biophysical analysis is described in more detail in [6, 16]). The structure of our mathematical model has been chosen according to the Volterra–Kosticyn hypothesis [2], as a system of three first order ordinary differential equations. This has let us, in modeling the VLF community, to create an “ecological constructor” based on system dynamics methods: the dynamics of biomasses in each of the three trophic levels is defined by three additive components—reproduction, alienation, and natural death rates, while each component, in turn, is constructed as a product of a constant and corresponding functions.

This approach corresponds to the level of our knowledge in the biophysics of ecological processes, the variety of assumptions, and lets us take into account different ecological hypotheses in different modifications of the model. We have created a large number of versions of this model: at first, we have used the idea of strong trophic interactions (of the “predator–prey” kind) literally, but then we have switched to using the threshold dependence hypothesis for the rate of lemming biomass growth depending on the vegetation biomass [6] and other hypotheses.

Based on the expert data we collected, we have constructed the first version of the model, which is a union of Forrester’s and V. Volterra’s approaches emphasizing Volterra’s “meeting hypotheses” [1], which appear to be the main reason for the success of our modeling. Failures in the implementation (the model “deconstructed” when one of the species died, and soon afterwards the entire system died too) have led us to search for alternative approaches and methods of simplified description. Studies of zero isoclinic lines in the “vegetation–lemmings” system have led to the idea of using an analogy with a neural cell and introduce, in the second version of the model, a threshold dependence of the lemming biomass growth on the availability of fodder: when a certain critical vegetation biomass is reached, a “population explosion” happens with the lemmings, and soon afterwards the food supply becomes depleted. Controlling regeneration rate for the vegetation has let us make the model tuning process controllable and thus “prove” a kind of “existence theorem” about the possibility of reconstruction of the necessary dynamic modes with a model from the chosen class. Our use of the “threshold model” has made it possible to find, in a computational experiment, relations between parameters of the corresponding expert estimates and average interval between population peaks.

The second version of the model turned out to be unsatisfactory; hence, we attempted to restructure the modeling process. Restructuring was done in two directions: extending (deepening) the biophysical knowledge about biological properties of the biocenoses and searching for efficient mathematical ways to express them. Having analyzed the results of computational experiments and ecological information, we have understood the great importance of intrapopulation dynamics of lemmings in population size fluctuations of all animals in the tundra community. We have introduced a new type of nonlinearity, the Allee principle [5, 6], that brings into the model the lemming density which is optimal for reproduction. A large number of other modifying assumptions was related to increasing stability (trajectory “boundedness”) of the model. In testing these assumptions, we have used two biophysical criteria (independent of expert estimates and axioms of classical models): keeping the trajectories in the positive square and reproducing the corresponding dynamic modes. A description of this version of the “vegetation–lemmings–arctic foxes” (VLF) model is given in the Appendix.

In computational experiments, we have obtained three- and four-year cycles in lemming and arctic fox population sizes fluctuations that are characteristic for tundra. Figure 1a shows the

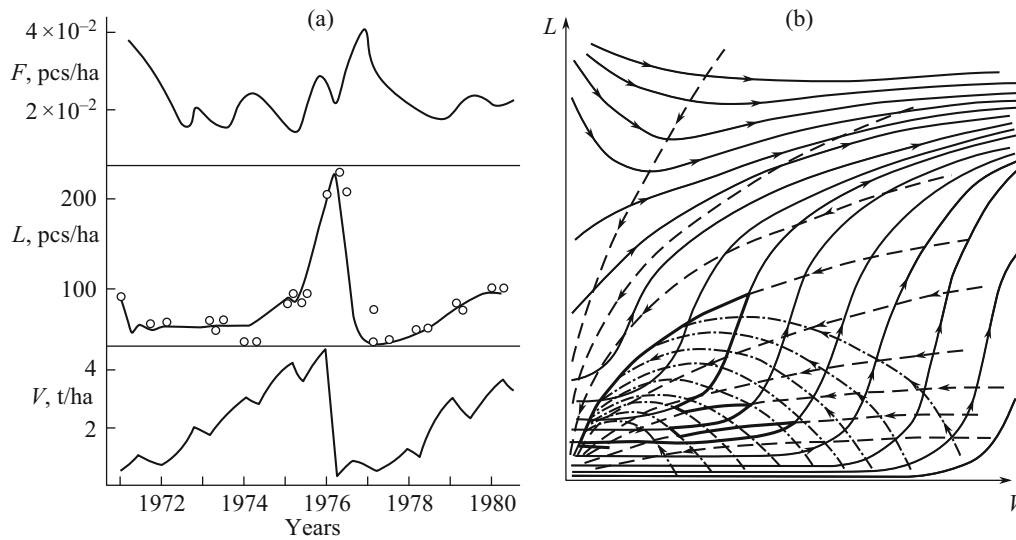


Fig. 1. (a) The results of one imitational experiment with the VLF model (V —vegetation, L —lemmings, F —arctic foxes), and the population dynamics of arctic lemmings registered on Wrangel island denoted by “circles;” (b) the phase portrait of the VL subsystem (V —vegetation, L —lemmings).

results of one imitational experiment with the VLF model and the population dynamics of arctic lemming registered on Wrangel island [14] denoted by circles; Fig. 1b shows the phase portrait of the “vegetation–lemmings” subsystem constructed with numerical computations on the entire model for each of the seasons. Here the bold line represents one of the actually realized trajectories; thin lines, phase curves in various seasons: dashed line, in winter (when lemmings do not reproduce); dot-and-dash line, in the nival reproduction period; solid, in summer (vegetation V along the horizontal axis, lemmings L along the vertical axis).

As Fig. 1b clearly shows, during winter and spring seasons the trajectories are attracted to the origin, while in summer the attractor is in a region of high lemming and vegetation density. Due to seasonal switchings of the trajectories, fluctuations appear in the model.

3. METHODOLOGY OF THE COMPLEX STUDIES (COST)

Modeling results described above were a continuation of the “biosphere topic.” We also planned to conduct computational experiments in order to determine the change in population dynamics under various scenarios of environmental changes: the constructed model of the tundra community was used to estimate the reaction of the tundra ecosystem to global planetary warming [6]. The goal to achieve a better understanding of the mechanisms that form the dynamics of tundra animal populations has led to a model of the population of lemmings who determine the fluctuations of the tundra animal community populations [6, 11].

Analysis of computational experiments results with both complementary models has led to a justification for the simplified model as a one-dimensional difference equation (sequence function) $L_{n+1} = F(L_n)$ that relates normalized lemming populations L_n in two consecutive years [6, 11, 16, 17]. The equation is graphically represented on Fig. 2. Here A is the equilibrium population; d —lemming population in the optimal biotope: the notion of an “optimal biotope” means a region of inhabitation space with optimal living conditions; in an optimal biotope, under any conditions a certain number of animal survives; P —the yearly increase in lemming population; $1/P$, the point when the maximal value of lemming population is reached.

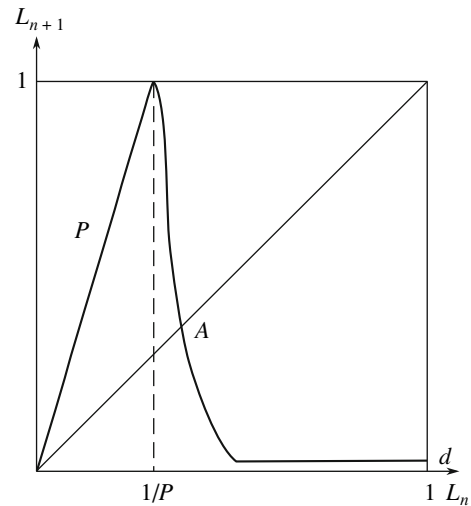


Fig. 2. Graphical representation of difference equation.

The special role of the sequence function in the studies of population fluctuations of tundra animals has led to looking for a closer connection of sequence functions and the original VLF model. Based on joint analysis of ecologo-biological information and results of computational experiments, we have been able to formulate and solve the “inverse imitational problem” (see Appendix), namely to introduce additional assumptions that let us obtain formulas relating the parameters of the original community model with parameters of the difference equation. This transition is based on the fact that at a certain time interval (season), the corresponding variables change in a relatively narrow range, which lets us linearize the original (expert) functions in a given range.

After solving the “inverse imitational problem,” we can tune the original (imitational) VLF model as follows: first, by the sequence function we find what its parameters should be to get the necessary dynamics. Then, using transition functions we find what parameters in the original models can be changed in order to change the necessary parameter or several parameters in the sequence function. Since nearly all of them depend on several original parameters, we have implemented a possibility to choose different versions and introduce the most biologically meaningful changes.

Using the complex approach to model tundra populations and communities [6, 17] has let us *formulate quantitative hypotheses on the leading (main, determining) mechanisms that create population fluctuations for tundra animals*. As we have already noted, the leading factor that determines these fluctuations is the dynamics of lemming population. This *dynamic*, in turn, *is determined by three parameters*: (1) rate of biomass growth in a favorable year; (2) maximal population; (3) survival rate under the least favorable conditions. The first parameter characterizes the balance between birth and death processes under no “environmental pressure”; the second characterizes the ecosystem as a whole and reflects the coevolution of lemmings and the food supply; the third characterizes adaptive properties of lemmings in extreme conditions and is in many ways determined by local characteristics, in particular the landscape in wintering places. Our results agree well with one of the widely accepted hypotheses that states that there is no single factor that forms population fluctuations but rather a combination of factors [13–15]. The resulting quantitative relations that link generalized parameters with population dynamic parameters can be used in parameter estimation procedures for real populations with parameters such as birth rate, death rate, etc. Difference equations can serve as a simple instrument to forecast the possible population of

lemmings and arctic foxes. At the same time, in order to adapt this approach to study different tundra regions and analyze significant changes in its properties, in particular due to anthropogenic factors (climate changes, etc.) one has to use the full imitational model.

4. DISCUSSION

Imitational modeling in an ecologo–biological domain is the art of using computer technology in an interdisciplinary process of creating mathematical models under incomplete and *always distorted* data of various nature about the properties of the object under study [8]. It is the art of compromise between ecological and mathematical requirements: for efficient modeling, we need not only to accommodate the informational fundamentals of the model with data and biologists' perceptions but also successfully tune mathematical tools needed to express the specifics of the object; it is hard to predict in advance what these properties may be. Only a computational experiment with a complete model (from the informational point of view) can show the possibility of reconstructing the population dynamics time series with a combination of the chosen model structure and corresponding informational base.

The search for such successful combinations is based on the idea of an “ecological constructor” (EC), an algorithmic structure of the model that lets one relatively easily modify it. The implementation of this idea is based on joining Forrester's system dynamics with the Volterra–Kosticyn hypothesis on the possibility to use systems of ordinary differential equations to describe ecological objects [2].

Imitational modeling lets one immediately, based on expert data and models left over from previous studies, begin model construction. EC allows for a relatively simple (on the formal level) implementation of various ideas. One can consider alternative possibilities (various “perceptrons”) and use the knowledge about similar processes of different nature. As the subject domain is internalized, the mathematician's role in model modification becomes more prominent, the “modeling mathematician” takes on the functions of an expert and filters information from the point of view of modeling efficiency. Informal (intuitive) considerations play an important role in the mutual adaptation of the information base and its representations; one can use his knowledge about similar processes of other nature, consider alternative descriptions (various “perceptrons”). The thesis of removing the dependency of modeling results on a specific parameterization, which dates back to the works of A.N. Kolmogorov [3], is implemented here.

However, purely imitational techniques are hard pressed to get a satisfactory description of the mechanisms of the phenomenon under study, distinguish its most important mechanisms even under perfect conditions for interdisciplinary interactions. A combination of imitational and analytic approaches, considering sets of interrelated models, including simplified ones that admit an analytic (parametric) study, presents an attractive option. The search for ways to implement such combinations has led to the creation of complex studies (COST). In justifying simplified models, we use the original detailed imitational model. This model serves as a kind of filter that the entire spectrum of available biological information is passed through. The iterative process of model modification leads to an enumeration of possible versions. The process of modifying and justifying simplified models is performed under expert control over the assumptions being used. Thus, unfoundedness claims regarding the analytic model can only be made concerning the trust put into experts and original biological data and the possibility to use mathematical means of representing them, whose scope has been greatly widened by computer technology.

Simplified models that admit parametric studies have completely changes the possibilities and potential of the modeling. This is both a tool for tuning the original imitational model in corresponding dynamic modes and a way to generate hypotheses regarding the leading mechanisms of the phenomenon under consideration.

Our complex approach shows how we can use the computer not only to produce corollaries of known facts or input a huge number of parameters but also to simplify the model and generate hypotheses regarding the mechanisms of the phenomenon under study. Using this approach to model tundra populations and communities has let us implement the idea of efficiency in imitational technologies in order to justify simplified equations that admit parametric studies. We have created a special class of models that take into account both seasonality [17–19] and the type of difference equations for which, under a certain scenario of sequential parameter changes, there arise stability zones with stable cycles, their periods change as natural numbers, and stability zones are divided from each other by transition zones with more complex modes [16]. Our previous modeling experience has let us move on to another level of description, namely using individually-oriented models [17, 20, 21]. Development of adequate mathematical models for various biological processes is necessary to form the framework of theoretical biology. Besides, under increasing global anthropogenic influences the model approach is virtually the only way to preserve an integral concept of biospheric objects being destroyed.

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APPENDIX

Description of the imitational model “vegetation–lemmings–arctic foxes.”

Biomass dynamics in a tundra community is given by a non-autonomous system:

$$\frac{dV}{dt} = f_V(V, L, \gamma), \quad \frac{dL}{dt} = f_L(V, L, F, \gamma), \quad \frac{dF}{dt} = f_F(L, F, \gamma),$$

where F, L, V are biomass (population) dynamics for arctic foxes, lemmings, and vegetation (their fodder) respectively; γ , the vector of system parameters. For each variable X , $f_X = R_X - M_X - D_X$, R_X denotes the growth rate; M_X , the natural death rate; D_X , alienation. Seasonal influences on the dynamics are modeled with auxiliary functions s_1 and s_2 . In winter, $s_1 = s_2 = 0$. In spring, $s_1 = 1, s_2 = 0$. In summer, $s_1 = s_2 = 1$.

During winter and spring, a part of the vegetation $V(1 - \omega)$ is unavailable for the lemmings, where ω is the fraction of territory on which vegetation is available throughout the year. As summer comes, both parts of the vegetation are united. Besides, lemmings can eat out only a fraction \tilde{d} of the total vegetation biomass (mainly above-ground). Eating becomes energetically detrimental and stops if the biomass of available vegetation drops under a certain number α .

Vegetation dynamics V is determined by the Verhulst formula in the summer, undergoes exponential dying out in winter, and matches dying and growth in spring:

$$R_V = a_4(1 - V/V_{\max})s_1V, \\ M_V = a_3V(1 - s_2).$$

Here a_4, a_3 are growth and dying coefficients for the vegetation biomass respectively, and V_{\max} is the capacity of the ecological niche.

Alienation of the vegetation by lemmings, taking into account seasonality, is given by the formula $D_V = \{a_1(1 - s_1) + a_2s_1\}L$, where a_1, a_2 are vegetation alienation coefficients: the first corresponds to winter and spring, the second, to summer. Lemming biomass growth R_L is proportional to the product of three factors: the amount of alienated vegetation D_V and the functions

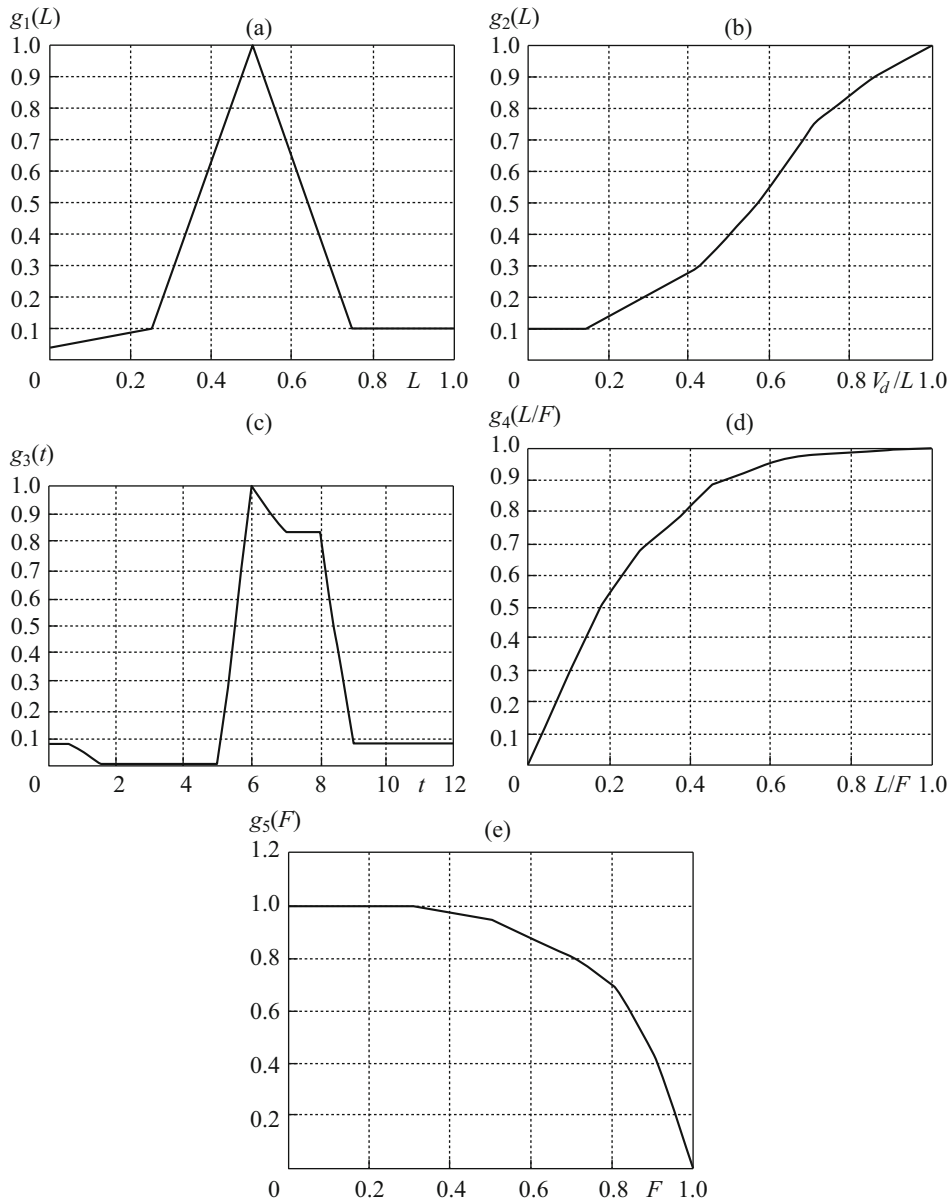


Fig. 3. Auxiliary functions the used in model: (a) functions of optimal density of lemmings (Allee functions); (b) function that formalize the decrease in the utility of fodders when they are in shortage; (c) function that define natural lemmings death rate depending on the season; (d) saturation function of lemming grazing by the arctic foxes; (e) function of the arctic foxes selflimitation.

$g_1(L)$ and $g_2(V_d/L)$, where V_d is the vegetation available for eating ($V_d = 0$ for $V \leq \alpha$, $V_d = \tilde{d}V$ for $V > \alpha$):

$$R_L = D_V g_1(L) g_2(V_d/L) [b_9 s_2 + b_{10} s_1].$$

The function $g_1(L)$ has been introduced according to the Allee principle that states that lemmings have an optimal density, while the function $g_2(V_d/L)$ is a trophic function and reflects the decrease in the utility of fodders when they are in shortage (see Figs. 3a and 3b). Coefficients b_9 and b_{10} characterize seasonal changes.

Natural lemming death rate M_L depends on the season and fodder availability and is given by:

- (1) $M_L = b_5 g_3(t) L$ —when fodder is available in sufficient quantities;

- (2) $M_L = b_4 [1 - V_d/(Lq)] g_3(t) L$ —when the fodder is in shortage ($V_d/L < q$);
- (3) $M_L = b_2 g_3(t) L$ —when there is no fodder ($V_d = 0$) in case everything has been eaten in spring;
- (4) $M_L = b_\beta L$ —when there is no fodder ($V_d = 0$) in case everything has been already eaten in winter, and by the end of winter lemmings remain only in the optimal biotope and their population in it equals β , and then the population is computed as in the third item.

Here the function $g_3(t)$ describes seasonal changes in the death rate (see Fig. 3c); q , the critical unit weight of vegetation below which fodder is in shortage; b_5, b_4, b_2, b_β , death rate coefficients: b_5 if there is sufficient fodder, b_4 in case of fodder shortage, b_2 if there is no fodder in spring, and b_β if there is no fodder in winter.

Alienation of lemmings by arctic foxes, D_L , is proportional to the product of biomasses of both species when lemming density is relatively low (the ratio L/F is small) and proportional to the arctic fox biomass when the density is high (the ratio L/F is large):

$$D_L = F g_4(L/F) (b_6 + b_7 s_1).$$

Here coefficients b_6, b_7 characterize seasonal changes in the intensity of harvesting lemmings, and the function $g_4(L/F)$ describes the trophic function of arctic foxes (see Fig. 3d).

Increase in the arctic fox biomass R_F due to the lemmings is proportional to the product of the biomass of hunted lemmings and the function $g_5(F)$ (it reflect the limiting influence of high density). Apart from lemmings, arctic foxes also eat other, nonspecific fodder whose consumption is assumed to be proportional to the foxes' biomass:

$$R_F = c_1 g_5(F) D_L + (c_2 + c_3 s_1) F.$$

Here c_1 is the coefficient of lemming biomass transition into arctic fox biomass, while coefficients c_2, c_3 describe the influence of nonspecific diet on seasonal changes.

Natural death rate and hunting-related deaths are assumed to be proportional to the total arctic fox biomass: $M_F = c_4 F$, $D_F = c_5 F$, where c_4, c_5 are natural death rate and hunting intensity coefficients respectively.

The numerical study was conducted for the following values of coefficients: the vector $a = (0.05; 0.12; 0.05; 1.35)$, $b = (500.00; 9.60; 0.00; 0.80; 0.05; 0.10; 0.20; 0.10; 3.40; 1.00)$, $c = (1.000; 0.025; 0.095; 0.055; 0.005)$, $\omega = 0.15$, $\tilde{d} = 0.6$, $\alpha = 2.0$, $V_{\max} = 30.0$, $q = 0.3$, $\beta = 2.5$. Initial conditions under which numerical experiments were conducted: $V_0 = 10$, $L_0 = \beta$, $F_0 = 5$.

Inverse imitational problem (constructing the simplified model).

Based on joint analysis of ecologo–biological information and results of computational experiments, we have been able to formulate and solve the so-called “*inverse imitational problem*” [6], namely choose such axioms in the original imitational model that would let us get, based on this original model, the difference equation shown above.

To solve this problem from the results of computational experiments (and in accordance with ecologo–biological data), we have made the following simplifying assumptions:

(1) we have removed the arctic fox subsystem from consideration since their influence on the lemming population dynamics is small;

(2) we have assumed that at the end of the summer period vegetation biomass reaches its maximum $V = V_{\max}$, and in all periods except winter and spring after the population peak the food supply (vegetation) does not limit the lemmings' population dynamics;

(3) the function $g_1(L)$ was replaced with a constant \hat{g}_1 during the entire year; the trophic function $g_2(V_d/L)$ equals the constant \hat{g}_2^1 under a shortage of fodder and \hat{g}_2^2 when fodder is plentiful; the dependence of the lemming death rate on fodder availability was described in two ways: either

fodder is sufficient (minimal death rate) or fodder is not available at all (maximal death rate). The function $g_3(t)$ that reflects the dependence of the lemmings' death rate on the season was chosen to be constant in each season: \hat{g}_3^i , $i = 1$ for winter, $i = 2$ for spring, and $i = 3$ for summer.

According to these assumptions, changes in the lemming population biomass in a "good year," when fodder is plentiful throughout the year, is governed in each season by an autonomous first order differential equation. As a result, for this case we get a difference equation that *relates lemming population in two consecutive years*:

$$\tilde{L}_{n+1} = P\tilde{L}_n.$$

Here $\tilde{L} = L/L_{\max}$, $P = \eta\nu\mu_1$ is the biomass increase rate in a good year; $\eta = \exp(pst_S)$, $\mu_1 = \exp(p_{P1}t_P)$, $\nu = \exp(p_Wt_W)$ is the ratio of lemming biomass at the end and beginning of a season in summer, spring, and winter respectively, assuming that fodder is available throughout the entire season; t_S, t_W, t_P are the durations of summer, winter, and spring; $p_S = a_2(b_9 + b_{10})\hat{g}_1\hat{g}_2^2 - b_5\hat{g}_3^3$, $p_{P1} = a_2b_{10}\hat{g}_1\hat{g}_2^2 - b_5\hat{g}_3^2$, $p_W = -b_5\hat{g}_3^2$, and parameters a_i and b_i have been defined above.

When lemming population is high, vegetation can serve as a limiting influence. In winter, vegetation biomass is governed by the formula

$$\frac{dV}{dt} = -M_V - D_V = \begin{cases} -a_3V - a_2L, & \text{if } V > \alpha \\ -a_3V, & \text{if } V \leq \alpha, \end{cases}$$

with initial conditions $V = V_{\max}$, and changes in the lemming population biomass are given either by formula

$$\frac{dL}{dt} = p_W L, \quad \text{if } V > \alpha,$$

where $p_W = -b_5\hat{g}_3^1$, or, if $V = \alpha$, we assume that lemmings remain only in the optimal biotope, i.e., at the end of winter $L = \beta$.

In spring, in turn, according to the assumptions of the original base model vegetation growth and death processes compensate for each other, and vegetation biomass dynamics is defined by lemming influence:

$$\frac{dV}{dt} = -D_V = \begin{cases} -a_1L, & \text{if } V < \alpha \\ 0, & \text{if } V \leq \alpha, \end{cases}$$

while lemming population biomass dynamics is given by

$$\frac{dL}{dt} = R_L - M_L = p_{Pi}L.$$

Here $p_{Pi} = \begin{cases} a_2(b_{10}\hat{g}_1\hat{g}_2^2) - b_5\hat{g}_3^2, & \text{if } V < \alpha \\ -b_2\hat{g}_3^2, & \text{if } V \leq \alpha. \end{cases}$

Let us use these formulas to get the necessary difference equation. Under our assumptions, it consists of three fragments. First fragment: fodder is plentiful throughout the year, and lemming biomass (population) grows linearly; third: fodder is not available already in winter, and only lemmings in the optimal biotope survive, so the biomass (population) is constant in this range (the horizontal segment, a "step"); second fragment: the transition zone when fodder runs out in sprint. While the first and third fragments have a simple representation, computations of the difference equation form in the transition zone yield cumbersome expressions. However, this is not really justified. Computational experiments show that the transition zone is rather narrow, and assuming that the influence of variations in this zone's description have a small influence on the population dynamics, we can describe the transition zone by a straight line segment connecting the

first and third fragments. To do so, we find the condition of transitioning into the third fragment, namely the value of B , lemming population at the end of summer when available fodder is eaten out by the end of winter, i.e., by end of winter the vegetation biomass equals α . Due to linearity of the corresponding equation, vegetation biomass changes additively based on its own intrapopulational processes and based on lemmings feasting on it.

The corresponding equation for finding B has the following form:

$$B = \frac{V_S z - \alpha}{a_1 p_W t_W (1 - \nu) / 2}.$$

Here $z = \exp(-a_3 t_W)$ is the ratio of vegetation biomasses at the end and beginning of winter given that there is no influence by the lemmings, and $B(1 - \nu) / 2$ is the average lemming biomass during winter.

The difference equation whose graphic representation is given on Fig. 2 relates lemming population in two consecutive years and has the following form for the normalized variable $\tilde{L} = L/L_{\max}$:

$$\tilde{L}_{n+1} = \begin{cases} P\tilde{L}_n, & \tilde{L}_n \leq 1/P \\ 1 - r(\tilde{L}_n - 1/P), & 1/P < \tilde{L}_n \leq B \\ d, & \tilde{L}_n > B. \end{cases}$$

Here $d = \frac{\beta\mu_2}{P}$, $r = \frac{P(1-d)}{BP-1}$, $\mu_2 = \exp(p_{P2}t_P)$ is the ratio of lemming biomass at the end and beginning of spring if fodder is unavailable during the entire season; β is the lemming's biomass by end of winter if fodder shortage occurred already in winter (capacity of the optimal biotope).

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