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COMPUTER MODELLING OF DENSITY DYNAMICS OF SINGLE-SPECIES LABORATORY INSECTS' POPULATION

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Abstract. The large number of recently created mathematical models of single-species insects' population density dynamics has confirmed the continuing interest of scientists to this problem. Beginning with Thompson's work [34] there have been suggested some mathematical models both for practical purposes (simulation models), and for revealing some general ecological patterns (qualitative models) [31].

The different approaches that could be applied to mathematical modelling of density dynamics of single-species laboratory insects' population by means of nonlinear difference-differential equations with delay are discussed. The main attention is paid to the mathematical model proposed by Kolesov [15], which takes into account the age structure within insects' population.

A computer implementation of all proposed mathematical models has been fulfilled by using Model Maker simulation system. Various scenarios for simulation of environmental factors impact on the population dynamics are realized. Simulation results are compared with results from well-known laboratory experiments on the single-species population.

Key words: mathematical modelling, insects' population, differential equations with delay

1. Introduction

Many species of insects are pests for agriculture and foresting. Therefore the questions of density dynamics of insects have been widely discussed in ecological literature for a long time. Main causes of mass reproduction of insects were explained by some universal theories with an one decisive factor only. However, accumulation of knowledge concerning density dynamics of insects has proved that such one-sided approach is insufficient to explain this complicated phenomenon. At present there aren't contradictory opinions about the important role of both abiotic and biotic factors affecting the density of insects. The existing differences of opinions are mainly determined by different approaches to mechanism of density control. The most acceptable seems to be an idea of automatic density control of insects, it is supported by numerous theoretical and experimental works together with mathematical methods [38].

The large number of recently created mathematical models has confirmed the continuing interest of scientists to this problem. Probably, the problem of insects' density dynamics is the most difficult in mathematical ecology. Beginning with Thompson's works [34] there have been suggested some mathematical models both for practical purposes (simulation models), and for revealing some general ecological patterns (qualitative models) [31]. The "biological model" (i.e. laboratory populations) is extremely effective for development of such models. They are very important for outlining phenomena that could explain mathematical models. A good review of the well-known laboratory experiments and data obtained in field experiments is given in the Victorov's [38, 39], Isajev's and Girs' [10], Varley's, Gradwell's and Hassle's monographs [36].

The mathematical models by means of which mechanisms of density oscillations of insects are investigated can be divided into three groups [11]. Firstly, they are discrete time models where difference equations are used to describe density dynamics of insects with non-overlapping generations. Secondly, they are continuous time models where various classes of non-linear differential equations are used and which can be used to describe density dynamics of insects' populations for both overlapping, and non-overlapping generations [14]. Thirdly, they are stochastic (non-deterministic) models, which in opposite to deterministic models take into account sporadic changes of environment.

The density dynamics for groups of insects with non-overlapping generations has been described by a logistic differential equation [26]

$$\frac{dN(t)}{dt} = r\left(1 - \frac{N(t)}{K}\right)N(t)\,, \tag{1.1}$$

where $N(t)$ is the number of individuals, r linear growth rate, K the maximum sustainable population.

The main biological importance of this population dynamics model is due to the fact of existence of feedback between the size of population and its growing rate. The logistic law has widely been used by a lot of researches for explaining the results of experiments. We can mention here well-known Pearl's works [26] on laboratory fruit fly (*Drosophila melanogaster*) population, Gause's works [6] on confused flour beetle (*Tribolium confusum Duv.*), Bodenheimer's works [2] on home bee population and others. Crombie [4] achieved a very satisfying correlation between the logistic curve and the number of *Rizopertha dominica* obtained in a laboratory experiment. However, many other experimental data have been described unsatisfactorily by the logistic law. For example, Sang [30] while analysing his own results and those of Bodenheimer's [2] experiments on fruit fly (*Drosophila melanogaster*) came to conclusion that the logistic law can be used to describe only the strictly restricted initial stage of population growth of adult specimens. Attempts to explain the growth curves of adult specimens on the base of equation (1.1) seem unsound mainly due to the fact that the age structure of population is completely ignored in this equation. Sang shows that density dynamics of adult specimens depends on many factors and there are only rare cases where it can be explained by the logistic law. The authors of work [3] on the base of their own analysis of density dynamics of Drosophila laboratory population draw attention to the fact that the behaviour of ups-and-downs type is more typical.

In natural conditions numerous species of insects have only one generation a year. Different development stages of such insects don't overlap or overlap only a little in the course of time. In this case the density dynamics can be modelled by difference equations. It is well–known that the solutions of such equations can possess very complex dynamics [19]. This approach to the mathematical modelling of insects' density dynamics hasn't shown any significant progress yet. As an example let's take Fujita-Utida's model [5]:

$$P_n = P_{n-1}\Big(\frac{1}{f + gP_{n-1}} - \sigma\Big)\,, \tag{1.2}$$

where P_n is a population density in n-th generation, $f = e^{-rT}$, $g = \dfrac{(1-f)h}{r}$, T is duration of one generation, $h = \dfrac{r}{K}$, r is growth rate, K average number of individuals, σ average mortality rate of adult specimens in one generation $(0 \le \sigma \le 1)$.

Utida [35] has used this model to explain damped oscillations of laboratory *Calosobruchus maculatus* population. Rabinovich [28] was trying to explain results of laboratory experiments on parasitic wasp (*N. Vitripennis*) population with the help of model (1.2). But he failed because the model gave quickly damped oscillations.

Further, the complex impact of various interacting factors on population dynamics leads to more and more complicated mathematical models. A lot of environmental factors simultaneously and differently affect the population density. On the other hand, importance of particular factors is specified not so much by the intensity as by variability.

The intention for creating more realistic models leads to necessity of including into them the age specific mortality rate [36]. This fact demands making life tables for several years covering different environmental conditions and different population density. Key factors playing the decisive role in density dynamics are determined by means of this life tables. To describe the impact of these factors the corresponding mathematical models are developed [37]. One of the methods frequently used to analyze density dynamics and to develop mathematical models is multiple regression [21, 40]. This method is mainly used for construction of prognostic equations. Whether the equation is usable or not, depends on precision of calculations. However, this method is not unique by means of which we can clarify in what way and what biological mechanisms influence the population density dynamics. The problems in using multiple regression for population density prediction also occur when certain interactions between independent variables exist.

2. Single-Species Laboratory Insects' Population Model with Delay

2.1. Mathematical analysis of model

The first who drew attention to importance of delay for density dynamics was Hutchinson [9]. He suggested differential-difference equation:

$$\frac{dN(t)}{dt} = r\Big(1 - \frac{N(t-h)}{K}\Big)N(t), \tag{2.1}$$

where r is the coefficient of linear growth, h the average age of adult individuals in population, K the maximum sustainable population.

The main features of equation (2.1) are [13]:

1. All solutions with positive initial conditions are positive and bounded;
2. When $0 < rh \le \frac{1}{e}$, the solution $N(t)$ monotonically converges to K (Fig. 1, the dashed line);
3. When $\frac{1}{e} < rh \le \frac{\pi}{2}$, the solution $N(t)$ converges to K with oscillations near equilibrium (Fig. 1, the solid line);
4. When $rh > \frac{\pi}{2}$, there is only one stable periodic solution (Fig. 1, the dotted line).

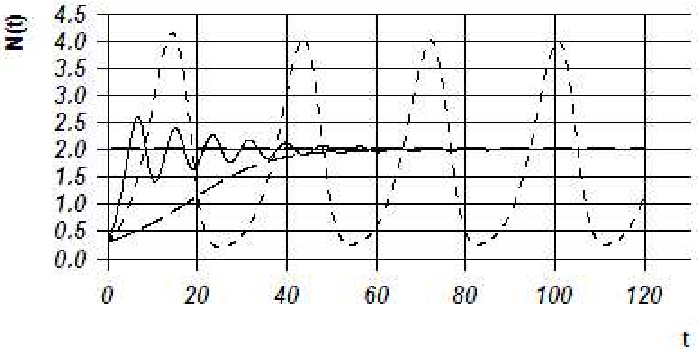


Figure 1. Solutions of equation (2.1): when $h = 1$, $r = 0.1$, $K = 2$ solution $N(t)$ monotonically converges to K (dashed line); when $h = 1$, $r = 0.7$, $K = 2$ solution $N(t)$ converges to K with oscillations near equilibrium (solid line); when $h = 5.3$, $r = 0.3$, $K = 2$ solution $N(t)$ is periodic and stable (dotted line).

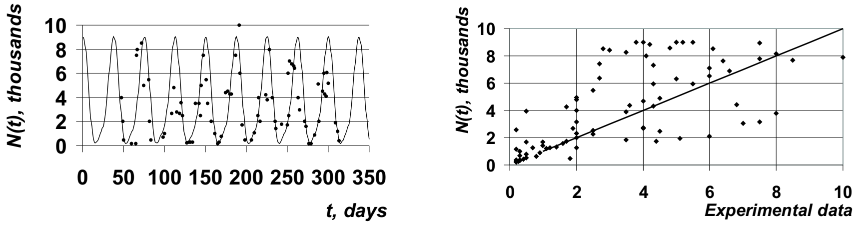
The approximate solution was constructed after analysis of equation (2.1) by means of bifurcation theory [13]:

$$N(t) \approx K\big[1 + 2.32\sqrt{rh - 1.57}\cos\big(\frac{\pi}{2}\tau\big) + 0.54(rh - 1.57) \times \big(\sin(\pi\tau) + 2\cos(\pi\tau)\big)\big], \tag{2.2}$$

where $h\tau[1 + 0.17(rh - 1.57)] = t$.

2.2. Modelling results

There were efforts to explain the cases of cyclic changes in insects' population density by means of equation (2.1) [13, 18, 28]. May in his monograph [18] compared the results of numerical analysis of equation (2.1) with experimental data from the classical work by Nicholson [24] on oscillations of density laboratory population of Australian sheep-bowfly (*Lucilia cuprina*) and got satisfying results. The approximate solution (2.2) also fits quite well to the Nicholson's experimental data. However, it should be noted that correlation between theoretical and experimental oscillations could be better (Fig. 2).



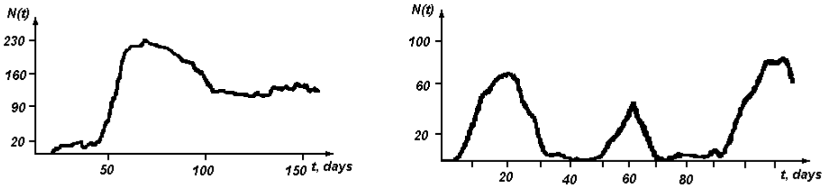
a) b)

Figure 2. a) Comparison of Nicholson's [24] experimental data on laboratory population of Australian sheep-bowfly (*Lucilia cuprina*) with approximate solution $N(t)$ (2.2), b) correlation coefficient $r = 0.67$.

D. Pratt's laboratorial researches [27] of Daphnia population in 1943 can be considered as a classical ecological experiment. Daphnia ontogenesis resembles the development stages of beetle population. Daphnia density dynamics for different temperatures is shown in Fig. 3.

Let us consider four methods for definition of parameters r and h of Daphnia population. Parameter r is the Maltusian coefficient of exponential growth, which can be observed only at the beginning of population growth under "competition vacuum" conditions. Let $[t_1, t_1 + \Delta t]$ be such time interval within which $N(t)$ and $N(t - h)$ values are small. Then $N'(t) \approx rN(t)$ and

$$r \approx \frac{lnN(t_1 + \Delta t)}{\Delta t}. \tag{2.3}$$



a) b)

Figure 3. Daphnia density dynamics: a) T=18^{0}C, b) T=25^{0}C.

Delay h is period of time which equals Daphnia development cycle period. Daphnia development cycle consists of two parts (see Fig. 4):

1) Period of 3-5 days, during which a young Daphnia can be hatched out;

2) Period of at least 2-3 days, which are needed for a young Daphnia to accumulate fat substances to be ready for laying eggs.

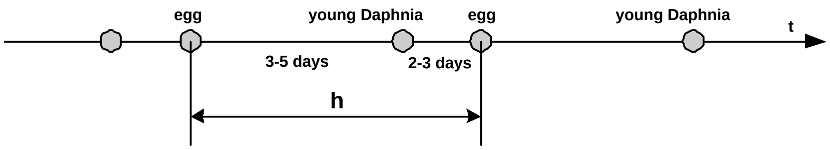
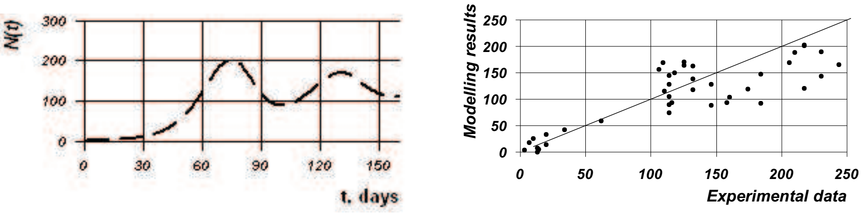


Figure 4. Life cycle of Daphnia.

The value of h depends on temperature. When the temperature changes, this parameter can also vary from 4 till 8 days and even more. From Pratt's data charts on birth and death rate dynamics it follows that at T=18^{0}C delay $h \approx 12$ days and at T=25^{0}C delay $h \approx 9$ days. So, when $rh = 1.2$ $(\frac{1}{e} < 1.2 \leq \frac{\pi}{2})$, $K = 135$ and $r = 0.1$, equation (2.1) describes quite well Daphnia density dynamics at T=18^0. When $rh = 1.62$ $(1.62 > \frac{\pi}{2})$, $K = 30$ and $r = 0.18$, equation (2.1) describes quite well Daphnia density dynamics on T=25^0 (see Fig. 5 and Fig. 6).

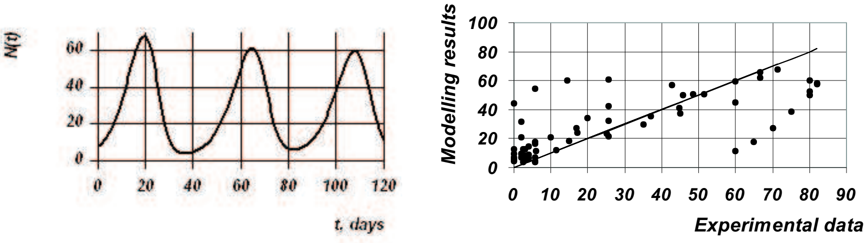
3. Single-Species Laboratory Insects' Population Models with Distributed Delays

Three stages of development - egg, larva and adult species are considered in Rudd's mathematical model on insect population dynamics [29]. Distributed delays are introduced into a system of three differential equations. Such introduction of distributed delays into a model is caused by the inability of discrete delay model adequately describe some extraordinary factors, e.g., it is impossible to simulate a usage of pesticides including some additional functions into



a) b)

Figure 5. Modelling of Daphnia density dynamics when T=18^{0}C: a) simulation results when $r = 0.1$, $h = 12$ and $K = 135$, b) comparison of Pratt's [27] experimental data presented in Fig. 3a with modelling results. Correlation coefficient $r = 0.83$.



a) b)

Figure 6. Modelling of Daphnia density dynamics when T=25^{0}C: a) simulation results when $r = 0.18$, $h = 9$ and $K = 30$. b) Comparison of Pratt's [27] experimental data presented in Fig. 3b with modelling results. Correlation coefficient $r = 0.73$.

a model. The model has been tested by experimental data on insects' population of *Anticarsia gemmatalis Hubner*. The correlation between theoretical and experimental curves appeared to be quite good. However, it should be mentioned, that practical usage of model demands vast amount of information. We should know the birth and death rate functions at each development stage, and also functions of age distribution at the initial time moment $t = 0$.

In work [8] a methodology of construction of single-species laboratory population dynamics models with respect to age structure is described. The given methodology can be used for those insects the life cycle of which can be divided into separated development stages. There has been constructed the system of differential equations with several delays, which can be used as a model of the above insect population. The model has been applied to explain laboratory population dynamics from a classical Nicholson's experiment [24]. The numerical analysis of the model has shown quite a good correlation with Nicholson's experimental data.

The same method was used to construct mathematical models of laboratory population dynamics with consideration of various possible effects due to limited food for larva [25].

4. Self-Excited Single-Species Laboratory Insects' Population Models

4.1. Model construction and mathematical analysis

A basically new approach to the problem of insects' population dynamics modelling has been started in works by Kolesov [14, 15]. He assumed that the main cause for density oscillations is a competition within population. Thus, differential equations describing population dynamics should have auto–oscillating solutions. Hutchinson's equation (2.1) is an example of such model. It is supposed in [15] that insects' density dynamics can be determined by two active phases - larva and imago. Therefore, the following mathematical model is suggested for description of two insects' development stages:

$$\begin{cases} N_1'(t) = r_1\big[1 - a(1 - \dfrac{N_2(t-h_1)}{K_2}) - \dfrac{N_1(t-h_2)}{K_1}\big]N_1(t)\,, \\ N_2'(t) = r_2\big[\dfrac{N_1(t-(1-h_1-h_2))}{K_1} - \dfrac{N_2(t)}{K_2}\big]N_2(t)\,. \end{cases} \tag{4.1}$$

In system (4.1) $N_1(t)$ is the number of imago, $N_2(t)$ the number of larva, $h_1(t)$ time period between larva and imago appearance, $1-h_1$ time period between imago and larva appearance, h_2 average imago's population life period per year, K_1, K_2 average number of imago and larva, $a<1$ characterizes power of relation between imago's and larva's populations, $r_1^0 = r_1(1-a)$ Maltusian's coefficient of linear growth, r_2 larva's population linear growth coefficient.

When $r_2 \longrightarrow \infty$ and the other parameters are constant, solutions of system (4.1) are similar to solutions of equation

$$N'(t) = r\big[1 - a\big(1 - N(t-(1-h))\big) - N(t-h)\big]N, \tag{4.2}$$

where

$$N(t) = \frac{N_1(t)}{K_1}, \quad r = r_1, \quad h = h_2, \quad \frac{N_2(t)}{K_2} = N\big(t-(1-h_1-h_2)\big).$$

Differential-difference equation (4.2) is simpler than the system (4.1) and approximates it satisfactorily.

Numerical analysis of system (4.1) and equation (4.2) has been done in [12]. The biological period is close to one, however, there are modes with a period significantly less than one. The stationary modes of equation (4.2) often have a complicated form. One can observe gradual increase of oscillations with the following depression stage, which is a good example of well-known natural phenomena of density outburst. However, the stationary modes [12] are very sensitive to even minor changes of model parameters and the ranges of parameters values for which the mode period is close to one are very narrow. Thus such comparison of theoretical and experimental data gives rise to difficulties because some parameters of models (4.1) and (4.2) are not known. It should be also noted that the stationary modes of equation (4.2) are more sensitive to changes of parameters than the same modes for system (4.1).

In order to explain the laboratory data of insects' population density, a modification of model from [15] has been proposed in [7]:

$$\begin{cases} N_1'(t) = r_1\Big[1 - a\big(1 - \dfrac{N_2(t-h_1)}{K_2}\big) + c\Big(1 - \dfrac{N_1(t)}{K_1}\Big) - \dfrac{N_1(t-h_2)}{K_1}\Big]N_1(t), \\ N_2'(t) = r_2\Big[\dfrac{N_1\big(t-(\alpha T - h_1 - h_2)\big)}{K_1} + b\Big(1 - \dfrac{N_2(t-h_3)}{K_2}\Big) - \dfrac{N_2(t)}{K_2}\Big]N_2(t), \end{cases} \tag{4.3}$$

where T is one generation duration, i.e. time period from egg till imago, h_3 is larva final development stage duration, $\alpha \geq 1$ reflects the generations overlapping fact.

Model (4.3) has been constructed on the base of special laboratory experiment on *Drosophila melanogaster* population. When

$$b = 0, \quad c = 0, \quad \alpha = 1, \quad T = 1$$

we get the system of equations (4.1).

Item $c(1 - \frac{N_1(t)}{K_1})$ in the first equation of (4.3) shows reduction of fertility of adult species in case their density becomes more than average, as well as increase of their death rate within such periods of time. Parameter $0 \leq c < 1$ characterizes the power of this additional inner feedback at the imago stage of insects' population. The additional term in the second equation of (4.3) reflects the impact of competition within population on density dynamics of larva. Delay h_3 equals the period of time within which the competition between larva is the strongest. Parameter b characterizes the acuteness of this competition. Factor $\alpha \geq 1$ appears due to overlapping of generations in laboratory population (see Fig. 7).

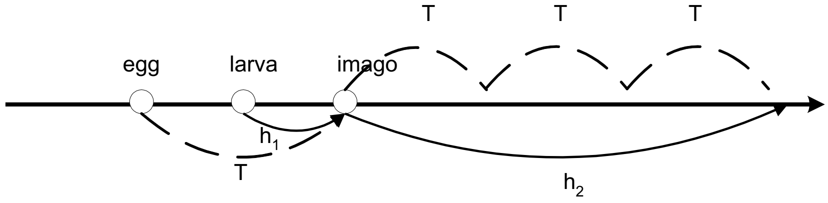


Figure 7. Life cycle of Drosophila.

The linear analysis has shown that when

$$cr_1h_2 > \frac{\pi}{2}, \quad c < 1, \quad br_2h_3 > \frac{\pi}{2}, \quad b > 1$$

and a is small, system (4.3) has two–frequency steady mode near steady state $N_1(t) \equiv K_1$, $N_2(t) \equiv K_2$.

Let consider the following model:

$$N'(t) = \frac{\alpha N(t-h)}{1 + \left(\frac{N(t-h)}{K}\right)^n} - \beta N(t), \tag{4.4}$$

where $\alpha > 0$ is coefficient of production, $\beta > 0$ coefficient of reduction, $n > 0$ the order of environment non-linearity, $K > 0$ average number of individuals.

The differential–difference equation (4.4) has a more complicated dynamics of solutions than equation (2.1) and a smaller sensitivity for changing the model's parameters compared with equation (4.2). Production rate in (4.4) is described by the Michaelis–Menten law for fermentative kinetics [20]. The delay has been introduced with respect to the Mackey–Glass work [17]. Electronic analog of (4.4) has been presented in [23].

The main properties of equation (4.4) are the following [32, 33]:

1. The convergence of $N(t)$ to the steady state $N(t) \equiv K \sqrt[n]{\frac{\alpha}{\beta} - 1}$ follows in two ways:
   a) monotonically, if
   $$0 < \frac{(\alpha - \beta)\beta n}{\alpha} - \beta \leq \frac{1}{he^{1+\beta h}};$$
   b) oscillating around the nontrivial steady state, if
   $$\frac{1}{he^{1+\beta h}} < \frac{(\alpha - \beta)\beta n}{\alpha} - \beta \leq \sqrt{(\frac{\omega_*}{h})^2 + \beta^2}\,,$$
   where ω_* is the solution of the equation
   $$-\frac{1}{\beta h}\omega = \tan\omega, \quad \omega_* \in (0, \pi)\,.$$
2. Differential-difference equation (4.4) has non-constant periodic solutions.
3. Solutions of equation (4.4) can behave chaotically.

The same properties are also valid for the equation:

$$N'(t) = \frac{\alpha N(t-h)}{1 + (\frac{\alpha}{\beta} - 1)(\frac{N(t-h)}{K})^n} - \beta N(t)\,, \tag{4.5}$$

which has a steady state solution $N(t) \equiv K$ and for the equation:

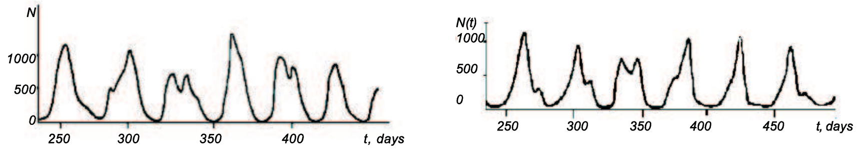
$$\begin{cases} N'(t) = \alpha \dfrac{N(t-\tau(N))}{1 + (\dfrac{N(t-\tau(N))}{K})^n} - \beta N(t), \\ \tau(N) = h \exp\left(\gamma(1 - \dfrac{N}{K\sqrt[n]{\alpha/\beta - 1}})\right). \end{cases} \tag{4.6}$$

where the delay $\tau = \tau(N)$ depends on $N(t)$.

4.2. Modelling results

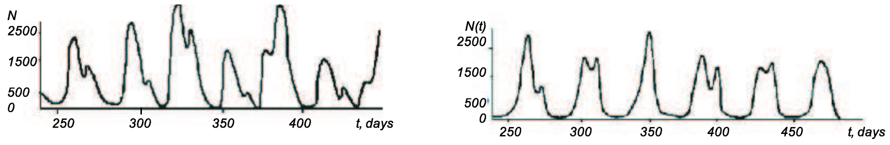
All numerical results were obtained by applying fourth order Runge–Kutta method built in the Model Maker simulation package [22].

Modelling results of system (4.3) were compared with the laboratory experiments data on *Drosophila melanogaster* population, Birch's laboratory experiments on *Sitophilus oryzae L.* population [1], Lloyd's laboratory experiments on *Tribolium castaneum Hrbst.* population [16] and others. In Fig. 8, Fig. 9 results of numerical solutions of model (4.3) are compared with insects' density dynamics data from Nickolson's laboratory experiments on Australian sheep-bowfly (*Lucilia cuprina*) population [24].



a) b)

Figure 8. Adult flys' density dynamics when larva have got 25 g of meat per day. a) Nickolson's laboratory experiments data. b) Modelling results when $T = 15; h_1 = 10; h_2 = 13; h_3 = 6; r_1 = 13.8; r_2 = 24; a = 0.495; b = 1.8; c = 0.715; \alpha = 3; K_1 = 350; K_2 = 700$.

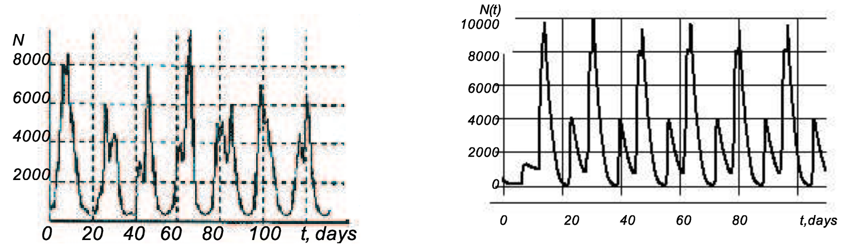


a) b)

Figure 9. Adult flys' density dynamics when larva have got 50 g of meat per day. a) Nickolson's laboratory experiments data. b) Modelling results when $T = 15; h_1 = 10; h_2 = 13; h_3 = 6; r_1 = 13.8; r_2 = 24; a = 0.495; b = 1.8; c = 0.715; \alpha = 3; K_1 = 900; K_2 = 1700$.

Model (4.6) has been applied to compare with the Nicholson's experimental data [24]. The data and computer simulation results are shown in Fig. 10.

A qualitative comparison of numerical solutions received for models (4.3) and (4.6) with experimental population density can be regarded as good. However, a calculated correlation of numerical solutions with experimental data is not high enough in these cases ($r \leq 0.6$). It should be mentioned that systems (4.3) and (4.6) contain a number of different delays and their solutions demonstrate the periodic behaviour, which is very sensible to the initial conditions. Therefore, small changes in parameters values could cause



a) b)

Figure 10. Modelling of Australian sheep-bowfly (*Lucilia cuprina*) population density. a) Nicholson's experimental data [24]. b) $N(t)$ modelling results when $\alpha = 10; \beta = 1; \gamma = 0.5; h = 4; n = 7.7; K = 2800$.

a switch from periodic solution to chaotic behaviour. In such a situation a correlation coefficient and some other quantitative measures of the fitting are not very useful for comparison of simulation results with experimental data.

References

[1] L.C. Birth. Experimental background to the study of the distribution and abundance of insects. I. The influence of temperature, moisture and food on the innate capacity for increase of three grain beetles. *Ecology*, **34**, 608 – 711, 1953.

[2] F.S. Bodenheimer. *Problems of animal ecology.* Oxford University Press, Oxford, 1938.

[3] H.C. Chiang and A.C. Hodson. An analytical study of population growth in Drosophila melanogaster. *Ecol. Monog.*, **20**, 173 – 206, 1950.

[4] A. C. Crombie. On competition between different species of graminivorous insects. *Proc. R. Soc. (B)*, **132**, 362 – 395, 1945.

[5] H. Fujita and S. Utida. The effect of population density on the growth of an animal population. *Ecology*, **34**, 488 – 498, 1953.

[6] G. P. Gause. *The struggle for existence.* Williams and Norgate, Baltimore, 1934.

[7] R. A. Grikėnis, V. P. Jonaitis, S. A. Pakalniškis and D. Švitra. The single-species insects' population density dynamics. *The works of Lith. Ac. Sci*, **4**, 28 – 38, 1986.

[8] W.S.C. Gurney, R.M. Nisbet and Lawton J.H. The systematic formulation of tractable single-species population models incorporating age structure. *J. of Animal Ecology*, **52**, 479 – 495, 1983.

[9] G. E. Hutchinson. Circular caused systems in ecology. *Ann. N. Y. Acad. Sci*, **50**, 221 – 246, 1948.

[10] A.S. Isajev and G.I. Girs. *Interaction between tree and insects-xilophagues.* Nauka, Novosibirsk, 1975.

[11] V. P. Jonaitis and D. I. Švitra. About insects density dynamics. *Acta entomologica Lithuanics*, **7**, 5 – 14, 1984.

[12] Y. S. Kolesov and E. P. Kubyshkin. Some properties of solution of differential-difference equation modelling insects' population density dynamics. *Oscillation theory and stability researches*, 64 – 86, 1983.

[13] Y. S. Kolesov and D.I Švitra. *Autooscillations in systems with delay.* Mokslas, Vilnius, 1979.

[14] Y.S. Kolesov. About some problems from oscillation theory. *Oscillation theory and stability researches*, 20 – 41, 1982.

[15] Y.S. Kolesov. Modelling of insects' population. *Biophysics*, **3**, 513 – 514, 1983.

[16] M. Lloyd. Self regulation of adult numbers by cannibalism in two laboratory strains of flour beetles (Tribolium casraneum). *Ecology*, **49**, 245 – 259, 1968.

[17] M.C. Mackey and L. Glass. Oscillation and chaos in physiological control systems. *Science*, **197**, 287 – 289, 1977.

[18] R.M. May. Stability and complexity in model ecosystems. *Ecol. Monog*, **20**, 173 – 206, 1950.

[19] R.M. May. Biological populations obeying difference equations: stable points, stable cycles, and chaos. *J. Theor. Biol.*, **51**, 511 – 524, 1975.

[20] N. Michaelis and M. Menten. Die kinetik der invertinwirkung. *Biochem. Z.*, **49**, 333 – 369, 1913.

[21] R.F. Morris. The dynamics of epidemic spruce budworm populations. *Mem. Ent. Soc. Can.*, **31**, 1 – 332, 1963.

[22] *Model Maker. Version 3.0.* Cherwell Scientific Publishing Limited, Oxford, 1997.

[23] A. Namajūnas, K. Pyragas and A. Tamaševičius. An electronic analog of the Mackey-Glass system. *Phis. Lett*, **A201**, 42 – 46, 1995.

[24] A.J. Nicholson. An outline of the dynamics of animal populations. *Aust. J. Zool.*, **2**, 9 – 25, 1954.

[25] R.M. Nisbet and W.S.C. Gurney. *Stage structure models of uniform larval competition.* Lect. Notes Biomath., 1985.

[26] R. Pearl. *The biology of population growth.* Williams and Norgate, London, 1926.

[27] D.M. Pratt. Analysis of population development in Daphnia at different temperatures. *Biol. Bull*, **85**, 116 – 140, 1943.

[28] J.E. Rabinovich. The applicability of some population growth models in a single-species laboratory population. *Annals of the Entomological Soc. of America*, **62**, 437 – 442, 1969.

[29] W.G. Rudd. Population modeling for pest managament studies. *Mathematical biosciences*, **26**, 283 – 302, 1975.

[30] J.H. Sang. Population growth in Drosophila cultures. *Biological Reviews of the Cambridge Philos. Soc.*, **25**, 188 – 219, 1950.

[31] J.M. Smith. *Models in ecology.* Mir, Moscow, 1973.

[32] D. Švitra and R. Retkutė. The analysis of modificated Mono equation. *The Scientific works of Lithuanian Society of Mathematicians*, **3**, 353 – 358, 1999.

[33] D. Švitra and R. Retkutė. The analysis of chemical kinetics equations with time delay. *Mathematical Modelling and Analysis*, **5**, 175 – 180, 2000.

[34] W.R. Thompson. Theorie mathematique de l'action des parasites entomophages et le facteur du hazard. *Annls. Fac. Sci.*, **2**, 69 – 89, 1924.

[35] S. Utida. Damped oscillation of population density at equilibrium. *Researches Popul. Ecology*, **9**, 1 – 9, 1967.

[36] G. Varley, G. Gradwell and M. Hassle. *Insect population ecology.* Oxford, 1975.

[37] G.C. Varley and G.R. Gradwell. Recent advances in insect population dynamics. *A. Rev. Ent.*, **15**, 1 – 24, 1970.

[38] G.A. Viktorov. *Problems of insect density dynamics: a case of tortoise beetle.* Nauka, Moscow, 1965.

[39] G.A. Viktorov. *Ecology of parasites-entomophages.* Nauka, Moscow, 1976.

[40] K.E.F. Watt. Mathematical models for use in insect pest control. *Canad. Entomol*, **19**, 18 – 23, 1961.

LABORATORINIŲ VABZDŽIŲ POPULIACIJŲ SKAITLINGUMO DINAMIKOS KOMPIUTERINIS MODELIAVIMAS

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Straipsnyje nagrinėjami izoliuotos vabzdžių populiacijos skaitlingumo dinamikos kompiuterinio modeliavimo klausimai. Šalia klasikinių šios srities darbų apžvalgos pateikiami autorių gauti rezultatai. Siūlomi netiesinių diferencialinių-skirtuminių lygčių pagrindu sudaryti matematiniai modeliai buvo realizuoti modeliavimo aplinkoje Model Maker. Kompiuterinio modeliavimo rezultatai palyginti su klasikiniais laboratoriniais bandymais.