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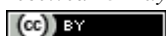
Classic models of population dynamics: assumptions about self-regulative mechanisms and numbers of interactions between individuals

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Abstract

Stochastic model of migrations of individuals within the limits of finite domain on a plane is considered. It is assumed that population size scale is homogeneous, and there doesn't exist an interval of optimal values of population size (Alley effect doesn't realize for population). For every fixed value of population size number of interactions between individuals is calculated (as average in space and time). Correspondence between several classic models and numbers of interactions between individuals is analyzed.

Keywords stochastic models; migrations; mechanistic models; self-regulative mechanisms.

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1 Introduction

Verhulst model (Verhulst, 1838) is one of the basic models in ecological modeling:

$$\frac{dx}{dt} = \alpha x - \beta x^2. \quad (1)$$

In (1) $x(t)$ is population size (or population density) at time t ; parameter α is equal to difference between intensity of birth rate and intensity of death rate; parameter β , $\beta = \text{const} > 0$, is coefficient of influence of self-regulative mechanisms on population dynamics; parameter $K = \alpha / \beta$ (when $\alpha > 0$, and population doesn't eliminate for all initial values of population size) is maximum of population size which can be achieved asymptotically. This is standard explanation of biological sense of model (1) parameters.

In (1) it is assumed that increasing of influence of self-regulative mechanisms on population size changing (and, respectively, increasing of death rate) is proportional to population size squared (or population density squared). This assumption is based on *physical* idea about paired interactions between *physical* objects. In other words, it is assumed that number of interactions between individuals during rather short time period

$\Delta t \rightarrow 0$ is equal to $\beta x^2 \Delta t$. Increasing of number of interactions leads, for example, to increase of intra-population competition for food and space, to increase of speed of a spread of diseases in population and so on. Thus, it leads to increase of influence of self-regulative mechanisms on population dynamics. But we have some differences between physical and biological objects... Moreover, it isn't obvious how we have to determine "number of interactions" for individuals even in most primitive cases (when space is homogenous, Allee effect doesn't realize for considering population etc.; Allee, 1931; Odum, 1983).

Comparison of theoretical results obtained with model (1) with empirical and experimental time series showed that in various cases this model doesn't allow obtaining good fitting for existing datasets (see, for example, Gause, 1934; Maynard, 1968, 1974; Pielou, 1977; Isaev et al., 1984, 2001; Brauer and Castillo-Chavez, 2001; Nedorezov and Utyupin, 2011 and many others). In situations when model (1) allows obtaining good fitting it is possible to point out some other models which can give better results (Nedorezov, 2011, 2012). Attempts in modifying of Verhulst' model (1) led to appearance of some other models. In particular, within the framework of Gompertz' model (Gompertz, 1825) it was assumed that influence of self-regulative mechanisms is proportional to product $x \ln(x)$:

$$\frac{dx}{dt} = \alpha x \ln\left(\frac{K}{x}\right). \quad (2)$$

In model (2) both parameters are positive. If initial value $0 < x_0 < K$ then $x(t) \uparrow K$ at $t \rightarrow \infty$. If $x_0 > K$ then $x(t) \downarrow K$. Note, expression $x \ln(x)$ describes influence of self-regulative mechanisms if and only if $x > 1$ (Nedorezov, 1997; Nedorezov and Utyupin, 2011). Model (2) can be modified with saving all basic properties:

$$\frac{dx}{dt} = \alpha x \left(\ln\left(\frac{K+1}{x+1}\right) \right)^\theta. \quad (3)$$

In model (2) all parameters are positive, $\alpha, K, \theta = const > 0$. Below model (3) will be called as "theta-Gompertz model". Within the framework of model (3) influence of self-regulative mechanisms is described by the expression $\alpha x \ln^\theta(x+1)$, and this expression was used for fitting of datasets.

In Svirezhev' model (Svirezhev, 1987) negative influence of self-regulative mechanisms was described with expression βx^3 , and increase of population size was proportional to αx^2 , $\alpha, \beta = const > 0$:

$$\frac{dx}{dt} = \alpha x^2 - \beta x^3. \quad (4)$$

Within the framework of theta-logistic model (Rosenzweig, 1969; Gilpin, Ayala, 1973) which is modification of Verhulst' model (1), respective expression has the form βx^θ , where θ is positive parameter, $\theta = const > 1$. In literature (see overview Nedorezov and Utyupin, 2011) it is possible to find a lot of various modifications of pointed out models (1)-(4) but in most cases influence of self-regulative mechanisms is described as monotonic increasing function with respect to population size in any power.

Use of physical ideas for modeling of ecological processes can be very useful. In various situations it allows obtaining important results. On the other hand, as it was pointed out above, interaction between *biological individuals* doesn't look like *colliding of absolutely elastic balls*. There exists a lot of various types of interaction between individuals: it can be a competition for food and space; it can be transmission of diseases from one individual to another one etc. Moreover, scale of population size changing may be a non-homogenous set: for biggest part of analyzed species Allee effect is observed (Allee, 1931; Odum, 1983).

Influence of this effect (existence of favorable levels of local population size) leads to changing of distribution of individuals in habitat, and respectively to changing of a number of interactions (like average of interactions in space) between individuals. Thus, these remarks allow concluding that question about types of functions which can be applied for description of influence of self-regulative mechanisms on population dynamics is open.

Problem pointed out above cannot be solved analyzing empirical or experimental datasets: self-regulation contains a lot of various biological mechanisms, real population density is unknown amount and out of control etc. Limits of favorable zone (Allee effect) are unknown too. Thus, this problem can be solved using mathematical model of migrations only. In such a situation all basic population parameters are under the control, and computer experiments can be provided with important artificial assumptions. One of such models is described and analyzed below.

2 Model

2.1 Description

Let N be a total population size, and $N = \text{const}$ during the time of providing of computer experiments. Let Z_{nm}^2 be an integer rectangular lattice on the plane R^2 :

$$Z_{nm}^2 = \{(i, j) : 1 \leq i \leq n, 1 \leq j \leq m\}.$$

We'll assume that local population size is determined in knots (i, j) of the lattice Z_{nm}^2 only. Denote it as $x_{ij}(t)$ for $(i, j) \in Z_{nm}^2$ at time moment t . Thus, for all time moments $t, t = 0, 1, 2, \dots$, the following relation is truthful:

$$\sum_{i=1}^n \sum_{j=1}^m x_{ij}(t) = N.$$

It means that there are no migrations outside the domain Z_{nm}^2 ; birth and death processes are absent too. We'll say that two elements of the lattice $(i_1, j_1), (i_2, j_2) \in Z_{nm}^2$ are neighboring knots if and only if the following relation is truthful:

$$|i_1 - i_2| + |j_1 - j_2| = 1.$$

Within the framework of model it will be assumed that migration processes from the knot (i, j) can be observed to neighboring knots only. Within the framework of considering model we'll assume that every individual with equal probabilities can migrate to nearest knots or stay in initial knot. Thus, $p = 0.2$.

2.2 Initial conditions

As it was pointed out above, for modeling of migration processes it was assumed that total population size N is constant; thus, theoretical population density μ was known and equal to $\mu = N/nm$. Initial population state was modeled with discrete uniform distribution: every individual with equal probabilities could appear in every knot of the lattice Z_{nm}^2 . After determination of initial positions the process of individual's migrations was started. During T time steps (for providing calculations it was assumed that $T = 20000$) model was run free. It is important moment because we have to have on the lattice the situation which is determined by the rules of population migration only, and doesn't depend on the initial state of population.

2.3 Number of interactions between individuals

Let's assume that at any fixed time moment t local population size $x_{ij}(t) = l$. The basic question is: how can we calculate number of interactions between individuals? First of all, it is naturally to assume that there are no

interactions between individuals from different knots. The second, if epizootics play most important role in self-regulation, we have a good background for assumption that every individual contacts with all other individuals in determined knot. Thus, in this case the number of *paired interactions* is equal to $l(l-1)/2$. Below results of computer experiments for this assumption about number of interactions are called “first dataset”. But it isn’t a unique type of grouping of individuals and their paired interactions (Odum, 1983; Maynard, 1968, 1974).

Together with pointed out variant of local interactions of individuals we’ll consider the following situation. It will be assumed that in every knot individuals can stay separately (i.e. without contacts with other individuals in a knot), or can stay in pair, or form a group of three individuals. Let ξ and η be stochastic variables with geometric distribution with parameter q . Number of pairs assumed to be equal to $\xi^* = \min\{\xi, l/2\}$. Number of groups with three individuals was equal to $\eta^* = \{(l - 2\xi^*)/3, \eta\}$. Other individuals $(l - 2\xi^* - 3\eta^*)$ were assumed to stayed separately. In this case the number of *paired interactions* was determined as $\xi^* + 3\eta^*$. Below results of computer experiments for this assumption about number of interactions are called “second dataset”.

3 Results of Calculations

After 20000 free steps of model during 20000 steps number of interactions between individuals was calculated as average in space and time (for both variants). For every fixed time moment number of interactions was calculated for every knot of lattice, and total sum of interactions was divided on product mn . All 20000 values of averages were summarized and divided on 20000 respectively. This procedure was repeated a certain number of times for various values of population size.

Population size N was changed from zero up to 100000 with step 1000. Respectively, population density $\mu \in [0,10]$ and was changed with step 0.1. Results of calculations of numbers of interactions between individuals are presented on Fig. 1.

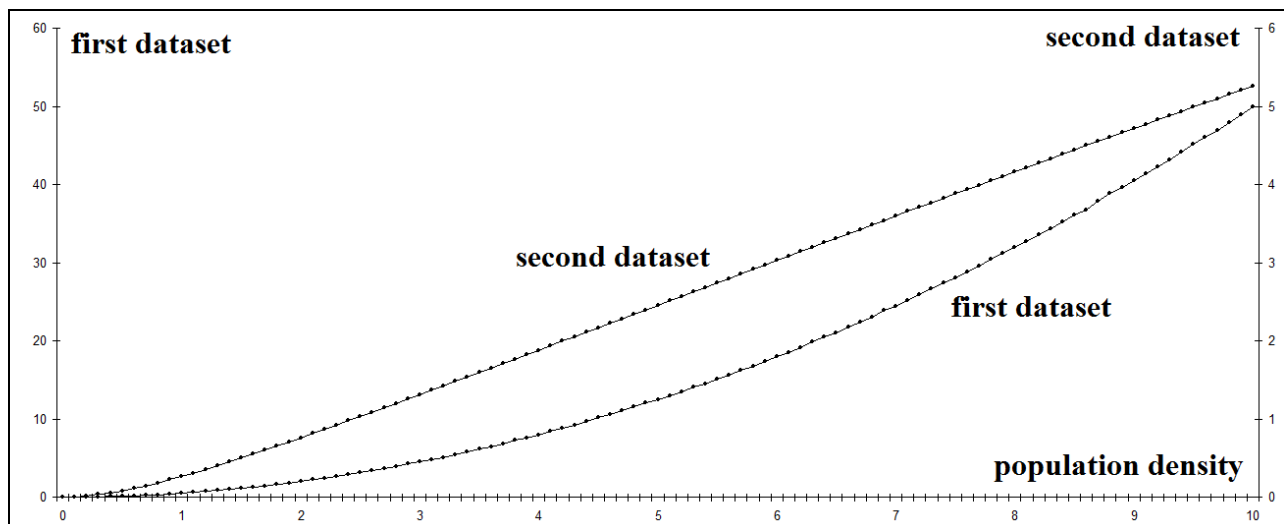


Fig. 1 Results of computer experiments: changing of numbers of interaction between individuals in two different cases with respect to changing of population density.

For fitting of obtained samples (Fig. 1) four different functions pointed out above were used. Deviations between theoretical functions and obtained samples were tested on Normality and symmetry of distributions (Kolmogorov – Smirnov test, Lilliefors test, Shapiro – Wilk test, Mann – Whitney test, and Wald – Wolfowitz

test), and on existence/absence of serial correlation (Draper and Smith, 1986, 1987; Lilliefors, 1967; Shapiro et al., 1968; Bolshev and Smirnov, 1983; Hollander and Wolfe, 1973; Bard, 1974). Note, that all computer experiments were provided independently; thus, if any curve gives good fitting of obtained datasets no serial correlations must be observed.

Table 1 Results of testing on normality for deviations (first dataset).

Models:	Parameters	Q_{\min}^*	KS ¹	L ²	SW ³
Verhulst	$\beta = 0.4993$	0.18	$p < 0.15$	$p < 0.01$	$p < 10^{-5}$
Theta-Gompertz	$\alpha = 0.636$ $\theta = 2.34$	7.06	$p < 0.2$	$p < 0.01$	$p = 0.00006$
Svirezhev	$\beta = 0.058$	1420.4	$p < 0.05$	$p < 0.01$	$p < 10^{-5}$
Theta-logistic	$\beta = 0.5$, $\theta = 2.0$	0.18	$p < 0.15$	$p < 0.01$	$p < 10^{-5}$

¹KS – Kolmogorov – Smirnov test; ²L – Lilliefors test; ³SW – Shapiro – Wilk test; Q_{\min}^* is minimal value of minimized functional form.

For the case when $m = n = 100$, and parameter of geometric distribution q is equal to 0.2, results of testing on Normality of deviations for four classic models (more precisely, deviations between computer results of calculation of number of interactions and functions in classic models which describe the influence of self-regulative mechanisms) are presented in Tables 1 and 2. Parameters of functions were determined with Least Square Method.

Results presented in table 1 show that best approximations were obtained with Verhulst and Theta-logistic models. For both models $R^2 = 0.999992$. For Svirezhev model $R^2 = 0.9379$, and for Theta-Gompertz model $R^2 = 0.9997$. As we can see in all cases correlation coefficient R^2 is very close to one, and it means that we have rather good approximation for first dataset. On the other hand, Lilliefors test and Shapiro – Wilk test showed that in all four considering cases with 1% significance level we have to reject hypotheses about Normality of residuals. Thus, from the standpoint of traditional imagination about good model (Bard, 1974) all functions are not suitable for fitting of first dataset.

Table 2 Results of testing on Normality for deviations (second dataset).

Models:	Parameters	Q_{\min}^*	KS ¹	L ²	SW ³
Verhulst	$\beta = 0.0642$	38.268	$p < 0.05$	$p < 0.01$	$p < 10^{-5}$
Theta-Gompertz	$\alpha = 0.3947$, $\theta = 0.3468$	0.1957	$p < 0.15$	$p < 0.01$	$p < 10^{-5}$
Svirezhev	$\beta = 0.0072$	117.35	$p < 0.05$	$p < 0.01$	$p < 10^{-5}$
Theta-logistic	$\beta = 0.3758$, $\theta = 1.1543$	0.327	$p < 0.15$	$p < 0.01$	$p < 10^{-5}$

¹KS – Kolmogorov – Smirnov test; ²L – Lilliefors test; ³SW – Shapiro – Wilk test; Q_{\min}^* is minimal value of minimized functional form.

The similar situation is observed for results presented in Table 2: Lilliefors test and Shapiro – Wilk test showed that in all four considering cases with 1% significance level we have to reject hypotheses about Normality of residuals. The best result was obtained for Theta-Gompertz model with $R^2 = 0.999258$. For Theta-logistic model $R^2 = 0.99876$. For Svirezhev model this characteristics is rather small: $R^2 = 0.5548$. Like in previous case, from the standpoint of traditional imagination about good model (Bard, 1974) all functions are not suitable for fitting of second dataset.

It is important to note that assumption about Normality of deviations between theoretical curves and experimental datasets (in considering situation we have to talk about results of computer experiments) is rather strong. Softer assumption is following: distribution density must be symmetric with respect to origin. Results of checking of hypotheses about symmetry for both datasets are presented in Tables 3 and 4.

Table 3 Results of testing on symmetry for deviations (first dataset).

Models:	KS ¹	WW ²	MW ³
Verhulst	$p > 0.1$	$p = 0.9968$	$p = 0.3573$
Theta-Gompertz	$p < 0.005$	$p = 0.3792$	$p = 0.016$
Svirezhev	$p > 0.1$	$p = 0.3196$	$p = 0.5335$
Theta-logistic	$p > 0.1$	$p = 0.5352$	$p = 0.5156$

¹KS – Kolmogorov – Smirnov test; ²WW – Wald – Wolfowitz test;

³MW – Mann – Whitney test

In creation of conclusions about properties of datasets we'll follow to the next basic principle: *if one of using tests gives a negative result we have to reject Null hypothesis, and it doesn't depend on results obtained with other tests.* In particular, Kolmogorov – Smirnov test showed that we have to reject hypothesis about symmetry of residuals obtained for Theta-Gompertz model with very small significance level (Table 3). In other cases we cannot reject Null hypothesis about symmetry even with 10% significance level.

Table 4 Results of testing on symmetry for deviations (second dataset).

Models:	KS ¹	WW ²	MW ³
Verhulst	$p > 0.1$	$p = 0.5586$	$p = 0.7887$
Theta-Gompertz	$p < 0.001$	$p = 0.009$	$p = 0.0009$
Svirezhev	$p > 0.1$	$p = 0.8422$	$p = 0.9423$
Theta-logistic	$p < 0.001$	$p = 0.0049$	$p = 0.0005$

¹KS – Kolmogorov – Smirnov test; ²WW – Wald – Wolfowitz test;

³MW – Mann – Whitney test

Results presented in Table 4 allow concluding that deviations obtained for Theta-Gompertz model and Theta-logistic model haven't symmetric distributions: we have to reject hypotheses about symmetry even with 1% significance level. It is interesting to note that biggest values of probabilities were obtained for Svirezhev model which has biggest value of minimizing functional form (Table 2).

As it was pointed out above for every value of population size (density μ) computer experiments were provided independently (Fig. 1). Additionally, we can consider population density as independent variable, as

a sequence of fixed *time moments*. Independence of computer experiments means that deviations between theoretical and experimental results are independent stochastic variables. Thus, we cannot have correlation in sequence of residuals if used model gives good fitting of dataset.

Critical values for Durbin – Watson test for 100 experimental points and one predictor variable are following: $d_L = 1.65$ and $d_U = 1.69$ for 5% significance level and $d_L = 1.52$ and $d_U = 1.56$ for 1% significance level (Draper and Smith, 1986, 1987). For first dataset we have the following results: for Verhulst model $d = 0.0268$; for Svirezhev model $d = 0.3901$; for Theta-logistic model $d = 0.0268$. Thus, in all cases we have to reject hypothesis about absence of correlation with 1% significance level. For second dataset we have the following results: for Verhulst model $d = 0.0047$; for Svirezhev model $d = 0.0153$. For this dataset we have also to reject hypothesis about absence of serial correlation.

For checking hypothesis about absence/existence of serial correlation we also used *serial test* (Draper and Smith, 1986, 1987). For first dataset we have the following results: for Verhulst model number of positive deviations is equal to 49, $n_1 = 49$, number of negative deviation is equal to 51, $n_2 = 51$, number of groups is equal to 50, $u = 50$, and $z = -0.0965$ (standard normal stochastic variable). Taking into account that $P\{z \leq -0.1\} = 0.47$ we can conclude that observed combination of deviations with different signs and their groups has very big probability. Thus, in this case we have no reasons for rejecting hypothesis about absence of serial correlation. The same results we have for Theta-logistic model. For Svirezhev model $n_1 = 85$, $n_2 = 15$, $u = 2$, $z = -9.554$; thus, for this model combination of deviations with different signs and their groups has very small probability, thus, we have to reject hypothesis about absence of serial correlation.

For second dataset we have the following results: for Verhulst model number of positive deviations is equal to 81, $n_1 = 81$, number of negative deviation is equal to 19, $n_2 = 19$, number of groups is equal to 2, $u = 2$, and $z = -9.623$; probability that z less or equal to -9.623 is very small, $P\{z \leq -3\} = 0.002$. For Svirezhev model $n_1 = 85$, $n_2 = 15$, $u = 2$, $z = -9.554$. For both models we have to reject hypotheses about absence of serial correlations in sequences of residuals.

4 Conclusion

Computer experiments with stochastic model of migrations of individuals on a plane under conditions that population size is constant (no birth and death rates, no migrations out of and in to considering domain, homogenous structure of locations) allowed obtain two various datasets of interactions between individuals. First dataset was obtained for the case when in every location every individual connected with all other individuals. Second dataset was obtained for the situation when in locations individuals could stay separately or organize group in two or three individuals.

A lot of classic models of population dynamics were constructed under the assumption that influence of self-regulative mechanisms is determined by numbers of interactions between individuals. Approximation of obtained datasets by various functions describing influence of self-regulative mechanisms (in Verhulst, Theta-Gompertz, Svirezhev, and Theta-logistic models) showed that all functions are not suitable for fitting of second dataset. For the first dataset Verhulst model and Theta-logistic model can be used for fitting. More precisely, last models have good backgrounds for it; but from the standpoint of traditional imagination about good and bad models (Bard, 1974) Verhulst and Theta-logistic equations are not suitable for approximation. When requirements for used model are not so strong (in particular, when distribution of residuals must be symmetric only, and in sequence of residuals serial correlation cannot be observed) these model can be used for fitting.

Obtained results don't allow concluding that used models cannot be applied for modeling of population dynamics. We obtained the background for conclusion that within the frameworks of considered models

influence of intra-population self-regulative mechanisms haven't strong correlation with numbers of interactions between individuals.

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