Computational Ecology and Software, 2014, 4(4): 234-247

Article

About a model of biological population data collection: Can heteroscedasticity problem be solved or not?

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Received 6 September 2014; *Accepted 12 October 2014*; *Published online 1 December 2014*

Abstract
In paper stochastic model with discrete time of migrations in finite part of plane is considered. It is assumed that migrations can be from every node of integer lattice to nearest nodes only, and these migrations depend on numbers of individuals in the respective nodes. Population size is assumed to be constant for every sequence of population size measurements. It is also assumed that there are two limits D_1 and D_2, D_1, $D_1 < D_2$, of local population size in node when respective node is attractable for migrants (Alley effect). If local population size is bigger than D_2 node becomes unsuitable for migrants, and all individuals try to leave the respective node. After a certain number of time steps local population size is determined in randomly selected nodes (it looks like method of "throwing of frame" or "cutting of model trees" of entomological data collection but in considering situation it doesn't lead to changing of conditions for population). Dependence of standard deviations of samples of various sizes on fixed values of population density are analyzed. In particular, it is shown that well-known problem of heteroscedasticity cannot be solved in principle for the situation when ecological model parameters must be estimated using empirical or experimental time series. Analysis of dependence of number of interactions of individuals per time step (average in time and space) on total population size allows pointing out new ways in modification of Verhulst model.

Keywords migration process; methods; biological population; data collection; stochastic mathematical model; Alley effect; heteroscedasticity problem.

Computational Ecology and Software
ISSN 2220-721X
URL: http://www.iaees.org/publications/journals/ces/online-version.asp
RSS: http://www.iaees.org/publications/journals/ces/rss.xml
E-mail: ces@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Estimation of model parameters using empirical time series is among of very important problems of modern ecological modeling (Bard, 1974; Isaev et al., 1984, 2001, 2009; McCallum, 2000; Brauer and Castillo-Chavez, 2001; Wood, 2001; Nedorezov, 2012; Sharma and Raborn, 2011; Haidar et al., 2011 and others). Finding of best estimations is important as for constructing of forecasts of various lengths as for determination of optimal methods of population management.

Least square method is one of popular methods for estimating of model parameters (Bard, 1974; Bolshev and Smirnov, 1983; Draper and Smith, 1998; Lakin, 1990). For example, let's assume that following equation describes population dynamics:

$$x_{k+1} = x_k F(\alpha, x_k) . \tag{1}$$

In model (1) x_k is population size (or density) at moment k, $k = 0,1,2...$; α is a vector of unknown model parameters; F is non-negative nonlinear function (birth rate). It is possible to point out a big number of models of (1) type which are used for approximation of entomological time series (Kostitzin, 1937; Moran, 1950; Varley, Gradwell, Hassell, 1975; Hassell, 1975; Bellows, 1981; Berryman, 1981; Turchin, 2003; Nedorezov, 1986, 2012).

Let x_0 be initial value of population size, $x = x(k, x_0, \alpha)$ be a solution of equation (1) for fixed values of model parameters α and fixed initial population size x_0, and let x_k^*, $k = 0,1,..., N$, be an empirical sample (time series). $N+1$ is a sample size. Best estimations of model (1) parameters can be obtained finding global minimum for the following expression:

$$Q(x_0, \alpha) = \sum_{k=0}^{N} (x_k^* - x(k, x_0, \alpha))^2 . \tag{2}$$

Note, that in (2) initial population size x_0 is unknown parameter too, and amount of x_0 must be estimated using the same sample. Real sense of expression (2) is following: in a set of all solutions of model (1) we have to find nearest to considering sample trajectory.

On a practice use of expression (2) meets with problems which have a direct relation as to finding of global minimum as to explanation of form of this expression. There exists one more important problem: influence of small values of initial sample on final results (values of model parameters) is much less than influence of big values.

Every term in sum (2) $e_k = x_k^* - x(k, x_0, \alpha)$ is a difference between empirical stochastic value and theoretical value which is obtained with model (1). It is assumed that theoretical values are real amounts, and observed differences can be explained as results of errors in measurements, influences of external factors etc. Consequently, every term in (2) is value of stochastic variable with zero average. But at the same time variances of these variables are different. Thus, (2) is sum of squared differences of stochastic variables e_k with different distributions (heteroscedasticity problem; see, for example, White, 1980; Gupta, Tang, 1984; Tofallis, 2008 and many others). If we want to have a situation when all terms in (2) have similar influences on final results, first of all we have to have equal variances for all e_k. This problem one tries to solve introducing into expression (2) non-negative "weights" $\{w_k\}$:

$$Q(x_0, \alpha) = \sum_{k=0}^{N} w_k (x_k^* - x(k, x_0, \alpha))^2 . \tag{3}$$

In (3) $w_k \geq 0$ are non-negative constants. Note, if we can find such constants it doesn't mean that we have a total solution of heteroscedasticity problem – this is particular solution only, and terms $e_k^{'}$, $e_k^{'} = \sqrt{w_k}(x_k^* - x(k, x_0, \alpha))$ in (3) may have various distributions.

Thus, particular solution of heteroscedasticity problem can be transformed into problem of finding of set of non-negative weights $\{w_k\}$ for expression (3). But up to current moment there are no real criterions (with good mathematical background) for selection process. We have the following recommendation only: we have to put big weights for small terms and small weights for big terms.

The following approach to the process of selection of weights $\{w_k\}$ looks better than recommendation pointed out above: all weights must be equal to variances of stochastic variables e_k to the power of minus one. If we can determine these weights all terms of (3) $e_k^{'}$ will have zero averages and variances equal to one. Note, that in this situation weights $\{w_k\}$ in (3) are not equal to constants – their values depend on the respective theoretical amounts $x(k, x_0, \alpha)$. We have to take it into account minimizing functional (3).

Thus, in some cases heteroscedasticity problem can be deduced to the problem of analysis of dependence of standard deviations of empirical data on real values of population size or density. If this dependence corresponds to monotonic function (in ideal variant it must be linear function) we have a certain possibility to estimate this dependence. But if this dependence corresponds to non-monotonic function it means that in considering case heteroscedasticity problem cannot be solved in principle: in practice it is impossible to determine non-monotonic sequence of weights $\{w_k\}$ for natural conditions. If this situation is truthful it means that heteroscedasticity problem hasn't a general solution.

The problem described above can be solved in the only way. It can be solved using mathematical model of individual's migrations. Below we use a model of individual migrations on a lattice (Harris, 1963; Bailey, 1967; Hanski, 1998) with local Allee effect (Allee, 1931; Odum, 1983). Process of data collection was modeled in the following manner: local population size was fixed in 100 various stochastically selected points of a lattice (discrete uniform distribution on the respective sets of nodes; Mikhailov, 1974; Ermakov, 1975). It looks like direct analog of *throwing of frame into a field*, or *shaking of model trees*, or *cutting of squared meter of forest floor in autumn*.

Within the framework of model it was assumed that total population size is constant during every separated set of "computer experiments" on data collection and estimating of average of population density. Dependence of sample variances, dependence of number of interactions between individuals, and dependence of estimation of probability that distribution of obtained sample corresponds to Normal on known population density are analyzed.

2 Model

Let's consider a model of migrations which are organized in simplest manner. Let's assume that all migrations (in finite part of plane) have stochastic nature, and transition from one part to another depends on relations of sizes in nearest parts of plane. Additionally, we'll assume that total population size doesn't change during certain time interval: there are no birth and death processes in population. Periodically population size is fixed in 100 stochastically selected points. It looks like a method of "throwing of frame" (for determination of density of insects on a field) or "cutting or shaking of model trees" (methods which are used in forest entomology; Isaev et al., 1984, 2001, 2009; Vorontsov, 1975, 1978; Dunaev, 1997).

Let N be a population size. We'll assume that this amount is constant, $N = const$, during a certain time interval of providing a set of "measurements" of local population size. Let Z_{nm}^2 be an integer lattice on a plane R^2:

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

It will be assumed that population size is determined in points of lattice Z_{nm}^2 only. Let $x_{ij}(t)$ be a number of individuals in node (i, j), $(i, j) \in Z_{nm}^2$, at moment t. It is naturally to assume that there are no migrations out of the lattice, thus the following relation is truthful for all t:

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

It is obvious that for all t $x_{ij}(t)$ and N are integer numbers. We'll also assume that time is discrete, $t = 0,1,2\ldots$.

Within the framework of model we'll assume that migrations of individuals can be observed to nearest nodes only. Two nodes of lattice (i_1, j_1), $(i_2, j_2) \in Z^2_{nm}$ are nearest to each other if the following relation is truthful: $|i_1 - i_2| + |j_1 - j_2| = 1$. In literature it is possible to find other variants of this definition (Harris, 1963; Bailey, 1967).

About migrations of individuals from point (i, j) it will be assumed that for all $x_{ij}(t)$ a certain quota of individuals δ, $\delta = const > 0$, $\delta < 1$, migrates to nearest nodes with equal probabilities. Number of these individuals ("crazy migrants") is equal to $[\delta x_{ij}(t)]$ where $[\cdot]$ is integer part of number. Other individuals, $x_{ij}(t) - [\delta x_{ij}(t)]$, migrate to other nodes with probabilities which depend on local sizes in these points.

It is naturally to divide all points of lattice Z^2_{nm} onto three qualitative different types. It is possible to point out two critical levels D_1 and D_2, $D_1 < D_2$, which determine "comfortable zone" for individuals (local Alley effect; Allee, 1931; Odum, 1983). If local population size belongs to the respective segment, $D_1 \le x_{ij}(t) \le D_2$, we'll assume that nobody wants to migrate from this comfortable zone; in such a situation we have "crazy migrants" only.

If $x_{ij}(t) < D_1$ individuals are out of "comfortable zone"; for this situation we'll assume that all individuals want to leave this point. Thus, probability for individual to stay in this node more than one time step is equal to zero.

If $x_{ij}(t) > D_2$ population size is out of "comfortable zone" too; for this situation we'll also assume that individuals want to leave this node (it can be called as "repulsion zone"). But probability for individual to stay in this point more than one time step is bigger than zero.

Within the framework of model we'll also assume that level of attractiveness for migrants of point (i, j) depends not on current number $x_{ij}(t)$ but on the state of node. Let coefficient of attractiveness for migrants to be equal to one, $q_1 = 1$, if $x_{ij}(t) < D_1$. It is obvious that coefficient of attractiveness is bigger than one if local population size in "comfortable zone", $q_2 = const > 1$ (Allee effect; Allee, 1931; Odum, 1983). If $x_{ij}(t) > D_2$ coefficient of attractiveness must be less than one, $q_3 < q_1$: such kind of nodes must have minimal attractiveness. In natural conditions it is possible to find other types of points with other relations between coefficients q_i (Isaev et al., 1984, 2001, 2009).

Denote as $q_{ij}(t)$ a level of attractiveness of point (i, j) at moment t. Depending on value of $x_{ij}(t)$ coefficient $q_{ij}(t)$ can be equal to q_1, q_2 or q_3. We'll assume that probability of individual to migrate to nearest node is proportional to coefficient of attractiveness of this node and inversely proportional to total sum of coefficients of all nodes individual can migrate to. As it was assumed above if $x_{ij}(t) < D_1$ all individuals leave point (i, j). If this node doesn't belong to boundary, $i \ne 1$, of lattice than probability for individual to migrate to point $(i-1, j)$ is determined by the following expression:

$$p_{i-1j} = \frac{q_{i-1j}(t)}{q_{i-1j}(t) + q_{i+1j}(t) + q_{ij-1}(t) + q_{ij+1}(t)}. \tag{4}$$

It is obvious that for points $(1, j)$, $j = 1,\ldots,m$, probability (4) is equal to zero. Respective formulas can be presented for other three probabilities.

For the case when $x_{ij}(t) > D_2$ it was assumed that probability for individual doesn't migrate to nearest node is greater than zero. If this point doesn't belong to boundary of lattice this probability is determined by the following formula:

$$p_{ij} = \frac{q_2}{q_2 + q_{i-1j}(t) + q_{i+1j}(t) + q_{ij-1}(t) + q_{ij+1}(t)} . \quad (5)$$

If $i = 1$, $1 < j < m$, formula (5) will have the following form:

$$p_{1j} = \frac{q_2}{q_2 + q_{2j}(t) + q_{1j-1}(t) + q_{1j+1}(t)} . \quad (6)$$

If $i = 1$, $j = 1$, formula (5) will have the form:

$$p_{11} = \frac{q_2}{q_2 + q_{i+1j}(t) + q_{ij+1}(t)} . \quad (7)$$

Note that amount of migration flow which is determined by formulas (4)-(7) increases at increase of attractiveness of node. It is necessary to note that stochastic process described above is a modification of processes described in modern literature (see, for example, Harris, 1963; Bailey, 1967; Hanski, 1998 and many others). But main goal of current publication isn’t in analysis of properties of described model but in analysis of properties of samples which can be generated by *methods of data collection* using in modern biology.

3 Data CollectioniIn Model

Initial population condition was modeled by the following way: every individual with equal probabilities could appear in one of nodes of lattice Z_{nm}^2. After that migration process was started (in correspondence of formulas (4)-(7)), and model worked free during T time steps; after that we had new distribution of individuals on the plane which is determined by basic laws (4)-(7) only. Computer experiments had been provided with $T = 1000$.

After T time steps data collection process was provided: in 100 various stochastically selected points of lattice local population size was fixed. It looks like direct analog of “throwing of frame into a field”, or “shaking of model trees”, or “cutting of squared meter of forest floor in autumn”. After fixation of local population sizes model worked free again during T time steps. After that the similar procedure of data collection was organized again. It was repeated 100 times for every selected values of total population size N.

4 Results of Calculations

For calculated datasets various problems were solved. In particular, dependence of standard deviation s_μ on $\mu = N / mn$ (the local population size averaged over the lattice of habitats) was analyzed for various numbers of sample sizes:

$$s_\mu = \left(\frac{1}{K-1} \sum_{k=1}^{K} (x_k^{**} - \mu)^2 \right)^{0.5} . \quad (8)$$

In (8) x_k^{**} are terms of sample (averages for all independent samples of the length M); K is a number of samples of the length M. For $m = n = 100$ and $M = 3$ we had $K = 3300$, for $M = 4$ - $K = 2500$, for $M = 5$ - $K = 2000$, for $M = 6$ - $K = 1600$, for $M = 7$ - $K = 1400$, for $M = 10$ - $K = 1000$, for $M = 20$ - $K = 500$, and for $M = 40$ - $K = 200$. Thus, sample’s sizes are rather big for obtaining “good estimations” for standard deviations s_μ (8) for various values of M.

4.1 Non-monotonic behavior of standard deviation

For the next values of model parameters $m = n = 100$, $D_1 = 10$, $D_2 = 30$, $\delta = 0.1$, $q_1 = 1$, $q_2 = 10$, $q_3 = 0.2$, “typical picture” of changing of standard deviations s_μ was observed. We are talking about “comfortable zone” because similar results were obtained for some other sets of parameters. When population density is rather small, $\mu \in [0.1,1.5]$, changing of standard deviation (Fig. 1) for various sample sizes $M = 3,4,5,7,10,20,40$ can be effectively described by linear function ($R^2 \in [0.9579,0.9739]$).

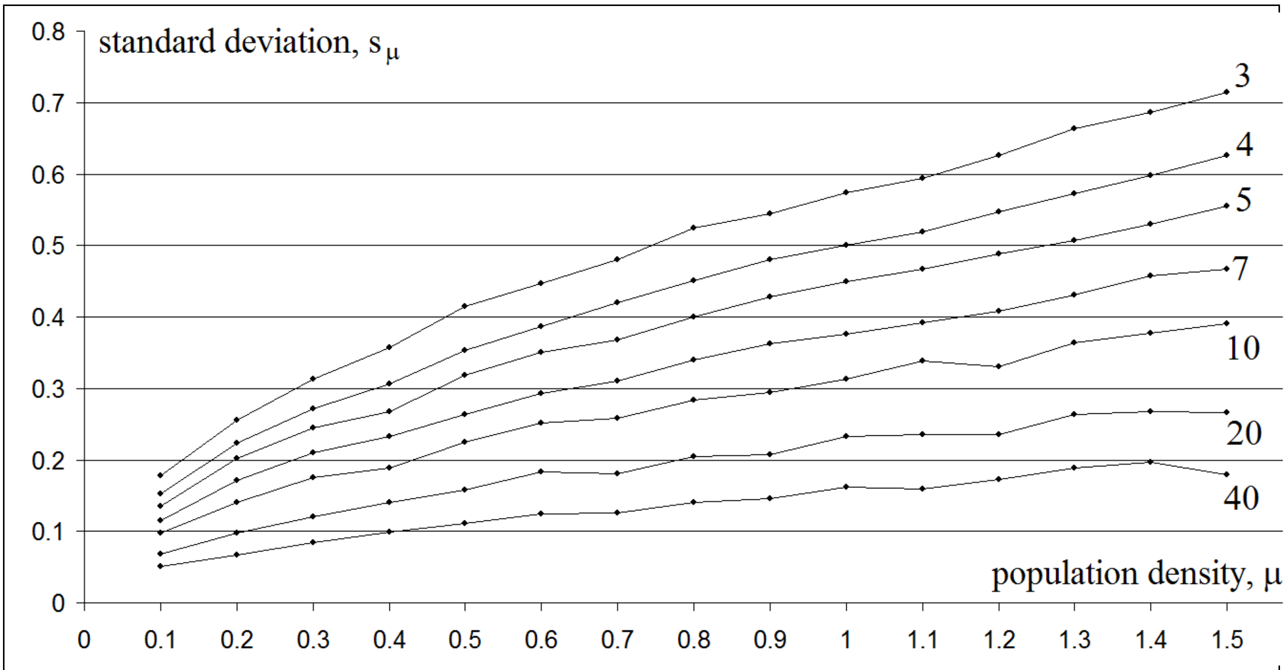

Fig. 1 Changing of values of standard deviation on population density μ ($0.1 \le \mu \le 1.5$) and sample size $M = 3,4,5,7,10,20,40$.

On the segment [1.5,1.6] there is a transition through any threshold value – after intersection sharp increasing of s_μ is observed and type of dependence of standard deviation on population density has different nature (Fig. 2). If $\mu \in [1.8,31]$ changing of standard deviation s_μ can be effectively described by parabolic function with $R^2 \in [0.926,0.963]$. Note that maximum value of standard deviation is observed near mid point of “comfortable zone”.

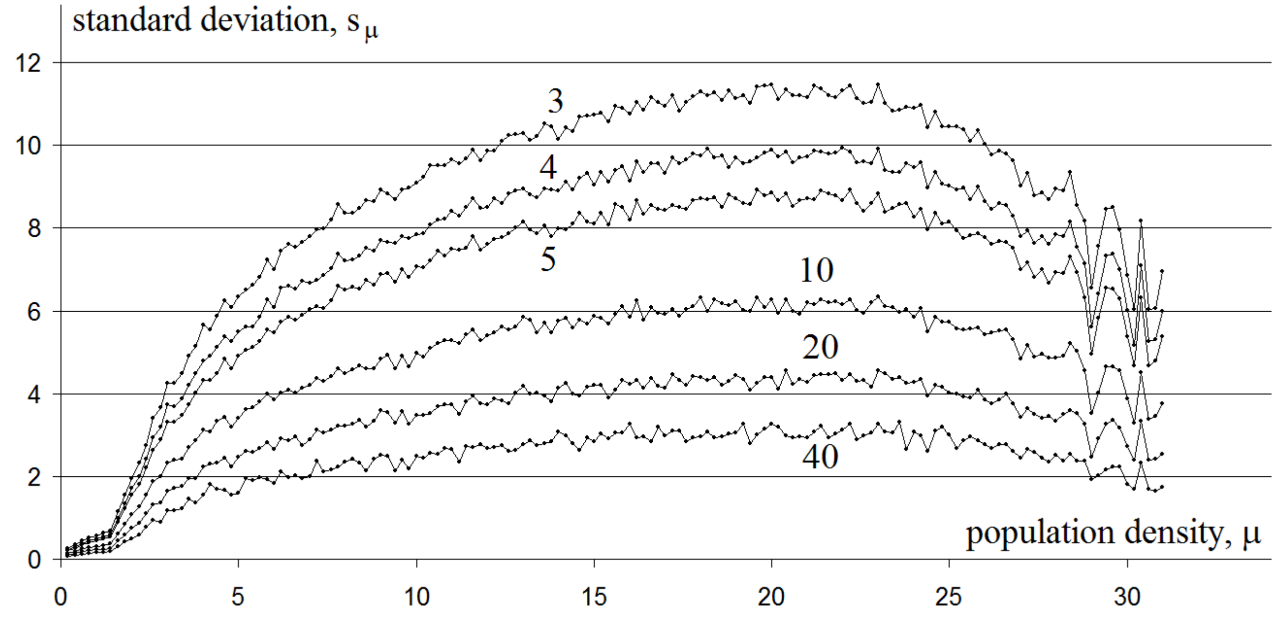

Fig. 2 Changing of values of standard deviation on population density μ ($0.2 \le \mu \le 31$) and sample size $M = 3,4,5,10,20,40$.

Thus, we can conditionally select at least two critical points on the curve of changing of standard deviation. First point is $\mu \approx 1.6$: after this value rather strong influence of “comfortable zones” on migrations is observed. The second point is $\mu \approx 20$: after intersection of this level decreasing of standard deviation is observed (fig. 2). Important question is following: can we find these critical points for *real* populations in *real* conditions? If yes, we have a principle possibility to solve heteroscedasticity problem and find optimal weights for expression (3). If not, heteroscedasticity problem hasn’t a solution.

Taking into account that in real conditions problems can arise with estimation of population density, estimation of boundaries of *comfortable zone* becomes unsolvable problem. Thus, we can conclude that at present time heteroscedasticity problem cannot be solved in principle. Finally, we can also conclude that using in (3) monotonic increasing or decreasing weights cannot lead to better results in estimating of model parameters. Close results were obtained for similar models with other laws of migrations (Nedorezov, 2012, 2013).

4.2 Confidence interval and density μ

For obtained datasets quotas of errors were estimated for various sample sizes M and density μ. It was assumed that we have an error when density μ was out of the limits of confidence interval when its boundaries were determined using standard formula: $\overline{\mu} \pm s_\mu \cdot t(M-1,0.05)$. In this expression $\overline{\mu}$ is estimation of density (average) for respective sample, s_μ is standard deviation for sample, and $t(M-1,0.05)$ is respective value of Student’s distribution for $M-1$ degrees of freedom and significance level 0.05 (Lakin, 1990).

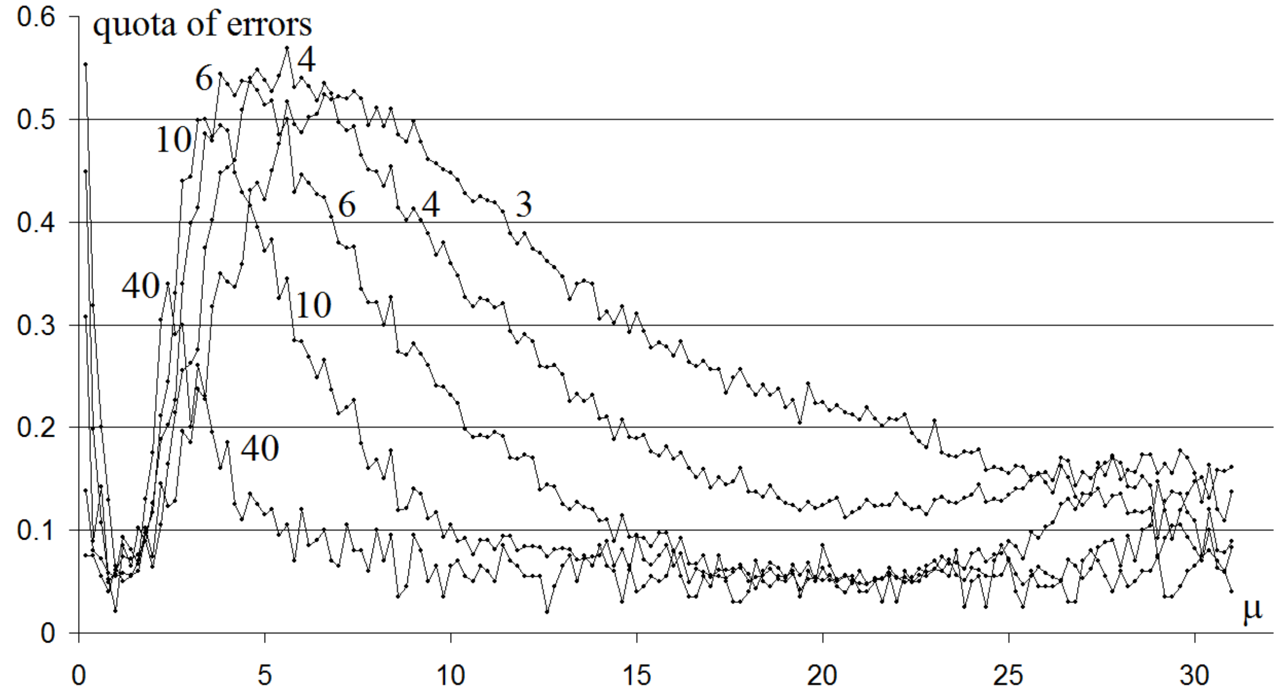

Fig. 3 Changing of values of quota of errors on population density μ ($0.2 \le \mu \le 31$) for sample sizes $M = 3,4,6,10,40$.

When population density μ is rather small (Fig. 3), $\mu = 0.2$, we may have errors in 55% of all cases. If $\mu = 0.1$ and $M = 3$ we may have errors in 74% cases. It means that results of data analysis provided with standard methods have no relations to reality with big probability. Increase of population density initially leads to decrease of quotas of errors; but after an intersection of critical level (fig. 3) quotas of errors increase, and local maximums can be rather big. Even when sample size is very big, $M = 40$, maximum of errors is equal to 34%.

Increase of sample size M leads to changing of points where maximums of errors are observed: it moves toward smaller values of population density (Fig. 3). It is interesting to note that observed situation is rather paradoxical one. With probability 0.95 real value of population density must belong to confidence interval but with probability 0.74 ($\mu = 0.1, M = 3$) it is out of this interval. And this result has no relation to (possible) problems of providing of computer experiments (for example, with appearance of any dependencies in obtained samples): for every selected value of population density all values of stochastic variables modeled independently.

Note that appeared situation cannot be explained by the small number of “free” working of model ($T = 1000$) between measurements of local population size: similar behavior was observed when T was increased in ten times. In our opinion non-monotonic behavior of quotas of errors can be explained by non-homogeneity of nodes of lattice, and existence of “comfortable zones” and “repulsion zones”. Partly it can be explained by basic properties of samples – with big probabilities samples are not Normal (see next Chapter of manuscript).

Taking into account that for natural populations “comfortable zones” and “repulsion zones” exist we can conclude that to analysis of considering situation (and similar situations) some of standard statistical methods cannot be applied.

4.3 About Normality of initial samples

For application of parametric methods of statistics to analysis of existing samples elements of these samples must have Normal distribution (or distribution which is close to Normal). For testing of Normality of existing sample Kolmogorov – Smirnov test, Lilliefors test, and Shapiro – Wolk test were used (Bolshev and Smirnov, 1983; Lilliefors, 1967; Shapiro et al., 1968). Results of application of these tests to 100 independent samples with $M = 6$ are presented on Fig. 4. On this picture quota of rejected hypotheses (in %) of Normality for 100 samples are presented for 5% significance level.

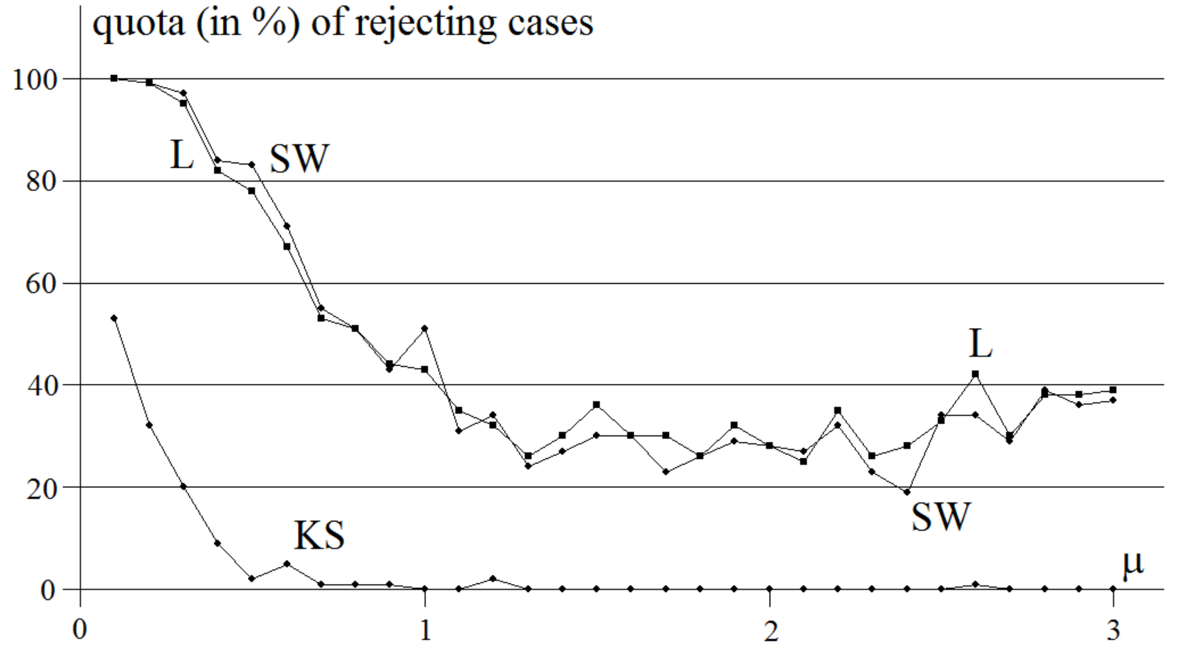

Fig. 4 Quota (in percentages) of situations when hypothesis about Normality of a sample with.

As we can see on this picture when population density is rather small ($\mu \in [0.1, 0.3]$), Null hypothesis was rejected in about 100% cases (Shapiro – Wilk test and Lilliefors test). Iven for situations when population density is big, $0.3 \le \mu \le 3$, these tests allow rejecting of Null hypothesis in (about or more) 20% of cases. Kolmogorov – Smirnov test isn't so strong like Shapiro – Wilk' and Lilliefors' tests but its use shows that we have to reject Null hypothesis in 20% or more cases when population density is small, $\mu \in [0.1, 0.3]$ (Fig. 4).

It is important to note that when hypothesis about Normality cannot be rejected, it doesn't mean that we have to accept this hypothesis. It means that used tests don't allow rejecting. Thus, like in previous case, we have to conclude that use of parametric statistical methods for estimating of population density when its amount is rather small, hasn't a good background.

4.4 Interaction between individuals, and new mechanistic model

For description of isolated population dynamics Verhulst' model and some other models of the respective class are used (Verhulst, 1838; Gompertz, 1825; Kostitzin, 1937; Odum, 1983; Brauer and Castillo-Chavez, 2001; Nedorezov, 1986, 2012; Nedorezov and Utyupin, 2011 and others). In particular, Verhulst model has the following form:

$$\frac{dx}{dt} = \alpha x - \beta x^2 . \qquad (9)$$

In model (9) α is intrinsic rate of natural increase; β is positive parameter of self-regulation; $x(t)$ is population size (or density) at time moment t.

Within the framework of model (9) it is assumed that influence of self-regulative mechanisms is proportional to number of interaction between individuals (it has influence on spread of diseases in population; it corresponds to level of competition between individuals for food etc.). It is also assumed that number of interaction between individuals is proportional to current population size squared. Within frameworks of some other models it is assumed that speed of interactions between individuals is proportional to $x \ln x$ and $x^{1+\theta}$, where θ is positive parameter (Gompertz, 1825; Brauer and Castillo-Chavez, 2001; Nedorezov and Utyupin, 2011). All these models were compared with real time series and allowed obtaining interesting results (Gause, 1934; Pielou, 1977; Nedorezov, 2011, 2012 and others).

But what does it mean "number of interactions between individuals"? How can we calculate it within the framework of model (4)-(7) considering in current publication? These questions are very important because these questions are about backgrounds for classic models.

Let's assume that we have homogeneous space (points of lattice) and homogeneous scale for local population sizes (i.e. there are no "comfortable zones"). Respectively, we have to assume that migration processes must be organized like in model (4)-(7) when local population size is bigger than upper level D_2. In this situation every individual can migrate to nearest points and probability to stay in current point is positive. Results of modeling are presented on Fig. 5.

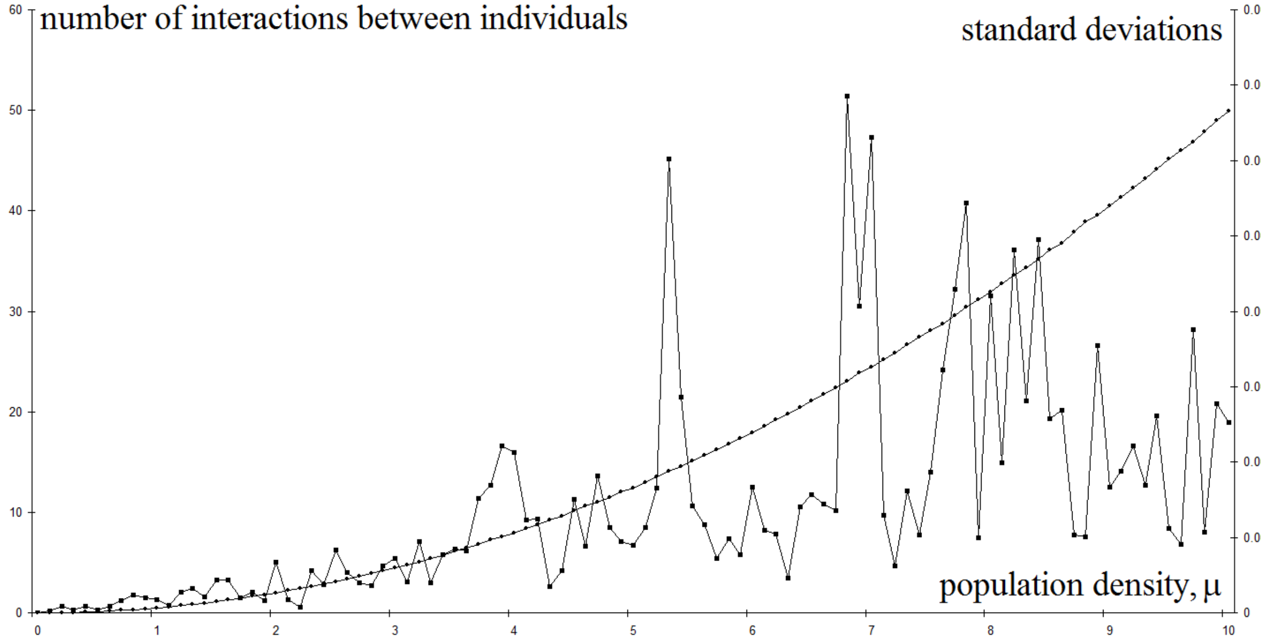

Fig. 5 Dependence of number of interaction between individuals on population density for homogenous space and scale of population size.

Number of (average) interactions was calculated by the following way. At the beginning model (4)-(7) worked free during 20000 time steps. For every of the next 20000 time steps average value of number of interactions was calculated: it was determined for all nodes of lattice. If in any point (i, j) at moment t we had $x_{ij}(t)$ individuals it was assumed that every individual has interactions with all other individuals in this node. Thus, it was assumed that number of “paired” interactions in point (i, j) is equal to $x_{ij}(t)(x_{ij}(t)+1)/2$. For every time moment t these amounts were summarized for all nodes of lattice and divided on mn (average number of interaction for fixed time moment). For this new sample – it contained 20000 values, - mean value was calculated too. Finally we got average (in space and time) number of interactions. It was provided for 100 various values of population density presented on Fig. 5. The same procedures were realized for situations when we had “comfortable zones” for individuals.

As we can see on this picture (Fig. 5) in considering case number of interactions can be effectively described by the function $z = \beta x^2$. For the same values of model parameters: $m = n = 100$, $q_1 = 1$, $q_2 = 10$, $q_3 = 0.2$, - minimum of function Q (2) is equal to 0.17987, parameter $\beta = 0.499291$ with standard error 0.000094, and $R = 0.99999607$. It allows concluding that Verhulst model (9) has background and can be used, in particular, for population dynamics description in situations when population size is rather small and, respectively, far from “comfortable zones” (in situations when these zones haven’t strong influence on behavior of individuals).

Computer experiments when “comfortable zones” exist, showed that attraction of “comfortable zones” can qualitatively change behavior of individuals and their distribution on the plane. For small values of population size ($\mu \le 1$) computer experiments were provided with step on density $h = 0.01$. Approximation of dataset using the function $z = cx^2$ showed that final value of squared deviations (function Q (2)) is equal to 0.00000265 with $R = 0.99999943$; parameter $c = 0.501264$ with standard error 0.000036. Thus, we have the same situation like in previous case.

For bigger values of population density, $\mu \ge 1$, we have situation presented on Fig. 6. Analysis of the dependence of number of interactions on μ shows that at the beginning we have “quadratic phase of growth” like on Fig. 5. After that we have “linear phase of growth”. On segment $\mu \in [2.5, 23.2]$ changing of number of interactions can be approximated by linear function $z = 20.56153\mu - 31.7648$ with $R^2 = 0.999919$.

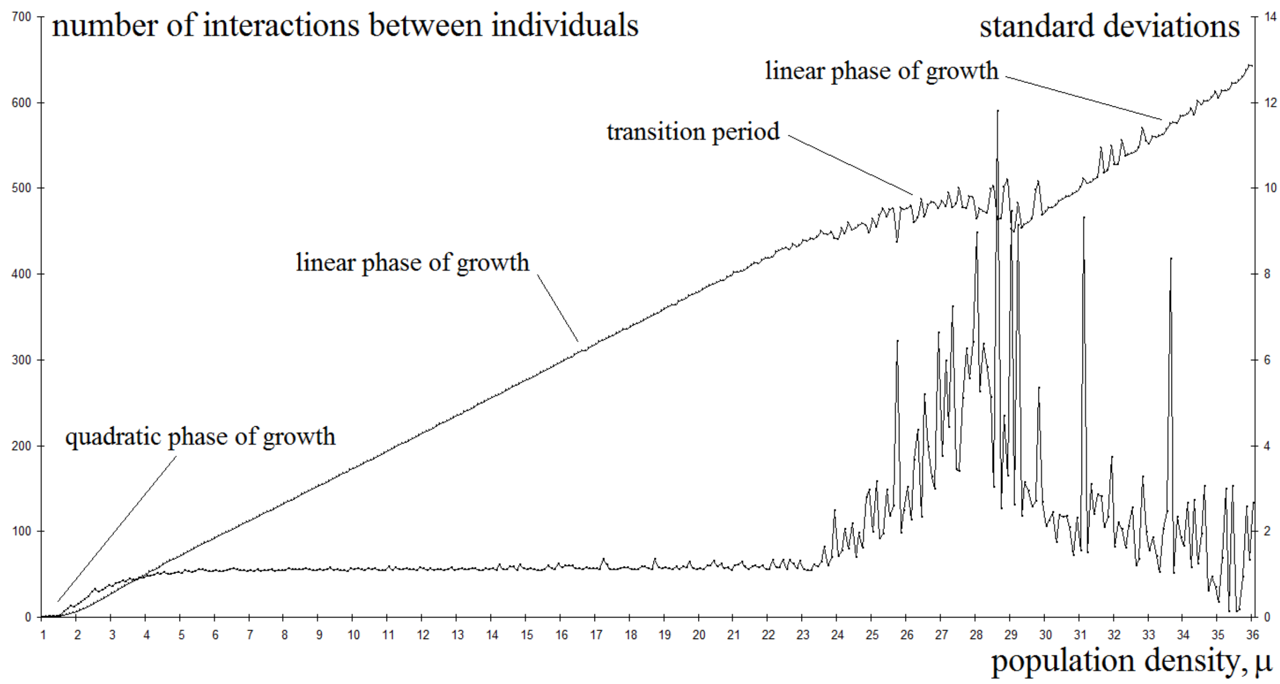

Fig. 6 Dependence of number of interaction between individuals on population density for the situation when $\mu \ge 1$.

When influence of zones where local population size is bigger than D_2, becomes rather strong we have “transition period” (fig. 6) without obvious dependence of number of interactions on density μ. We have to note that this interval of changing of μ is characterized by very big values of standard deviations (Fig. 6). When μ belongs to segment [30, 36] dataset can also be approximated by linear function with other parameters: $z = 27.30781\mu - 343.688$ with $R^2 = 0.980903$.

Consequently, we have to conclude that for description of population dynamics with Allee effect functions of (9) type are not suitable, and we have to use other functions. In particular, function $g(x)$ may have the following form:

$$g(x) = \begin{cases} b_1 x^2, \ x \in [0, \mu_1] \\ b_2 x + b_3, \ x \in [\mu_1, \mu_2] \\ r(x), \ x \in [\mu_2, \mu_3] \\ b_4 x + b_5, \ \mu \geq \mu_3 \end{cases} \tag{10}$$

In (10) b_j, $j = 1,...,5$, are constants, b_1, b_2, b_4>0; $[\mu_j, \mu_{j+1}]$ are segments corresponding to various types of changing of function $g(x)$; $r(x)$ is sub-function corresponding to “transition period” (Fig. 6). In modification of model (9) with function (10) we have to put $b_4 \geq \alpha$; if this inequality is truthful it is possible to point out upper limit of population size K. It is obvious that parameters of function (10) are not independent, and we have the following relations:

$b_1 \mu_1^2 = b_2 \mu_1 + b_3$, $r(\mu_2) = b_2 \mu_2 + b_3$, $r(\mu_3) = b_4 \mu_3 + b_5$.

The second, for modification of model (9) with function (10) it is easy to point out conditions for parameters when in phase space we can observe two stable attractors. It is important that realization of this dynamic regime (trigger regime, or fixed outbreak; Isaev et al., 1984, 2001, 2009) can be explained by the specific organization of self-regulative mechanisms only. And, finally, questions about possible backgrounds for various well-known models (Gompertz, 1825; Kostitzin, 1937; Brauer and Castillo-Chavez, 2001; Nedorezov, 1986, 2012; Nedorezov and Utyupin, 2011 and others) are open now.

5 Discussion

Analysis of dependence of standard deviations (from “real values of densities) on population density shows that changing of these deviations (for various sample sizes) isn’t linear or monotonic function. On some short intervals it can be approximated by linear function but in general it has non-monotonic character (Fig. 2). In reality situations are more difficult, and respectively there are no possibilities to estimate critical values of population density when derivatives change their signs. Moreover, for real situations we have no possibility to find real values of density – every time we work with estimations of this amount only. It means that practically we have no chance to choose a system of weights for expression (3) for estimation of model parameters: we cannot find weights which transform expression (2), and all elements of minimizing functional form have similar influence onto final estimations of model parameters.

If we follow the principle “to put bigger values of weights for smaller values of sample” every time we will have a situation when we put bigger value instead of smaller one (in a result of non-monotonic behavior of standard deviations). It means the following of pointed out principle can lead to unpredictable results in estimation of model parameters. Thus, introduction of weights into formula (2) of minimizing functional form must be avowed as untenable method. Additionally, heteroscedasticity problem must be avowed as unsolvable problem at estimation of non-linear ecological model parameters.

Analysis of results of computer experiments with very simple stochastic model of migrations showed also that there is no background for application of parametric statistical methods for analysis of datasets when population density is rather small. It has a direct relation to various methods of entomological data collection and, in particular, to methods of “cutting of squared meter of forest floor in autumn” or “shaking of model trees”. Use of these methods when population density is small leads to obtaining of non-Normal samples.

Calculation of average (in space and time) of number of interactions of individuals for every fixed value of population density within the framework of stochastic model allowed presenting of background for Verhulst model (Verhulst, 1838). In particular, number of interactions can be described by quadratic law when population density is rather small, or when influence of attracting zones in space isn’t strong. For other well-known models of the same class questions about kind of functions describing influence of self-regulative mechanisms are open. When influence of attracting zones onto behavior of individuals is rather strong kind of function can be difficult (10).

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