# Dynamics of pine beauty (*Panolis flammea*): search for stationary dynamical regimes

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**Abstract**

In current publication possible population dynamics regimes are analyzed using pre-model statistical method. Method was applied to well-known pine beauty moth (*Panolis flammea* L.) time series (Schwerdtfeger, 1944, 1968). Provided statistical analysis showed that observed dynamics of pine beauty doesn't correspond to strong 2-, 3-,…, or 9-year cycles which can be generated by one-dimensional discrete models, and doesn't correspond to fluctuations near stable level.

**Keywords:** pine beauty moth population fluctuations, time series, pre-model statistical analysis, approximation, stationary dynamical regime

## Introduction

Search for suitable mathematical model, estimation of model parameters using empirical datasets, and determination of basic features of population phase portraits are among of the main elements of population dynamics analysis (Isaev et al., 1984, 2001; McCallum, 2000; Tonnang et al., 2009, 2010, 2012; Turchin, 2003; Wood, 2001 and many others). Without finding of a suitable model (or without constructing of new suitable model) it is impossible to prepare strong scientifically-based forecasts of pest population changing in time and optimal methods of its management. But up to current moment there are no criterions, which can help in finding of a suitable model before comparison of theoretical and empirical datasets (Isaev et al., 1984, 2001; Nedorezov, Utyupin, 2011). Even comparison of model trajectories with empirical time series can give us a set of suitable models (for fitting of empirical datasets), and again we may have a situation when it is necessary to find a best model (Nedorezov, 2010, 2011 a, b, 2012). In such a situation preliminary and pre-model statistical analysis of existing time series can be very useful in a process of searching of suitable model and/or group of suitable models.

Pre-model analysis is a testing of correspondence of observed population fluctuations to any dynamical regimes which can be generated by various mathematical models. For example, it is a testing of correspondence of population dynamics to 1-cycle (fluctuations near stable level), 2-cycle etc. (Nedorezov, 2012, 2013 a). All deviations from coordinates of $n$-cycle must be explained as results of influence of external stochastic factors, by used methods of data collection etc. In other words, before choosing of model we can try to determine a dynamical regime which is observed in natural conditions. More precisely, we can try to find a dynamical regime with the following property: modern statistical methods don't allow us concluding that considering regime doesn't correspond to observed fluctuations (Nedorezov, 2011a, 2012).

It is known, that for estimation of model parameters under the use of *global fitting* for empirical time series, researches use *initial parts* of model trajectories, and don't use parts of trajectories which correspond to *stabilized regime* of population fluctuations (McCallum, 2000; Nedorezov, 2010, 2012; Turchin, 2003; Wood, 2001 and others). Approximation of empirical time series by initial parts of model trajectories is correct if we analyze a process of population size changing in time which corresponds to *non-stabilized dynamic regime* (Nedorezov, 2011 b, 2012). But if we analyze dynamics of species which exist in local habitat (and where datasets were collected) during long time period the use of initial parts of model trajectories for fitting of empirical time series needs in additional explanation.

**Algorithm**

Let $x_1,\ x_2,\dots,x_N$ be a time series of considering hypothetical population. Time step is equal to one year, thus $x_k$ is a population size (or density) at $k$ th year. First of all, we have to solve the following question: what kind of datasets we have now? If, for example, we analyze time series presented in book by G.F. Gause (1934), it is obvious, that for every trajectory we can point out initial part (it can be exponential phase of population growth), mid part of trajectory (where we can observe growth of influence of intra-population self-regulative mechanisms on process of population size changing), and stabilized behavior (fluctuations near asymptotical stable level). In such a situation we have a good background for application of initial parts of trajectories for fitting of experimental datasets (Nedorezov, 2011 b, 2012).

But in the case when we analyze insect population dynamics in locations where insects live thousands and thousands years, we haven't a background with the same properties. In these situations we observe *stabilized dynamical regime*. Thus, for the estimation of model parameters we have to minimize, for example, the sum of squared deviations of real datasets from coordinates of *asymptotically stable attractors*.

First of all, we must determine a dynamical regime which is realized for population: it is hypothesis we have to check. For example, we can start with assumption that observed fluctuations of population size correspond to cycle of the length two: *ababab*... Let's assume that minimizing functional form is equal to sum of deviations squared. In this case we have:

$$Q(a,b) = \sum_k (x_k - a)^2 + \sum_k (x_k - b)^2 \to \min_{a,b} . \quad (1)$$

From (1) we get the following estimations for coordinates of 2-cycle:

$$a = \frac{1}{N^*}\sum_k x_k \ , \ b = \frac{1}{N^{**}}\sum_k x_k \ , \quad (2)$$

where $N^* + N^{**} = N$, and $N^* = N^{**}$ or $N^* = N^{**} + 1$. After estimation of coordinates of 2-cycle (2) we have to check hypothesis that observed regime is 2-cycle: more precisely, we have to analyze two sequences $x_1 - a$ , $x_3 - a$ ,... and $x_2 - b$, $x_4 - b$ ,… and to show that arithmetic averages are equal to zeros, distribution functions for both sets are symmetric functions, and there are no serial correlation in sequence $x_1 - a$ , $x_2 - b$, $x_3 - a$,... ((Draper, Smith, 1986, 1987)). In the end we have to reject Null hypothesis about equivalence of coordinates of cycle: Null hypothesis is $a = b$ .

If all used tests show that there are no reasons for rejecting of the respective Null hypotheses and Null hypothesis $a = b$ must be rejected for selected significance level, we have to start the process of selection of mathematical model. It is obvious, if observed changing of population size corresponds to 2-cycle there are no reasons for consideration of the Skellam model or Kostitzin model – in both models there are the regimes of asymptotic stabilizations of population size at any levels only for all values of model parameters (Skellam, 1951; Kostitzin, 1937). In this situation it is better to use Moran – Ricker model or discrete logistic model: both models contain a lot of various dynamical regimes (Moran, 1950; Ricker, 1954; Isaev et al., 1984, 2001; Bazykin, 1985; Nedorezov, 1986, 1997; Svirezhev, 1987).

**Datasets**

In current publication algorithm described above was applied to time series of pine beauty moth (*Panolis flammea* L.) (Schwerdtfeger, 1944, 1968; Varley, 1949; NERC Centre for Population Biology, Imperial College (1999) The Global Population Dynamics Database, N 3756). Population densities are presented in units "logarithm of individuals (pupae) per squared meter" from 1881 to 1940. Total sample size is equal to 60.

On figure 1 there are graphics of changing of density of pupae of pine beauty moth (curve 2) and logarithm of density (curve 1) in time. These fluctuations look like as periodic process under (very) strong influence of external stochastic factors: hypothesis about periodicity of observed fluctuations cannot be rejected a'priori.

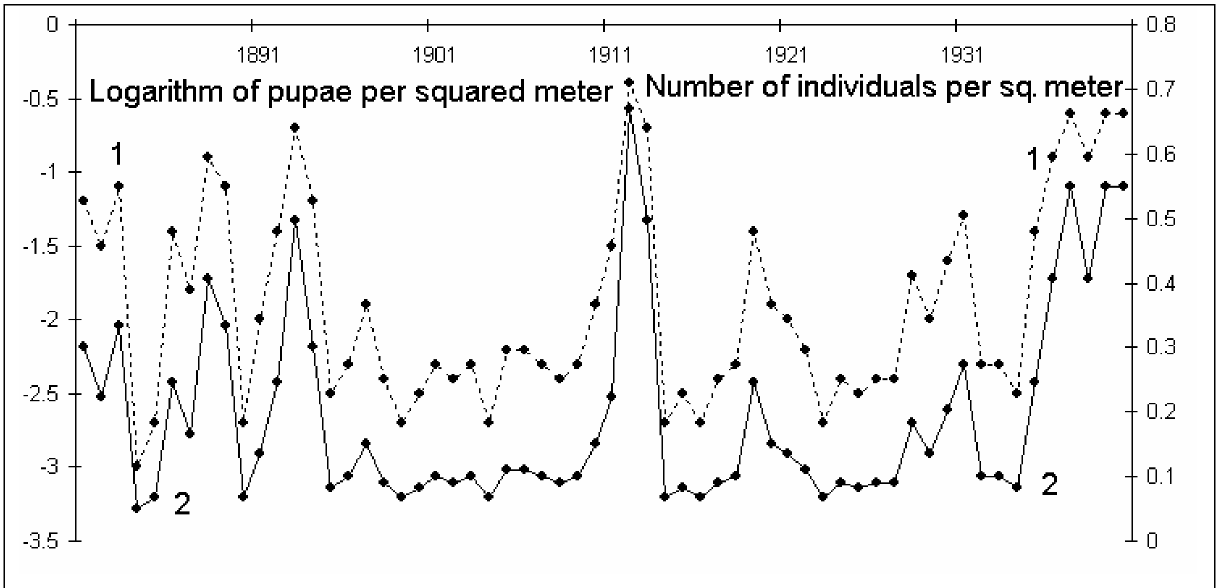


**Fig. 1** Changing in time of logarithm of pupae per squared meter (curve 1, left ordinate line) and density of individuals per squared meter (curve 2, right ordinate line).

**Results**

In table 1 there are the estimations of cycle's coordinates (under the assumptions that one or other attractor is realized for pine beauty fluctuations), and respective values of minimizing functional form $Q$ (it is a sum of squared deviations of real values from the estimated coordinates of cycle; in particular case $Q$ is presented for 2-cycle with formula (1)). It was assumed that maximum length of cycle is 9.

It is obvious that increasing of the length of cycle must lead to decreasing of the value of minimizing functional form $Q$ (as we can see from the table 1, process of decreasing can be non-monotonic). If length of cycle is equal to 60 (it is equal to sample size) $Q = 0$. But in table 1 there is no strong decreasing of $Q$: local minima are observed for 3-cycle, 6-cycle, and 9-cycle. At the same time, differences between values of functional $Q$ are rather small.

If we assume that considering time series correspondents to stochastic fluctuations near one stable level, we have to check Normality of deviations and existing/absence of serial correlation. Kolmogorov – Smirnov test gives $d = 0.2295$, and probability $p < 0.01$ (this is the probability of event that distribution of deviations is Normal); Lilliefors test shows $p < 0.01$; Shapiro – Wilk test: $W = 0.7883$ and $p < 10^{-5}$ (Lilliefors, 1967; Shapiro, Wilk, Chen, 1968;

Bolshev, Smirnov, 1983). Thus, with 1% significance level hypotheses about Normality of residuals must be rejected.

Table 1
Estimations of coordinates of cycles and respective values of sums of squared deviations between theoretical and empirical trajectories

| | 1* | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.193 | 0.2 | 0.156 | 0.217 | 0.182 | 0.19 | 0.207 | 0.276 | 0.136 |
| 2 | | 0.187 | 0.205 | 0.156 | 0.216 | 0.259 | 0.196 | 0.16 | 0.163 |
| 3 | | | 0.219 | 0.184 | 0.239 | 0.259 | 0.186 | 0.201 | 0.258 |
| 4 | | | | 0.217 | 0.174 | 0.121 | 0.227 | 0.16 | 0.222 |
| 5 | | | | | 0.156 | 0.151 | 0.164 | 0.148 | 0.289 |
| 6 | | | | | | 0.179 | 0.195 | 0.152 | 0.261 |
| 7 | | | | | | | 0.174 | 0.165 | 0.102 |
| 8 | | | | | | | | 0.283 | 0.157 |
| 9 | | | | | | | | | 0.126 |
| *Q* | 1.383 | 1.38 | 1.338 | 1.344 | 1.329 | 1.223 | 1.36 | 1.22 | 1.136 |

*1-cycle is stationary level

Durbin – Watson criteria (Draper, Smith, 1986, 1987) is equal to 0.773, and it means that in sequence of residuals there is a serial correlation (for sample size 60 and one predictor critical values of this criterion for 5% significance level are following: $d_L = 1.549$ and $d_U = 1.616$; and $d_L = 1.383$ and $d_U = 1.449$ for 1% significance level).

If we assume that observed fluctuations correspond to 2-cycle *abab...*, we have to divide initial sample on two sub-samples $x_1$, $x_3$,… and $x_2$, $x_4$,…, and to analyze two sequence of deviations. For first sub-sample $x_1 - a$ , $x_3 - a$ ,… the following results were obtained: Kolmogorov – Smirnov test – $d = 0.232$ , $p < 0.1$; Lilliefors test – $p < 0.01$; Shapiro – Wilk test – $W = 0.79017$ , $p = 0.00004$. For the second sub-sample $x_2 - a$ , $x_4 - a$ ,… obtained results are following: Kolmogorov – Smirnov test – $d = 0.2524$ , $p < 0.05$ ; Lilliefors test – $p < 0.01$ ; Shapiro – Wilk test – $W = 0.7682$ , $p < 0.00002$. Thus, with 1% significance level hypotheses about Normality for every sub-samples must be rejected. Durbin – Watson criteria is equal to 0.7618: in sequence of residuals there is a serial correlation.

In tables 2-8 there are the results of analyses of sets of deviations between coordinates of cycles and time series. Application of Durbin – Watson criteria showed that for 3-cycle $d = 0.7199$ , for 4-cycle $d = 0.7339$ , for 5-cycle $d = 0.7316$ , for 6-cycle $d = 0.6597$ , for 7-cycle $d = 0.7697$ , for 8-cycle $d = 0.6896$ , for 9-cycle $d = 0.7679$ .

Table 2

Results of analyses of deviations between time series and 3-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.156±0.027 | 0.244/p<0.2 | p<0.01 | 0.766/p=0.00028 |
| 0.205±0.039 | 0.276/p<0.1 | p<0.01 | 0.75/p=0.00017 |
| 0.219±0.036 | 0.2/p>0.2 | p<0.05 | 0.833/p=0.0028 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

Table 3

Results of analyses of deviations between time series and 4-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.217±0.044 | 0.318/p<0.1 | p<0.01 | 0.765/p=0.00136 |
| 0.156±0.026 | 0.274/p<0.2 | p<0.01 | 0.82/p=0.00671 |
| 0.184±0.034 | 0.203/p>0.2 | p<0.1 | 0.82/p=0.00667 |
| 0.217±0.051 | 0.257/p>0.2 | p<0.05 | 0.79/ p=0.00275 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

Table 4

Results of analyses of deviations between time series and 5-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.182±0.031 | 0.255/ p>0.2 | p<0.05 | 0.884/ p=0.0998 |
| 0.216±0.056 | 0.27/p>0.2 | p<0.05 | 0.693/p=0.00071 |
| 0.239±0.05 | 0.288/p>0.2 | p<0.01 | 0.804/p=0.01047 |
| 0.174±0.044 | 0.268/p>0.2 | p<0.05 | 0.782/p=0.00587 |
| 0.156±0.039 | 0.268/p>0.2 | p<0.05 | 0.667/p=0.00041 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

Table 5

Results of analyses of deviations between time series and 6-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.19±0.042 | 0.178/p>0.2 | p>0.2 | 0.861/p=0.0778 |
| 0.259±0.06 | 0.183/ p>0.2 | p>0.2 | 0.866/p=0.09028 |
| 0.259±0.054 | 0.223/ p>0.2 | p<0.2 | 0.884/p=0.1433 |
| 0.121±0.033 | 0.38/p<0.1 | p<0.01 | 0.595/p=0.00005 |
| 0.151±0.045 | 0.404/p<0.1 | p<0.01 | 0.537/p=0.00001 |
| 0.179±0.046 | 0.223/ p>0.2 | p<0.2 | 0.759/p=0.00464 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

Table 6

Results of analyses of deviations between time series and 7-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.207±0.058 | 0.285/ p>0.2 | p<0.05 | 0.817/p=0.03187 |
| 0.196±0.039 | 0.236/p>0.2 | p<0.15 | 0.857/ p=0.0892 |
| 0.186±0.054 | 0.257/p>0.2 | p<0.1 | 0.772/p=0.00975 |
| 0.227±0.075 | 0.324/p>0.2 | p<0.01 | 0.738/p=0.00394 |
| 0.164±0.052 | 0.289/p>0.2 | p<0.05 | 0.718/p=0.00356 |
| 0.195±0.05 | 0.231/p>0.2 | p>0.2 | 0.838/p=0.07196 |
| 0.174±0.042 | 0.28/p>0.2 | p<0.1 | 0.786/p=0.0204 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

Table 7

Results of analyses of deviations between time series and 8-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.276±0.061 | 0.268/p>0.2 | p<0.1 | 0.851/p=0.09661 |
| 0.16±0.041 | 0.289/p>0.2 | p<0.05 | 0.805/p=0.03201 |
| 0.201±0.061 | 0.273/p>0.2 | p<0.1 | 0.812/p=0.03808 |
| 0.16±0.06 | 0.388/p<0.15 | p<0.01 | 0.659/p=0.00077 |
| 0.148±0.058 | 0.479/p<0.1 | p<0.01 | 0.528/p=0.00004 |
| 0.152±0.033 | 0.292/p>0.2 | p<0.1 | 0.797/p=0.03822 |
| 0.165±0.028 | 0.236/p>0.2 | p>0.2 | 0.839/p=0.09696 |
| 0.283±0.083 | 0.248/p>0.2 | p<0.2 | 0.884/p=0.2446 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

Table 8

Results of analyses of deviations between time series and 9-cycle

| Estimations of coordinates of cycle* | KS[1] | Lilliefors | SW[2] |
|---|---|---|---|
| 0.136±0.036 | 0.397/p<0.2 | p<0.01 | 0.727/p=0.00719 |
| 0.163±0.045 | 0.306/p>0.2 | p<0.05 | 0.734/p=0.00851 |
| 0.258±0.056 | 0.245/p>0.2 | p>0.2 | 0.892/p=0.28386 |
| 0.222±0.063 | 0.238/p>0.2 | p>0.2 | 0.883/p=0.2417 |
| 0.289±0.089 | 0.217/p>0.2 | p>0.2 | 0.87/p=0.18648 |
| 0.261±0.074 | 0.206/p>0.2 | p>0.2 | 0.872/p=0.19173 |
| 0.102±0.015 | 0.235/p>0.2 | p>0.2 | 0.871/p=0.23 |
| 0.157±0.051 | 0.356/p>0.2 | p<0.05 | 0.658/p=0.00216 |
| 0.126±0.042 | 0.432/p<0.2 | p<0.01 | 0.6/p=0.00046 |

*Average ± Standard Error

[1]KS – Kolmogorov-Smirnov test, [2]SW – Shapiro-Wilk test

For all coordinates of 3-cycle and 4-cycle application of Lilliefors test and Shapiro – Wilk test allows rejecting of hypotheses about Normality of sets of deviations with 1% significance level (tables 2 and 3). For 5-cycle in 4 cases we have to reject hypotheses about Normality of sets of deviations with 1% significance level, and in one case we have to reject Null hypothesis with 5% significance level (table 4).

For 6-cycle (table 5) the situation is much better: in 3 cases the Null hypothesis must be rejected with 1% significance level but in other 3 cases Null hypothesis cannot be rejected even with 5% significance level. For 7-cycle (table 6) in 3 cases Null hypothesis must be rejected with 1% significance level, and in 2 cases hypothesis must be rejected with 5% significance level, and in 2 cases Null hypothesis must be rejected with 10% significance level.

For 8-cycle (table 7) in 2 cases Null hypotheses must be rejected with 1% significance level; in 3 cases hypothesis must be rejected with 5% significance level, and in 2 cases hypothesis must be rejected with 10% significance level. For 9-cycle in 4 cases hypothesis must be rejected with 1% significance level (table 8), but in other 5 cases it cannot be rejected with 10% significance level. Thus, taking into account results obtaining for 1% significance level we can conclude that best situations are observed for 8-cycle and 9-cycle. But these results don't allow saying that observed fluctuations of pine beauty moth correspond to these dynamic regimes. Moreover, application of Durbin – Watson criteria showed that for all considering situations we found strong serial correlation in sequences of residuals.

## Non-traditional approach to problem

Within the limits of traditional approach to analysis of the correspondence between theoretical and empirical datasets it is assumed, for example, that all deviations have zero averages and finite equal dispersions. Moreover, it is assumed that distribution of deviations is Normal.

Modelling and analysis of process of data collection within the limits of very simple mathematical model of individual's migrations showed (Nedorezov, 2012, 2013 b) that we have no reasons for assumption about Normality of collected datasets. It is obvious a'priori that this is unrealistic assumption. We have to check some other properties of initial samples, in particular:

- symmetry of sample (with respect to origin) that can be provided with Kolmogorov – Smirnov test, Mann – Whitney test, Lehmann –Rosenblatt test, and some other tests,
- monotonic decreasing of density function (absence of local minima).

In other words, we have to be sure that deviations have uni-modal density function, and maximum of density function is in origin. Note that these two requirements are not as strong as a requirement of correspondence to Normal distribution.

If these two requirements are observed for set of deviations hypotheses about absence of dependencies in a sequence of residuals must be checked. It can be provided with various tests, and, in particular, with Durbin – Watson test (Draper, Smith, 1986, 1987), analyzing behavior of autocorrelation function etc.

If all used tests show that there are no correlations in a sequence of residuals (for selected significance level Null hypothesis about absence of correlation cannot be rejected) we have to analyze a correspondence between theoretical curve and empirical datasets. This analysis must contain the following basic steps:

- comparison of increments for theoretical and empirical trajectories; we have to compare number of cases when we have “positive-positive” behaviour and “negative-negative” behaviour with number of cases when we have “positive-negative” and “negative-positive” behaviour; dividing first number on total number (sample size minus one) we get a frequency of “successful” results; after that we have to check hypothesis about equivalence of this frequency to 0.5 (we have a positive result if we have to reject this hypothesis);
- comparison of signs of “second derivatives” which can be estimated with formula:

$$x_k^{''} \approx \frac{x_{k+1} - 2x_k + x_{k-1}}{h^2},$$

where $h$ is time step. Taking into account that time interval between two nearest measurements is equal to one year in formula we can put $h = 1$. Like in previous case we have to calculate the value of frequency of cases when we have the same signs for theoretical and empirical time series, and reject Null hypothesis that this frequency is equal to 0.5. If we cannot reject hypotheses about equivalence of the respective frequencies to 0.5 it means that we haven’t good background for conclusion that considering model gives good fitting of empirical time series.

This line of tests can be continued. It doesn’t mean that we have to check a correspondence between all possible “derivatives” (it is limited by sample size and requirements to used model). But two first steps pointed out above must be obligatory.

In table 9 there are the results of application of Mann – Whitney test, Lehmann – Rosenblatt test, and Kolmogorov – Smirnov test (for two independent samples) to sets of deviations of empirical values from estimated coordinates of cycles. It was pointed out above that distribution of deviations must be symmetric with respect to origin. For checking of this hypothesis every set of deviations was transformed into two subsets: positive values $\{e_i^+\}$ and negative values $\{e_i^-\}$. It is obvious, if distribution of deviations is symmetric with respect to origin distribution function $F(x)$ for $\{e_i^+\}$ must be equal to distribution function $G(x)$ for $\{-e_i^-\}$. Null hypothesis for Lehmann –Rosenblatt test, and for Kolmogorov – Smirnov test is $F(x) = G(x)$. For significance level $\alpha = 0.001$ critical level for Lehmann –Rosenblatt test is 1.17. Thus, for all cycles (tabl. 9) we have to reject Null hypotheses. The similar results were obtained for Kolmogorov – Smirnov test: in 7 cases we have to reject Null hypothesis with 1% significance level; in 2 cases this hypothesis can be rejected with 10% significance level.

Table 9
Results of application of Mann – Whitney test, Lehmann –Rosenblatt test, and Kolmogorov-Smirnov test

| Cycles | MW[1] | LR[2] | KS[3] |
|---|---|---|---|
| 1 | 511/517 | 12.858 | 0.4982/p=0.001 |
| 2 | 503/517 | 13.432 | 0.4286/p=0.009 |
| 3 | 509/517 | 13.743 | 0.4286/p=0.009 |
| 4 | 535/517 | 13.035 | 0.4286/p=0.009 |
| 5 | 540/517 | 11.003 | 0.4505/p=0.005 |
| 6 | 509/506 | 13.326 | 0.35/p=0.058 |
| 7 | 540/506 | 15.296 | 0.475/p=0.003 |
| 8 | 524/526 | 12.798 | 0.3182/p=0.095 |
| 9 | 554/494 | 15.11 | 0.457/p=0.006 |

[1]Mann – Whitney test: Empirical values/Critical values (for 5% significance level); [2]Lehmann –Rosenblatt test; [3]KS is Kolmogorov-Smirnov test for two independent samples

**Discussion**

Provided analysis of dynamics of pine beauty moth showed that best results are observed for 8-cycle and 9-cycle. Results of analysis of these cases are presented in tables 7 and 8. For both cycles Shapiro – Wilk test allows rejecting Null hypotheses with 1% significance level in 2 and 4 cases respectively. These results don't allow saying that observed fluctuations of pine beauty moth correspond to these dynamic regimes.

Analysis of distributions of residuals for all considered situations with the help of Lehmann –Rosenblatt test and Kolmogorov – Smirnov test (for two independent samples) showed that with very small value of significance level we have to reject the hypothesis about symmetry of density functions with respect to origin. It allows concluding that observed dynamics of pine beauty doesn't correspond to stochastic fluctuations near stable level and to cyclic fluctuations in 2,…,9 years.

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