

Algorithm for Experimental Estimation of the Conditional Threshold for the Duration of Low Temperatures Exposure on the Example of the Laboratory-Reared Population of *Lymantria Dispar*

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Abstract: The paper substantiates the introduction of a new parameter into the development model of the laboratory-reared population of *Lymantria dispar*, formulates and mathematically formalizes the parameter, and develops an algorithm for its experimental evaluation. It increases the correctness and adequacy of the mathematical description of the population development in terms of assessing the main parameters of its development used earlier in the model. The obtained results can be used to study the development of laboratory-reared populations of *Lymantria dispar*, as well as to understand the dynamics of population development in the natural environment.

Key-Words: *Lymantria dispar*, laboratory-reared population, development model, algorithm for experimental estimation.

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1 Introduction

Modeling the development of laboratory-reared populations requires a rigorous mathematical formalization of the development process itself. At the same time, it is necessary to formulate model parameters that allow taking into account the impact of certain factors on the process of population development in order to build a correct and adequate model. Modern models do not describe this complex multifactorial process in sufficient detail even under conditions of long-term observation of the population. Therefore, their clarification and addition is an important and urgent task in studying the development of populations. This clarification can take various forms.

For example, there is no general opinion regarding the temperature threshold from which the sum of effective temperatures should be calculated when hatching caterpillars from eggs, when studying the development of *Lymantria dispar* caterpillars. The article in [1] presents different approaches to this issue. At the same time, the approaches are fundamentally different from each other. The concept of some fixed threshold value can be found in most works like [2], [3], [4] and others. However, there are more complex ideas about the threshold values, for example, that they vary depending on the period of eggs stay at low temperatures, [5], or some other factors, [6], [7]. In

this case, it is necessary to supplement the composition of the model parameters and experimentally study the temperature threshold, [8], [9]. At the same time, the introduction of a critical value of the parameter will make it possible to combine these concepts, considering them within the framework of one model. The temperature threshold can be considered constant before reaching the critical value. It can be considered variable after reaching the critical value.

The work in [10], [11], [12] and [13] consider the development of the laboratory-reared population of *Lymantria dispar* in the framework of the Eigen quasispecies model. [14], [15]. Here, the main parameters are singled out for studying their dynamics when fixing external conditions that affect the development of the population. At the same time, the main parameters should tend in probability to some optimal values corresponding to fixed external conditions according to the Eigen model. In this case, the introduction and experimental study of the dynamics of a new model parameter will increase confidence or, conversely, doubts about the correctness of using the Eigen quasispecies model in describing the development of a laboratory-reared population.

Thus, the presented work is aimed at supplementing the development model of the laboratory-reared population of *Lymantria dispar*

with a new parameter and developing an algorithm for its experimental evaluation. It will increase the adequacy and correctness of the development model.

2 Conditional threshold for the duration of exposure to low temperatures as an important factor in the population development

It is known that under natural conditions the formation and development of *Lymantria dispar* caterpillars in the egg occurs in autumn, [7]. They, as a rule, go into diapause after full formation. In the literature, cases of caterpillars' non-diapause development are known both in nature, [16], and under laboratory conditions, [1]. The introduced parameter will not make sense for a non-diapause population since during the development of such a population there is no effect of low temperatures on eggs. However, non-diapause individuals, as a rule, do not complete their development and die under natural conditions, [1]. Laboratory-reared populations in some cases are quite viable, [16]. In this regard, it should be noted that we are talking about diapause populations of *Lymantria dispar*.

It has been established that for the formation of caterpillars in eggs and the normal course of diapause, a sufficient amount of heat in autumn and moderate cold at the beginning of winter are necessary, [7]. It is possible to fix one of the parameters in laboratories. Thus, the sum of effective positive summer-autumn temperatures was recorded for all generations at the level of $+580 \pm 10$ °C for the studied laboratory-reared population. It was experimentally established that with such a sum, the onset of embryonic and temperature diapauses occurs almost simultaneously. The embryonic diapause precedes the temperature diapause in nature. Otherwise, the caterpillars in the eggs are underdeveloped and often die. However, the significantly more complex temperature distribution in nature compared to laboratory conditions does not make it possible to obtain a relatively simple mathematical model.

Further, the egg-laying of the laboratory-reared population is placed in a refrigerator at a temperature of $-2 - +6$ °C. An important issue for constructing a development model is the duration of the period of exposure to low temperatures, during which normal development of caterpillars will be observed. It is obvious that this duration should have upper and lower bounds. Moreover, the concept of a lower bound is not so obvious and can

be interpreted in different ways. Indeed, in fact, we are talking about the minimum value of the period of exposure to low temperatures, at which normal development of caterpillars is possible. However, non-diapause populations of *Lymantria dispar* indicate a zero boundary, especially since we are talking not only about laboratory-reared populations, but also about natural phenomena. Therefore, there is no unconditional duration threshold. On the other hand, the existence of non-diapause populations has not been described in nature, and the habitat of *Lymantria dispar* in nature is limited in the west by 30–60 parallels north latitude, in the east by 50 parallel north latitude and by the northern tropic, [7]. Therefore, we can assume that the normal development of *Lymantria dispar* in nature with a zero unconditional threshold is not observed. At the same time, the unconditional duration threshold is a low-value parameter for formulating a population development model.

Let us introduce the concept of a conditional threshold for the duration of the period of exposure to low temperatures. Various restrictions can be selected as a condition. For example, it is proposed to use the condition of hatching at least a third of viable eggs. Thus, we can write:

$$D \left(t \left| N_+ \geq \frac{N_0}{3} \right. \right) = D_{need \ min}, \quad (1)$$

where D is the duration of the period of exposure to low temperatures; t is the time parameter; N_+ is the number of hatched caterpillars; N_0 is the total number of eggs involved in the experiment; $D_{need \ min}$ is the period duration threshold for exposure to low temperatures.

It should be understood that $D_{need \ min}$ is a parameter that depends both on the sum of effective positive summer-autumn temperatures and on the temperature values during the period of low temperatures. Therefore, it is more correct to characterize it as a conditional threshold for the duration of the period of exposure to low temperatures (provided that at least 1/3 of viable eggs are hatched). This threshold corresponds to a certain value of the sum of effective positive summer-autumn temperatures (for example, $+580$ °C as in the experiments) and the average temperature during the period of low temperatures (for example, $+4$ °C). All fertilized eggs can be considered viable under laboratory conditions.

It should also be noted that when the conditional threshold is reached, the hatching rate is an increasing function. Then the increase is replaced by a decrease. Starting from some value of D ,

caterpillars will stop hatching altogether. The condition for the hatching of at least a third of viable eggs will be fulfilled in a certain range of D values since hatchability is a continuous function of D . Of course, $D_{need\ min}$ will be the minimum value of this segment.

The dynamics of the conditional threshold is an important indicator of population development. In nature, global warming is observed, which leads to a reduction in the period of low temperatures and its gradual disappearance. It means either a reduction in the habitat or the adaptability of the population to new conditions. The first scenario is the most probable with the $D_{need\ min}$ value not changing significantly. If, on the contrary, its value tends to decrease, then this indicates a gradual adaptability and development towards a non-diapause population. Global warming can lead to the formation of a stable natural non-diapause population, especially since such laboratory-reared populations exist and are successfully developing.

3 Algorithm for estimating the conditional threshold for the duration of exposure to low temperatures

3.1 Estimating the value of the conditional threshold for the duration of exposure to low temperatures

Based on the problem being solved, two approaches to estimation are possible: according to the required accuracy and according to the available source material. The first approach assumes the presence of a large amount of biological material (eggs) that can satisfy the required estimation accuracy. We choose a confidence level β (usually 0.95 or 0.99). Then the average value of hatched caterpillars will be in the confidence interval:

$$\left(\bar{N}_+ - \frac{\sigma}{\sqrt{N_0}} t_\beta; \bar{N}_+ + \frac{\sigma}{\sqrt{N_0}} t_\beta \right),$$

with the probability β , where σ is the sample mean-square deviation; $t_\beta = \Phi_0^{-1}\left(\frac{\beta}{2}\right)$, and $\Phi_0(x)$ are the Laplace's function.

In this case, the required sample size (the number of eggs required for the experiment) is determined as follows:

$$N_0 > \left(\frac{\sigma t_\beta}{\varepsilon} \right)^2,$$

(2)

where ε is the prescribed accuracy.

Next, we should determine experimentally or assign the value of the time step. Apparently, a uniform step can be used initially. In fact, this value has a certain meaning, besides a simple time scale. It denotes the period of time during which changes are so serious that they significantly affect the hatching rate. However, most likely, its value is not constant and, at least, depends on the duration of exposure to low temperatures. The following algorithm can be used when experimentally determining the time step. It is necessary to select a certain sufficient number of early egg-laying at the end of the generation development. We divide them into separate batches and, using a different time step value for different batches, estimate the statistically most probable step size. At the same time, we assume that this value will not change significantly for later egg-laying. You can also use the experience of previous generations, if the conditions for their development and the main indicators of the population do not differ notably from each other. In order to insure yourself against possible outliers of early egg-laying in the presence of previous experience, it is possible to estimate the step in two ways, followed by a comparison of these estimates. You can build an integral estimate using weighting factors if it's necessary. The biological material should be removed from the refrigerator and the number of hatched caterpillars should be recorded using the sample size calculated by formula (2) and the time step. As a result, a correlation dependence of the conditionally average number of hatched caterpillars on the duration of the period of exposure to low temperatures will be obtained. Next, it is necessary to identify the trend of this correlation dependence. The trend will be a linear or non-linear functional relationship. Substituting condition (1) into this dependence will give the estimate $D_{need\ min}$. However, it should be understood that the accuracy of this estimate will decrease due to the addition of an error in the approximation of the correlation dependence by a functional trend. This fact should be taken into account especially when using a linear trend as the simplest functional relationship.

The second approach assumes the presence of a limited amount of biological material (eggs). From here it follows, using formula (2), to determine the maximum accuracy of estimating the conditional average value of hatched caterpillars:

$$\varepsilon < \frac{\sigma t_\beta}{\sqrt{N_0}}.$$

(3)

Most likely, we will have to be content with a uniform time step in this case. Its experimental estimation may not be available, as in the first approach. Therefore, we will have to use previous experience, if available, and simple considerations. For example, it hardly makes sense to use a step size of less than one day. In this case, it will be difficult to calculate the effective temperature, which can lead to a decrease in the estimate accuracy. Otherwise, the algorithm for estimating the conditional threshold for the duration of exposure to low temperatures will coincide with the first approach.

3.2 Estimation of the error in the value of the conditional threshold for the duration of exposure to low temperatures

An important issue is not only the estimation of the value of the conditional threshold for the duration of exposure to low temperatures, but also the error estimation. There are two types of errors to consider. The first of them is a statistical error associated with the limited sample N_0 . The second error, as mentioned above, is related to the approximation error. Then the total error will be the sum of these two errors. For the number of hatched caterpillars, the statistical error will be determined by inequation (3). Table 1 provides some data on the estimation accuracy and the sample size required to achieve this accuracy.

Table 1. There are data on accuracy, volume of biological material (eggs) and confidence interval

ε	β	σ	t_β	N_0	Confidence interval
1	0.95	10	1.645	271	$\bar{N}_+ \pm 1$
1	0.99	10	2.326	542	$\bar{N}_+ \pm 1$

The following considerations can be used to estimate the approximation error. It is necessary to calculate the part of the variance of the correlation dependence that is not explained by the functional dependence. For this purpose, we need to calculate the regression residuals ξ_i :

$$\xi_i = (N_+)_i - \hat{N}_+(D_i),$$

(4)

where $(N_+)_i$ are the experimental values of the hatched caterpillars number for the duration of the exposure period to low temperatures D_i ; $\hat{N}_+(D_i)$ are the same values approximated by the functional dependence.

Then the unexplained part of the variance will be equal to:

$$ESS = \sum_{i=1}^n \xi_i^2,$$

(5)

where n is the total number of experimental points.

The approximation error can be estimated as follows using (4) and (5):

$$\hat{\varepsilon} = \sqrt{\frac{ESS}{n}}.$$

(6)

Then for the value of hatched caterpillars we can write: $\bar{N}_+ \pm (\varepsilon + \hat{\varepsilon})$. We use the functional dependence $\hat{N}_+ = f(D)$ to estimate the approximation error in the value of the conditional threshold for the duration of exposure to low temperatures. Substituting the values of $\bar{N}_+ - (\varepsilon + \hat{\varepsilon})$ and $\bar{N}_+ + (\varepsilon + \hat{\varepsilon})$ for \hat{N}_+ , we obtain, respectively, the values of D_{min} and D_{max} . Then we have:

$$\left\{ \begin{array}{l} \bar{D}_{need\ min} = \frac{D_{max} + D_{min}}{2}; \\ \delta = \frac{D_{max} - D_{min}}{2}. \end{array} \right.$$

(7)

δ is the required error in estimating the value of the conditional threshold for the duration of exposure to low temperatures in system (7). It also includes the statistical error (limitation of the sample) and the error in approximating the experimental correlation dependence $(N_+)_i = f(D_i)$ by the functional dependence $\hat{N}_+ = f(D)$.

Thus, a new indicator is introduced in the work in the form of a conditional threshold for the duration of the period of exposure to low temperatures. This indicator allows you to control the stability of external conditions when growing a laboratory population of *Lymantria dispar*. Permissible values of the percentage of hatching of caterpillars from eggs with the help of this indicator are transformed into the minimum required duration of the period of exposure to low temperatures. It is very useful when developing a plan for rearing generations of the laboratory population. Since this

indicator is reasonable and is associated with the main parameters describing the development of the laboratory population.

4 Experimental part

4.1 Experimental material

14 egg-laying of the semiannual laboratory-reared population of *Lymantria dispar* were selected, [12], [13], [17] for the experimental study. This is the seventh generation of the population grown in artificial laboratory conditions. Data on the studied parameters for previous generations are shown in Table 2.

Table 2. There are data on the studied parameters of six generations of the semiannual laboratory-reared population of *Lymantria dispar*

Year	Genera- tion designati on	D, days	N ₀	Hatching, %	T _{hat} ^{min} , °C	T _{hat} , °C
2018	F0	No data	280	89	90	100
2018	0,5F1	49	62	82	153	230
2019	0,5F2	133	100	95	72	106
	0,5F3a	42	22	50	170	306
2019	0,5F3b	42	27	89	133	224
	0,5F4a	153	100	66	89	119
2020	0,5F4b	153	100	45	89	119
	0,5F5a	35	50	84	151	216
2020	0,5F5b	38	50	88	135	229
	0,5F5c	86	50	94	73	95
	0,5F6a	97	50	94	110	130
2021	0,5F6b	102	50	48	110	131

Table 2 uses the designations: T_{hat}^{min} is the hatching threshold, which denotes the minimum sum of effective positive temperatures from +6 °C, after which caterpillars hatch, [17]; T_{hat} is the average sum of effective temperatures, which denotes the average value of the sum of effective positive hatching temperatures of all hatched caterpillars from +6 °C, [17].

At the same time, the sums of effective positive temperatures from +6 °C at the egg stage fluctuated in the range of +580...+590 °C. This parameter can be considered constant taking into account the estimation errors. The ambient temperature was +20...+25 °C during this period. A total of 768 fertilized eggs were used in the experiments.

4.2 Experimental results

All experimental material was divided into 10 parts and was exposed to low temperatures in the range of -2...+2 °C for different periods of time. Then the eggs were taken out of the refrigerator for hatching at a temperature of +20...+25 °C. The hatched caterpillars developed normally to the adult stage in all ten batches. The results of the evaluation of the parameters studied during the experiment are presented in Table 3.

Table 3. There are data on the studied parameters of the semiannual laboratory-reared population of *Lymantria dispar*

Population labeling	D, days	N ₀	Hatching, %	T _{hat} ^{min} , °C	T _{hat} , °C
0,5F7a	34	51	39	175	289
0,5F7b	44	77	83	173	262
0,5F7c	56	83	37	160	198
0,5F7d	64	137	94	137	169
0,5F7e	74	89	97	130	148
0,5F7f	84	84	95	135	152
0,5F7g	94	36	97	160	171
0,5F7h	105	85	75	124	146
0,5F7i	116	46	78	130	167
0,5F7j	148	90	32	150	171

Figure 1 shows the experimental data (Table 3) and the approximation of the experimental data by a third-order polynomial.

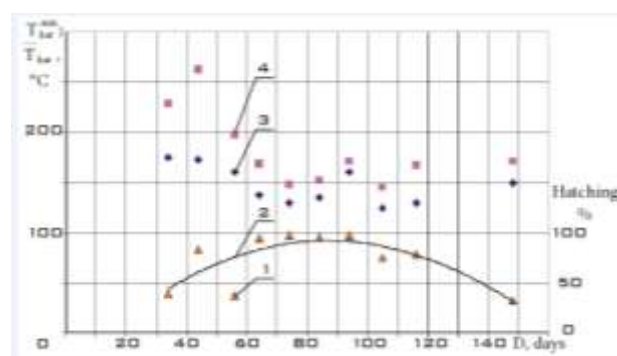


Fig. 1. There are experimental data and approximation: 1 is hatching, 2 is approximation of the hatching, 3 is minimum sum of effective positive temperatures from +6 °C, after which caterpillars, 4 is average sum of effective positive temperatures from +6 °C, after which caterpillars

In this case, the estimated value is $\bar{D}_{need\ min} = 29\ days$ or, taking into account errors (3) and (6), is $D_{need\ min} = 29 \pm 8\ days$. One can obtain an estimate of the upper bound on the duration of exposure to low temperatures arguing in a similar way. We calculate $\bar{D}_{need\ max} = 147\ days$ using the approximation in Figure 1. Taking into

account errors (3) and (6), we obtain:
 $D_{need\ max} = 147 \pm 8\ days$.

Thus, it was found that for the duration of exposure to low temperatures $D \in [37, 139]\ days$, the condition $N_+ \geq \frac{N_0}{3}$ will almost certainly be met in the experiment course.

5 Conclusion

Thus, this paper describes a new parameter for the development of the laboratory-reared population of *Lymantria dispar*, which is a conditional threshold for the duration of exposure to low temperatures. An algorithm for estimating this parameter using experimental data is given. The calculation of the estimation error is presented. This parameter can be used to study the applicability of the Eigen quasi-species model for the correct description of the development of the laboratory-reared population of *Lymantria dispar*.

The presented parameter can be interpreted more broadly than it is described in this paper. Depending on the problem being solved, condition (1) can be replaced by another condition. At the same time, the presented studies can be considered as an example of the parameter formation for a specific task posed in this paper.

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