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Influence of Biotic and Abiotic Factors on the Duration of Development of the Spongy Moth *Lymantria dispar* (L.) (Lepidoptera: Erebidae) in the West Siberian Population of Different Latitudinal Origin

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Abstract—The study of the effect of biotic and abiotic factors on the duration of development of the spongy moth (*Lymantria dispar* (L.)) and the establishment of thresholds for the development of stages in individuals of the West Siberian population of different latitudinal origins (56°33′ N, 76°37′ E) (northern part of the range) and (53°44′ N, 78°02′ E) (central part of the range) has been carried out. We analyze possible ways to accelerate the development of individuals of this species in the northern part of the range: reducing the number of instars, increasing the developmental rate of instars without reducing their number, and lowering the development thresholds. It is found that the reduction in the number of larval instars is not a significant factor of the analyzed effect in this population. The threshold of late embryonic development in the West Siberian population is significantly lower than that defined for populations of the European part of Russia, and a lower threshold for the development of individuals in the northern part of the population with a low sum of effective temperatures (SET) of early embryonic development is noted. The SET of early embryonic development has a significant impact on the acceleration of the development of active stages on the northern border of the area, and the smaller it is, the higher the impact. The high plasticity of the adaptation of the species to temperature conditions allows the spongy moth to become established in new, more northern regions. This plasticity is provided both by natural selection and the reduction in threshold temperatures of development and by epigenetic mechanisms that allow adjusting the rate of development depending on the temperature conditions of the habitat.

Keywords: *Lymantria dispar* (L.), temperature thresholds of development, sum of effective temperatures, developmental biology, climate change

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INTRODUCTION

Global climatic processes lead to changes in the range boundaries of species. Territories that had been previously unavailable to species such as the spongy moth *Lymantria dispar* (L.) (Lepidoptera: Erebidae) become more favorable for penetration. However, the establishment of a species in new territories requires the maintenance of a minimum number that would allow the population to be preserved without regard to migration (Tobin et al., 2009). In the northern part of the range, one of the leading factors of mortality is temperature conditions. In winter, when the spongy moth experiences unfavorable conditions in the state of diapause and quiescence, the most important factor is frost reaching the point of maximum hypothermia (Madrid and Stewart, 1981; Waggoner, 1985; Andersen et al., 2001). However, at formally low atmospheric temperatures, the spongy moth is an ecologically plastic species, including in an ethological context. In particular, depending on the climatic zone, the spongy moth lays its eggs in different biotopes (Kurenshchikov et al., 2020). In the conditions of the flat part of Western Siberia, almost all egg masses are laid on the base of a tree trunk and covered with a layer of snow, where the temperature does not down below −5°C (Martemyanov, unpublished data). This is also confirmed for other populations of this species, where the thickness of the snow cover plays a significant role in the increase in the population size (Inoue et al., 2019). At the same time, in mountainous conditions, insects prefer to lay their eggs on rocks, where the temperature also does not even come close to the atmospheric minimum (Ananko et al., 2022). Thus, for this species, the heat availability of the growing season may turn out to be the most limiting factor even under conditions of a pronounced sharply continental climate with extreme winter temperatures. Forecasts created on the basis of CLIMEX modeling indicate the advance of the species for hundreds of kilometers with a change in the average annual temperature by 2–3°C (Vanhanen et al., 2007; Yasyukevich et al., 2013). The northward movement of the species is also confirmed by field observations. Thus, the species is found 200 km north of the previously established boundaries (Ilyinykh and Krivets, 2011). Along with the change in climatic conditions observed in recent decades, northern populations can develop adaptive mechanisms for successfully moving into less favorable temperature conditions. It is believed that a decrease in the sum of effective temperatures (SET) necessary for development is one of the mechanisms of adaptation of species of the family Erebidae (Leach) to a lack of heat availability and instability of weather conditions as they move north (Kozhanchikov, 1950). It is quite possible that such a mechanism can also manifest itself at the intraspecific level.

Since insects are poikilothermic animals, to calculate both the SET of the development of individuals in the population and the heat availability of the growing season of the region in which monitoring is carried out, a temperature threshold for the development of individuals is required. In the literature, different thresholds for the development of the spongy moth are noted depending on the stage and population. Thresholds of spring development of embryos before hatching according to different authors vary from 3 to 7°C (Meshkova, 2009; Johnson et al., 1983). Thresholds of larval development vary from 6 to 10°C (Carter et al., 1992; Meshkova, 2009; Vanhanen et al., 2007; Limbu et al., 2017). For pupae, the threshold of development is indicated at 10°C (Kozhanchikov, 1950) and 9°C (Ilyinsky and Tropin, 1965). For the summer–autumn development of embryos, the threshold is 6.8°C (Kozhanchikov, 1950) and 7°C (Ilyinsky and Tropin, 1965). According to Gray et al. (2001), the threshold for the development of this stage is 10°C.

In the Russian literature (Kozhanchikov 1950; Ilyinsky, Tropin, 1965), it is indicated that, for spring–summer development from the late embryonic stage to adults, 930–990 degree days are required above the development threshold of 7°C and, for early embryonic (summer–autumn) development over 7°C, 300–320 degree days. According to these data, the development of the longest active stage, the larval stage, requires 650 degree days for males and 730 for females (Ilyinsky and Tropin, 1965). However, based on the data obtained in laboratory studies, this is not its physiological limit of development. Thus, in a laboratory line grown for several dozen generations under constant conditions on an artificial diet (Keena and O'Dell, 1994) at an average daily temperature of 23.3°C with selection for a high rate of development, males develop in 31.6 days and females in 35.8 days, which, at a developmental threshold of 7°C, gives 515 and 584 degree days of larval development SET, respectively. These data may indicate the achievement of a certain limit of the SET of the development of the species, which is significantly lower than the classical ideas about the development of natural populations. Experiments on growing natural populations showed a slightly larger SET of larval development: 588 degree days (27.6 days) for males and 651 (31.2 days) for females at $T = 28$°C (Casagrande et al., 1987).

Based on the analysis of pheromone monitoring of the spongy moth in populations of different latitudinal origins, we found that, in the northern part of the spongy moth range, the SET required to reach the adult stage is significantly lower than in its more southern parts (Ponomarev et al., 2019). Such a change in the rate of development to adults in the northern part may be associated with different mechanisms of adaptation to the reduced heat availability of the region. In particular, we found that the SET obtained during early embryonic development affects not only the "wintering" of spongy moth embryos, but also the rate of development of the subsequent stages of ontogeny of individuals of this species. (Ponomarev et al., 2016). In addition, changes in the rate of development from the late embryonic stage to adults can be affected by changes in the developmental thresholds of different stages.

The aim of the study was to find out the influence of biotic and abiotic factors on the duration of development of the stages of the spongy moth and the establishment of thresholds for the development of these stages in the same geographical population but of different latitudinal origins.

EXPERIMENTAL

The object of the study was the West Siberian population (Novosibirsk oblast). According to the literature data (Ilyinykh and Krivets, 2011), the northern boundary of the range of the spongy moth in this population is located at a latitude of 57° N. Egg masses of spongy moth for experiments were collected in 2020 in birch stands near the village of Kyshtovka (56° 33′ N, 76° 37′ E) (northern part of the range) and city of Karasuk (central part of the range) (53°44′ N, 78°02′ E). Stands in the area of Kyshtovka are included in the taiga forest zone, West Siberian south taiga plain region; stands in the area of the city of Karasuk are included in the forest steppe zone, West Siberian subtaiga forest steppe region (Order of the MPR..., 2014).

The main host plant species of the spongy moth in this population are the silver birch (*Betula pendula* Roth.) and downy birch *B. pubescens* (Ehrh.).

Both locations belong to the formation zones of outbreak locations of the studied species (Ponomarev et al., 2012, Martemyanov et al., 2019). Pheromone monitoring to determine the SET of development to adults in the area of Kyshtovka was carried out in 2019, 2021, and 2022 and in the area of Karasuk in 2013 and 2022 using closed pheromone-baited milk-carton traps with dispensers containing 500 μg (+)-disparlure (made in the United States). During the period of pheromone monitoring, the population at both counting points was in the phase of peak numbers. Males start flight earlier than females; however, the differences in the average date of the emergence of adults of males and females of both the laboratory culture and the wild population are marginal and amount to about 2 days (Keena, O'Dell, 1994). According to a study by Limbu et al. (2017) for Eurasian populations at 50% adult yield, the difference in SET between males and females is about 40 degree days, which at a threshold of 8–9°C and rearing temperature of 25°C is about 2–2.5 days. Taking into account all these points, as well as the fact that the curve of the dynamics of the flight of males is nonparametric, which is confirmed by our calculations using the Kolmogorov–Smirnov criterion, to characterize the flight of adults and calculate the SET of their development, we took the date of the median of the flight of males, which characterizes the flight of about 50% of adults in that location.

The SET of development to adults and the heat availability of the regions were calculated using temperature data from weather stations for these settlements (WMO id: 29405 (Kyshtovka) and 29814 (Karasuk) Weather and Climate website). To calculate the SET of development, we used weather data in the years of monitoring, and to assess the heat availability, weather data for the last 11 years.

Since we previously discovered the influence of temperature conditions of early embryonic development on the rate of development of subsequent stages (Ponomarev et al., 2016), in order to correctly compare individuals from the central and northern parts of the range, the collection of egg masses was carried out during the period of active flight of individuals and certain SETs were set in laboratory conditions.

An additional SET was set by exposure of egg masses after collection in a climatic chamber at a temperature of 24°C. Two levels of SETs were chosen: relatively small (750 degree days) and large (1600 degree days) at a threshold of 7°C. Upon completion of the set of the specified SET, the egg masses were placed in refrigeration equipment to undergo the cold termination of diapause at a temperature 2°C. After the completion of the cold termination, the egg masses were exposed for eclosion simultaneously. For each variant, five Petri dishes with 100 eggs each were exposed at temperatures of 14, 20, and 26°C; humidity of 60–70%; and light mode 14 h a day and 10 h a night. Due to the fact that larvae hatch within several days, individuals for rearing were selected every day, taking into account the share of the total hatching; 50 larvae were selected for each variant. Cultivation was carried out in a single regime on an artificial diet (Ilyinykh, 1996) with the addition of ferrous sulfate. The initial number of eggs was 9000 individuals and, reared larvae, 600 individuals.

The results were analyzed using the Statistica program. Significance of differences in the rate of development was assessed using GRM analysis with a post hoc comparison of mean values according to the Tukey test ($p < 0.05$). The selection of optimal models is made according to the principle of the minimum of the Mallows criterion: C*p* (Mallows, 1973). When analyzing the developmental duration data, the following factors were taken into account: (1) sex: female and male, (2) origin: northern and central parts of the population, (3) early embryonic SET: 750 and 1600 degree days (as discrete predictors), and (4) temperature (as a continuum predictor). Data normalization was carried out by transformation using the function $at = 1/x$. To determine the degree of predictor collinearity, the dispersion inflation factor (VIF) was evaluated.

The effect of temperatures on insect development was assessed using linear regression $y = -a + bx$, where y is the rate of development (1/days of development), X is the temperature, and a and b are the regression coefficients. Development temperature threshold (Tt) was calculated using the formula: $Tt = -a/b$ (Campbell et al., 1974).

RESULTS

The average long-term heat availability of the growing season at a threshold of 7°C in the area of the village of Kyshtovka (northern part of the range) is 1161 ± 41 degree days (mean ± standard error). The average value of the SET of development up to the median of the flight of imagoes according to the results of pheromone monitoring in 2019, 2021, 2022 is 672 ± 35 degree days. In the area of Karasuk (the central part of the range), the heat availability of the growing season is 1534 ± 56 degree days. The average value of the SET of development before the median of flight according to the results of pheromone monitoring in 2013 and 2022 is 870 ± 48 degree days. Despite the lower heat availability in the northern part of the range, due to the higher rate of development of the active stages, most of the eggs laid by females have time to obtain a SET sufficient for the successful completion of early embryonic development and subsequent passage through diapause and wintering.

The acceleration of development to imago is possible in several ways. One way is to reduce the number of instars and the second is to increase the developmental rate of the instars. The third is lowering the development thresholds.

An analysis of the results of larval rearing of the West Siberian population of different latitudinal origins with different SETs of early embryonic develop-

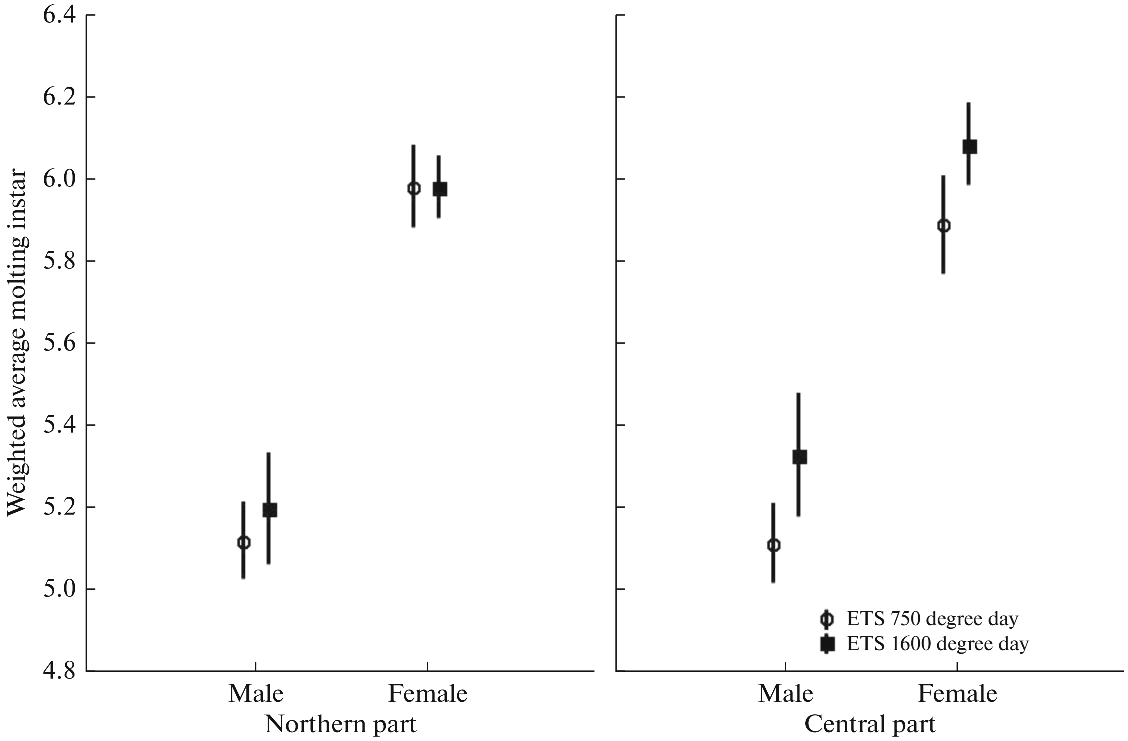

Fig. 1. Number of instars depending on the SET of early embryonic development and latitudinal origin of individuals of the West Siberian population of the spongy moth.

ment and under different temperature conditions of rearing is given below.

An analysis of the number of instars depending on the rearing regimes and the latitudinal origin of the individuals of the bpopulation according to χ^2 showed that the reduction in the number of instars is not a significant factor in increasing the rate of development (Fig. 1). Only a significant increase in the number of instars in males in the central part of the range was noted with an increase in the SET of early embryonic development ($p = 0.021$); in all other cases, $p = 0.4–0.5$.

The survival rate of individuals of different geographic origins does not differ under the same temperature growing conditions: at 14°C, a high mortality rate is observed at the larval and pupal stages, which indicates the general pessimal nature of the conditions for these stages compared to the embryonic one. No variation in the duration of pupal development at the same temperatures was noted. Differences in the duration of development of a pharate larva (a larva of the first instar inside the chorion) depending on the latitudinal origin and SET are significant, but not decisive (Table 1).

The choice of optimal models according to the Mallows criterion describing the influence of factors on the rate of larval development showed that the optimal model includes four predictors: temperature, sex of an individual, SET of early embryonic development, and origin of individuals (Table 2). The effects of the interaction of factors are not observed. The results of the analysis of variance reject the null hypothesis of no effects ($r^2 = 0.83$; $F_{(4.373)} = 467.0$; $p < 0.0001$ with VIF < 1.01).

Temperature conditions and the sex of the individual are expected to play a decisive role. To a lesser extent, the SET of early embryonic development are significant factors in the development of the larval stage: with its increase, the rate of development decreases ($F_{(1.376)} = 16.05$ $p < 0.001$), and geographical origin ($F_{(1.376)} = 4.51$ $p < 0.05$). Differences in geographical origin appear at low temperatures: individuals from the northern part of the population range develop faster than larvae from the central part (Table 1). The regression coefficients for the development rate of larvae before pupation are shown in Table 3.

The calculation of threshold temperatures (Table 4) showed that the lowest threshold temperature for development is in Kyshtovka, but at a low SET of early embryonic development. With a large SET, the threshold changes towards an increase and differs from individuals in the central part of the range.

DISCUSSION

The results allow us to conclude that the reduction in the number of larval instars is not a significant factor acceleration of their development in the northern part of the range, at least in the studied population.

Table 1. Indicators of the development of individuals of the West Siberian population of different latitudinal origins and different SETs of early embryonic development

T, °C	Origin	SET degree days	Pharate larva		Larva		Pupa	
			survival rate* %	duration of development, days	survival, %	duration of development, days	survival, %	duration of development, days
14	Kyshtovka	750	76.2	15.5 ± 0.2a**	34	104 ± 4.0a	18	43.2 ± 1.8
		1600	73.9	17.0 ± 0.1b	34	112 ± 4.0a	30	41.3 ± 1.4
	Karasuk	750	74.3	16.0 ± 0.2c	14	121 ± 6.2ab	28	45.0 ± 2.8
		1600	74.7	15.7 ± 0.1ac	34	128 ± 4.0b	40	40.8 ± 1.6
20	Kyshtovka	750	82	8.3 ± 0.1a	86	47 ± 1.1a	96	16.2 ± 0.2
		1600	74.7	9.9 ± 0.1b	82	51 ± 1.2ab	95	16.5 ± 0.2
	Karasuk	750	85.3	8.5 ± 0.1a	86	48 ± 1.1ab	77	16.7 ± 0.2
		1600	82.4	8.9 ± 0.1c	84	52 ± 1.1b	98	16.7 ± 0.2
26	Kyshtovka	750	84.6	6.8 ± 0.1a	74	35 ± 1.1ab	95	10.7 ± 0.2
		1600	73.1	8.4 ± 0.1b	70	34 ± 1.1ab	93	10.7 ± 0.2
	Karasuk	750	86.4	7.3 ± 0.1c	76	34 ± 1.1a	95	10.7 ± 0.2
		1600	77.9	7.5 ± 0.1d	78	38 ± 1.1b	97	10.8 ± 0.2

* Survival is indicated relative to the previous stage of development.

** Different letters indicate significant differences for a specific stage of development under the same temperature conditions ($p < 0.05$).

Table 2. Selection of optimal models according to the Mallows criterion (C_p = min) to describe the rate of development (1/days of development) of spongy moth larvae before pupation

Model rank	C_p	N*	Temperature	Sex (1)	Summer–autumn SET (2)	Origin (3)	(1) × (2)	(1) × (3)	(2) × (3)	(1) × (2) × (3)
1	**5.6**	**4**	**0.877**	**0.244**	**0.085**	**0.045**				
2	6.8	4	0.872	0.245	0.087		–0.038			
3	8.1	3	0.874	0.244	0.086					
4	9.1	4	0.875	0.245	0.086				0.021	
5	9.6	4	0.874	0.244	0.086					0.014

* Number of factors. Categorical predictors and their interaction are indicated in round brackets.

Table 3. Parameter estimates for the best (C_p = min) of the regression model to describe the rate of development of larvae (1/days of development) before pupation: $y = b_o + \Sigma b_i x_i + \varepsilon_i$

Predictors	Level factor a	b	se	t	$p <$	+95% CI	–95% CI
b_0#		–0.0125	0.00085	–14.7	0.00001	–0.014	–0.011
Temperature		0.00162	0.00004	41.4	0.00001	0.0015	0.0017
Floor	Female	0.00189	0.00016	11.55	0.00001	0.0016	0.0022
Summer–autumn SET	Large	0.00066	0.00016	4.01	0.0001	0.0003	0.0010
Origin	Central	0.00035	0.00016	2.12	0.04	0.00003	0.00067

is the reference level—the expected value of 1/days of development with zero values of continuous predictors and all dummy variables remaining in the model; i.e., here, in b_0, male, small SET (750 degree days), northern origin; t is the criterion for the significance of the linear regression coefficient.

This does not mean that such a mechanism cannot be activated under other conditions, as is evidenced by the data of American researchers on the reduction in the number of instars to five in 80% of females in laboratory culture (F_{15}) selected for a high rate of development (Keena and O'Dell, 1994).

A significant acceleration in the development of individuals to adults during long-term pheromone monitoring was noted by us in the northern part of the Trans-Ural population (Ponomarev et al., 2016) in years preceded by years with very late flights of imagoes, which could be associated with the elimination

Table 4. Threshold temperatures for the development of individuals of the West Siberian population from the central and northern parts of the range with different SETs of early embryonic development

Part of the range/early embryonic SET	Late embryonic development	Larval development	Pupal development	Full development
	Tt	*Tt*	*Tt*	*Tt*
Northern/750	3.2	6.8	9.5	4.8
Northern/1600	2.3	8.3	9.4	7.5
Central/750	3.2	7.5	9.4	6.0
Central/1600	2.3	8.1	9.5	6.2

Tt is the threshold development temperature.

of the offspring of females with slow development that did not receive the SET necessary for successful wintering. A shortening of the duration of development of the offspring of females with a high rate of development is also indicated by data on the characteristics of specimens of the laboratory culture (Keena and O'Dell, 1994).

A significant influence on the acceleration of the development of active stages in the northern part of the range is also exerted by the SET of early embryonic development; the smaller it is, the greater the effect is. For the northern part of the Trans-Ural population in the same work (Ponomarev et al., 2016), it was shown that, when receiving a different SET (420 and 1230 degree days), with a low SET, the duration of development before pupation of both males and females was reduced by 7–8 days, mainly due to a reduction in the duration of development of younger instars, while for in the southern, lower Volga population (Volgograd, 48°42′ N–44°30′ E), a significant reduction in the duration of development was found only in females; the duration of development in males and younger instars of both sexes did not change. These data indicate the epigenetic nature of the change in the rate of development of offspring. According to the results of this study, in the northern part of the West Siberian population, the influence of the SET of early embryonic development is also significant (Table 3) but, at a value higher (750 degree days, Table 1) than in the earlier experiment (420 degree days) (Ponomarev et al., 2016), it is less pronounced.

An assessment of temperature thresholds for the development of different stages (Table 4) showed that the threshold of late embryonic development in the West Siberian population is significantly lower than the threshold established for the populations of the European part of Russia at 6°C (Ilyinsky and Tropin, 1965) and closer to the temperature threshold for the development of this stage established for North American populations at 3°C (Johnson et al., 1983). Considering the high survival rate of embryos under different temperature conditions of cultivation (Table 1), the reliability of these values is quite high. Larval development thresholds slightly differ from the literature data, but given the high mortality rate of larvae and pupae at 14°C rearing, they require additional clarification. The threshold of pupal development coincides with the literature data and does not depend on the origin or SET. The lower threshold of complete development of individuals in the northern part of the population with a small SET of early embryonic development may be one of the reasons for the successful passage of the life cycle under conditions of limited heat availability in this part of the range.

CONCLUSIONS

The high plasticity of the type of adaptation to temperature conditions allows the spongy moth to develop new, more northern regions. This plasticity may be due to natural selection and a decrease in the threshold temperatures of development, as well as due to epigenetic mechanisms that make it possible to adjust the rate of development depending on the temperature conditions of the habitat.

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CONFLICT OF INTEREST

The authors confirm that there is no conflict of interest.

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