ISSN 1067-4136, Russian Journal of Ecology, 2021, Vol. 52, No. 6, pp. 514–522. © Pleiades Publishing, Ltd., 2021.
Russian Text © The Author(s), 2021, published in Ekologiya, 2021, No. 6, pp. 450–459.

Influence of the Density Dynamics Phase and External Conditions on the Manifestation of the Group Effect in Gypsy Moth *Lymantria dispar* (L.)

V. I. Ponomarev[a], *, G. I. Klobukov[a], V. V. Napalkova[a], E. M. Andreeva[a], and I. A. Kshnyasev[b]

[a] *Botanical Garden, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*

[b] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*

**e-mail: v_i_ponomarev@mail.ru*

Received August 11, 2020; revised April 16, 2021; accepted April 25, 2021

Abstract—Based on the long-term laboratory rearing of gypsy moth larvae on an artificial diet with different modifications, which were taken from egg masses in the same forest area in different phases of the population dynamics, we have studied the effect of biotic and abiotic factors on the duration of the development and survival rate of larvae at younger instars in the group- and solitary-rearing regimes. It is shown that the duration of larval development at younger instars is influenced by the sum of effective temperatures at the early embryonic stage of development, as well as by the duration of embryo exposure to temperatures below the developmental threshold and by the food composition. The effect of the group rearing regime (group effect) on the rate of larval development is associated with the population dynamics phase; its most significant positive effect has been recorded in the eruptive period. It has been revealed that the response of larvae to the food composition through the development duration differs in different rearing regimes, depending on the population density phase. With respect to the food composition, the group effect can be determined both by the acceleration of larval development in the group regime and by the deceleration of larval development in the solitary rearing regime. The studied effects have been quantitatively assessed.

Keywords: gypsy moth, group effect, younger instars, eruptive phase, food composition, density-dependent phenomena in populations

DOI: 10.1134/S1067413621060102

While reaching a high density during outbreaks, insects face problems, such as increased competition for food substrate and space [1, 2], increased pressure from predators and parasites [3, 4], and acceleration of the spread of infectious diseases [5, 6]. However, the mortality rate during the period of high density is often lower than the expected level as a result of physiological and behavioral changes determined by the high density of individuals [7]. B.P. Uvarov [8], who was one of the first to reveal density-dependent population effects in locusts, called them "phase polymorphism." This phenomenon, which can be considered as a component of the Allee effect [9], is termed the "group effect" [10].

The group effect is defined as the structural and functional features of a species that depend on the population density (different colors of insect integuments, accelerated development as a result of aggregation, changes in the oxygen consumption rate in aquatic animals, etc.) [11]. E. Wilson [12] characterizes the group effect as a behavioral or physiological change at the species level due to signals that are not oriented in space or time.

It is most relevant to study the group effect in species with periodic outbreaks, since the patterns of this effect make it possible to more completely understand the processes that occur in populations of these species when their density increases. With account of the variety of factors influencing the group effect, the optimal way to study this phenomenon is to use a species that develops well under laboratory conditions at fixed abiotic parameters on a diet with constant composition. Gypsy moth *Lymantria dispar* (L.) corresponds to these requirements; however, long-term studies of the group effect have not yet been carried out for this species.

The purpose of this research is to analyze the manifestation of the group effect in gypsy moth, depending on the food composition, abiotic conditions of development, and phase of the gradation cycle of the parental generation.

MATERIAL AND METHODS

The objects of this research were larvae of the Trans-Ural population. The main host species for this population are silver birch (*Betula pendula* Roth) and

downy birch (*B. pubescens* Ehrh.). Gypsy moth egg masses were collected for experiments from the birch stand near the village of Pokrovskoe (Kamensk-Uralsk district, Sverdlovsk oblast, 56°28′ N and 61°37′ E). The stand consisted of silver birch (quality class II, age 70–80 years, relative density 0.7). There was an outbreak of gypsy moth with a strong and continuous defoliation of stands in this area from 2005 to 2011. A significant increase in the population density was also recorded in 2016–2017. In these years, an outbreak with significant defoliation was recorded throughout the southern part of Sverdlovsk oblast and in the adjacent regions (Kurgan and Tyumen oblasts). In the egg mass sampling area, the density increased according to the prodromal type, without significant defoliation. Egg masses were collected in August–September (not less than 50 egg masses per year). The egg mass density is given in Table 1. The eggs from masses were mixed to neutralize the effect of genetic differences on the results.

Larvae that hatched from egg masses were reared in the group and solitary regimes on a standard artificial diet (AD) [13] in a climatic chamber at 26°C and 60% humidity; the photoperiod was 14 h day : 10 h night.

The following aspects were taken into account during the planning of the experiments:

(1) The container volume per larva should be comparable at different densities to determine the stable values of the contribution of intraspecific contacts to the group effect [14]. Therefore, solitary larvae were kept in Petri dishes with a volume of 10 mL until reaching the third instar and group larvae were kept in Petri dishes with a volume of 100 mL (20 larvae per dish at the first instar and ten individuals per dish at the second instar). The choice of the larva as an experimental unit both in the group and solitary rearing regimes is determined by the fact that the choice of the container as an experimental unit leads to additional effects that make it difficult to interpret the results [14].

(2) The sum of effective temperatures (SET) accumulated over the larval hatching period influences both the duration of further larval development and the manifestation of the group effect [15]. Therefore, the experiments were started after the appearance of not less than 80% of larvae within 2 days. Larvae that hatched on the same day were selected for rearing and larvae that hatched before that day were removed from the container.

(3) Since a number of researchers believe that the group effect is determined by the intensification of physiological processes [16], ADs with addition of iron sulfate ($FeSO_4 \cdot 7H_2O$) at the rate of 150 mg per 500 g of the food for activating metabolic processes [17] were used in some experiments involving larvae, the embryos of which received different summer–autumn SETs and, accordingly, developed at different rates [18].

The summer–autumn SET, accumulated over the period of early embryonic development and diapausing, was calculated based on the results of annual pheromone monitoring in the study area according to the meteorological station data [19]. Temperatures above the threshold level of 6°C were recorded from the date of the emergence median (the date when more than half of adults emerged from pupae). We recorded data for the period before the stable transition of mean daily temperatures to the level below the threshold value or before placing the eggs in refrigeration equipment at temperatures of 0...2°C for "overwintering" (the cold termination of embryonic diapause) (in variants with the artificial variation of the summer–autumn SET) [20]. The data on the year of egg mass collection, summer–autumn SET received by embryos, dates of hatching from clutches, overwintering duration, rearing regime, and diet are given in Table 1.

Larvae were reared taking into account the duration of their development at the first and second instars and their mortality. The results were statistically processed using the standard STATISTICA 6.0 software package. The survival rate of larvae at the initial instars was analyzed by the method of generalized linear models (GLZ) using logit regression; the effect of rearing conditions on the development duration was analyzed by the method of general regression models - GRM (the dependent variable is the development duration, which previously was normalized by taking it's log).

Collinearity of predictors was estimated by calculating the variance inflation factor (VIF). We took into account both continuous predictors ((1) overwintering duration (days), i.e., the period with temperatures close to 0°C, and (2) summer–autumn SET (degree days) accumulated before the onset of overwintering) and categorical factors, (3) type of AD (with or without addition of $FeSO_4$), (4) phase of population dynamics (outbreak or other periods) (the years with the population density of more than 0.5 egg masses per tree were classified as outbreak years, since outbreak foci of this species begin to be recorded at this density [16]), and (5) rearing regime (solitary or group rearing). Continuous predictors (summer–autumn SET and overwintering duration) were converted to the range from 0 to 1. The interaction of the latter three predictors was also included in the analysis. The optimal models for the GRM analysis were selected from the list of competing models according to the principle of the minimum of Mallows' C_p test [21]. The effects were considered statistically significant at $p < 0.01$.

RESULTS

Analysis of the data on larval mortality showed that the important conditions for the larval survival at the first instar were the type of diet and pattern of early embryonic development (the optimal SET for the suc-

Table 1. Years of egg mass sampling, rearing conditions and regimes, and mortality rate of gypsy moth larvae of the Trans-Ural population

Year of sampling	Egg mass density, pcs./tree	Summer–autumn SET, degree days	Hatching date	Rearing regime (pcs.), 1st instar/2nd instar	Overwintering duration, days	Number of larvae, pcs.	Mortality, 1st/2nd instars, %
Rearing on the standard AD							
2008	3–4	385	29.01.09	20/10	132	100	5/48
				1/1		50	8/9
2009	15–20	490	01.02.10	20/10	116	60	33/13
				1/1		100	4/0
2010	15–20	660	22.02.11	20/10	138	60	4/0
				1/1		100	10/33
2011	10–12	660	30.01.12	20/10	147	40	11/0
				1/1		90	15/27
2012	0.2	440	09.02.13	20/10	128	100	23/10
				1/1		50	16/2
2013	0.1	510	06.02.14	20/10	118	100	32/16
				1/1		50	34/9
2014	0.02	320	20.04.15	20/–*	192	100	59/–*
				1/1		40	0/45
2015	0.02	350	29.04.16	20/10	217	100	30/44
				1/1		50	10/18
2016	0.3–0.4	730	23.03.17	20/10	175	100	11/12
				1/1		50	7/2
2017	0.7	350	10.02.18	20/10	130	100	33/42
				1/1		51	22/10
2017	0.7	350	27.02.18	20/10	147	100	18/11
				1/1		50	12/7
2018	0.02	775	23.03.19	20/10	147	100	6/2
				1/1		50	8/2
Rearing on the AD with $FeSO_4$							
2008	3–4	385	29.01.09	20/10	132	100	6/1
				1/1		50	5/48
2012	0.2	440	09.02.13	20/10	128	100	20/4
				1/1		50	8/0
2017	0.7	350	27.04.18	20/10	147	100	16/7
				1/1		50	6/2
2018	0.02	775	23.03.19	20/10	147	80	4/1
				1/1		50	6/0

* Rearing was carried out until the 25th day; all the individuals that did not reach the third instar were eliminated.

cessful completion of embryogenesis and transition to the diapausing state) (Table 2). Group rearing does not lead to a significant increase of the mortality rate; however, the survival rate increases in the group regime during outbreaks. The addition of iron compounds to the AD increases the survival rate under the group rearing regime and during outbreaks in general. At the second instar (Table 3), the mortality increases under the group rearing regime; this is apparently due to the cannibalism, which is not manifested at the first instar [22].

Analysis of the duration of development of the first instar showed that the optimal model included six predictors ($F_{6,2072} = 82.94$, $p < 0.0001$): (1) type of diet, (2) overwintering duration, (3) summer–autumn SET, (4) population density phase, and two paired interac-

Table 2. Assessment of the effect of the conditions of development of the embryonic and larval stages of gypsy moth on the rate of survival to the second instar using generalized linear models (GLZ)

Predictors	Factor level	*b*	*se*	Wald	*p*	95% CI	
b_0#		1.597	0.128	155.64	<0.001	1.35	1.85
Summer–autumn SET (0–1)		**1.074**	**0.179**	**35.98**	**<0.001**	**0.72**	**1.42**
Overwintering (0–1)		0.055	0.214	0.07	=0.798	–0.36	0.47
AD [1]	**$FeSO_4$**	**0.300**	**0.093**	**10.28**	**<0.001**	**0.12**	**0.48**
Regime [2]	Group	–0.139	0.092	2.27	=0.132	0.32	0.04
Phase [3]	Outbreak	0.154	0.098	2.49	=0.115	0.04	0.35
[1] × [2]		**0.250**	**0.092**	**7.33**	**=0.007**	**0.07**	**0.43**
[1] × [3]		–0.077	0.094	0.68	=0.410	–0.26	0.11
[2] × [3]		**0.263**	**0.092**	**8.07**	**=0.004**	**0.08**	**0.44**
[1] × [2] × [3]		**0.244**	**0.092**	**6.96**	**=0.008**	**0.06**	**0.43**

Here and in Table 3, the # symbol indicates the reference level (the expected value of the survival rate at zero values of continuous predictors and all dummy variables remaining in the model; i.e., here b_0 refers to solitary rearing on the standard AD during the inter-outbreak period). Categorical predictors and their interactions are in square brackets. Significant effects are in bold.

Table 3. Assessment of the influence of the conditions of development of the embryonic and larval stages of gypsy moth on the rate of survival to the third instar using generalized linear models (GLZ)

Predictors	Factor level	*b*	*se*	Wald	*p*	95% CI	
b_0#		1.09	0.116	88.3	<0.001	0.87	1.32
Summer–autumn SET (0–1)		**1.46**	**0.165**	**78.6**	**<0.001**	**1.14**	**1.79**
Overwintering (0–1)		–0.117	0.201	0.34	=0.561	–0.51	0.28
AD [1]	**$FeSO_4$**	**0.632**	**0.088**	**51.9**	**<0.001**	**0.46**	**0.80**
Regime [2]	**Group**	**–0.221**	**0.086**	**6.53**	**=0.011**	**–0.39**	**–0.05**
Phase [3]	Outbreak	0.063	0.091	0.49	0.485	–0.11	0.24
[1] × [2]		**0.248**	**0.086**	**8.25**	**=0.004**	**0.08**	**0.42**
[1] × [3]		0.073	0.087	0.70	=0.403	–0.10	0.24
[2] × [3]		**0.214**	**0.086**	**6.17**	**=0.013**	**0.05**	**0.38**
[1] × [2] × [3]		**0.294**	**0.086**	**11.6**	**<0.001**	**0.12**	**0.46**

tions, (5) population density phase and larval rearing regime and (6) the population density phase and type of diet (Table 4). Magnitudes of the standardized coefficients serve as a relative measure of the effect value.

The development at the first instar is significantly influenced by the overwintering duration. This period is characterized by the cold termination of diapause, which covers embryos formed at the end of summer. As in the case of the increased period of the summer–autumn SET, the overwintering duration also has a positive effect on the rate of development.

The regression coefficients of predictors of the duration of larval development to the second instar are given in Table 5. The relationship between the overwintering duration and rate of development only at the first instar is possibly determined by the effect of the overwintering duration on the SET accumulated over the larval hatching period: the longer the period of clutch exposure to low temperatures, the earlier and more concurrent the emergence of larvae from them [23]. In our previous laboratory experiments [24], we showed a more rapid development of larvae that were first to hatch and, hence, required a lower SET. The larval development is significantly accelerated by the addition of iron to the AD as an active microelement, which is contained in enzymes and highly active in the ionic form.

The outbreak state of the population also has a positive effect on the developmental parameters compared to the inter-outbreak period. In particular, the interaction of this factor with the conditions of aggregation of individuals and type of diet is of greatest interest. It is during an outbreak when the group effect

Table 4. Standardized regression coefficients and choice of optimal models (C_p = min) describing the duration of development of gypsy moth larvae to the second instar

Model rank	C_p	N	Overwintering	Summer–autumn SET	Phase [1]	AD [2]	Regime [3]	[1] × [2]	[1] × [3]	[2] × [3]	[1] × [2] × [3]
1	**8.78**	**6**	**–0.16**	**–0.12**	**–0.26**	**–0.44**		**–0.25**	**–0.15**		
2	8.84	7	–0.16	–0.12	–0.25	–0.44		–0.24	–0.17		–0.033
3	9.65	8	–0.16	–0.12	–0.25	–0.43		–0.24	–0.17	–0.023	–0.041
4	10.0	9	–0.16	–0.12	–0.24	–0.42	–0.034	–0.23	–0.18	–0.044	–0.054
5	10.4	7	–0.16	–0.12	–0.26	–0.44		–0.25	–0.15	–0.012	
6	10.7	8	–0.16	–0.12	–0.25	–0.44	–0.007	–0.24	–0.17		–0.034
7	10.8	7	–0.16	–0.12	–0.26	–0.44	–0.003	–0.25	–0.15		
8	12.1	8	–0.16	–0.12	–0.26	–0.43	–0.014	–0.25	–0.15	–0.020	
9	42.9	6	–0.15		–0.23	–0.41		–0.20	–0.17		–0.035
10	43.0	7	–0.15		–0.22	–0.41		–0.20	–0.17	–0.029	–0.045

The most optimal model is in bold.

Table 5. Parameters of the best regression model (C_p = min) describing the duration of larval development to the second instar: $\log(\text{days}) = b_0 + \Sigma b_i x_i + \varepsilon_i$

Predictors	Factor level	b	se	$t(2072)$	$p <$	CI	
b_0#		2.32	0.014	160.0	0.0001	2.29	2.35
Overwintering (0–1)		–0.20	0.030	–6.8	0.0001	–0.26	–0.14
Summer–autumn SET (0–1)		–0.11	0.019	–6.0	0.0001	–0.15	–0.08
Population density phase [1]	Outbreak	–0.09	0.009	–9.4	0.0001	–0.11	–0.07
AD [2]	$FeSO_4$	–0.17	0.009	–19.4	0.0001	–0.18	–0.15
Regime [3]	Group	–	–	–	–	–	–
[1] × [2]		–0.08	0.009	–9.4	0.0001	–0.10	–0.06
[1] × [3]		–0.05	0.007	–7.4	0.0001	–0.06	–0.04

#, reference level (the expected value of log (days) at zero values of continuous predictors and all dummy variables remaining in the model, i.e., here b_0 refers to solitary rearing on the standard AD during the inter-outbreak period). Categorical predictors and their interactions are in square brackets.

is positive and the presence of iron in the feed enhances the effect.

The picture somewhat changes when larvae reach the third instar. Here, the optimal model also includes six predictors ($F_{6.1761}$ =170.3, $p < 0.001$ at VIF not more than 1.48). The main factors maintain their effect, except the overwintering period; at the same time, three of these factors—the population density phase, type of diet, and rearing regime—begin to interact with each other (Table 6).

The coefficients of regression of the duration of larval development to the third instar are given in Table 7. The contribution of the summer–autumn SET to the acceleration of larval development continues to be significant. The most significant factor is addition of iron to the AD, which accelerates the larval development during outbreaks. The effect of group rearing on the rate of development was observed only during outbreaks and the effect of other predictors did not change.

Analysis of differences in the development rate of larvae to the third instar showed that the development rate was higher during outbreaks and lower during other phases of population dynamics in the group regime than in the solitary regime. At the same time, the differences in this parameter are significant only in the inter-outbreak period on the AD with addition of $FeSO_4 \cdot 7H_2O$ (Fig. 1).

DISCUSSION

Numerous studies on representatives of different insect orders (Orthoptera, Lepidoptera, Blattodea, Hymenoptera, etc.) indicate similar trends in the manifestation of the group effect, which are often expressed in such processes as a decrease of the devel-

Table 6. Choice of optimal models (C_p = min) describing the duration of larval development to the third instar

Model rank	C_p	N	Overwintering	Summer–autumn SET	Phase [1]	AD [2]	Regime [3]	[1] × [2]	[1] × [3]	[2] × [3]	[1] × [2] × [3]
1	**4.55**	**6**		**–0.15**	**–0.10**	**–0.65**		**–0.28**	**–0.16**		**–0.06**
2	6.26	7	–0.012	–0.15	–0.11	–0.65		–0.28	–0.15		–0.06
3	6.38	7		–0.15	–0.10	–0.65		–0.28	–0.16	–0.009	–0.06
4	6.55	7		–0.15	–0.10	–0.65	–0.001	–0.28	–0.16		–0.06
5	8.10	8	–0.012	–0.15	–0.10	–0.65		–0.28	–0.16	–0.008	–0.06
6	8.26	8	–0.012	–0.15	–0.11	–0.65	–0.001	–0.28	–0.16		–0.06
7	8.28	8		–0.15	–0.10	–0.64	–0.007	–0.28	–0.16	–0.013	–0.06
8	9.58	5		–0.15	–0.11	–0.65		–0.29	–0.13		
9	10.00	9	–0.012	–0.15	–0.10	–0.65	–0.008	–0.28	–0.16	–0.012	–0.06
10	11.34	6		–0.15	–0.11	–0.65		–0.29	–0.13	0.009	

The most optimal model is in bold.

Table 7. Parameters of the best regression model (C_p = min) describing the duration of larval development to the third instar: $\log(\text{days}) = b_0 + \Sigma b_i x_i + \varepsilon_i$

Predictors	Factor level	b	se	$t(1761)$	$p <$	95% CI	
b_0#		2.71	0.008	323.0	0.0001	2.70	2.73
Summer–autumn SET		–0.11	0.014	–7.6	0.0001	–0.14	–0.08
Phase [1]	Outbreak	–0.03	0.006	–4.3	0.0001	–0.04	–0.01
AD [2]	$FeSO_4$	–0.19	0.006	–29.8	0.0001	–0.20	–0.17
Regime [3]	Group	–	–	–	–	–	–
[1] × [2]		–0.07	0.006	–11.5	0.0001	–0.09	–0.06
[1] × [3]		–0.04	0.006	–7.2	0.0001	–0.05	–0.03
[1] × [2] × [3]		–0.02	0.006	–2.7	0.001	–0.026	0.004

#, reference level (the expected value of log(days) at zero values of continuous predictors and all dummy variables remaining in the model, i.e., here b_0 refers to solitary rearing on the standard AD during the inter-outbreak period. Categorical predictors and their interactions are in square brackets.

opment period of population individuals (or its increase for some species), a decrease in their average size, a decrease in their mortality and fertility, an increased melanization of integumentary tissues, and an increased motor activity [2, 8, 25, 26]. This effect also involves the enhancement of the immune activity, which is indirectly associated with the intensification of the phenol oxidase system and increase in the production of hemocytes [7].

The positive effect of high density on the developmental parameters in eruptive phyllophagous species, such as gypsy moth, is observed mainly in larvae at the first and second larval instars. In gypsy moth, the group effect is expressed primarily in its decreased mortality and an increased rate of its development [26–29]. The above-mentioned effects may be indirectly associated with changes in the enzyme activity of the digestive system under the group rearing regime [30], which influences the efficiency of food substrate digestion, as well as with an intensification of the phenol oxidase system [31] as a nonspecific stress response of the body to the increased density [5]. In some cases, there are no differences in the mortality rate [29, 31, 32] and development rate [29] between the larvae of this species that were kept at different levels of density.

We previously showed a significant variation in the degree of manifestation of the group effect in different years of laboratory rearing, depending on the food composition and indicators of population adaptation. Significant differences in the vector of manifestation of the group effect were revealed between different substrates during the low density period: a positive or negative effect during feeding on birch foliage or its absence during feeding on the AD [34]. The group effect on the AD was positive in the first years of outbreak and was absent on birch foliage [15]; however, it was unclear whether this was determined by the phase of population density dynamics or by some other factors.

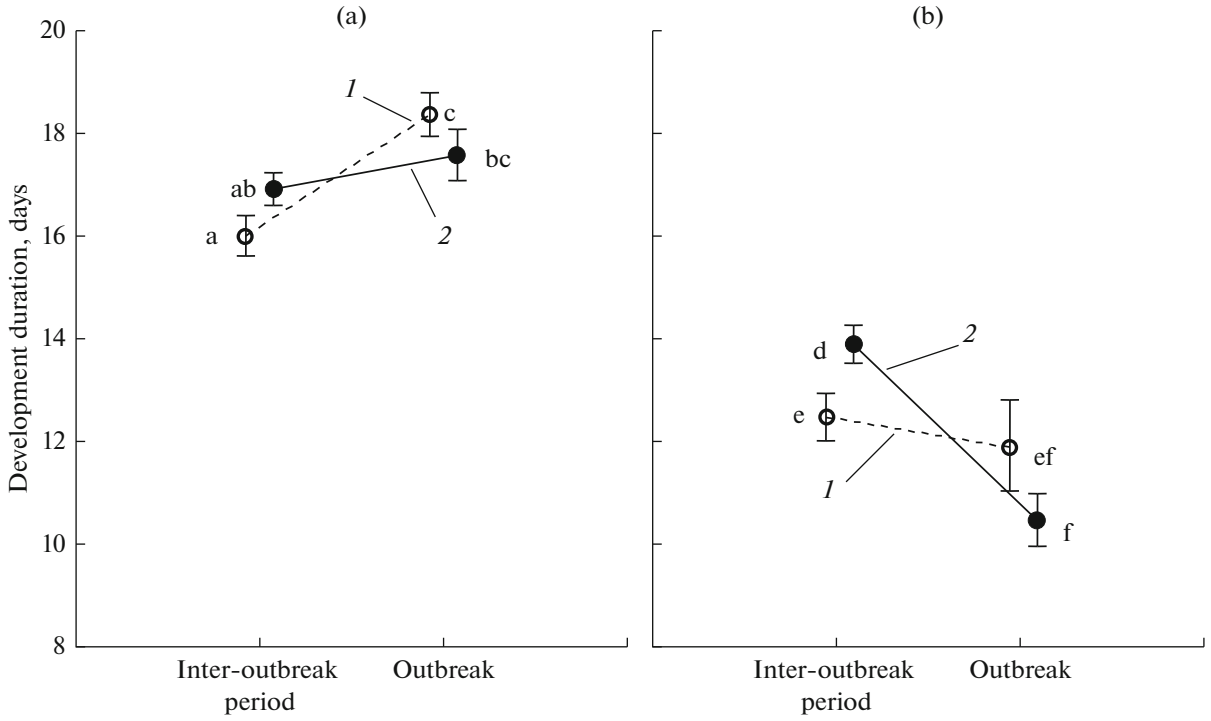

Fig. 1. Influence of the phase of population dynamics, type of diet ((a) standard AD, (b) AD with $FeSO_4$), and rearing regime ((1) solitary rearing, (2) group rearing) on the duration of larval development to the third instar ($F_{(1,1761)} = 7.03$, $p = 0.008$). Dots indicate the weighted average values; the error indicates the 95% confidence intervals ($\bar{x} \pm$ CI 95%). Significant differences calculated by Scheffe's test for multiple comparisons at significance threshold $p < 0.05$ are indicated by different letters.

The results of our study show that the response of larvae to the food composition differs under different rearing regimes, depending on the population density phase. On the standard AD, the developmental rate during the outbreak period does not change in the group regime, while it significantly slows down in the solitary regime. The absence of differences in the duration of development on the standard AD during the outbreak and inter-outbreak periods in the group rearing regime is apparently explained by the superimposition of the influence of the diet, since solitarily reared larvae significantly slow down their development during an outbreak. The observed phenomenon is possibly associated with changes in food preferences at different phases of the gradation cycle. This issue requires additional research, since there are literature data on the extension of the list of food plants during outbreaks [20, 35].

The situation is opposite when larvae are reared on the AD with $FeSO_4$: in this case, the larval development significantly accelerates in the group rearing regime during an outbreak. This suggests that the intensification of the physiological processes does not cause the manifestation of the group effect [16].

Under natural conditions, outbreaks are accompanied by a higher development rate and, as a consequence, earlier phenological periods of oviposition by gypsy moth females and an increase in the summer–autumn SET accumulated by embryos before the onset of cold spells. According to the analysis (see Tables 6 and 7), the value of the summer–autumn SET is significant along with other factors; however, it is not determining in the manifestation of the group effect.

As a result, this research revealed a significant influence of the phase of gypsy moth population dynamics on the manifestation of the group effect, which, in turn, positively influences the rate of larval development during the eruptive phase. The absence of the group effect or its negative manifestation that were previously recorded by us and other authors [29, 32–34] are possibly associated with the phase of dynamics of density of the initial population.

FUNDING

This study was performed under the state assignment of the Botanical Garden of the Ural Branch, Russian Academy of Sciences, and supported by the Russian Science Foundation (project no. 20-64-46011).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

1. Dethier, V.G., Food-plant distribution and density and larval dispersal as factors affecting insect populations, *Can. Entomol.,* 1959, vol. 91, no. 9, pp. 581–596. https://doi.org/10.4039/Ent91581-9
2. Applebaum, S.W. and Heifetz, Y., Density-dependent physiological phase in insects, *Annu. Rev. Entomol.,* 1999, vol. 44, pp. 317–341. https://doi.org/10.1146/annurev.ento.44.1.317
3. Stiling, P., Density-dependent processes and key factors in insect populations, *J. Anim. Ecol.,* 1988, vol. 57, no. 2, pp. 581–593. https://doi.org/10.2307/4926
4. Turchin, P., Taylor, A.D., and Reeve, J.D., Dynamical role of predators in population cycles of a forest insect: An experimental test, *Science,* 1999, vol. 285, no. 5430, pp. 1068–1071. https://doi.org/10.1126/science.285.5430.1068
5. Steinhaus, E.A., Crowding as a possible stress factor in insect disease, *Ecology,* 1958, vol. 39, no. 3, pp. 503–514. https://doi.org/10.2307/1931761
6. Andersron, R.M. and May, R.M., The population dynamics of microparasites and their invertebrate hosts, *Philos. Trans. R. Soc. Lond. B: Biol. Sci.,* 1981, vol. 291, no. 1054, pp. 451–524. https://doi.org/10.1098/rstb.1981.0005
7. Wilson, K. and Cotter, S.C., Density-dependent prophylaxis in insects, in *Phenotypic Plasticity of Insects: Mechanisms and Consequences,* Ananthakrishnan, T.N. and Whitman, T.W., Eds., Enfield, NH: Science Publsihers Inc., 2009, pp. 381–420. https://doi.org/10.1201/b10201-7
8. Uvarov, B.P., *Grasshoppers and Locusts,* Cambridge: Cambridge Univ. Press, 1966, vol. 1.
9. Courchamp, F., Berec, L., and Gascoigne, J., *Allee Effects in Ecology and Conservation,* Oxford: UK: Oxford Univ. Press, 2008. https://doi.org/10.1093/acprof:oso/9780198570301.001.0001
10. Grassé, P.P. and Chauvin, R., L'effet de groupe et la survie des neutres dans les sociétés d'insectes, *Rev. Sci.,* 1944, vol. 82, pp. 461–464.
11. Dedyu, I.I., *Ekologicheskii entsiklopedicheskii slovar'* (Encyclopedic Dictionary of Ecology), Kishinev: Mold. Sov. Entsikl., 1990. http://www.cnshb.ru/AKDiL/0039/Default.Shtm
12. Wilson, E.O., *Sociobiology: The New Synthesis,* Cambridge, MA: Belknap Press, 1975.
13. Il'inykh A.V. Optimized artificial cultivation medium for gypsy moth (*Ocneria dispar* L.), Biotekhnologiya, 1996, no. 7, pp. 42–43.
14. Ponomarev, V.I., Klobukov, G.I., Napalkova, V.V., and Kshnyasev I.A., Influence of experimental conditions on manifestation of the group effect in the gypsy moth, *Lymantria dispar* L., *Russ. J. Ecol.,* 2017, vo. 48, no. 4, pp. 377–383. https://doi.org/10.1134/S1067413617040129
15. Ponomarev, V.I., Shatalin, N.V., and Strelskaya, T.M., Effect of iron ions (Fe^{+3}) added to food on manifestation of group effect in gypsy moth (*Lymantria dispar* L.), Izv. S.-Peterb. Lesotekh. Akad., no. 187, St. Petersburg, 2009, pp. 249–258.
16. Il'inskii, A.I. and Tropin, I.V., *Nadzor, uchet i prognoz massovykh razmnozhenii khvoe- i listogryzushchikh nasekomykh v lesakh SSSR* (Surveillance, Census, and Prediction of Population Outbreaks in Needle- and Leafgnawing Insects in Forests of the Soviet Union), Moscow: Lesnaya Promyshlennost', 1965. https://search.rsl.ru/ru/record/01006414096.
17. Ponomarev, V.I., Andreeva, E.M., Shatalin, N.V., et al., Efficiency of endogenous activators of membrane lipid peroxidation in gypsy moth larvae of different instars, *Izv. Samar. Nauch. Tsentra Ross. Akad. Nauk,* 2009, vol. 11, no.1 (2), pp. 129–131. https://elibrary.ru/item.asp?id=13619367.
18. Ponomarev, V.I., Klobukov, G.I., and Napalkova, V.V., The dependence of morphophysiological parameters of postembryonic stages on temperature conditions during embryonic development in the gypsy moth *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), *Vestn. Tomsk. Gos. Univ., Ser. Biol.*, 2016, no.3 (35), pp. 107–127. https://doi.org/10.17223/19988591/35/7
19. Weather and Climate: Kamensk-Uralsky weather station (synoptic index 28449). http://www.pogodaiklimat.ru/
20. Benkevich, V.I., *Massovye poyavleniya neparnogo shelkopryada v evropeiskoi chasti SSSR* (Gypsy Moth Population Outbreaks in the European Soviet Union), Moscow: Nauka, 1984.
21. Mallows, C.L., Some comments on *C*p, *Technometrics,* 1973, vol. 15, no. 4, pp. 661–675. https://doi.org/10.1080/00401706.1973.10489103
22. Mason, C.J., Cannizzo, Z., and Raffa, K.F., Influence of diet and density on laboratory cannibalism behaviors in gypsy moth larvae (*Lymantria dispar* L.), *J. Insect Behav.,* 2014, vol. 27, pp. 693–700.
23. Ponomarev, V.I., Klobukov, G.I., Ilyinykh, A.V., and Dubovskii, I.M., Adaptation features of diapause duration of the gypsy moth *Lymantria dispar* (L.) from populations of different latitudinal origination, *Contemp. Probl. Ecol.,* 2019, vol. 12, no. 1, pp. 1–9. https://doi.org/10.1134/S1995425519010098
24. Ponomarev, V.I., Ilyinykh, A.V., Gnineko, Yu.I., et al., *Neparnyi shelkopryad v Zaural'e i Zapadnoi Sibiri* (The Gypsy Moth in the Transural Region and Western Siberia), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2012.
25. Long, D.B., Effects of population density on larvae of Lepidoptera, *Trans. R. Soc. Lond. B,* 1953, vol. 104, no. 15, pp. 544–585. https://doi.org/10.1111/j.1365-2311.1953.tb01247.x
26. Peters, T.M. and Barbosa, P., Influence of population density on size, fecundity and developmental rate of insects in culture, *Annu. Rev. Entomol.,* 1977, vol. 22, pp. 431–450. https://doi.org/10.1146/annurev.en.22.010177.002243
27. Leonard, D.E., Effects of density of larvae on the biology of the gypsy moth, *Porhetra dispar* (L.), *Entomol. Exp. Appl.,* 1968, vol. 11, no. 3, pp. 291–304. https://doi.org/10.1111/j.1570-7458.1968.tb02058.x

28. Konikov, A.S., *Regulyatory chislennosti lesnykh nasekomykh* (Regulators of Population Size in Forest Insects), Novosibirsk: Nauka, 1978.

29. Vasil'eva, T.G., Analysis of group effect in the gypsy moth, in *Neparnyi shelkopryad v Srednei i Vostochnoi Sibiri* (The Gypsy Moth in Central and Eastern Siberia), Novosibirsk: Nauka, 1982, pp. 51–58.

30. Lazarevic, J., Peric-Mataruga, V., Vlahovic, M., et al., Effects of rearing density on larval growth and activity of digestive enzymes in *Lymantria dispar* L. (Lepidoptera: Lymantriidae), *Folia Biol.,* 2004, vol. 52, nos. 1–2, pp. 105–112. http://www.isez.pan.krakow.pl/journals/folia/pdf/52(1-2)/17.pdf.

31. Pavlushin, S.V., Belousova, I.A., Chertkova, E.A., et al., The effect of population density of *Lymantria dispar* (Lepidoptera: Erebidae) on its fitness, physiology and activation of the covert nucleopolyhedrovirus, *Eur. J. Entomol.,* 2019, vol. 116, pp. 85–91. https://doi.org/10.14411/eje.2019.009

32. Zlotin, A.Z., Effect of density and chemical treatment of food on the development of *Ocneria dispar* L. cultivated in a laboratory, *Zool. Zh.*, 1965, vol. 44, no. 12, pp. 1809–1812.

33. Kireeva, I.M., *Ekologiya i fiziologiya neparnogo shelkopryada* (The Gypsy Moth: Ecology and Physiology), Kiev: Naukova Dumka, 1983.

34. Ponomarev, V.I., Andreeva, E.M., and Shatalin, N.V., Group effect in the gypsy moth (*Lymantria dispar,* Lepidoptera, Lymantriidae) depending on food composition and popuationparameters, *Zool. Zh.*, 2009, vol. 88, no. 4, pp. 446–453.

35. Montgomery, M.E. and Wallner, W.E., The gypsy moth: A westward migrant, in *Dynamics of Forest Insect Populations,* Berryman, A.A., Ed., New York: Springer, 1988, pp. 354–375.

Translated by D. Zabolotny