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Influence of Experimental Conditions on Manifestation of the Group Effect in the Gypsy Moth, *Lymantria dispar* L.

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Abstract—The effect of rearing conditions for gypsy moth larvae on parameters of their development (its duration and mortality) was studied in experiments with early instar larvae reared singly or in groups. The manifestation of the group effect was analyzed depending on the choice of experimental unit (the larva or the rearing container) and the amount of volume per larva. The observed effects were evaluated quantitatively.

Keywords: gypsy moth, group effect, survival rate, duration of development
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Intensification of intraspecific contacts may lead to changes in the behavior and physiological features of individuals within a population. This phenomenon is termed "group effect" [1]. Edward O. Wilson [2] describes this effect as change in behavior and physiology within the species caused by signals that have no orientation in time or space. This definition gives no qualitative estimation of the effect, i.e., whether group rearing has a positive or negative influence on parameters of individual development. At the same time, other definitions often include an estimation criterion. In particular, it is stated that this effect contributes to survival and reproduction, provides for more effective resource utilization, and stimulates metabolism [3]. The manifestation of group effect in insects is caused by signals of different nature, including visual [4], tactile [5], and chemical stimuli [6]. A considerable effect of group rearing on morphophysiological parameters of insects has been noted by many authors. In eruptive species of phyllophagous insects, such as the gypsy moth *Lymantria dispar* (L.), a positive group effect is manifested mainly in the first and second instar larvae, providing for lower mortality and higher developmental rate [7]. In some cases, however, these parameters do not differ between groups of *L. dispar* larvae kept at different densities [7, 8], or even an increase in mortality is observed among young instars larvae kept in groups [9]. As follows from the definition of group effect [2] and published data on the pattern of its manifestation, this is a multifactor and nonlinear phenomenon.

Analysis of the influence of different signals on the manifestation of group effect is possible only under controlled laboratory conditions, which make it possible to minimize bias caused by unforeseen abiotic conditions. Insects reared in climatic chambers are kept in containers (Petri dishes, plastic cups, etc.). In studies on the group effect, some larvae are reared singly, other in groups. If containers of the same volume are used, an additional possible source of variation appears, namely, resource amount per capita per larva. Another source of variation is a probable influence of larvae of a certain instar on larvae of different instars, which is excluded if groups consist of same-instar larvae. Therefore, prior to planning an experiment, it is necessary to estimate (1) the level of objectivity in the choice of experimental unit and (2) the influence of rearing conditions (container volume) on parameters of larval development.

As defined by Kozlov [10], "The experimental unit is the smallest division of material that can be exposed to the study factor *independently* of other experimental units... The measured (estimated) unit is an element of the experimental unit that serves as a basis for obtaining an individual estimate (measurement). Although the experimental unit plays the role of the smallest independent element of experimental action, it may (but not must) consist of several measured units" (p. 54).

Control larvae in laboratory studies on the group effect are reared singly in individual containers; i.e., the experimental and measured units are identical. The other larvae are reared in groups, and the experimental unit may differ depending on conditions of a given experiment: this may be a container nested within i-level of treatment or a larva within container. In the former case (container), the study object will be

a larva under solitary rearing and a group of larvae under group rearing.

The purpose of this study was to analyze the influence of rearing conditions (container volume per larva, embryo wintering duration, the choice of experimental units) on the results of experiments.

MATERIAL AND METHODS

The study was performed with gypsy moth larvae from two populations. The first, trans-Ural population was represented by two micropopulations from: (1a) birch stands in Kamensk-Uralsky district, Sverdlovsk oblast; egg masses collected in birch stands in the autumn of 2013, in the second year of decline after population outbreak (density 1 egg mass per 10–20 trees); (1b) mixed stands in a park within the Yekaterinburg city limits, proportion of the host tree species (birch *Betula pendula* Roth) about 20%; egg masses collected in the autumn of 2013, when their density slightly increased (1 per 25–50 birch trees) after remaining extremely low (<1 per 100 trees) for 2 years. The second, Western Siberian population was from Karasuksky district of Novosibirsk oblast. Egg masses were collected in birch stands in the autumn of 2013, at a peak of population outbreak (>3–5 per tree).

Experiments were performed with larvae hatched on the same day, taking into account significant differences in the manifestation of group effect depending on the sum of effective temperatures (SET) necessary for hatching [12]. Newly hatched larvae were placed singly or in groups in containers (Petri dishes 100, 50, or 10 mL in volume) with the optimized artificial diet [11] and reared in a climatic chamber at 26°C, 60% air humidity, and 16L : 8D photoperiod.

To evaluate the question of objectivity in choosing the experimental unit, group rearing was performed in three variants. Variant Group 1: the first-instar larvae were kept at a density of 20 ind. per dish and transferred to new 100-mL dishes after molting into the second instar (10 ind. per dish). Their density was maintained constant by adding larvae from other dishes. The experimental (measured) unit was the larva. Variant Group 2: the larvae in groups of 20 were kept in the same 100-mL dishes until the last one molted into the third instar. The experimental unit was the container (dish). Variant Group 3: the larvae kept in groups of 20 were removed from the dish as they molted into the second instar (i.e., their density was decreasing). The experimental unit was the container.

To evaluate the influence of container volume per larva on the manifestation of group effect, the first-instar larvae kept in groups of 20 or 10 were transferred to new dishes after molting into the second instar (10 or 5 larvae per dish, respectively), with their density being maintained constant.

In all experimental variants, the count of larvae molting into the next instar was taken once a day, before noon.

The larvae from the Western Siberian population hatched on March 31 and April 17, 2014; from the Transural population, on February 2 and 26, 2014. As noted above, experiments should have been performed with larvae hatched on the same day. However, the hatching period in the Kamensk-Uralsky subpopulation (in early February) was prolonged, and the larvae that hatched on the second day after its onset were also included in the experiment. In contrast, all larvae from the Yekaterinburg subpopulation hatched simultaneously, on February 26. The situation with the western Siberian population was similar: the larvae started to hatch on March 30, but their number was insufficient, and they were pooled with the larvae hatched on the next day. Hatching on April 17 was synchronous, and the number of larvae was sufficient for the experiment.

Statistical analysis of the duration of larval development was performed using the general regression modeling (GRM), which provides the possibility to evaluate the effects of solitary rearing and different variants of group rearing (parameterized as k – 1 indicator/dummy variables) and to take into account the influence of confounders. Optimal models were selected by the minimum of Mallows C_p-criterion [13]. Variables measured on a ratio scale (duration of development and container volume per larva) were logarithmically (to base 10) transformed prior to analysis.

RESULTS AND DISCUSSION

Table 1 shows the results of experiment on estimating the influence of the choice of experimental unit on the manifestation of group effect. Their analysis revealed no differences either in the duration of development to the second instar or in the mortality rate. However, when the container was used as the experimental unit, standard deviation reached 0.6 days. Since the count of larvae was taken once a day, almost the entire observed variance could be accounted for by the accuracy of measurement. When the larva was the experimental unit (variants Single and Group 1), standard deviations were similar: 2.11 and 2.16 days, respectively (Hartley's F_{max} (99, 49) = 1.05, $p = 0.870$).

Analysis of contribution from the nonidentity of experimental units (containers) to variance in the duration of larval development (Table 2) showed that the additive component of between-container variance in the first instar was negligible (2.95 and 2.83%). This component in the second instar increased 5.46% but remained statistically nonsignificant, while the mortality rate increased significantly, due mainly to cannibalism (88% of the total loss). The duration of development to the third instar in group variants was significantly smaller than in the solitary variant, with

Table 1. Duration of development and mortality rate of larvae reared singly or in groups (20 ind. per container) in 100-mL Petri dishes (Western Siberian population, egg masses collected in 2013)

Variant	Number of experimental units	Number of measurement units	Duration of development, days ± SD		Mortality rate, %	
			to 2nd instar	to 3rd instar	1st instar	2nd instar
Single	50	50	11.1 ± 2.11a	18.3 ± 2.29a	4a	4a
Group 1	100	100	10.8 ± 2.16a	16.8 ± 3.39b	6a	8a
Group 2	20	400	10.6 ± 0.60a	15.2 ± 1.37c	3a	45b
Group 3	20	400	10.7 ± 0.60a	–	5a	–

Variants of group rearing are designated as in Material and Methods (here and in Table 2). Statistically significant differences (F-test, $p < 0.05$) are indicated by different letter indices; statistical significance of differences in mortality rate was estimated by Pearson's χ^2 test; SD is standard deviation per experimental unit.

Table 2. Restricted maximum likelihood (REML) estimates of "between-container" variance. ANOVA with random or mixed effects: the container is a random factor, and the logarithm of the duration of larval development is a dependent variable

Source of variance	$E(\sigma^2)$	ase	Z	p	%
Group 2, development to the second instar					
Container	0.0002	0.0002	1.14	0.253	2.95
Error	0.0077				
Group 3, development to the second instar					
Container	0.0002	0.0002	1.09	0.275	2.83
Error	0.0073				
Group 2, development to the third instar					
Container	0.0002	0.00017	1.26	0.21	5.46
Error	0.0037				

the developmental rate being the highest in the Group 2 variant (Table 10).

A comparison of the time of development to the third instar in Group 1, where all larvae in a container were of the same (second) instar, and in Group 2, where different instars were in the same container, suggested that the acceleration of development observed in Group 2 may be explained by death of larvae with retarded development (figure).

Since the density of larvae within a container changed significantly in the course of their growth, it could be supposed that the change in feeding behavior (switch to cannibalism) was stimulated the insufficiency of individual space. However, this phenomenon can also be explained by contact between the larvae of different instars, with older instars preying on younger instars. Thus, parameters of larval development in groups recorded under laboratory conditions largely depend on the choice of experimental unit. If the larvae are reared in a climatic chamber to study the group effect, the choice of container as the experimental unit is inadequate, because between-container differences in the variance of developmental parameters are negligible; moreover, additional factors appear that may have an effect on these parameters (in particular, cannibalism).

The problem of choosing an appropriate experimental unit is closely related to the problem of pseudoreplication in ecological experiments [14]. The latter problem was concisely formulated by Oksanen [15]: "First, it is impossible to infer causal relationships from unreplicated experiments, because interactions between spatial and temporal variation can then account for apparent treatment effects. Second, logically sound induction of causality can also be prevented by compound treatments (e.g., consistent use of the same growth chamber for the same treatment), because even in this case, there are alternative explanations for the apparent treatment effect. Third, the use of inferential statistics without true replication is not informative, because the null hypothesis that two statistical populations are identical is trivially wrong in the living nature" (p. 27).

The abrupt increase in mortality due to cannibalism in the variant with container taken as the experimental unit is evidence that the use of Petri dishes to study the group effect directly touches upon the second item in the above formulation, which is related to

Table 3. Parameters of development of young instar gypsy moth larvae reared singly or in groups depending on Petri dish volume (egg masses collected in 2013)

mL/number of larvae	Number of larvae	Duration of development, days ± SE		Mortality rate, %		Cannibalism, % of overall mortality
		to 2nd instar	to 3rd instar	1st instar	2nd instar	
Western Siberian population, hatched March 3, 2014						
100/1	50	10.2 ± 0.46bc	16.3 ± 0.67ab	42a	6a	0
10/1	50	10.3 ± 0.37bc	16.8 ± 0.53a	36a	4a	0
100/10	100	11.7 ± 0.26a	17.8 ± 0.49a	36a	5a	0
50/10	100	10.9 ± 0.25b	16.8 ± 0.41a	36a	12a	13
10/10	100	10.1 ± 0.23c	15.4 ± 0.30b	32a	8a	3
Western Siberian population, hatched April 4, 2014						
100/1	50	11.1 ± 0.30a	18.2 ± 0.50e	4a	4ad	0
10/1	50	9.5 ± 0.28b	16.0 ± 0.54bc	0	0	0
100/10	100	10.9 ± 0.23a	17.1 ± 0.36ae	3a	14b	53
100/20	100	10.8 ± 0.23a	16.8 ± 0.36ad	6a	8bd	42
50/10	100	11.2 ± 0.25a	17.4 ± 0.37ae	3a	9bd	50
50/20	100	10.1 ± 0.23b	16.2 ± 0.30bd	5a	1a	33
10/10	100	10.0 ± 0.23b	15.1 ± 0.28c	17b	11b	86
10/20	100	9.6 ± 0.19b	15.1 ± 0.33c	2a	40c	81
Transural population, park in Yekaterinburg, hatched February 6, 2014						
100/1	50	–	16.6 ± 0.55a	30a	0	0
10/1	50	–	16.4 ± 0.35a	38a	2a	0
100/20	100	–	16.5 ± 0.25a	36a	6a	7
Transural population, Kamensk-Uralsky region, hatched February 26, 2014						
100/1	50	–	17.1 ± 0.41a	1a	0	0
10/1	50	–	16.6 ± 0.47a	2a	0	0
100/20	100	–	16.6 ± 0.34a	1a	5	0

Statistical significance of differences in the time of reaching a certain instar between larvae hatched on the same day was estimated by *F*-test ($p < 0.05$); of differences in mortality rate, by Pearson's χ^2 test. Statistically significant differences are indicated by different letter indices; (–) analysis was not performed; SE is standard error.

change in the situation in a dish with an increase in the biomass of growing larvae. Similar results were obtained by American researchers [16], who observed a sharp increase in the rate of cannibalism at high density of larvae in the container (taken as the experimental unit). The negligible between-container differences in the variance of developmental parameters in larvae reared in a climatic chamber (especially at the first instar) are directly related to the third item, since the two statistical populations in this case are almost identical.

With regard to these results, the effect of container volume per larva on the duration of larval development was evaluated taking the larva as the experimental unit, either during solitary rearing or group rearing under corresponding conditions (variant Group 1) (Table 3). Preliminary analysis showed that the rate of larval development increased with an increase in the number of larvae per group. This relationship is well known [7–9].

Differences in the mortality rate among first-instar larvae from the same population may depend on the SET necessary for successful hatching. We have previously noted an increased mortality rate among early instar larvae that require a higher SET for completing embryonic development in spring [12]. It may well be that it is this phenomenon that accounts for the relatively high mortality of the first-instar larvae that were included in experiments on the second day after the onset of mass hatching (on February 2, 2014 and March 31, 2014) (Table 3).

The effect of rearing conditions on the duration of larval development was analyzed by means of generalized regression models. The dependent variable was the duration of development of the larvae reared in the same container until the last one molted into the third instar. Variables measured on a ratio scale (duration of

Table 4. Selection of optimal models (C_p = min) describing the duration of larval development to the second instar: log(days) = $\Sigma b_i X_i$ + e

Model rank	C_p	P	Standardized regression coefficients (β) for predictors X_i				
			duration of wintering	group 1	group 3	single larvae	log (volume per larva)
1	**3.5**	**3**	**–0.107**			**–0.205**	**0.229**
2	4.5	4	–0.098	0.025		–0.197	0.238
3	5.5	4	–0.107		0.001	–0.205	0.229
4	6.0	5	–0.098	0.038	0.020	–0.188	0.238
5	17.7	3		0.060		–0.155	0.258

Here and in Table 6, P is the number of predictors, excluding the intercept (b_0, Group 2); boldface indicates the best model.

Table 5. Parameters of the best regression model (C_p = min) describing the duration of larval development to the second instar: log(days) = $\Sigma b_i X_i$ + e

Predictors	b	se	t(2081)	$p <$	95% CI	
b_0#	1.065	0.016	64.66	0.0001	1.032	1.097
Single larvae (x = 1)	–0.051	0.008	–6.74	0.0001	–0.066	–0.036
Duration of wintering, days	–0.0003	0.0001	–4.50	0.0001	–0.0002	–0.0004
Volume per larva, log(mL/n)	0.043	0.006	7.80	0.0001	0.032	0.054

The # symbol indicates the reference level, or the expected log(days) value at zero values of continuous predictors and all indicator/dummy variables remaining in the model; i.e., here b_0 combines all three variants of group rearing (Groups 1–3); CI is confidence interval.

development and container volume per larva) were converted into logarithmic form. Collinearity of predictors was estimated by calculating the variance inflation factor (VIF).

The model found to be optimal for the first instar includes three predictor variables: duration of wintering (the period with temperatures below the developmental threshold that the embryos survived prior to the onset of incubation for hatching), solitary/group rearing, and container volume per larva (Table 4).

ANOVA rejected the null hypothesis about the absence of effects (F(3; 2081) = 29.07; $p < 0.00001$), and VIF did not exceed 2.01, indicating that there was no problem of collinearity between the predictor variables in this parameterization model. Regression coefficients for the model describing the duration of larval development to the second instar are given in Table 5. The duration of the first instar shows no significant dependence on specific features of group rearing in different variants: b(Group 1) ≈ b(Group 3) ≈ 0. An increase in the duration of wintering (hatching on the later date) leads to a slight reduction in this parameter (by only 0.05%). Under conditions of solitary rearing (compared to group rearing), the duration of the first instar is reduced by an average of 5.1% (3.6–6.6%). A tenfold increase in container volume per larva (log10 = 1) will expectedly result in its prolongation by 4.3%.

The optimal model for larval development to the third instar takes into account three factors: container volume per larva; the variant of group rearing where the larvae molting to the next instar were removed from the container and the density of larvae was maintained constant (Group 1), with the larva taken as the experimental unit; and solitary rearing (Table 6). ANOVA rejected the null hypothesis about the absence of effects on the duration of larval development to the third instar (F(3; 1428) = 35.42; $p < 0.00001$), and VIF did not exceed 2.06.

Table 7 shows regression coefficients for the model describing the duration of larval development to the third instar. The onset time of incubation for hatching is irrelevant for this model. A tenfold increase in container volume per larva is expected to prolong the time of development by 4%, irrespective of rearing conditions. The effect of solitary rearing on this parameter is reduced almost to zero, while that of group rearing in the variant with the larva taken as the experimental unit (Group 1) is increased. In other words, the time of development to the third instar in the variant Group 2 (with the larvae remaining in the same container until the last one molted into the third instar and their density increasing significantly) is similar to that in solitary-reared larvae but 2.2% (1.6–2.9%) shorter than in variant Group 1 (with the larvae kept in even-aged groups, maintaining the density of different instars at a relatively equal level).

On the whole, the above data show that a significant influence of the group effect on the duration of larval development (independent of additional factors) manifests itself only at the first instar. A decrease in container volume per larva results in the accelerated development of the first and second instars, regardless

Table 6. Selection of optimal models (C_p = min) describing the duration of larval development to the third instar: log(days) = $\Sigma b_i X_i$ + e

Model rank	C_p	P	Standardized regression coefficients (β) for predictors X_i			
			duration of wintering	group 1	single larvae	log(volume per larva)
1	**3.05**	**3**		**0.22**	**–0.05**	**0.28**
2	5.00	4	0.006	0.22	–0.04	0.28
3	52.80	1				0.18

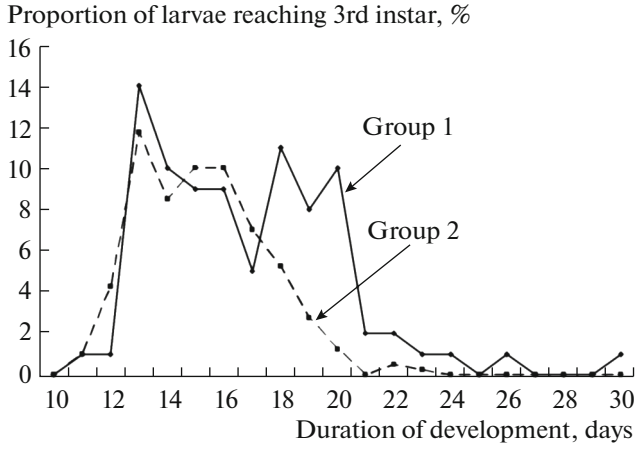
Table 7. Parameters of the best regression model (C_p = min) describing the duration of larval development to the third instar: log(days) = $\Sigma b_i X_i$ + e

Predictors	b	SE	t(1428)	p	95% CI	
b_0#	1.166	0.005	216.5	0.0001	1.156	1.177
Group 1	0.022	0.003	6.6	0.0001	0.016	0.029
Single larvae	–0.006	0.005	–1.2	0.216	–0.015	0.003
Volume per larva, log(mL/n)	0.040	0.005	7.6	0.0001	0.030	0.051

The # symbol indicates the reference b_0 level, or the expected log(days) value at zero values of continuous predictors and all indicator/dummy variables; i.e., here b_0 refers to the Group 2 variant of group rearing; CI is confidence interval.

of rearing conditions. Analysis of the causes of the observed phenomenon is beyond the scope of this study. What is important is that the rate of development increases significantly, but this increase has no relation to the group effect and is caused by some other factors. Further studies are needed to find out what these factors are.

Thus, to obtain consistent results in studies on the role of intraspecific contacts (or their absence) in the group effect, it is necessary to use containers of such size that provide approximately equal volume of space per larva. It should be noted here that almost all researchers dealing with the group effect have adhered to this principle [7, 8, 17, 18]. Studies by Kireeva [9], are an exception, since she has used containers of the same volume regardless of the number of larvae per group. According to her data, the survival rate of early instars decreased significantly with an increase in the number of larvae per group. Moreover, Konikov [17] has emphasizes that the manifestation of the group effect directly depends on the volume per larva, irrespective of group or solitary rearing. Unfortunately, the number of larvae used in his experiment was extremely small (four variants with 16–20 larvae each).



Duration of larval development to the third instar in different variants of group rearing (see Table 1), Kolmogorov–Smirnov test: $d_{max} = 0.27$, $p < 0.001$.

The results of this study provide a basis for certain conclusions. The influence of change in the volume of space per larva on the rate of its development may indicate that the group effect is largely conditioned by aggregation of larvae. The influence of change in the number of larvae per group on the manifestation of this effect may be due to the concomitant change in the volume of space per larva. The choice of experimental unit without preliminary analysis of the effect of this choice on experimental results may give additional problems (not taken into account during analysis) within the experimental unit.

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