=================== **COMPARATIVE AND ONTOGENIC** ===================
PHYSIOLOGY

The First Proof of a Possibility of Change of Temperature Norms of Insect Development as a Result of Artificial Selection for Fast or Slow Development by the Example of the Red Soldier Bug *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae)

S. V. Balashov and V. E. Kipyatkov

Department of Entomology, St. Petersburg State University, St. Petersburg, Russia

Received March 20, 2007

Abstract—For 3—4 generations, selection of the nymphs most rapidly and slowly developing at 28°C was performed in four families of the red soldier bug *Pyrrhocoris apterus* L. In each generation, duration of development of nymphs was determined at 5 constant temperatures from 20°C to 28°C. From these data the linear regression coefficient of the development rate against temperature (the development thermolability coefficient) for each generation was calculated. As a result of the selection the average duration of the nymph development was shortened or increased statistically significantly depending on its direction. The artificial selection for the development duration has been established to change not only this parameter, but also the temperature norms of the insect development. At selection for fast development the regression straight line slope (i.e., the regression coefficient value) increased statistically significantly, i.e., development became more dependent on temperature. As a rule, the temperature threshold of development increased. At selection for slow development the values of the regression coefficient and of the threshold decreased, but these differences were not statistically significant. The effect of artificial selection for the development duration on temperature norms of insect development has been revealed for the first time.

DOI: 10.1134/S0022093008020060

Key words: *Pyrrhocoris apterus*, temperature norm of reaction, thermal parameters of development, artificial selection.

INTRODUCTION

According to the theory of life cycles, physiological norms of poikilothermal animal reaction to temperature are to depend on climate, i.e., to show adaptive geographical variability, as the natural selection optimizes parameters of development and reproduction, by adjusting them to climatic conditions in each local population [1—4]. It is to expect the presence of similar intraspecies geographical variability also for the parameters describing temperature norms of the insect development—the development thermolability coefficient (i.e., coefficient of the linear regression equation of the development rate for temperature), and the temperature threshold of development [5]. Indeed, such variability has been found in several species (reviews [5, 6]).

There are many works in the literature on studying the temperature norms of development of insects from different populations of the same species. A part of species show appreciable stability of development norms overall areal, for example, golden-eyed lacewing *Chrysopa oculeata* [7], sev-

en-spotted ladybird *Coccinella septempunctata* [8], oleander aphid *Aphis nerii* [5]; while the other part—its variability, these changes involving both the temperature threshold—ground beetle *Pterostihus nigrita* [9], the European corn borer *Ostrinia nubilalis* [10], or the thermolability coefficient— mosquito *Toxorhynchites rutilus septentrionalis* [11], or both these parameters—common black ant *Lasius niger* [12], migratory grasshopper *Melanoplus sanguinipes* [13], the Colorado potato beetle *Leptinotarsa decemlineata* [14]. It is obvious that at least some insect species were adapting at diffusion over their areal to environmental conditions by change of the development temperature norms by natural selection.

The adaptive significance of intraspecies geographical variability of temperature norms of insect development is so far poorly understood. There are no clear proofs that it is the result of natural selection. As rightfully indicated by Groeters [5], all studies carried out till now have shown only the presence of interpopulational variability of the development temperature norms in some species, whereas to prove genetic inheritance of the thermolability coefficient and the development threshold, it is necessary to study intrapopulational variability of these parameters, which is a possible object of selection, or to prove a possibility of their change by artificial selection. So far such studies have been carried out by nobody yet.

There are very few works in the literature dealing with artificial selection for insect development duration [15, 16]. Some studies analyze correlated changes of the development duration at selection for the sign of body size [17, 18].

The goal of the present work was to study possible effect of artificial selection on temperature norms of insect development. The task was posed to find out how the thermolability coefficient and the temperature threshold of development would change at selection for the faster or slower rate of development of larvae at some particular temperature.

MATERIAL AND METHODS

The object of the study was the red soldier bug *Pyrrhocoris apterus* that quite fits our requirements due to its easy cultivation and maintenance in lab-

oratory. The imagoes of bugs were collected in Moscow in the spring 2006. During two generations the culture of bugs was kept in laboratory at 24°C and 20/4 light/dark duration, and then was used in the experiment. Males and females were placed pairwise in Petri dishes. Linden seeds were used as forage. Water was given in test tubes closed by cotton. The dishes were inspected once a day and the laid eggs were transported to photothermostats with 20-h light length and temperature varied in ranges 20.0 ± 0.5, 22.0 ± 0.5, 24.0 ± 0.5, 26.0 ± 0.5, and 28.0 ± 0.5°C. The temperatures over 28°C were not applied, as the development rate is too fast at elevated temperatures, which needs more often inspection for more precise measurement of the development duration, which is technically too difficult to perform. The temperature lower than 20°C is extremely unfavorable for development of this thermophilic bug. The temperature was measured using a Tinytalk® autonomous microprocessor sensors recording temperature each hour. This was necessary for more precise evaluation of the experimental temperatures. Larvae were supplied with forage and water and kept at the same temperature as the eggs, at the 20-h light length, which was chosen because it exceeded deliberately the critical duration (17 h 30 min for bugs from the Belgorod region population, after Volkovich and Goryshin [19]) and, hence, does cause formation of the imago diapause. To determine the moment of imago appearance, the nymphs were inspected once a day. In this case, the error of measurements of the nymph development duration amounted to ± 1 day.

Offspring from three females and three males from the original culture was used to create three experimental strains (families) inside which the reproduction and selection were subsequently. In the first generation, initial parameters of dependence of the nymphal development duration on temperature—the thermolability coefficient and the development threshold—were determined for each family (see below). In the same generation the selection was started. The selection for the faster or slower nymphal development was carried out among the individuals developing at temperature 28°C. For this purpose, in the first case, only the individuals were used for strain prolongation, whose larval development was finished foe 2 days

after the imago first appeared among this egg mass. In the second case the bugs with the slowest development were selected—5–6 individuals developed from one clutch, which were winged the last.

The data on nymph development durations (D) at designed temperatures were obtained and compared. The dropped-out values were discarded basing on the criterion equal to the normalized deviation from the drop-out. Then the values reciprocal to development duration— the development rates, $R = 1/D$—were calculated. Assuming the linear dependence of the development of temperature within the limits of the used interval, two coefficients of equation of the linear regression of development rate (R) for the temperature (T) were calculated:

$$R = a + bT,$$

where a—constant, b—linear regression coefficient, which is also the thermolability coefficient. The value of the low temperature threshold (t_0) was determined by extrapolation of the regression straight line down to $R = 0$, according to the formula: $t_0 = -a/b$. Standard errors of the constant and the regression coefficient were obtained by the regression analysis, and the error of t_0 was calculated under the formulas presented in the applied literature [20]. The calculations were carried out using specialized program DevRate 4.1 (© V. E. Kipyatkov, 2006) realized on the basis of Quattro Pro 9.0 software.

To estimate statistical significance of changes of the development duration as a result of the selection during several generations, the regression analysis module of package Statistica 6.0 was used. Statistical significance of differences between generations in the development duration of individuals was estimated by analysis of variance (ANOVA) and the subsequent pair wise comparison of the mean values with *a posteriori* (post hoc) test (Tukey HSD test) using package Statistical 6.0. In the cases of differences of the real mean values of temperature between samples in experiment, the statistical analysis was carried out for recalculation of the development duration for each individual in relation to standard temperatures (20, 22, 24, 26, and 28°C), using the corresponding equation of linear regression obtained in experiments.

Kolmogorov–Smirnov test was used to check normality of distribution. If the distribution of the

development durations differed statistically significantly from the normal one, logarithmic transformation of the data was used. The same transformation was applied in the cases of statistical significant correlation between the means and dispersions. If taking the logarithm did not eliminate the problem, the nonparametric methods (Kruskal–Wallis test) were used. Bartlett test was used to check homogeneity of dispersion. Values of the regression coefficients and the temperature thresholds were compared using Student's criterion.

RESULTS

Because of death of insects we failed to obtain the data on development duration at all five temperature regimes in some generations of the selection. In these cases we were unable to calculate parameters of the regression equation. Especially high lethality was observed at selection for slow development, probably, because of a high percent of insufficiently viable individuals among the insects with delayed development. Therefore, at selection for slow development, it was possible to estimate changes of the development thermolability only in two cases. We were interested first of all in the question whether the selection affected the nymphal development duration at temperature 28°C (Table 1), and then, whether the development temperature norms were changed in this case (Table 2). For convenience, the subsequent analysis of results is carried out in separate families.

Family I. With this family, we managed to perform selection for fast development in five generations, and for the slow one—in three generations. Nymphs of the initial, second, third and fourth generations developed at five temperatures; of the first—at 20, 22, and 28°C, of the fifth—at 20, 22, 26, and 28°C. At selection for fast development, indeed, there was a reduction of the nymphal development duration at 28°C in sequential generations (Table 1), of which statistical significance was confirmed by regression analysis ($F_{1.281} = 30.976$, $p < 0.001$; regression coefficient = -0.74 ± 0.26). Analysis of variance also revealed a statistically significant effect of the "generation" factor on the mean duration of nymphal development (ANOVA; $F_{3.755} = 73.229$, $p < 0.01$). The regression straight lines of the development rate against temperature were calcu-

Table 1. Change of the mean duration of nymphal development at temperature 28°C in three families of red soldier bug as a result of artificial selection for fast and slow development

Families	Parameters	Generation of selection					
		F_0	F_1	F_2	F_3	F_4	F_5
Family I (selection for fast development)	The mean duration	22.8	22.1	24.8	20.5	20.2	20.3
	Statistical error	0.26	0.42	0.35	030	0.25	0.39
	The number of individuals	47	28	103	48	46	11
Family I (selection for slow development)	The mean duration	22.8	–	23.8	25.5	–	–
	Statistical error	0.26	–	0.60	0.50	–	–
	The number of individuals	47	–	7	14	–	–
Family II (selection for fast development)	The mean duration	23.9	26.6	22.9	21.4	21.6	–
	Statistical error	0.31	1.34	0.21	0.33	0.28	–
	The number of individuals	48	7	175	40	8	–
Family III (selection for slow development)	The mean duration	21.9	–	26.2	24.9	26.4	–
	Statistical error	0.27	–	0.40	0.50	0.44	–
	The number of individuals	47	–	83	30	31	–

Note: "–" means that the count was not carried out.

Table 2. Change of temperature norms of nymphal development in three families of red soldier bug as a result of artificial selection for fast and slow development

Family	Direction of selection	Generation of selection	Regression coefficient ± standard error	Temperature threshold ± standard error (°C)	The number of individuals
Family I	For fast development	F_0	0.0037 ± 0.00073 [ab]	16.7 ± 0.15 [a]	299
		F_2	0.0032 ± 0.00105 [ab]	15.6 ± 0.36 [ab]	166
		F_3	0.0042 ± 0.00139 [a]	17.0 ± 0.25 [b]	204
		F_4	0.0045 ± 0.00169 [b]	17.6 ± 0.29 [a]	124
	For slow development	F_2	0.0034 ± 0.00281	15.9 ± 0.71	27
Family II	For fast development	F_0	0.0033 ± 0.00072 [ab]	16.3 ± 0.18 [ab]	294
		F_2	0.0042 ± 0.00127 [a]	17.6 ± 0.30 [a]	253
		F_3	0.0042 ± 0.00146 [b]	17.2 ± 0.26 [b]	136
Family III	For slow development	F_0	0.0039 ± 0.00078	17.1 ± 0.15	354
		F_3	0.0036 ± 0.00163	17.8 ± 0.30	112

Note: Identical letter indexes indicate statistically significant differences between parameters ($p < 0.05$) at comparison using Student's test within each family.

lated for the second–fourth generations. Comparison of the development temperature norms in the sequential generations has shown that the thermolability coefficient increases markedly and statistically significantly by the third and fourth generations of selection, and the temperature threshold was

statistically significantly higher than the initial one in the second and fourth generations.

At selection for slow development, as the initial one, the same generation was used as at selection for fast development. The parameters of development have not been evaluated in the first generation. Nymphs of the second generation were cultivated at the five temperatures mentioned above, the third—at 24, 26, at 28°C. As a result of the selection, there was an increase of the nymphal development duration at 28°C, whose statistical significance in the second and third generations was confirmed by regression analysis ($F_{1.66} = 24.529$, $p < 0.0001$; regression coefficient = 0.85 ± 0.34). The regression straight line of the development rate against temperature was obtained only for the second generation, as nymphs in the third generation finished their development only at 24, 26, and 28°C. Values of the thermolability coefficient and the development threshold in the second generation were somewhat lower in comparison with the initial generation of the selection, but these differences were statistically non-significant. Nevertheless, the analysis of variance has revealed as a whole the statistically significant effect of the generation factor on the development duration at three upper temperatures (24, 26, and 28°C) ($F_{2.199} = 29.7286$, $p < 0.000001$).

Family II. With this family, the selection was carried out only for fast development during four generations. Nymphs of the initial, second and third generations were cultivated at all five temperatures, the first—at 20 and 28°C, the fourth—at 24, 26, and 28°C. Regression analysis has shown in sequential generations a statistically significant reduction of nymphal development duration at 28°C ($F_{1.276} = 24.018$, $p < 0.0001$; regression coefficient = -0.78 ± 0.31). Dispersion analysis has revealed statistically significant effect of the generation factor on the mean duration of the nymphal development ($F_{2.668} = 27.738$, $p < 0.000001$). Regression straight lines of the development rate against temperature were obtained only for the second and third generations. Comparison of the development temperature norms has shown that the values of the thermolability coefficient and the development threshold were markedly and statistically significantly higher already in the second, and also in the third generations of the selection, than in the initial one.

Family III. In this family the selection for slow development was carried out during four generations. The parameters of development in the first generation were not evaluated. Nymphs of the initial and third generations were cultivated at five temperatures, the second—at 24 and 28°C, the fourth—only at 28°C. As a result of the selection, there was a rise of the nymphal development duration at temperature 28°C (Table 2), whose statistical significance in the second—fourth generations was confirmed by regression analysis ($F_{1.199} = 41.969$, $p < 0.0001$; regression coefficient = 1.10 ± 0.33). Reliability of the differences between all generations in the development duration at 28°C has shown by Kruskal—Wallis test as well ($H_{3, N = 191} = 74.58$, $p < 0.0001$). The regression straight line of the development rate against temperature has been obtained only for the third generation. The value of the thermolability coefficient in the third generation was somewhat lower, while of the development threshold—somewhat higher in comparison with the initial generation of the selection, but these differences were statistically non-significant. Nevertheless, the analysis of variance has revealed statistically significant differences in the mean duration of the nymphal development at all five temperatures between the initial and third generations (ANOVA: $F_{1.456} = 84.8$, $p < 0.001$, Tukey Hsd 0.000009).

DISCUSSION

The first result of our studies is demonstration of efficacy of the artificial selection for duration of nymphal development in *P. apterus*. This result, although very important in the context of this work, is to be considered sufficient trivial, as it follows from experience of selection that the artificial selection should lead to a desirable result, only if when the population contains hereditary variability for the specific feature. The development duration is a very important adaptive and undoubtedly inheritable sign that can be affected efficiently by the selection [3].

A considerably more interesting result is the proof that selection for the development duration not only changes this parameter, but also affects thermolability of development, i.e. changes the degree of dependence of the development rate on

temperature. At selection for fast development the slope of the regression straight line of the development rate against temperature (i.e., the value of the linear regression coefficient) is enhanced, i.e. the development becomes more dependent on temperature, more thermolabile. Thus, as a rule, the temperature threshold of development increases. We managed to prove this effect with a high degree of statistical significance (Table 2). It can be suggested that selection for slow development should lead to the opposite effect—to a decrease of the development thermolability and a decrease of the temperature threshold.

The effect of the artificial selection for the development duration on the thermolability coefficient and the development threshold is revealed in this work for the first time, as we failed to find in the literature any evidences for probable effects of the artificial selection action on the temperature norms of insect development. It was shown by Neifakh et al. [15] that inbred strains at selection of *Drosophila melanogaster* for fast embryonic development at temperature 32°C had a small increase of the development rate at 32 and 25°C in comparison with the control strain, whereas at 17°C such differences were absent. The coefficients of regression of the development rate against temperature, which we calculated from the data presented in this work, amounted to 0.054 ± 0.128 before selection and $0.058{-}0.060 \pm 0.118{-}0.122$ after selection. Hence, the angle of the regression straight line slope increased as a result of selection. However, since the egg development rate was measured only at three temperatures, and the obtained mean values poorly corresponded to the linear regression equation, the differences between these regression coefficients were statistically insignificant. The authors of that work do not discuss a possible effect of selection on the development thermolability, which we have revealed at analysis of their data.

A very important peculiarity of the revealed effect of selection is the coupling of the thermolability coefficient and the development threshold changes: with increase of the angle of the regression straight line slope, the threshold, as a rule, rises and *vice versa*. It is interesting that the direct correlation between the thermolability coefficient and the development threshold is detected for insects as a whole and for ants in particular, both at the interspecies [21—23] and at the interpopulational (intraspecies) level [6, 24]. It is suggested that there is a certain genetic or physiological association between the thermolability coefficient and the threshold; however, this is not proved by anything. To prove the presence of the genetic interconnection between the thermolability coefficient and the threshold, it is necessary to study the intrapopulational variability of these parameters, which nobody has done so far [5]. The results obtained in the present work have shown that in *P. apterus* at action of the artificial selection for the nymphal development duration the thermolability coefficient and the temperature threshold of development change coordinatively, which proves indirectly their genetic interconnection.

The proof of the presence of the genetic covariance between the thermolability coefficient and the temperature threshold of development is very important for more profound understanding of processes of microevolutionary adaptation of insect populations to local climatic conditions. For example, let us suggest that there is in population *P. apterus* the selection for faster development at rather high temperatures. Such situation is possible, if the season favorable for development is short, and the individuals with fast development mainly survive, which use more effectively the short seasons with high temperature, for example, in the northern part of the area or at a cold year. Such explanation is acceptable for our object, as it is known, that soldier bugs are searching actively for places with the temperatures more favorable for them [25]. However, selection for faster development at high temperatures will lead to an increase of the straight line slope angle of the regression of the development rate against temperature and, hence, to an increase of the threshold and deceleration of the development at lower temperatures. This could be unfavorable for the individuals whose development occurs under colder conditions, for example at the end of the summer season. As a result, the so-called trade-offs could appear, which inhibit action of selection and lead to compromise situations [5].

In opinion of Ikemoto [26], formation of related insect species from the ancestral form is accompanied by a change of the coefficient and the

threshold according to thermal conditions of the niches occupied by new species. This agrees with our obtained data and indicates the existence of mechanisms of evolutionary changes of the insect development temperature norms by change of the thermolability and the temperature threshold of development.

ACKNOWLEDGMENTS

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