

Intraspecific Variation of Thermal Reaction Norms for Development in Insects: New Approaches and Prospects

V. E. Kipyatkov and E. B. Lopatina

Department of Entomology, St. Petersburg State University, St. Petersburg, 199034 Russia

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Abstract—The main parameters (thermal constants) characterizing the effects of constant temperatures on the duration and rate of development in ectotherms are considered. The advantages and drawbacks of the linear and nonlinear models describing the dependence of the development rate on temperature are discussed. The main patterns of interspecific variation of thermal constants in insects are described. The development of new ideas in the study of intraspecific variation of thermal reaction norms for development in insects is examined. The discrepancies in the data and their interpretation in this field are shown to result mostly from using the traditional methods of determining thermal constants. According to this method, the development rates calculated as reciprocals of the mean development times at each experimental temperature are used for regression analysis. The standard errors calculated according to this method are usually too large. Instead, a fundamentally new method is employed by the authors, according to which the individual development rates calculated for each individual are used for regression analysis of the reciprocals of the mean development times. This method reduces the standard errors of thermal constants by about an order and reveals significant differences between populations and other groups of insects. New data on intraspecific variation of the thermal reaction norms for development in *Myrmica* ants, the linden bug *Pyrhocoris apterus*, and *Calliphora* blowflies are briefly described and discussed. The possible adaptive significance of these forms of intraspecific variation is discussed. The prospects of research in this new field are outlined.

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One of the most important forms of dependence of ectothermic organisms on the thermal conditions of the environment is the effect of the temperature on the growth rate and development time. This form of phenotypic plasticity of an organism is characterized by the thermal reaction norms (Roff, 1980, 1992; Groeters, 1992; Nylin, 1994). This communication presents a brief review of the principal parameters characterizing the effects of constant temperatures on the duration of development in insects. Special attention is focused on the relatively new direction of evolutionary ecology: studies of intraspecific variation of thermal reaction norms for development.

THE DURATION OF INSECT DEVELOPMENT IN RELATION TO TEMPERATURE: A LINEAR MODEL

It is well known (Kozhanchikov, 1961; Goryshin, 1966; Mednikov, 1966, 1977; Campbell et al., 1975; Wagner et al., 1984, etc.) that within the favorable temperature range, the duration of development of insects and other ectothermic organisms shows an approximately hyperbolic relation with temperature (see

Figs. 1A; 7). The main equation of this dependence is often referred to as “Blunck’s hyperbole” in the Russian literature (Blunck, 1914, 1923):

$$D = \frac{K}{T - T_0} \quad (1)$$

where D is duration of development, expressed in days, hours, etc.; T is the temperature at which development takes place; T_0 is the temperature, or thermal, development threshold; and K is a constant. In fact, equation (1) reflects the thermal reaction norm for duration of development, inherent in individuals of a given species, population, colony, etc. According to the equation, the duration of development increases hyperbolically as the temperature decreases and becomes an infinite quantity when the temperature T_0 is reached (Fig. 2). It follows that no development takes place at the threshold temperature. The practical application of hyperbolic equations is cumbersome, since they are difficult to represent and compare.

A hyperbolic relation can be easily transformed into a linear one by using the reciprocal values of the vari-

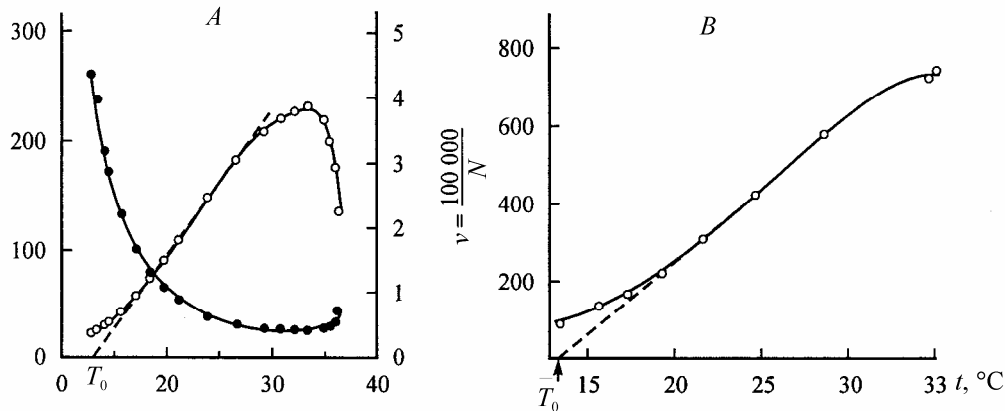


Fig. 1. Examples of experimental studies of the dependence of duration and rates of insect development on the temperature (original diagrams). (A) duration (black circles) and rate (100/hour; empty circles) of development of the oriental fruit fly *Dacus dorsalis* Hendel (Messenger and Flitters, 1958, cited after Ratte, 1985). The mean values of development duration are approximated by Janisch's catenary equation, and the values of development rates, by its reciprocal; the linear portion of the curve is approximated by a straight line (dashed), whose interception with the abscissa axis gives the value of the development threshold T_0 . Abscissa: temperature °C. Ordinate: on the left—duration of development, h ; on the right—rate of development, $h^{-1} \times 100\%$. (B) development rate of pupae of *Tenebrio molitor* L. in relation to temperature (Pütter, 1914, cited after Mednikov, 1966). Abscissa: temperature °C. Ordinate: rate of development, $\text{day}^{-1} \times 10^5$.

able. Therefore, if we define development rate (R) as the reciprocal of its duration ($R = 1/D$), equation (1) will be transformed into the linear form:

$$R = a + bT \quad (2)$$

where a is a constant and b is the coefficient of linear regression of development rate on temperature. Defined in this way, the development rate reflects the fraction of the complete development achieved per unit time, for example, in one day. In earlier works, $1/D$ was usually multiplied by 100%, perhaps for a better demonstrative value, so that the development rate was expressed as a percentage of complete development (see Figs. 1, 6). Now, the rate of development is more correctly expressed as a fraction of one (Fig. 2). The dimension of development rate is D^{-1} , for example, day^{-1} .

The graph of equation (2) shows the thermal reaction norm for development rate inherent in individuals of a particular species, population, colony, etc. (Fig. 2). It is a straight line crossing the abscissa axis at T_0 . Thus, the temperature threshold is the value at which the development rate equals zero. This threshold is sometimes called the "lower" threshold, implying that there is also an "upper" threshold (see Fig. 1A). However, since the nature of the latter is entirely different, it should be referred to as the upper limit of development.

The constant a in equation (2) determines the x-intercept of linear regression of the development rate

on temperature; its value is usually negative. The dimension of the constant is the same as that of the development rate: D^{-1} .

The coefficient of linear regression of development rate on temperature b has dimension $D^{-1} \times T^{-1}$ (for example, $\text{day}^{-1} \times \text{deg}^{-1}$); it determines how the development rate changes when the temperature increases or decreases by 1 degree. It is actually the slope of the regression line relative to the abscissa axis (Fig. 2). The greater the angle between the regression line and the abscissa axis (i.e., the value of b), the more profound will be changes in the development rate accompanying changes in the temperature, and vice versa. The coefficient of regression b is thus a very important parameter, characterizing the degree of dependence of the development rate on the temperature, or, in other words, the thermolability of development. Therefore, it may be also referred to as the development thermolability coefficient (Kozhanchikov, 1946, 1961; Mednikov, 1966, 1977).

The temperature threshold of development can be determined from the equation of linear regression of development rate on temperature by equaling the development rate to zero in equation (2):

$$T_0 = -a/b \quad (3)$$

One of the consequences of the linear relation between the development rate and temperature is the so-called "rule of the constant sum of effective

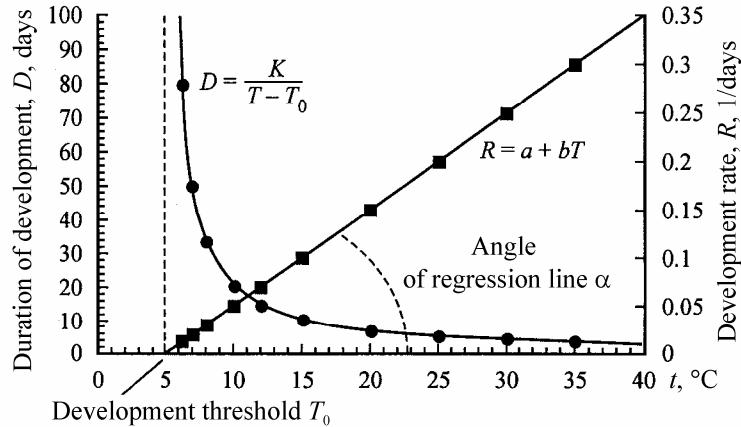


Fig. 2. The principal parameters characterizing the thermal reaction norms for insect development. For explanations, see text.

temperatures.” Indeed, equation (1) may be transformed as

$$D \times (T - T_0) = K \quad (4)$$

This implies that the product of the duration of development and the so-called effective temperature (i.e., temperature exceeding the threshold) must be a constant equal to K . If the mean daily temperature is not the same during all the days of development, equation (4) will be transformed as:

$$\sum_{n=1}^{n=D} d \times (T_n - T_0) = K \quad (5)$$

where d is a value with the same dimension as the time unit used in the study of development (usually one day); D is the number of days the development takes.

The parameter K has dimension $T \times D$, for example day \times deg. Therefore it would be most correct to refer to this value as the “sum of degree-days.” The common name “sum of effective temperatures” is basically incorrect since it does not reflect either the method of calculation or the dimension of this parameter. Even though equations (4) and (5) clearly define the mathematical nature and dimension of K , these equations can rarely be used for direct calculation of this parameter, mostly because of the natural variability of the duration of development. The sum of degree-days represents a reciprocal of the regression coefficient, and should be correctly calculated using the formula:

$$K = 1/b \quad (6)$$

This formula can be derived by replacing D in equation (4) by a reciprocal of the development rate from

equation (2); it should be taken into account that, according to equation (3), $a = -bT_0$.

It is completely incorrect to calculate the values of K for each experimental temperature separately, based on the mean duration of development at this temperature and the temperature threshold value determined from all the variants or taken from the literature, as some authors do (Saulich, 1999; Saulich and Volkovich, 2004). The sum of degree-days is in fact an integrative parameter determined by the regression equation and depending on the duration of development in all the temperature variants and on the development threshold which is also determined by the same regression equation. Therefore, each sample (experiment) may be characterized by only one value of the sum of degree-days, calculated from formula (6) (Mednikov, 1966, 1977; Campbell et al., 1974; Honěk and Kocourek, 1988, 1990; Honěk, 1996a, 1996b).

The parameters characterizing the linear dependence of the development rates of insects on the temperature, or, in other words, the thermal norms for development, namely the development threshold, the coefficient of regression (thermolability), and the sum of degree-days, are often referred to as thermal constants of development, even though these parameters have long been shown to be variable and cannot be regarded as constants in the biological sense. It should also be noted that, since the sum of degree-days is a reciprocal of the coefficient of regression, simultaneous use of both parameters would be redundant.

THE NONLINEAR MODELS

The classical linear model describes very well the dependence of the development rate of insects on the

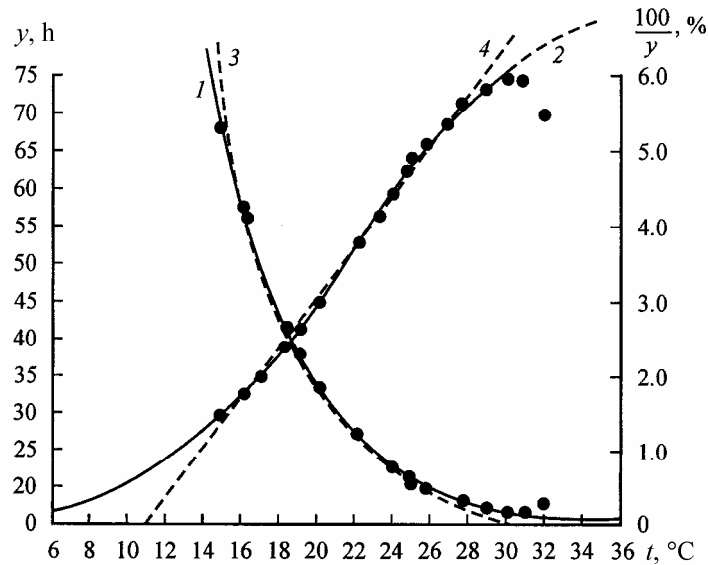


Fig. 3. Duration and rate of development of eggs of *Drosophila melanogaster* Mg. in relation to temperature. Curves 1 and 2 are calculated using a logistic equation, curve 3, a hyperbolic equation, and curve 4, a linear equation. Abscissa: temperature °C. Ordinate: on the left—duration of development, h ; on the right—rate of development, $h^{-1} \times 100\%$. Modified after Davidson, 1944.

temperature within the range of temperatures favorable for their active life. However, outside this range the relation deviates from the linear one: the development rate becomes higher than the predicted value at lower temperatures and lower at higher temperatures (Figs. 1; 6B). Thus, the actual dependence of the development rate of ectothermic organisms is shaped as a flattened sigmoid (Fig. 3) with the central portion (somewhat above and below the inflection point) only slightly deviating from the straight line (Davidson, 1944; Campbell et al., 1975; Ratte, 1985), so that a linear approximation of this part of the curve is possible (Campbell et al., 1975; Wagner et al., 1984).

It should be noted that at the temperature corresponding to the development threshold calculated from the linear regression equation, the actual development rate is not zero. This threshold is therefore a conditional parameter that can be used only in the linear model. The true physiological threshold of development at which the development rate indeed equals zero must be markedly lower (Figs. 1, 3). However, this threshold is virtually impossible to determine in an experiment, because development is very slow and the survival rate is low at near-threshold temperatures (Campbell et al., 1975; Wagner et al., 1984; Ratte, 1985). The indirect method of determining the physiological threshold proposed by J. De Wilde (1950) is very laborious and provides only rough estimates (see Saulich, 1999; Saulich and Volkovich, 2004). Moreover, it should be emphasized that even if the physio-

logical threshold has been successfully determined, it should on no account be used for calculating the sum of effective temperatures, as some authors assumed. Only the threshold value based on the linear regression model and determined from equation (3) will be suitable for this purpose.

At sufficiently high temperatures, not only deviation from the linear dependence but also a noticeable increase in the duration of development (a decrease in the development rate) is observed (Figs. 1, 3, 6). Based on this fact, some researchers postulated the presence of the so-called “development optimum,” i.e., a temperature value at which the development rate is the highest, and the “upper threshold of development” at which development stops (Blunck, 1923; Ludwig, 1928; Wagner et al., 1984; Ratte, 1985). However, almost all the species studied show a considerable increase in mortality already at the temperature of the “development optimum,” whereas the “upper threshold of development” cannot be determined at all because the insects cannot survive such high temperatures (Wagner et al., 1984). The available facts indicate that the thermal optimum of insect development lies approximately within the range of linear dependence of the development rate on the temperature (Campbell et al., 1975; Vinberg, 1983; Ratte, 1985; Trudgill et al., 2005).

Many nonlinear models have been proposed to describe the dependence of the development rate on the

temperature, from Janisch's catenary equation to more recent "biophysical" models. There are exponential, power-like, logistic, sigmoid, Gaussian, and other models (see reviews in Goryshin, 1966; Mednikov, 1977; Wagner et al., 1984). A detailed consideration of the various nonlinear models is beyond the scope of this communication.

The only advantage of nonlinear models is that they allow one to calculate the precise rate of development at temperatures strongly different from the optimum range (Taylor, 1981; Wagner et al., 1984; Marshakov, 1984; Lamb, 1992). However, application of these models in research, and especially in the practice of phenological predictions is limited due to many factors.

(1) It is difficult to select the appropriate model; the criteria for selection are obscure (Wagner et al., 1984; Marshakov, 1984).

(2) The development rates must be experimentally determined at many temperatures; this work is labor consuming and especially difficult to accomplish for the temperatures noticeably above and below the optimum range.

(3) The "optimum" temperature, at which the development rate is the highest, must be determined experimentally, which is also a difficult task.

(4) There are no parameters with a clear biological significance, such as the development threshold and the number of degree-days.

(5) Comparative studies involving many species are difficult or impossible to carry out.

Advantages of the Linear Model

The extensive use of the linear model is determined by the fact that in most (though not all) insects, the dependence of the development rate on the temperature is almost linear within the temperature range favorable for development (Campbell et al., 1975; Wagner et al., 1984; Lamb, 1992). The linear model has the following principal advantages.

(1) It is mathematically simple.

(2) All the parameters can be easily determined using regression analysis.

(3) There is no need to experiment at many temperatures, especially too low and too high ones; it is sufficient to study 3–5 variants within the optimum range.

(4) Statistical errors can be calculated for all the main parameters (Campbell et al., 1974).

(5) The thermal constants have a clear adaptive ecological significance.

(6) Extensive material is available for comparative studies (data on hundreds of species of insects have already been accumulated).

Owing to these features, the linear model, in spite of its being an approximate one, is very broadly used in insect ecology (Campbell et al., 1975; Wagner et al., 1984; Trudgill et al., 2005). The rule of the sum of effective temperatures proves acceptable in most cases (Lamb, 1992; Honěk, 1996) and provides quite adequate predictions of the development of pest populations (Pruess, 1983).

The use of the linear model and thermal constants appears to be especially promising in comparative studies of the life cycles of insects. The use of the coefficient of regression of the development rate on temperature and its reciprocal, the sum of degree-days, allows the species to be compared with respect to their thermal requirements and the degree of thermolability of development. The development threshold determined from the regression equation, even though it is a conditional parameter, is also convenient for comparing the species. There are strong grounds to believe that its value is closely related to that of the actual physiological threshold (Lamb, 1992). It seems obvious that if the threshold calculated from the regression equation for one species is several degrees lower than the corresponding value for another species, then the difference between the actual physiological thresholds of these species should be approximately the same. The species may thus be compared using objective parameters.

A serious drawback of the linear model is that the temperature range within which this model can be applied cannot be unambiguously determined. Inclusion into the analysis of too low or too high temperatures, at which regression in a given species noticeably deviates from the straight line, will lead to underestimation of the threshold and the regression coefficient (Wermelinger and Seifert, 1998; Saulich, 1999). Based on analysis of extensive published data, A. Honěk (1990) demonstrated that the lower temperatures were used in the experiment, the smaller mean values of the threshold and regression coefficient would be obtained for the same species. Therefore, during the experiments and material processing, it is essential to control

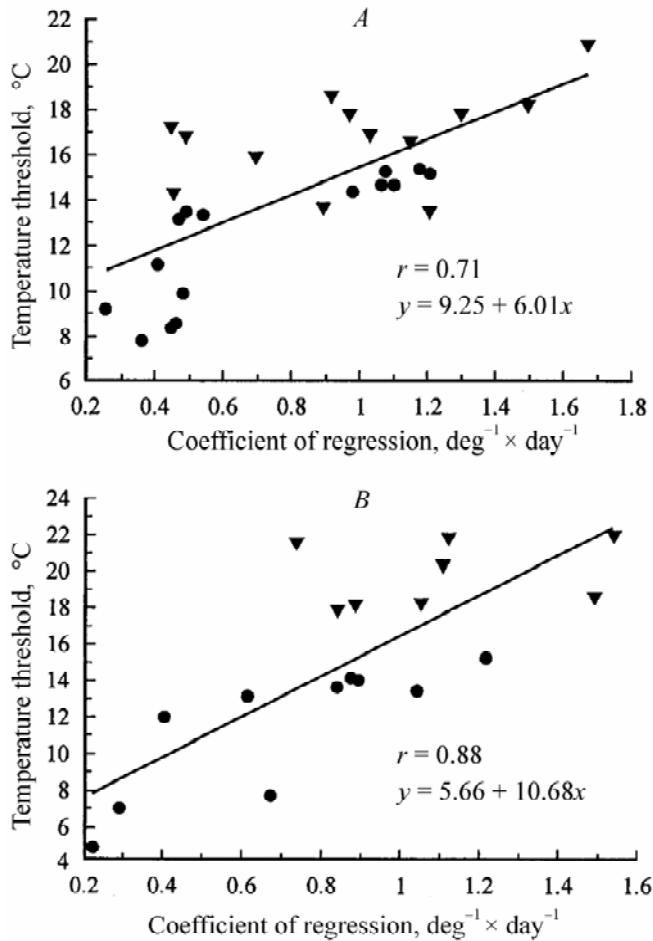


Fig. 4. Correlation between the coefficient of regression of development rates on temperature and the temperature development threshold in eggs (A) and larvae (B) of ants. The diagram shows Pearson's linear correlation coefficient (r) and linear regression equations approximating the experimental dots. The northern species are designated with circles, and the southern ones, with triangles. After Lopatina and Kipyatkov, 1998.

the linearity of the data obtained by means of special statistical tests (Campbell et al., 1975; Shaffer, 1983; Sokal and Rohlf, 1995). The points noticeably deviating from the linear relation should be discarded. The requirements concerning the minimum sample size, the number of experimental temperature variants, and statistical procedures described in the special literature (Campbell et al., 1975; Shaffer, 1983) should be strictly followed.

Interspecific Variability of the Thermal Development Norms in Insects

The end of the XX century was marked by a considerable achievement in the studies of the thermal norms for insect development, namely the discovery of common traits in the interspecific variability of ther-

mal constants (Honěk and Kocourek, 1988, 1990; Honěk, 1996a). A general negative correlation was revealed between the sum of degree-days and the temperature threshold: as a rule, the sum of degree-days increases as the threshold decreases, and vice versa. This also implies the presence of a positive correlation between the threshold and the coefficient of regression, because the latter is a reciprocal of the sum of degree-days. A functional explanation of this relation was proposed (Trudgill and Perry, 1994; Trudgill, 1995). The species living at higher latitudes benefit from lower development thresholds, which allow them to develop at lower temperatures but at the same time reduce the coefficient of thermolability. Thus, according to the cited authors, the negative correlation between the threshold and the sum of degree-days in different species may be explained by the existence of species adapted to life at various latitudes, i.e., under various climatic conditions.

Indeed, A. Honěk (1996b) was able to reveal a significant negative correlation in the northern hemisphere between the temperature threshold and the latitude of the species' locality. On the contrary, the sum of degree-days showed a trend for increasing from south to north, which was significant only for the egg stage. The same trends were revealed during our studies of Palearctic ants (Lopatina and Kipyatkov, 1998). We observed a significant positive correlation between the regression coefficient and the temperature threshold of development. In addition, the species occurring in more southern regions were found to have a higher mean thermolability of development and higher development thresholds, as compared to the species distributed in more northern territories (Fig. 4).

The reasoning of D.L. Trudgill and J.N. Perry (1994) is based on the assumption that a certain genetic or physiological relation should exist between the sum of degree-days (the regression coefficient) and the development threshold. Therefore, an evolutionary increase in thermolability is usually accompanied by an increase in the threshold, and vice versa (Trudgill et al., 2005). The genetic covariation of the regression coefficient and the threshold was proved for the first time in our research (see below).

Thus, the most important trend in the interspecific variability of the thermal norms for insect development is that in northern species, the lines of regression of development rates on temperature have on average a smaller slope to the abscissa axis, due to smaller

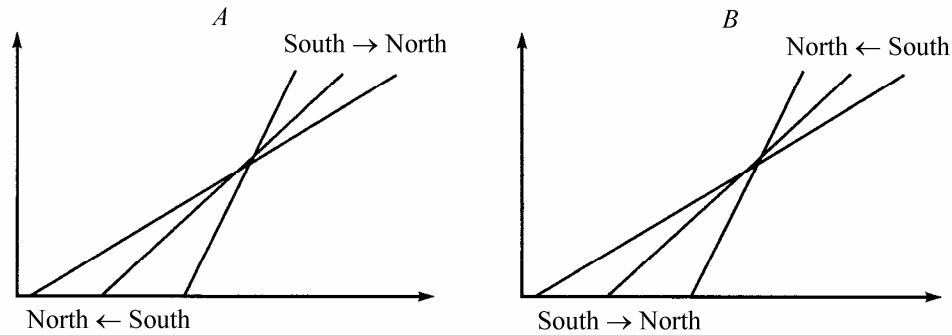


Fig. 5. Two types of latitudinal variation of thermal reaction norms for insect development. (A) The first type: the physiological response becomes less dependent on the temperature from south to north, which is indicated by a decreasing slope of the graph to the abscissa axis; the temperature threshold value decreases simultaneously. (B) The second type: the physiological response becomes more dependent on the temperature from south to north; the slope of the graph to the abscissa axis and the temperature threshold value increase. Abscissa: temperature. Ordinate: intensity of physiological response to temperature (for example, growth rate, development rate, intensity of metabolism, fecundity).

values of the coefficient of regression and the development threshold. The sum of degree-days tends to increase from south to north, corresponding to the first type of latitudinal variability of the thermal reaction norms (Fig. 5A).

Is There Intraspecific Variability of Thermal Reaction Norms for Development?

In the first half of XX century, the thermal constants characterizing the effect of temperature on the duration of development of insects were generally considered to be stable within a species. It was mostly for this reason that they were called constants and regarded as stable physiological characters determined by species-specific properties of proteins, cell cytoplasm, etc. (Bělehrádek, 1935; Kozhanchikov, 1946, 1961; Goryshin, 1966). Some researchers, however, noted that the thermal norms for larval development could change depending on the diet and other external factors (Ludwig, 1928).

The problem of intraspecific geographic variability of thermal constants was first addressed by A.S. Danilevsky (1957, 1961) by the example of two lepidopteran species: *Acronycta rumicis* and *Spilosoma menthastri*. The diagrams provided in the cited works demonstrate small but quite clear differences in the thermolability of development between the geographic populations (Fig. 6). Still, A.S. Danilevsky (1961: 133) wrote: "The development of the larvae from Sukhumi was slightly slower, therefore the sum of effective temperatures calculated for them exceeded those for the larvae from Belgorod and Leningrad by nearly 10%. Such differences, however, lie within the

acceptable experimental error." Later, A. Campbell and co-authors, considering the data of A.S. Danilevsky, noted that the differences, though small, were still statistically significant (Campbell et al., 1974).

Based on the original research and some published data, A.S. Danilevsky (1961: 137) made a conclusion about "... the relative constancy of temperature requirements of active stages in intraspecific geographic populations ..." and in fact regarded the thermal constants as a stable character of a species. The concept of the "species rank of thermal development norms" has been supported by some researchers until recently (Saulich, 1999: 258).

The progress of evolutionary ecology in the second half of the XX century raised some doubts as to intraspecific constancy of thermal development norms. If the thermal norms are different in closely related species, they might also be different in subspecies, ecotypes, and local populations. The life cycle theory (Stearns, 1992; Roff, 1992) predicted the existence of adaptive intraspecific variation of thermal development norms. According to this theory, all the principal parameters of the life cycle, including the physiological norms of reaction of ectothermic organisms to temperature, should depend on the climate, because natural selection optimizes the parameters of development and production in each population, adjusting them in accordance with the local climatic conditions (Roff, 1980; Taylor, 1981; Nylin, 1994). Intraspecific geographic variation of thermal norms for development was indeed discovered in a number of species (Campbell et al., 1974; Druzhelyubova, 1976; Gro-

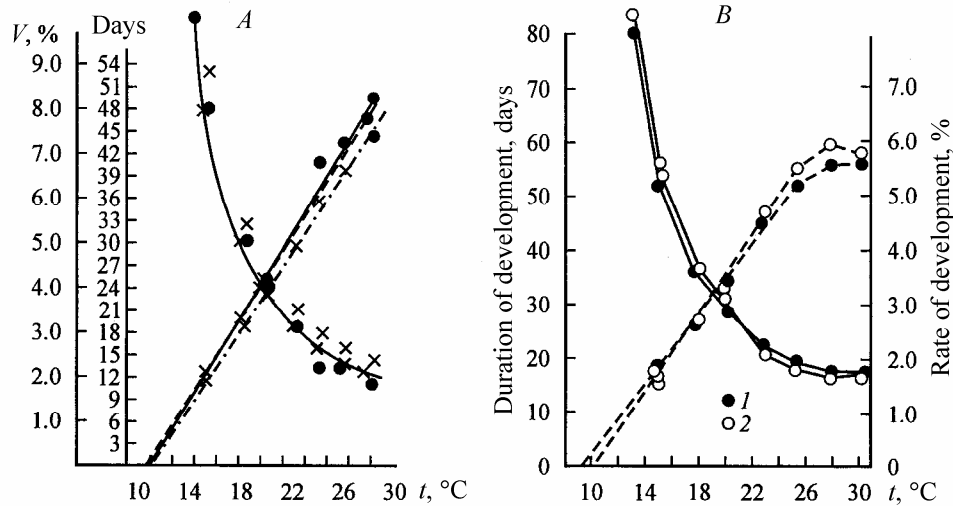


Fig. 6. The effect of temperature on the duration and rate of development of the larvae of *Acronycta rumicis* L. (A) and *Spilosoma menthastris* Esp. (B) from different geographic populations. Populations: (A) Leningrad (circles), Belgorod (\times), Sukhumi (+); (B) Leningrad (1), Sukhumi (2). Abscissa: temperature $^{\circ}\text{C}$. Ordinates: duration of development, day; rate of development, $\text{day}^{-1} \times 100\%$. Modified after Danilevsky, 1957, 1961.

eters, 1992), listed in A. Honěk's paper (1996b). There were also reports on intraspecific variation of thermal norms for insect development related to the differences in the diet (Goryshin et al., 1988), development on different hosts (Padua et al., 1996), and also to seasonal differences, namely, the presence or absence of diapause in the preceding development (Kozhanchikov, 1961; Morris and Fulton, 1970; Nechols et al., 1983; Turnock et al., 1983, 1985; Saulich and Volkovich, 2004).

It is very interesting that many researchers obtained data indicating a considerable stability of the thermal constants within species' ranges (Lamb et al., 1987; Nechols et al., 1987; Tauber et al., 1987; Groeters, 1992; Mogi, 1992, etc.), which apparently confirmed the views of A.S. Danilevsky (1961). It should be noted that some of these publications still reported small differences between geographic populations; however, these differences either proved to be statistically insignificant, or were regarded as too small by the authors of the cited works.

Considering the predictions based on the life cycle theory and the factual data concerning intraspecific variation in many insects, it should be admitted that the geographic stability of the thermal reaction norms cannot be explained by merely regarding these norms as species-specific characters; instead, the special mechanisms facilitating their stability should be revealed. A number of hypotheses were put forward to explain these mechanisms (Roff, 1980; Nechols et al.,

1987; Tauber et al., 1987; Groeters, 1992); a detailed consideration of all of them is beyond the scope of this work. Of the greatest interest from the standpoint of the life cycle theory are the hypotheses that explain the absence of adaptive geographic variation in thermolability of development by the trade-off action of natural selection. Even though an increase in development rates at high temperatures may be adaptive, it is inevitably accompanied by a decrease at lower temperatures, and also by an increase in the temperature threshold of development (since the threshold and the coefficient of thermolability are interrelated), which may be a disadvantage. Consequently, natural selection leads to a trade-off result, determining the absence of geographic variation of thermolability and the development threshold (Nechols et al., 1987; Tauber et al., 1987; Groeters, 1992).

There are contradictory views concerning the intraspecific variation of the thermal reaction norms for development (Groeters, 1992). In some cases, the latitudinal variability corresponds to the first type (Fig. 5A), i.e., is similar to the interspecific differences (Heron, 1972; Benson et al., 1994), while in other cases it shows a directly opposed pattern (Brenner et al., 1981; Obrycki and Tauber, 1982), i.e., corresponds to the second type (Fig. 5B). The adaptive significance of interspecific geographic variation of thermolability and the development threshold is still insufficiently studied. Our work has contributed to better understanding of this phenomenon.

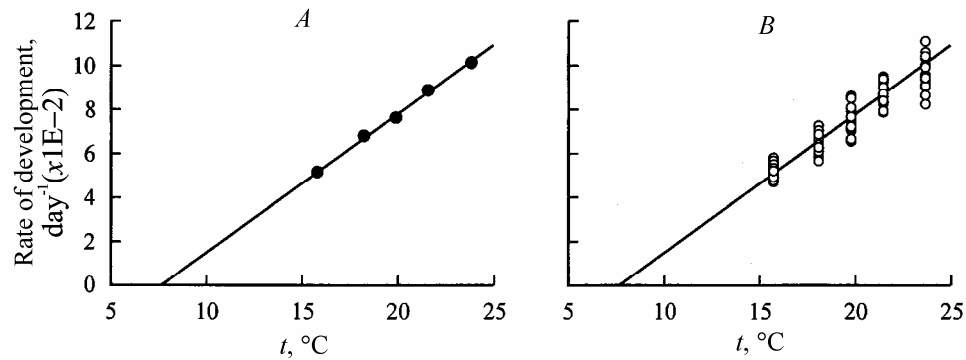


Fig. 7. The effect of temperature on the duration of development of pupae of the blowfly *Calliphora vicina* R.-D. from the Murmansk population. (A) The traditional method ($n = 5$). The values determined by regression analysis: development threshold, $7.6 \pm 1.41^\circ\text{C}$; coefficient of regression, $0.634 \pm 0.0191 \text{ day}^{-1} \times \text{deg}^{-1}$; sum of degree-days, $157.7 \pm 4.75 \text{ day} \times \text{deg}$. (B) The new method ($n = 2000$). The values determined by regression analysis: development threshold, $7.6 \pm 0.06^\circ\text{C}$; coefficient of regression, $0.636 \pm 0.00297 \text{ day}^{-1} \times \text{deg}^{-1}$; sum of degree-days, $157.3 \pm 0.73 \text{ day} \times \text{deg}$. For explanations, see text (Unpublished data of A.P. Nesin).

A New Method of Determining Thermal Constants

In our opinion, the controversy in the facts and views concerning the intraspecific variation of thermolability and the development threshold of insects can be explained by the following principal reasons.

(1) The differences in the thermal development norms between different populations or other groups of individuals of the same species are usually small (Campbell et al., 1974); based on this fact alone, many authors agree with A.S. Danilevsky's (1957, 1961) conclusion that intraspecific variation does not exist (Groeters, 1992; Jarošik et al., 2002b).

(2) In studies employing traditional methods, the statistical errors of the regression coefficient, sum of degree-days, and development threshold are either not calculated at all, or found to be very large. Therefore the differences revealed in most studies cannot be proved to be statistically significant.

This situation results to a considerable degree from the traditional method of determining thermal constants, based on the mean duration of development calculated for each experimental temperature variant. When the mean values have been obtained, their reciprocals (i.e., mean development rates at different temperatures) are calculated, plotted on a graph, and approximated with a straight line, either manually or by means of regression analysis. Many authors do not calculate the statistical errors of thermal constants at all (Goryshin, 1966; Mednikov, 1966; Ratte, 1985; Honěk and Kocourek, 1988; Groeters, 1992; Saulich, 1999; Saska and Honěk, 2003; Saulich and Volkovich, 2004). If the errors are calculated, they prove to be very large (Fig. 7A) owing to a small sample size,

which in this case corresponds to the number of experimental temperature variants (Campbell et al., 1974). In view of this it was even assumed that the thermal constants and especially the development threshold could never be determined with sufficient precision to demonstrate the statistical significance of the minute differences observed between intraspecific populations or life cycle stages (Jarošik et al., 2002). The concept of "developmental rate isomorphy" was thus formulated, presuming the existence of the same temperature threshold for all the stages of the species' life cycle (Jarošik et al., 2002, 2003; Saska and Honěk, 2003).

However, a completely different method based on individual development rates determined in different individuals at each experimental temperature was proposed already in 1974 (Campbell et al., 1974). Although the paper is often cited, almost no researchers have applied this method until recently. We have been using a considerably improved variant of this method since 1998.

The principal difference from the traditional approach is that in the new method, the development rate is determined for each individual participating in the experiment, as a reciprocal value of the duration of its development. After this, regression analysis is performed for the entire set of individual development rates obtained at all the experimental temperatures, and the constant a and the linear regression coefficient b with the corresponding statistical errors are calculated (Campbell et al., 1974; Sokal and Rohlf, 1995). After this, the temperature threshold and the sum of degree-days are calculated from equations (3) and (6). The statistical errors of the thermal constants are de-

terminated using special formulas (Campbell et al., 1974). Owing to a large sample size, which in this case is determined by the number of individuals, rather than the number of temperature variants in the experiment (Campbell et al., 1974), the standard errors are much smaller than in the case of the traditional method (Fig. 7B).

For a precise estimation of the thermal constants, the duration of development should be determined for no less than 50 individuals at each of 3 or 4 constant temperature values that are known to lie within the range of linearity (Campbell et al., 1974). We prefer to use 5 temperature variants, in which case the minimum sample size for each temperature may be decreased, if necessary, to 30 individuals. It should be remembered, however, that the greater the number of individuals studied, the smaller the standard errors of all the parameters in question. Analysis and statistical evaluation of such extensive data sets are performed using the DevRate 4.3 program developed by V.E. Kipyatkov and implemented within QuattroPro 9.0 software.

According to statistical requirements, when the duration of development is determined, the interval between the records should not exceed the standard deviation (even better, half the standard deviation) of the value in question (Nicholson, 1979; Shaffer, 1983). This means that in many cases, records should be made no less than twice a day, which is a very labor consuming task. We have therefore developed a new method of automatic recording of the duration of development of non-feeding stages in the insect life cycle. The method consists in monitoring of development by taking pictures of the tray with eggs or pupae in the wells at regular intervals, using a digital camera. The pictures are taken automatically every hour or even more frequently, allowing the duration of development of eggs and pupae to be calculated with precision of no less than ± 1 h. The duration of development could not be determined with such precision in most of the previous studies.

The precise measurement and control of temperature in the experiments are of utmost importance for obtaining reliable results. We have, for the first time in Russia, developed and introduced into eco-physiological experimental work the modern technology of measurement and control of temperature, based on laboratory analog and digital input-output controllers of RL and NL series equipped with DS1820 temperature sensors (available from Research Laboratory of Design Automation—RLDA, Taganrog, Russia). This

equipment provides means of computer-assisted control and recording of temperature in the photothermic chambers. The temperature can be recorded with an accuracy of 0.0625°C , continuously or at any intervals needed, yielding completely reliable values of the mean daily temperature. Computerized temperature control and the use of leak-tight chambers permitting lag-free heating and cooling by cool air pumping, allows one to maintain constant experimental regimes with an accuracy of $\pm 0.1^{\circ}\text{C}$. Such accuracy of temperature control exceeds that of the last-generation equipment by almost an order of magnitude, which is more than sufficient for studying the thermal reaction norms for insect development.

The use of the new method with all additions and improvements allowed us to increase the accuracy of calculation of the thermal constants, reducing their standard errors by an order of magnitude and in some cases even more profoundly (Fig. 7). In fact, this method revealed for the first time significant differences between the thermal constants characterizing the thermal norms for development of insects from different populations (Kipyatkov and Lopatina, 2002; Lopatina et al., 2002; Kipyatkov et al., 2004), colonies (Balashov and Kipyatkov, 2008b), and generations (Balashov et al., 2007). New data were also obtained concerning the phenotypic plasticity of the thermal norms of development, i.e., their changes under the action of environmental factors, such as photoperiodic conditions (Lopatina et al., 2007), diet (Balashov et al., 2007), and season (Kipyatkov et al., 2005).

NEW DATA ON THE INTRASPECIFIC VARIATION OF THE THERMAL NORMS FOR INSECT DEVELOPMENT

1. Intraspecific Geographic Variation

The fundamentally new results obtained in our studies allowed us to conclude that the temperature reaction norms in ants varied according to the local climatic parameters: egg production, brood rearing, and individual growth and development became more dependent on the temperature in the northern regions (Kipyatkov and Lopatina, 2002; Lopatina et al., 2002; Kipyatkov et al., 2004). In the graph, this phenomenon is reflected by a greater angle between the reaction norm line and the abscissa axis in the northern populations, i.e., the second type of latitudinal variation observed in the thermal reaction norms (Fig. 5B). Thus, the northern populations of ants demonstrate adaptations to faster development at relatively high tempera-

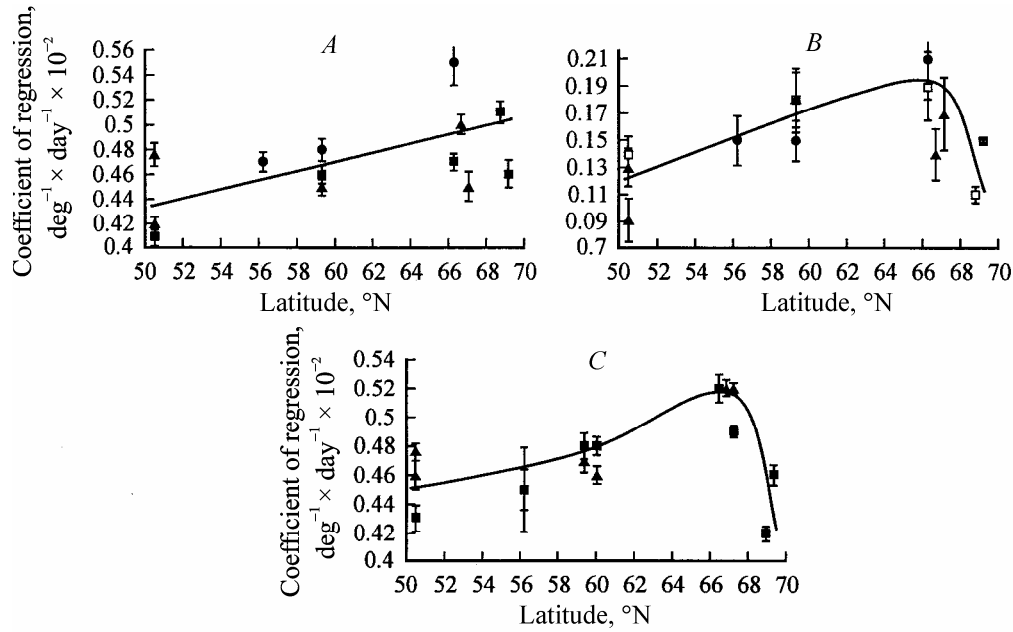


Fig. 8. Intraspecific latitudinal variation of the coefficient of regression of development rates on temperature in eggs (A), larvae (B), and pupae (C) of 3 species of ants of the genus *Myrmica* Latr.: *Myrmica ruginodis* Nyl. (squares), *M. rubra* L. (triangles), and *M. scabrinodis* Nyl. (circles). Vertical lines represent the standard errors.

tures; in other words, they are more thermophilic and stenothermic than the southern ones.

Exactly the same latitudinal changes in the temperature reaction norm were observed in our previous studies of respiration of ants of the genus *Myrmica* (Elmes et al., 1999; Nielsen et al., 1999). The worker ants from higher latitudes demonstrated higher values of Q10 coefficient, which means that they had a more intensive metabolism at high temperatures but a less intensive metabolism at low temperatures, as compared to individuals from southern regions. Thus, the respiratory metabolism of northern ants more strongly depended on temperature, which also corresponded to a greater slope of the reaction norm graph (Fig. 5B). These conclusions agree well with the fact that ants are highly thermophilic insects, which can exist in the temperate climate zone primarily owing to their social mode of life and the ability to create favorable thermal conditions for brood development in their nests, either by active thermoregulation, or by choosing the warmest microstations and the special construction of the nests ensuring their heating by the sun.

Further, more complete studies showed that the latitudinal variation of the thermal reaction norms for development in *Myrmica* ants was much more complicated (Kipyatkov et al., 2005a, 2005b; Kipyatkov and Lopatina, 2006, 2007). In particular, the values of the temperature development threshold and the coefficient

of linear regression of development rate on temperature in the larvae and pupae increased from south to north approximately as far as the Polar Circle and then decreased at the northern distribution boundary (Figs. 8B, 8C). At the same time, the corresponding parameters of the eggs did not decrease noticeably in the Far North (Fig. 8A). These trends evidently cannot be explained based on the simple reasoning that “it is warm in the south and cold in the north.”

In an attempt to understand the adaptive significance of this trait, we have studied the phenology of colony development and the nest microclimate of *Myrmica* ants within the latitude range from 50°N (Belgorod) to 69°N (Murmansk). The daily and seasonal temperature variations in the ant nests were studied using Tinytalk® II self-contained microprocessor-based temperature data loggers, capable of recording the local temperature with preset intervals and storing long-term data (up to 10–12 months). This work is still unfinished but has already produced interesting results (Lopatina and Kipyatkov, 2006, 2007). It was found that in June and July, when most of the brood was reared, the mean daily temperatures in the nests of northern ants were nearly the same as in the southern nests, except for the northernmost location (Murmansk) where the nest temperatures were noticeably lower (Fig. 9A). The maximum daily temperatures of June and July even increased from south to north,

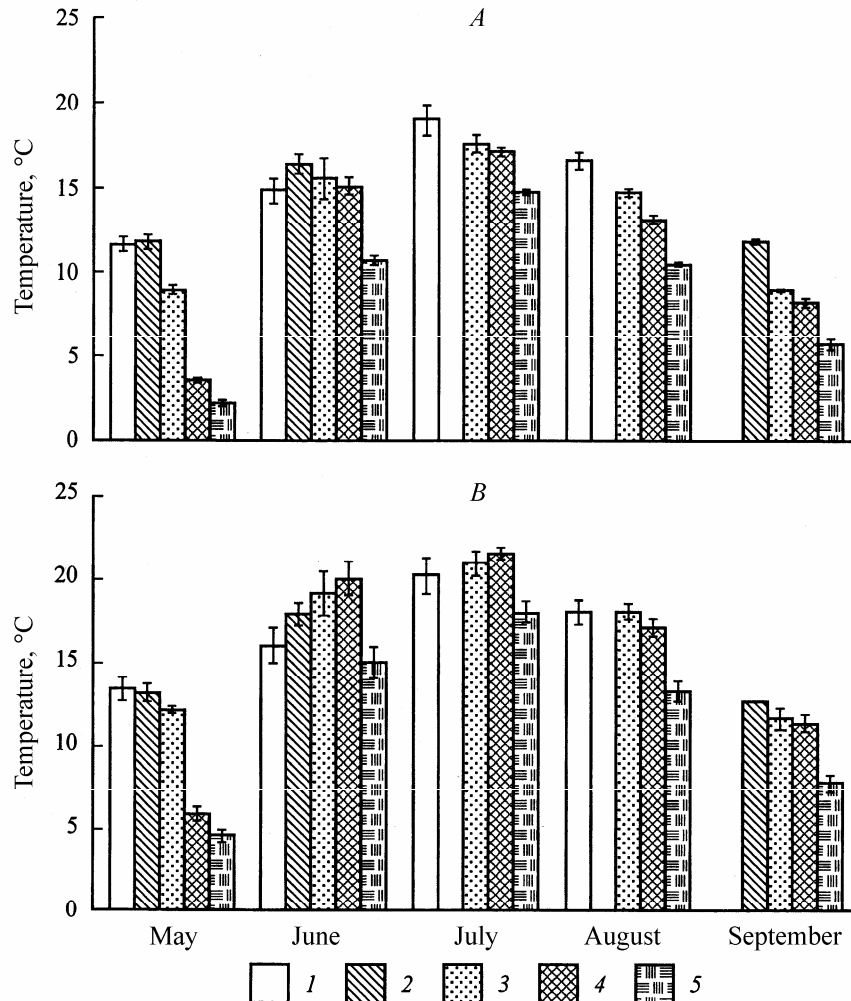


Fig. 9. Latitudinal variation of the thermal regime in nests of the ant *Myrmica ruginodis* Nyl. The mean daily temperature (A) and the mean maximum temperature (B). The measurements were taken at the center of the nest dome. (1) Borisovka, 50.5°N; (2) Kiev, 50.5°N; (3) St. Petersburg, 60°N; (4) Chupa, 66.3°N; (5) Murmansk, 69°N.

again with an exception of Murmansk area (Fig. 9B). Such changes in the microclimate can be accounted for by adaptive changes in the microhabitat preferences and the nest structure, facilitating better absorption of solar heat, that take place along the latitudinal gradient.

The results obtained demonstrated for the first time the adaptive significance of latitudinal variation of the thermal reaction norms for development observed in ants of the genus *Myrmica*. The coefficients of regression of development rates on temperature generally increase from south to north for all the stages of the ant life cycle (Fig. 8); correspondingly, the slope of the regression lines to the abscissa axis increases, and so does the development threshold (Fig. 10). It should be noted that in all the 3 species studied, the regression lines of different geographic populations intersect

at 14–16°C (Fig. 10). This means that northern populations have higher development rates at relatively high temperatures (above the intersection of the regression lines) and lower development rates at relatively low temperatures (below the intersection of the regression lines), as compared to southern populations. In other words, the northern populations of ants show adaptations to a faster development at relatively high temperatures. The increased thermolability of development of the northern populations of ants allows a more efficient utilization of high daytime temperatures for rapid brood rearing. According to our data, such temperature conditions do exist in ant nests in the north (Fig. 9). However, in the Far North, near the distribution boundary of *Myrmica* ants, where the climatic conditions do not allow such a favorable microclimate to be maintained in the nests (Fig. 9), high

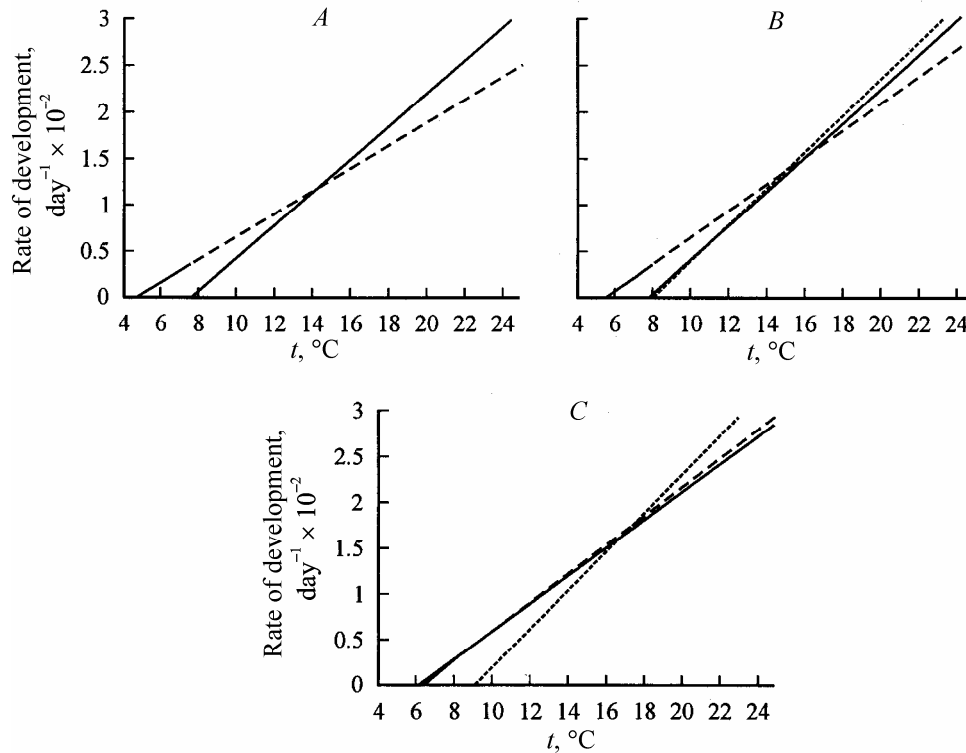


Fig. 10. Lines of regression of development rates on temperature in summer larvae of three ant species of the genus *Myrmica* Latr. from different geographic populations (after Kipyatkov and Lopatina, 2002): *Myrmica rubra* L. (A), *M. ruginodis* Nyl. (B), and *M. scabrinodis* Nyl. (C). Dashed line: Kiev (50°30'N); dashed line (C): Vladimir (56°12'N); solid line: St. Petersburg (59°55'N); dotted line: Chupa (66°15'N).

thermolability of development ceases to be adaptive. On the contrary, low thermolability, allowing a faster development at lower temperatures, may become an advantage under these conditions. Therefore, thermolability of development of the larvae and pupae decreases in the Far North (Figs. 8B, 8C). It is more difficult to explain why no decrease in thermolability of egg development is observed in the Far North (Fig. 8A). This fact may be related to noticeable differences in the thermopreferendum and vertical distribution of different kinds of brood in the ant nest. The eggs are known to be placed in the deeper and cooler layers of the nest, whereas the larvae are located above them, and the pupae, in the best heated areas. Therefore the larvae and pupae may utilize the high daytime temperatures to a greater extent, and the degree of thermolability of development may be a more important adaptive characteristic for these stages.

Another object studied by us in sufficient detail was the linden bug *Pyrrhocoris apterus*. The latitudinal variation in the duration and thermal norms of development of the eggs and nymphs of this species was found to be very complicated (Figs. 11, 12). Our stud-

ies allowed us to put forward hypotheses concerning its adaptive significance (Balashov et al., 2005). The regression coefficient of development rates on temperature and the threshold of development of the eggs and nymphs increase from south to north within the latitude range from 43 to 48°N (Fig. 11). This means that the slope of regression lines to the abscissa axis increases northwards, so that the development proceeds faster at relatively high temperatures in the northern populations. As a result, the duration of development of the eggs and nymphs decreases from south to north at all the temperature variants within this latitude range (Fig. 12), which probably allows the more northern populations of the species (up to 48–50°N) to remain bivoltine.

In the areas lying to the north of 50°N, where the second generation is produced by only a small fraction of individuals, the duration of nymphal development significantly increases northwards at all the temperatures (Figs. 12C, 12D), while the regression coefficient of nymphal development tends to decrease (Fig. 11C). In our opinion, this pattern of latitudinal variation may be related to the fact that as the duration of the warm season decreases from south to north, the

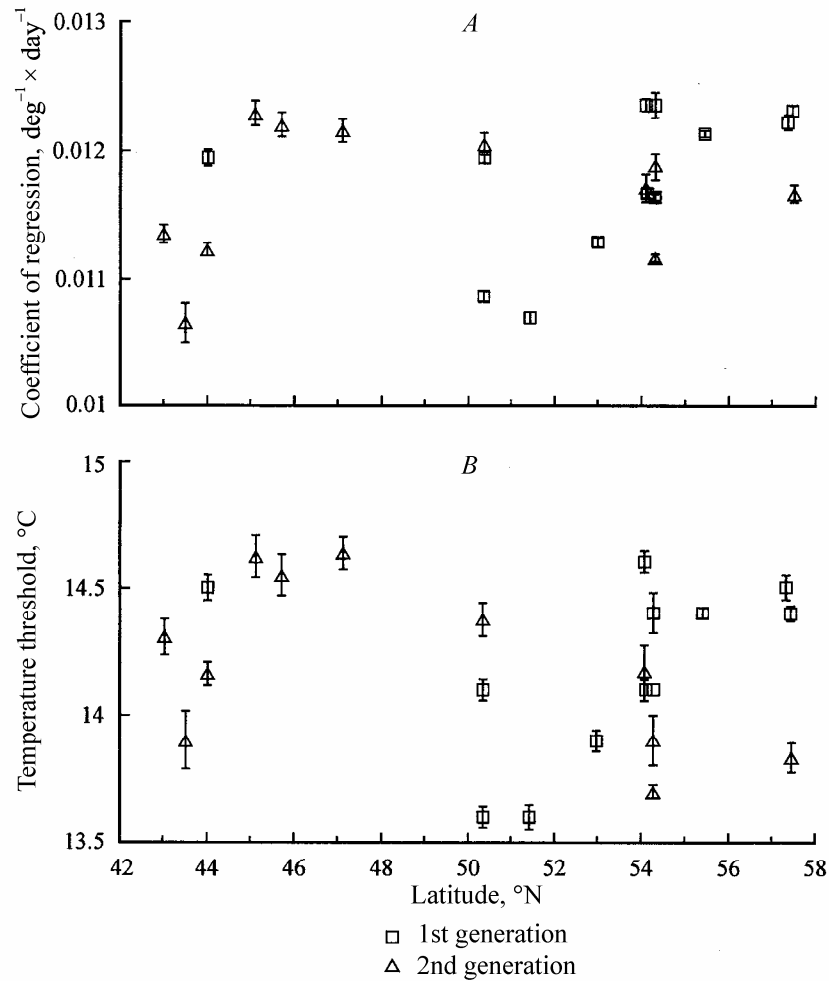


Fig. 11. Intraspecific latitudinal variation of the coefficient of regression of development rate on temperature and the temperature threshold in eggs (A, B) and nymphs (C, D) of the linden bug *Pyrrhocoris apterus* L. (Unpublished data of S.V. Balashov). Vertical lines represent the standard errors.

fraction of insects with a univoltine development cycle gradually increases. Since a sizable fraction of individuals cannot produce the second generation in northern populations, selection will act against rapid development and the expenses involved (Roff, 1980), leading to an increase in the mean duration of development (Figs. 12C, 12D) and a decrease in the thermolability of nymphal development (Fig. 11C) along the latitudinal gradient from 50 to 58 $^{\circ}\text{N}$.

At latitudes above 50 $^{\circ}\text{N}$, the development rates of linden bug eggs are generally lower than at 45–48 $^{\circ}\text{N}$, at temperatures above 24 $^{\circ}\text{C}$ (Fig. 12B), but noticeably higher at lower temperatures and especially at 20 $^{\circ}\text{C}$ (Fig. 12A). A faster development of eggs at relatively low temperatures may be an adaptation to the microclimate of the habitats where the eggs develop in the northern areas. The linden bugs lay eggs in the litter and soil. Even though they may select more or less

well-heated areas for oviposition, the mean daily temperatures at the places of egg development will undoubtedly be lower than those at which the nymphs can develop. These temperatures are unlikely to be noticeably above 20 $^{\circ}\text{C}$. It is obvious that under such conditions, the insects from northern populations will benefit more from faster egg development at low temperatures, which is exactly what is observed in the nature. Therefore, the regression coefficient and the threshold of egg development in the northern parts of the distribution range appear to be weakly dependent, or not dependent at all, on the latitude (Figs. 11A, 11B).

We have also found some species of insects with highly constant thermal reaction norms within the distribution ranges. For example, in the blowflies *Calliphora vicina*, *C. vomitoria*, and *C. uralensis* the latitudinal variability of thermal development norms was

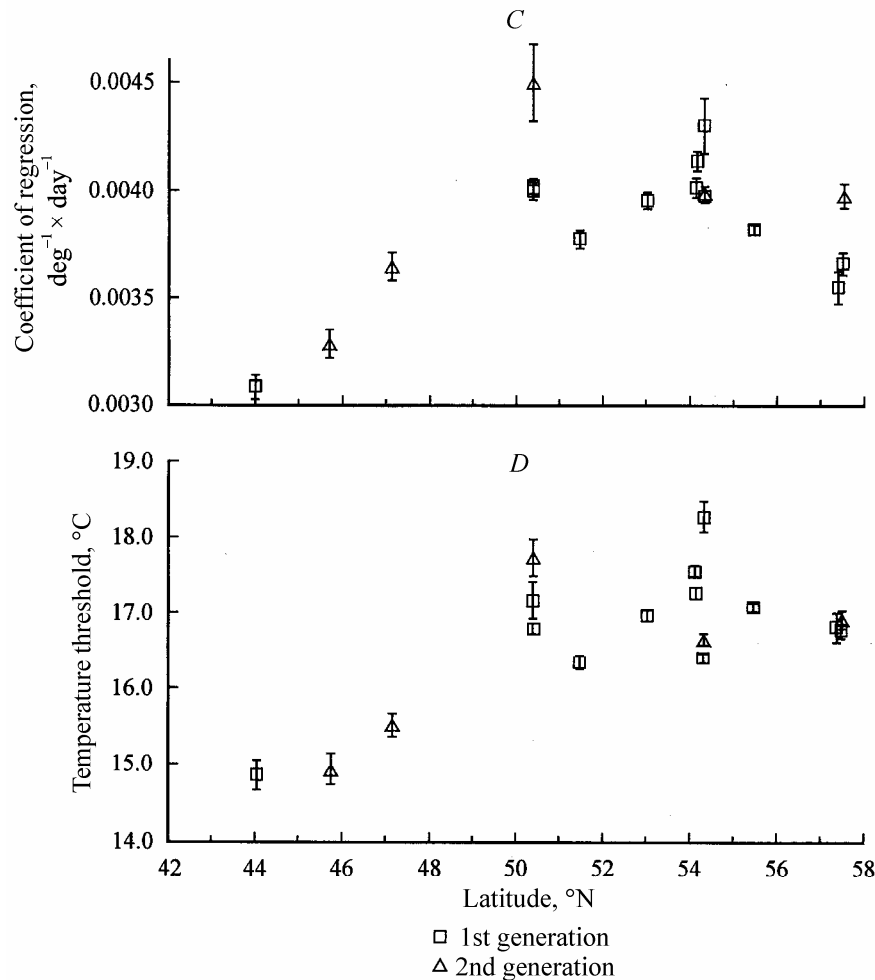


Fig. 11 (Contd.).

very low within the studied latitudinal range (about 9°) in northwest Russia. The coefficient of thermolability and the development thresholds in all the three species showed a weak trend for increasing from south to north; however, no significant differences were revealed between many geographic populations of these fly species (Nesin and Kipyatkov, 2007).

2. Seasonal Variation

Our experiments with the ants *Myrmica rubra* and *M. ruginodis* revealed a previously unknown form of seasonal variation in the duration and thermal norms of pupal development. The pupae of workers produced in early summer by overwintered larvae (the winter brood) were found to be somewhat larger in both species and to take significantly longer to develop (by 7–12% in *M. ruginodis* and by 9–11% in *M. rubra*), as compared to the pupae produced in the second half of summer by the larvae that had developed from eggs laid in spring (the summer brood). The lines of regression of development rates on temperature for the

summer brood pupae had a greater slope to the abscissa axis, indicating a greater thermolability of development than that of the winter brood pupae (Kipyatkov et al., 2005).

Studies of the linden bug *Pyrhcoris apterus* revealed a significant variation in the duration and thermal norms of development of the eggs and nymphs in two consecutive generations, which may also be interpreted as a form of seasonal variation (Balashov et al., 2007). The thermal norms for development of the linden bug nymphs were also shown to vary depending on the food quality. The thermolability and development threshold was significantly lower in the nymphs feeding on sunflower seeds (a less favorable diet) than in those feeding on linden seeds (a more favorable diet).

3. Thermal Norms for Development at Different Stages of the Life Cycle

The coefficients of regression of development rates on temperature of the eggs of the linden bug *Pyrrho-*

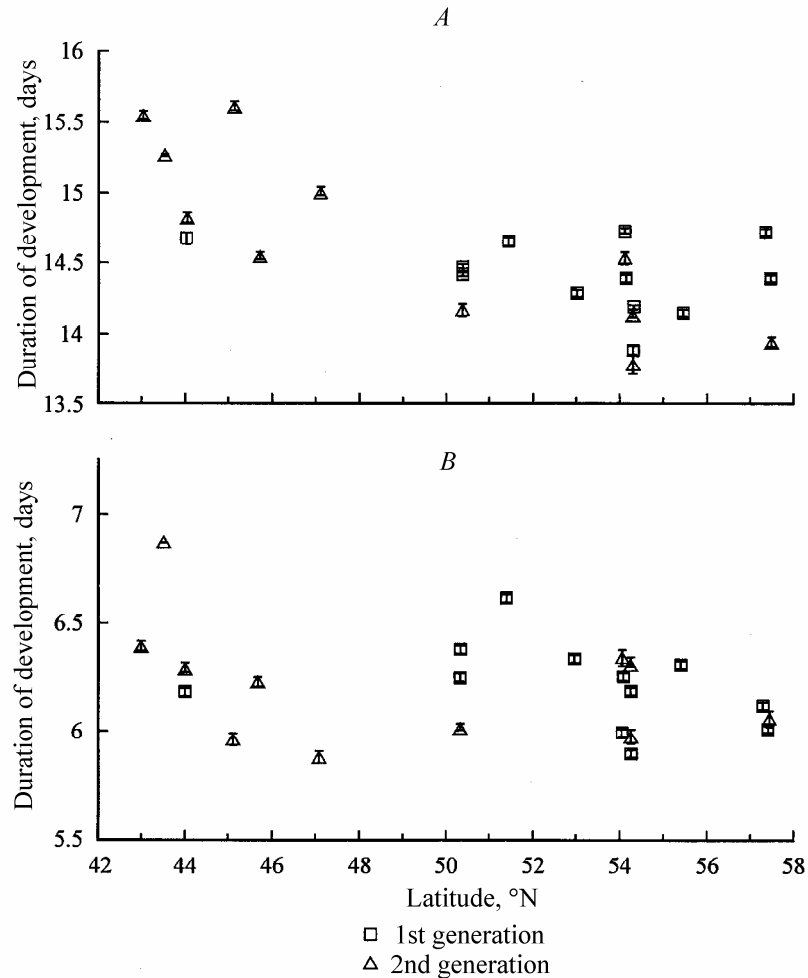


Fig. 12. Intraspecific latitudinal variation of the duration of development of eggs (A, B) and nymphs (C, D) of the linden bug *Pyrrhocoris apterus* L. at temperatures 20°C (A, C) and 28°C (B, D) (Unpublished data of S.V. Balashov). Vertical lines represent the standard errors.

coris apterus were found to be noticeably and significantly higher in all the cases, and the development thresholds to be lower than the corresponding parameters of the nymphs (Balashov and Kipyatkov, 2008b). The thermal reaction norms for development were also different in the eggs, larvae, and pupae of many species of ants (Lopatina and Kipyatkov, 1998). These results evidently disagree with the concept of “developmental rate isomorphy” (Jarošik et al., 2002), according to which the development thresholds of all the stages in the life cycle of a species should be the same, and only the slopes of the lines of regression of development rates on temperature may vary. In addition, the absence of significant correlation between the coefficients of thermolability of development and between the development thresholds of eggs and nymphs in linden bug colonies was demonstrated for the first time. All the coefficients of correlation between these

parameters are small, non-significant, and may accept positive or negative values in different populations, indicating the absence of any specific relation between the parameters in question. In other words, the absence of genetic covariation between the thermal reaction norms for development of different stages of the species’ life cycle: eggs and larvae, was proved for the first time. This means that the regression coefficient (as well as the sum of degree-days) and the development threshold of the eggs and larvae are inherited independently; therefore, these parameters may change independently in the course of evolution, according to the specific environmental conditions under which these stages of the life cycle exist.

In our opinion, the “developmental rate isomorphy” cannot be regarded as a universal phenomenon among insects. Isomorphy may be ecologically justified in

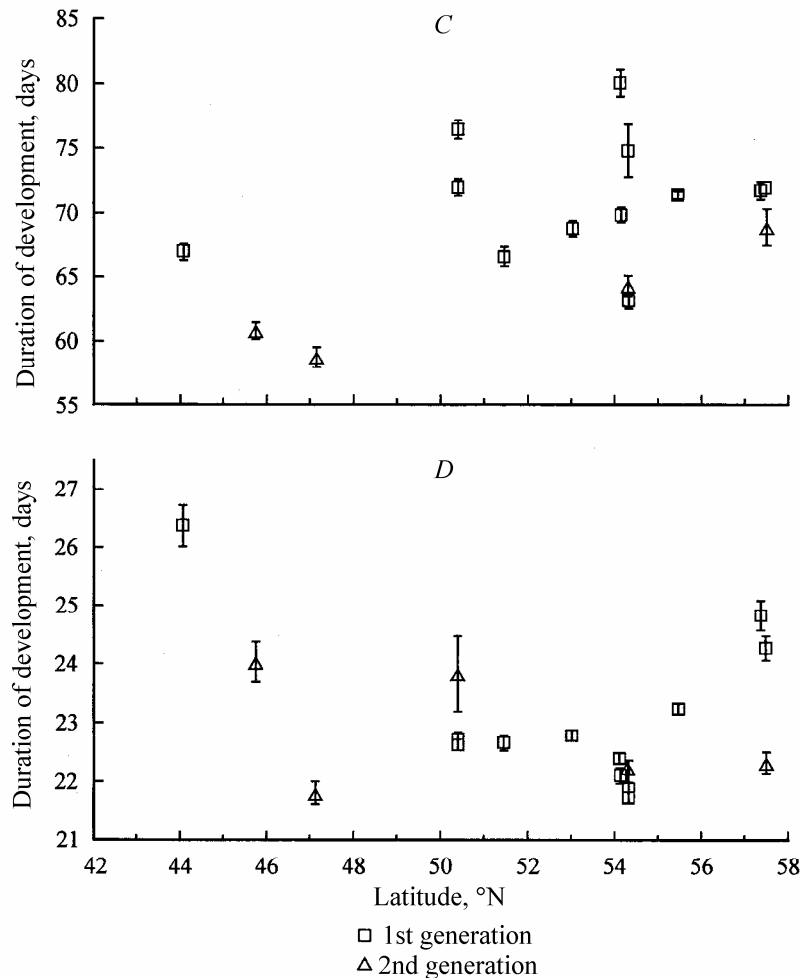


Fig. 12 (Contd.).

some groups, such as ladybugs (Jarošik et al., 2002) or ground beetles (Saska and Honěk, 2003), in which all the stages of the life cycle occur in the same habitats and under similar thermal conditions. However, if ecological conditions differ strongly at different stages of the life cycle, as observed in the linden bug, then the thermal norms for development of these stages may also be noticeably different. This conclusion agrees well with the life cycle theory.

4. The Effect of the Size of Pupae on the Thermal Norms for Their Development

Experiments carried out by A.P. Nesin on the blowfly *Calliphora vicina* showed the duration and thermolability of development of the pupae to depend on their mass. The duration of development of smaller pupae was noticeably and significantly shorter at all the temperatures exceeding the development threshold, while the coefficient of thermolability of their development was significantly greater (i.e., the slope of the line of

regression of development rates on temperature to the abscissa axis was greater) than those of larger individuals (Fig. 13). The temperature thresholds of development of small and large pupae were almost the same. A significant correlation was observed between the body mass and the duration of development of pupae at all the 5 experimental temperature variants. The duration and thermal norms of development were not affected by the sex of the larva and the presence of a diapause in its preceding development. It is interesting that our studies of ants (Kipyatkov et al., 2005) also indirectly confirm the idea that the size of the pupae might affect the duration and thermal norms of their development: the pupae of the summer brood, which are on the average smaller than the spring pupae, demonstrate faster development and higher thermolability.

The size (body mass) of individual insects is often positively correlated with the duration of their larval development, which can be easily explained from the

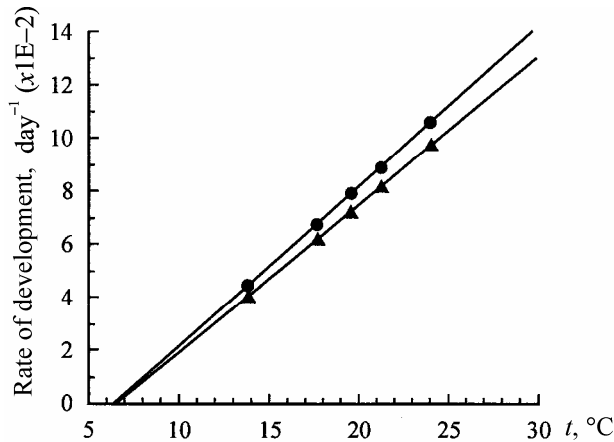


Fig. 13. Lines of regression of development rate on temperature for small (circles) and large (triangles) pupae of the blowfly *Caliphora vicina* R.-D. from the St. Petersburg population (Unpublished data of A.P. Nesin).

physiological standpoint (Ratte, 1985; Atkinson, 1994). In such cases, the duration of development of the larva is a factor affecting its size by the end of the growth period. However, as far as we know, no one has ever raised a question as to the possible inverse relation, i.e., whether the body mass might affect the duration of development. This question would be justified only with respect to non-feeding and non-growing stages of the life cycle, namely eggs and pupae, which are characterized by a certain initial mass that may only be reduced in the process of development. The effect of the initial mass of the pupae on the rates and thermal norms of their development was demonstrated in insects for the first time. These findings open a new promising line of research.

5. Photoperiodic Regulation of the Thermal Norms for Development

Our studies carried out on the linden bug *Pyrrhocoris apterus* (Lopatina et al., 2007) revealed for the first time the effects of photoperiodic conditions on the temperature threshold and thermolability of development in insects. In experiments with individuals from four geographic populations, a decrease in daylength was shown to modify the thermal dependence of the duration of development: the temperature threshold and the coefficient of thermolability of nymphal development decreased. Thus, under short-day conditions the nymphal development becomes less thermolabile but proceeds more rapidly at relatively low temperatures (below 24°C). As a result, the nymphal development is accelerated at the end of summer, which

represents an advantage since the insect can successfully reach the stage of a diapausing adult before autumn.

There is extensive factual material indicating the influence of photoperiodic conditions on the duration of insect development (Danilevsky, 1961; Danks, 1987; Saulich and Volkovich, 2004). Most of the cited researchers studied the effects of photoperiods (usually long-day and short-day ones) on insect development at only one, less frequently two variants of temperature. According to the traditional views, different photoperiods may “hasten” or “impede” development, which may have an adaptive significance of synchronization of the life cycle with the seasonal climatic changes (Danilevsky, 1961; Danks, 1987; Nylin, 1994; Saulich and Volkovich, 2004). Our studies of the linden bug demonstrated for the first time that photoperiodic conditions did not merely hasten or impede growth and development of insects but modified the thermal reaction norms for their development. The effect of a particular photoperiod on development is therefore ambiguous: at some temperature values it may accelerate development as compared to other photoperiods, whereas an opposite effect may be observed at other temperatures. In graphical form, this effect is manifested by the mutual arrangement of the lines of regression of development rates on temperature, characterizing the reaction norms at different photoperiods (Lopatina et al., 2007).

We could find several published reports of experiments carried out at different photoperiods and two or three temperature values. Using these data, we calculated the values of thermal constants at different photoperiods in several species of insects and in all the cases revealed the sought-for effect (Lopatina et al., 2007), which had not been noticed by the original researchers owing to the prevalence of the traditional perspective: nobody had ever considered the idea that the duration of development could depend on photoperiodic conditions and be based on the corresponding changes in the thermal norms for development. The results obtained suggest that the photoperiod affecting the thermal reaction norms for development is a widespread phenomenon among insects. The influence of a short-day or long-day photoperiod does not simply hasten or impede development, as most researchers assume, but changes the thermal reaction norm as a whole.

6. *Inheritability of the Thermal Norms for Development and the Possibility of Changing Them by Artificial Selection*

Our studies of populations of the linden bug *Pyr-rhocoris apterus* (Balashov and Kipyatkov, 2008b) revealed a considerable variation of the duration and thermal norms of development of the eggs and nymphs. This variation was observed between the colonies and was therefore inherited. Another important result was the finding of a positive correlation between the coefficient of regression of development rates on temperature and the development threshold of individuals (eggs and nymphs) from different colonies. The greater the slope of the line of regression of development rates on temperature in a particular colony, the higher the temperature threshold of development in this colony. Therefore, the lines of regression of development rates on temperature drawn for different linden bug colonies usually intersect. A positive correlation at the species level between the temperature threshold and the coefficient of thermolability was also observed in our experiments with ants (Kipyatkov et al., 2005a, 2005b). These results demonstrate for the first time the presence of a genetic interrelation (covariation) of the regression coefficient and the development threshold in insect populations.

F.R. Groeters (1992) justly noted that all the research carried out so far only demonstrated the presence of interpopulation variation in the thermal norms for development. At the same time, in order to prove the genetic interrelation of the regression coefficient and the threshold, one should study intrapopulation variation, representing a necessary condition for natural selection, and prove the existence of a genetic covariation of these two characters. This problem was solved for the first time by our research.

It was also found out that artificial selection of linden bugs for faster or slower completion of development at 28°C resulted in noticeable and significant changes in the thermal reaction norms for nymphal development (Balashov and Kipyatkov, 2008a). During selection for faster development, both the temperature threshold and the coefficient of thermolability increase, which is reflected in the graphical form by a decreasing slope of the line of regression of development rates on temperature. As a result, the nymphal development becomes faster at higher temperatures but slower at lower temperatures. Selection for slower development has an opposite effect (Balashov and Kipyatkov, 2008a).

Significant differences between different linden bug colonies with respect to duration of development, coefficient of regression, and temperature threshold, the presence of genetic covariation between the coefficient of thermolability and the development threshold, and also the possibility of changing thermolability by selection indicate that there is a hereditary component in the variation of thermal norms for development. These results suggest that interspecific and interpopulation differences in the thermal norms for insect development may be the result of intrapopulation hereditary variation of the duration of development, coefficient of regression, and development threshold, which is subject to natural selection.

CONCLUSION

Studies of the intraspecific variation of thermal reaction norms for development of insects are a promising field of evolutionary ecology and the life cycle theory. The discovery of significant intra- and interpopulation variation of thermal constants in several species of insects sets a number of important problems. First, one should obtain evidence of inheritability of the thermal development norms and their possible changes by artificial selection in several species from different insect taxa, in order to demonstrate the general nature of this phenomenon. Second, comprehensive studies of the thermal constants, phenology of seasonal development, and microclimate of the habitats should be carried out in different geographic populations of the species studied. Such an approach will allow one to estimate the adaptive significance of intraspecific variation of thermal constants and to reveal the microevolutionary mechanisms of its origin and selective maintenance. The factors determining the geographic stability of thermal constants in some insect species, such as blowflies of the genus *Calliphora*, should also be characterized. Finally, the most important task is studying the phenotypic plasticity of thermal development norms, i.e., the possibility of their modification by environmental factors, under particular photoperiodic conditions.

ACKNOWLEDGMENTS

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