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COMPARATIVE AND ONTOGENIC  
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## Effect of Temperature on Rearing of the First Brood by the Founder Females of the Ant *Lasius niger* (Hymenoptera, Formicidae): Latitude-Dependent Variability of the Response Norm

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**Abstract**—It has been established that duration of brood development and success of rearing of the first worker individuals by founder females of the ant *Lasius niger* from the northern population (St. Petersburg) depend on temperature conditions to a larger extent than of individuals from the southern areal (Borisovka Village, Belgorod Region). The development rate of individuals from the northern population is lower as compared with individuals from the southern population in the low temperature range (17–20°C), but is higher at elevated temperatures (22–27°C). This leads to a greater slope of the temperature regression line of the development rate on the temperature, to lower values of the sum of effective temperatures, and to a higher temperature threshold of development in the northern population. Lower temperatures have a stronger effect on development of larvae from the northern population by inducing diapause in the greater number of individuals as compared with larvae from the southern population. The *L. niger* founder females require, on average, higher temperatures than the females from the southern populations of this species for rearing the first worker ants during the same summer season (i.e., without winter diapause). Thus, ants of the southern populations, when rearing the first brood, use a strategy of faster development at higher temperatures, while low temperatures restrict to the greater extent the development of their brood as compared with ants from the southern populations. It is concluded that one of the ways of physiological adaptation of ants for inhabitation on the North is such change of the norm of response to temperature, at which development becomes more temperature-dependent, the physiological response to higher temperatures increasing at the cost of its decrease at lower temperatures.

### INTRODUCTION

One of the central problems of the current evolutionary biology is evaluation of the relative role of natural selection and internal genetic and physiological factors restricting processes of development in maintenance of stability of species in the course of evolution. Numerous facts have been collected about the existence of morphological, behavioral, and physiological differences between geographic species populations. At the same time, only occasional

authors focused on geographically stable and conservative signs and discussed possible causes of such constancy. For theoretical solution of the problem of variability/stability of species and population signs, quite necessary are new data dealing not only with morphology, but also with physiology, ecology, and behavior of various organisms [1–8].

One of the most important ecophysiological features of insects is the character of dependence of the duration of species development on the temperature, i.e., the thermolability of development

measured by such parameters (thermal constants) as the temperature threshold of development, coefficient of thermolability of development, and sum of effective temperatures [9]. For the last few years, a considerable progress has been achieved: general regularities of interspecies variability of thermal constants have been established [10–12]. A negative correlation was found to exist on the whole between values of the sum of effective temperatures and the lower temperature threshold, i.e., when the threshold decreased, the effective temperature sum as a rule increased, and *vice versa*. Recently, Tradgill and Perry [13, 14] have proposed a functional explanation of this dependence: it is advantageous for species inhabiting at higher latitudes to have lower thresholds, which permits their development possible at lower temperatures but at the same time leads to an increase of the sum of effective temperatures. Thus, the authors believe that the negative correlation between the threshold values and the sum of effective temperatures revealed at the interspecies level is accounted for by the existence of the species adapted to inhabitation at different latitudes, i.e., under different climate conditions. This suggestion was confirmed in the subsequent work of Honek [15] who at the interspecies level revealed statistically significant correlations between the thermal constants and the geographical latitude of the place inhabited by the species: a negative correlation for the temperature threshold and a positive one for the sum of temperatures. Our studies on the ants of Paleoarctic [16, 17] have permitted revealing the same regularities: a statistically significant negative correlation between values of the lower temperature threshold of development and the sum of effective temperatures. It has also been established that the ant species inhabiting more southern regions have, on average, higher thresholds of development and lower values of the sum of effective temperatures as compared with the species spread to more northern areas.

At the same time, the works dealing with a possible intraspecies geographic variability of the thermolability of insect development are not that numerous (see reviews [12, 15, 18]). Some of them report data on stability of thermal constants within the species [19, 20], which basically confirms a viewpoint of Danilevskii [21] who considered the thermal constants as a stable species sign. Howev-

er, there also are data about the existence in some insects of an intraspecies geographic variability of the lower temperature threshold and the sum of effective temperatures; in some cases, the direction of this variability turns out to be the same as at the interspecies level [22, 23], whereas in other cases, directly opposite [24, 25]. In our recent studies on ants [26–29], the data have been obtained about an opposite direction of this variability within the species (they will be considered in “Discussion”).

According to the theory of life cycles (nowadays, a rapidly developing part of evolutionary ecology), the response norm of poikilothermic organisms to the temperature factor, including that to thermolability of development, is to depend on climate, i.e. to have an adaptive geographic variability, as natural selection optimizes parameters of development to make them corresponding with the temperature conditions in each local population [5, 30–32]. Therefore, to explain the absence of such variability, i.e., the facts of geographic stability of thermal constants, the term “species sign” is not sufficient and the mechanisms responsible for this needs to be revealed. For this purpose, various authors put forward several hypotheses [19–21, 30] that cannot be completely considered here due to the lack of place. However, it is clear that studies on geographic variability of the response norm of developing insects to the temperature factor, which could promote solution of this fundamental problem of the theory of life cycles, are quite actual. That was the main goal of our study.

## MATERIALS AND METHODS

Founder females of *Lasius niger* L. were collected after their nuptial flight in July–August on vegetation-free soil areas, when they threw down wings and were looking for places for the nest building. In laboratory, the females were placed in individual plastic Petri dishes, 40 mm in diameter, which also contains a piece of a regularly moistened cotton wool ball, and were kept in thermostats without illumination. The ant founder females during rearing of the first brood do not eat and live owing to internal reserves. Therefore, the animals were not fed during the experiments.

The main experiment was carried out in 1994 on

the females collected in the farmstead of the reserve "Forest on Vorskle" (the current name "Belogorie," the Borisovka Village, Belgorod Region), and in St. Petersburg. Ninety eight females from the first population and 117 insects from the second one were used. They were kept at five temperature regimes: 17, 20.5, 22.5, 25, and 27°C; the temperature was regulated with an accuracy of  $\pm 0.5^\circ\text{C}$ . Each group consisted of 20–25 females. Since the temperature fluctuated markedly during the experiment, it was measured 3 times a day and, for each ontogenetic stage, the mean temperature, at which the development occurred in each temperature regime, was determined. The mean temperature values used for calculation of the constants of regression equations are presented in Table 2.

In similar experiments carried out in 1987 on the *L. niger* females of three geographic populations: from Borisovka of the Belgorod Region, Novosibirsk (Akademgorodok) and St.-Petersburg environs, 33, 49 and 18 females were used, respectively; they kept at four constant temperatures: 17, 20, 22 and 25°C. Only the duration of egg development was determined.

Depending on the temperature, the females started to lay eggs in 2–8 days, from which the larvae and then pupae of worker ants and worker imagines developed. The Petri dishes with the females were examined under a binocular microscope every day, approximately at the same day period, to record the presence of eggs and all subsequent development stages of the first brood. Hence, duration of development of each stage and of the entire ontogenesis could be determined with an accuracy of  $\pm 0.5$  day. As early as at the first day after the beginning of egg laying, each females laid quite a few eggs (usually more than 10). Therefore, the duration of egg development was determined as the length of the period from the day of the appearance of eggs to the day of the appearance of the first larvae, whose number was counted. Subsequently, the duration of the period was determined from the day of the appearance of the first larvae to the appearance of the same number of pupae and, then, of the same number of workers. Thereby, for each female, we determined duration of all ontogenetic stages of several (usually 4–6) worker individuals.

The duration of development of the larvae was measured from the time of leaving the egg to for-

mation of pre-pupae, i.e., till the moment of defecation that occurs as early as in the cocoon and may be recorded by the appearance of a dark clump of excrement, meconium, in one of its ends. The existence of cocoon did not permit measuring separately duration of the pre-pupa and pupa stages; therefore, they were pooled, i.e., we determined duration of the period from the larva defecation to the moment when the imago left the cocoon.

The data obtained were processed using Quattro Pro 7.0. For each obtained value of the development duration ( $D$ ), the value of the development rate ( $R = 1/D$ ) was calculated. The correlation between the rate of development and the temperature in insects and other poikilothermic organisms is known to be non-linear at sufficiently high and low temperatures, but at intermediate temperatures, not too far from the optimal ones, it is practically linear. The existence of the linear dependence of the rate of development on the temperature permits calculating the so-called lower temperature threshold of development (LTT), a temperature, at which development already does not occur, i.e., its rate is equal to zero, and the sum of effective temperatures (SET), i.e., the number of degree-days at the temperature higher than LTT, which is required for completion of development of insect populations under the climate conditions [9–12, 15, 17–20, 22–25, 30, 33]. Therefore, we also used the linear regression analysis in our work.

Assuming the linear dependence of the development rate on the temperature within the limits of the used temperature interval (17–27°C), two coefficients of the linear regression equation of the development rate  $R_T$  against  $T$  were calculated:

$$R_T = a + bT,$$

where  $a$ —constant,  $b$ —coefficient of linear regression. The value of LTT was determined by extrapolation of the regression line to  $R_T = 0$  by the formula  $LTT = -a/b$ . SET was calculated as an inverse value of the regression coefficient:  $SET = 1/b$ . The standard errors of the constant and regression coefficient were obtained from the regression analysis and the errors of SET and LTT were calculated according to the formulas given in [33, 35]. The statistical significance of differences between the values of the regression coefficient, LTT and SET were determined from their standard errors, using Student's  $t$ -test.

**Table 1.** Success of rearing of the first worker ants by founder females *Lasius niger* from two geographic populations at different temperatures (1994)

Region of collection	Temperature (°C)	The total number of females	Females rearing worker ants	
			the number	the percent $\pm$ error (%)
Borisovka, Belgorod Region	17	20	0	0 $\pm$ 4.8
	20.5	19	12	63 $\pm$ 11.4
	22.5	21	20	95 $\pm$ 4.8
	25	20	20	100 $\pm$ 4.8
	27	18	18	100 $\pm$ 5.3
St. Petersburg	17	23	0	0 $\pm$ 4.2
	20.5	23	8	35 $\pm$ 10.2
	22.5	25	21	84 $\pm$ 7.5
	25	22	22	100 $\pm$ 4.3
	27	24	24	100 $\pm$ 4.0

The statistical significance of differences in duration of the development between populations were determined with aid of the dispersion analysis (ANOVA) and a subsequent paired comparison of the mean values by *post hoc* criteria (Tukey HSH test) using the program Statistica 4.3. Since the character of distribution of the values of development duration quite often differed statistically significantly from the normal one and the statistically significant correlation between the means and the dispersions was observed, we used a logarithmic transformation of the data, which permitted us to normalize to a considerable extent the distribution and to practically eliminate a correlation between the means and the dispersions. The statistical significance of differences between the percentages was determined by the Fisher method using Student's criterion.

## RESULTS

*Success of rearing of the first workers.* Only at temperatures of 25 and 27°C, all females reared successfully the first worker ants. A decrease of

temperature increased the percentage of females in which the workers never appeared, and at 17°C, no females reared workers (Table 1). In such females, all larvae entered diapause and subsequently were not developed by reaching the dimensions not exceeding the mean ones. Thus, a decrease of temperature increased the percentage of larvae in the state of diapause, which is typical of insects with facultative diapause [36].

However, the most interesting are differences in the response to temperature between two studied populations: a decrease of temperature seemed to promote to the greater degree the appearance of the diapause in the offspring of the females from the northern population (St. Petersburg), and therefore the percent of the females rearing workers at 22.5 and 20.5°C in the Belgorod population was statistically significantly higher ( $t = 2.03$ ,  $p = 0.026$ ) than in the St. Petersburg population (Table 1).

*Effect of temperature on duration of development.* The data on duration of development of the brood of the founder females at different temperatures, which were obtained in the main experiment, are presented in Table 2, while the parameters characterizing the dependence of the brood development rate on temperature, in Table 3. For 17°C, the data were obtained only on duration of egg development, as at this temperature all larvae entered diapause and did not pupate.

On the whole, for the entire diapason of temperatures studied, the effect of the factor of geographic origin on the development duration turned out to be statistically significant for eggs (ANOVA:  $F_{1,939} = 83.02$ ,  $p < 0.000001$ ; Tukey HSD:  $p < 0.000009$ ), for larvae (ANOVA:  $F_{1,548} = 5.0$ ,  $p < 0.026$ ; Tukey HSD:  $p < 0.0006$ ), and for the entire ontogenesis as a whole (ANOVA:  $F_{1,543} = 4.95$ ,  $p < 0.027$ ; Tukey HSD:  $p < 0.000009$ ), but not statistically significant for pre-pupae and pupae (ANOVA:  $F_{1,470} = 0.32$ ,  $p < 0.57$ ). The reason for this fact will be considered below.

The differences between the two geographic populations are to be analyzed taking into account the character of dependence of the development rate on temperature (Table 3, figure). It is clearly seen from figure that regression lines of the development rate for temperature for the eggs, larvae, pupae and the whole ontogenesis differ in two studied populations in a quite certain manner: in the

**Table 2.** Duration of development of the first brood (days) of founder females *Lasius niger* from two geographical populations at different temperatures (1994) (in parentheses—the number of individuals)

Ontogenetic stages	Parameters	Temperature regimen (°C)				
		17	20.5	22.5	25	27
Borisovka, Belgorod Region						
Egg	mean temperature (°C)	17.1	20.7	22.8	24.7	26.8
	min–max	52–57	23–33	18–22	15–18	13–16
	mean ± error	53.7 ± 0.26 (31)	25.3 ± 0.24 (72)	20.7 ± 0.09 (86)	16.7 ± 0.07 (138)	14.7 ± 0.08 (115)
Larva	mean temperature (°C)	–	20.6	23.0	24.8	27.0
	min–max	–	16–27	11–15	7–14	7–10
	mean ± error	–	21.1 ± 0.50 (32)	13.5 ± 0.13 (77)	10.2 ± 0.09 (127)	8.7 ± 0.07 (133)
Prepupa+pupa	mean temperature (°C)	–	20.2	22.0	25.4	27.2
	min–max	–	20–31	18–22	13–16	11–14
	mean ± error	–	24.5 ± 0.67 (32)	20.4 ± 0.13 (66)	14.5 ± 0.08 (112)	12.5 ± 0.07 (104)
Total ontogenesis	mean temperature (°C)	–	20.5	22.6	25.0	27.0
	min–max	–	64–76	52–57	39–47	33–38
	mean ± error	–	70.5 ± 1.76 (7)	54.4 ± 0.19 (57)	41.1 ± 0.14 (110)	35.7 ± 0.12 (99)
St. Petersburg						
Egg	mean temperature (°C)	17.1	20.7	22.8	24.7	26.8
	min–max	51–55	22–27	18–22	14–19	13–15.5
	mean ± error	53.4 ± 0.19 (43)	24.9 ± 0.13 (112)	19.9 ± 0.12 (96)	15.7 ± 0.08 (130)	14.1 ± 0.07 (136)
Larva	mean temperature (°C)	–	20.6	22.2	24.8	27.0
	min–max	–	18.5–32	13–19	8.5–12.5	7–10
	mean ± error	–	23.3 ± 1.53 (11)	15.8 ± 0.19 (84)	10.6 ± 0.09 (114)	8.4 ± 0.06 (137)
Prepupa+pupa	mean temperature (°C)	–	20.2	22.8	25.4	27.2
	min–max	–	24–28	14–21	12–16	11–14
	mean ± error	–	26.0 ± 2.00 (2)	18.3 ± 0.17 (77)	13.6 ± 0.09 (109)	12.3 ± 0.06 (127)
Total ontogenesis	mean temperature (°C)	–	20.5	22.6	25.0	27.0
	min–max	–	70–72	50–59	37–44	33–36
	mean ± error	–	71.0 ± 1.00 (2)	53.8 ± 0.30 (59)	39.9 ± 0.16 (104)	34.8 ± 0.09 (113)

northern population, the slope angle of the regression line (i.e., the regression coefficient) and the

LTT values always are slightly greater than in the southern population. The differences between the

**Table 3.** Parameters of dependence of development rate ( $R_T$ ) of the first brood of founder females *Lasius niger* from two geographic populations on temperature (T) (1994)

Ontogenetic stages	The number of temperature points	The number of individuals	Parameters of the equation of linear regression ( $R_T = a + bT$ )		LTT $\pm$ standard error ( $^{\circ}\text{C}$ )	SET $\pm$ standard error (degree-days)
			constant (a) $\pm$ standard error	regression coefficient (b) $\pm$ standard error		
Borisovka, Belgorod Region						
Eggs	5	442	$-6.55 \pm 0.335$	$0.50 \pm 0.006^{***}$	$13.0 \pm 0.13$	$199 \pm 2.3^{***}$
Larvae	4	365	$-16.26 \pm 0.985^*$	$1.04 \pm 0.026^{***}$	$15.7 \pm 0.23^{***}$	$96 \pm 2.4^{***}$
Prepupa+pupa	4	304	$-7.84 \pm 0.420$	$0.58 \pm 0.010$	$13.5 \pm 0.21$	$172 \pm 3.1$
Total ontogenesis	4	273	$-3.01 \pm 0.087$	$0.22 \pm 0.003^*$	$13.9 \pm 0.16$	$463 \pm 6.4^{**}$
St. Petersburg						
Eggs	5	517	$-7.15 \pm 0.54$	$0.54 \pm 0.006^{***}$	$13.3 \pm 0.11$	$186 \pm 1.9^{***}$
Larvae	4	346	$-19.32 \pm 0.929^*$	$1.16 \pm 0.025^{***}$	$16.7 \pm 0.18^{***}$	$86 \pm 1.8^{***}$
Prepupa+pupa	4	315	$-8.17 \pm 0.503$	$0.61 \pm 0.016$	$13.5 \pm 0.32$	$165 \pm 4.4$
Total ontogenesis	4	278	$-3.24 \pm 0.097$	$0.23 \pm 0.003^{**}$	$14.2 \pm 0.17$	$439 \pm 6.6^{**}$

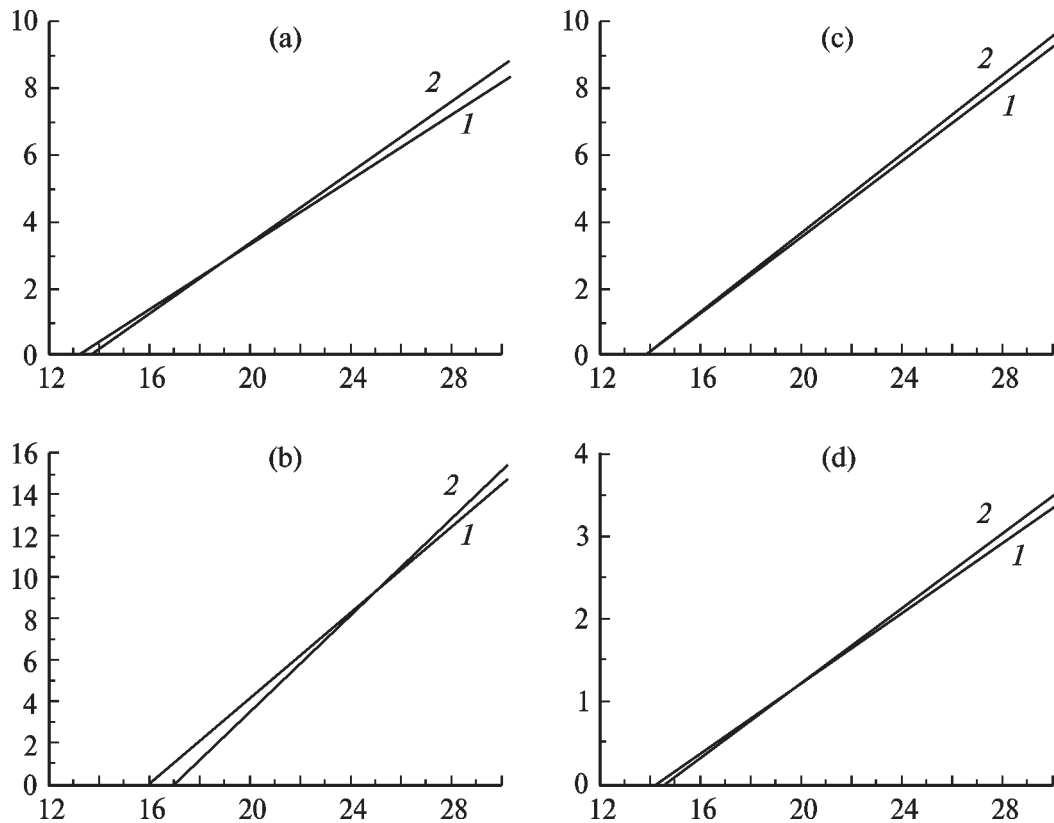
Note: LTT—the lower temperature threshold; SET—the sum of effective temperatures (the same for Table 5). The values of parameters designated by asterisks differed statistically significantly at the given stage of development: one:  $p < 0.05$ , two:  $p < 0.01$ , three:  $p < 0.001$ .

regression coefficients calculated for the two populations for eggs, larvae and the whole ontogenesis are statistically significant, and so are the differences between SET whose values always are lower for the northern population (Table 3). The differences between LTT are not marked and are statistically significant only for larvae in which they reach  $1^{\circ}\text{C}$  (Table 3). It is also important that the regression lines for the two populations are always crossed in the region of intermediate temperatures (figure).

Thus, duration of development of brood of founder females from the northern population depends to a greater extent on temperature. The development rate of individuals from the northern population is lower as compared with those from the southern population in the region of low temperatures, but higher at high temperatures. Therefore, the effect of the geographic factor on duration of pupa development turned out to be statistically insignificant. The pupae from St. Petersburg population developed much faster at temperatures of  $25$  and  $27^{\circ}\text{C}$ , whereas considerably slower at  $20$  and

$22^{\circ}\text{C}$  than the pupae from the Belgorod Region (Table 2), which resulted, on the whole, in the absence of statistically significant differences. When low temperatures were eliminated from consideration, the effect of the geographic factor on the development duration became even more statistically significant. For instance, for pre-pupae and pupae (at  $25$  and  $27^{\circ}\text{C}$ ), ANOVA:  $F_{1,448} = 49.2$ ,  $p < 0.000001$ ; Tukey HSD:  $p < 0.000009$ .

The revealed regularities are confirmed by the results of the experiment of 1987: the development of eggs of founder females from St. Petersburg turned out longer as compared with the eggs of the females from Belgorod at  $17^{\circ}\text{C}$ , but occurred somewhat faster at  $20$ – $25^{\circ}\text{C}$  (Table 4). The values of LTT and of the regression coefficient of the temperature-related development rate in the St. Petersburg population also turned out to be higher than in the Belgorod population (Table 5). All these parameters in the Novosibirsk population were intermediate or even closer to the Petersburg population (Table 5). This might be due to the more continental



Temperature regression lines of the development rate for eggs (a), larvae (b), pupae (c), and the complete ontogenesis (d) of the first brood of the founder females *Lasius niger* from two geographic populations. Abscissa: temperature ( $^{\circ}\text{C}$ ), ordinate: development rate ( $\text{day}^{-1} \times 10^{-2}$ ). (1) females from Borisovka, Belgorod Region; (2) females from St. Petersburg.

**Table 4.** Duration of development of eggs (days) of the founder females of *Lasius niger* from three geographic populations at different temperatures (in parentheses—the number of individuals)

Region of collection	Parameters	Temperature regimen ( $^{\circ}\text{C}$ )			
		17	20	22	25
Borisovka, Belgorod Region	min–max	46–62	25–31.5	20–25	15.5–17
	mean $\pm$ error	$52.7 \pm 2.28$ (7)	$28.5 \pm 0.63$ (10)	$23.1 \pm 0.62$ (9)	$16.5 \pm 0.19$ (7)
Novosibirsk	min–max	43–58	25–31.5	18.5–23.5	15–17
	mean $\pm$ error	$50.00 \pm 1.76$ (9)	$28.5 \pm 0.42$ (17)	$21.6 \pm 0.47$ (9)	$15.8 \pm 0.25$ (14)
St. Petersburg	min–max	52.2–55.5	25–30.5	21–23	15–17
	mean $\pm$ error	$54.0 \pm 1.50$ (2)	$27.9 \pm 1.13$ (4)	$22.0 \pm 0.32$ (5)	$16.0 \pm 0.36$ (7)

climate of Novosibirsk. However, for more certain conclusions, additional studies are required.

It is also to be emphasized that all parameters of the linear regression equation as well as the LTT

and SET values determined for eggs turned out to be very similar to those in the experiments of 1987 and 1994 (comp. Tables 3 and 5), which indicates a high temporal stability of these parameters.

**Table 5.** Parameters of dependence of the development rate ( $R_T$ ) of eggs of founder females *Lasius niger* from three geographic populations on temperature ( $T$ ) (1987)

Region of selection	The number of eggs	Parameters of the equation of linear regression ( $R_T = a + bT$ )		LTT $\pm$ standard error ( $^{\circ}\text{C}$ )	SET $\pm$ standard error (degree -days)
		constant (a) $\pm$ standard error	regression coefficient (b) $\pm$ standard error		
Borisovka, Belgorod Region	33	$-6.75 \pm 0.275$	$0.51 \pm 0.018$	$13.2 \pm 0.28$	$196 \pm 6.8$
Novosibirsk	49	$-7.37 \pm 0.288$	$0.55 \pm 0.015$	$13.4 \pm 0.22$	$182 \pm 4.8$
St. Petersburg	18	$-7.39 \pm 0.282$	$0.55 \pm 0.025$	$13.5 \pm 0.99$	$183 \pm 8.3$

Note: For ants from each region, 4 temperature points were studied.

## DISCUSSION

The obtained results permit concluding that one of the ways of physiological adaptation of ants to inhabit northern areals, under conditions of colder climate and shorter summer, is such change of the response norm to the temperature factor, at which development becomes to the greater extent temperature-dependent, the physiological response to higher temperatures increasing at the cost of its decrease at lower temperatures. This is seen from the change in the slope angle of temperature regression lines of the development rate (figure), which reflect, in fact, the norm of response of developing individuals to the temperature factor. The change in the response norm, i.e., the slope angle of regression lines, leads to that the development rate of individuals from the northern regions decreases at low, but increases at high temperatures. At the same time, LTT somewhat increases. In our opinion, it is the shortening of duration of ant development at higher temperatures that is of the main adaptive significance. Besides, the simultaneous elongation of the development at low temperatures and a slight increase of LTT do not produce any negative effect, as the development occurs mainly at higher temperatures (see below).

There remains unsolved question as to why the norm of response to the temperature cannot be changed by in such a way that the physiological response (for instance, the development rate) would increase in a full temperature diapason? This could have been of high adaptive significance

in many situations. Probably, such changes are prevented by some physiological mechanisms whose nature has not been yet known at present. Nevertheless, extensive comparative data have established [11, 12, 15] that the geographic variability of parameters of the temperature dependence of insect development takes place in most cases in the form of a change of the angle of the temperature regression line slope of the development rate, which usually leads to corresponding changes of the LTT value.

The change in the norm of response to temperature in *L. niger* affects not only the development duration, but also its other parameters, such as, for instance, induction of diapause. Indeed, we have established the low temperatures to act on larvae of the northern population much stronger by inducing diapause in the greater number of individuals as compared with larvae of the southern population. Hence, in the northern population larvae, the temperature threshold of the diapause induction is higher than in the southern population individuals. The founder females of *L. niger* need, on average, higher temperatures to rear successfully the first workers for the same summer season (i.e., without the winter diapause) as compared with females of the same species from the southern populations. Thus, the boreal ants, when rearing the first brood, use the strategy of a faster development at higher temperatures; at the same time, low temperatures restrict to the greater extent the development of their brood, than the ants from the southern populations.



We obtained quite similar data on a latitude-related variability of the norm of response to temperature of developing individuals in three species of ants of the genus *Myrmica* by an example of rearing the fast (i.e., developing without diapause) brood [26–28] as well as of development of pupae [29]. In the northern populations of these ants, the angle of the temperature regression line slope of the development rate also is greater, while low temperatures limit to a greater extent the development without diapause in comparison with colonies of ants from the southern regions.

Besides, in our joint studies with foreign colleagues on the latitude-related variability of respiratory metabolism in the same three species of ants of the genus *Myrmica*, it was shown [37, 38] respiration of worker individuals from the northern populations to be characterized by higher values of the  $Q_{10}$  coefficient as compared with ants from the southern regions, the northern ants breathing at 25°C more intensively, while at 5°C, less intensively, than the southern individuals. Thereby, respiratory metabolism of individuals from the northern populations depends to a greater degree on temperature (a change of the response norm) than that in southern representatives of the same species. This allows the boreal ants “to live more intensively” at higher temperatures by using more effectively for faster development a relatively short warm season at northern latitudes.

Our studies of the seasonal dynamics of temperature in nests of the ants *Myrmica rubra* and *M. ruginodis* [26, 28] have shown that the mean temperatures at which ants rear the brood on the North and even on the Subarctic by no means is lower than in the southern regions. This becomes possible, as ants on the North choose the warmest habitats and due to adaptive peculiarities of their nests, which permits them to better trap solar radiation. It is known [39] that ants initially are a thermophil group of insects that preserve on the whole their elevated temperature requirements when spreading on the North, which is provided by adaptive choice of habitats or thermoregulation in the nest. Our data permit us to think that on spreading to the North, thermophilicity of ants is not only preserved at the same high level but in many cases even increases.

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