

Reaction norm in response to temperature may change to adapt rapid brood development to boreal and subarctic climates in *Myrmica* ants (Hymenoptera: Formicidae)

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Key words. Formicidae, ants, *Myrmica rubra*, *Myrmica ruginodis*, *Myrmica scabrinodis*, latitude, reaction norm, temperature, rapid brood rearing, development rate, thermal threshold, thermal constants

Abstract. Colonies of *M. rubra*, *M. ruginodis* and *M. scabrinodis* were collected in four geographic regions: Kiev, Ukraine (50.5°N, 30.5°E – first two species), Vladimir, Russia (56.2°N, 40.4°E – only last species), St. Petersburg, Russia (59.3°N, 30.3°E – all three species) and Chupa, Murmansk prov., Russia (66.3°N, 33.7°E – last two species). After artificial overwintering experimental cultures consisting of 150 workers and one queen were established and kept at 16, 18, 20, 22, 24 and 26°C under long (22 h) day lengths. The workers reared eggs laid by queens into rapid (non-diapause) brood pupae and diapause larvae, which were removed and counted. The results showed the distinct latitudinal variation in the temperature effects on rapid brood rearing and in the thermal requirements for development. First, the period during which new rapid brood pupae appeared was found to be longer and the total number of pupae produced to be greater in ants from more southern populations. The number of diapause larvae reared by ant cultures was also usually greater, in ants from southern sites. Second, low temperatures reduced the period of rapid brood production and the number of pupae reared to a greater degree in ants from northern populations. It means that northern *Myrmica* colonies rear rapid brood under lower temperatures evidently worse in comparison with ants from southern regions. Third, eggs and larvae from more northern sites appeared to develop faster than southern brood at temperatures above 16–18°C. This was because brood development in northern populations was more temperature dependent, i.e. characterised by higher slopes of regression lines of development rate on temperature. The sum of effective temperatures decreased with the advance to North. The higher slopes were always associated with higher thermal thresholds for development. We conclude that the reaction norm of *Myrmica* colonies, in response to temperature, changes according to the local climate in such a way that brood rearing, growth and development of individuals become more temperature dependent in more severe environments with colder and shorter summers. This led to the increase of the physiological and developmental responses at higher temperatures at the expense of a decrease within lower temperature range. In fact *Myrmica* colonies from northern populations need on average higher temperatures in their nests for successful production of new adults as compared to southern ants.

INTRODUCTION

Ants, despite being generally thermophilic, have successfully penetrated as far to the North as the sub-arctic forest-tundra zone (Holgersen, 1942; Kusnezov, 1957). Although the importance of ants in boreal ecosystems is well acknowledged (e.g. Brian, 1983; Nielsen, 1987) surprisingly few studies have been devoted to the adaptations of these insects to the harsh climatic conditions of the North (Heinze & Hölldobler, 1994). In particular, almost nothing is known about the thermal requirements of development in boreal and sub-arctic species and populations of ants.

Our preliminary studies (Lopatina et al., 1999) suggested that southern and northern populations of *Myrmica* ants differed in the physiological response of colonies to temperature. We expected that such changes of the reaction norm to temperature in response to differences in local climate might be detected in the best way in experiments with ant colonies collected in several regions along latitudinal gradient from South to North. To make such experiments was the main goal of our study.

It is generally supposed that arctic and subarctic poikilotherms should be better adapted to grow and develop at low temperatures compared to their temperate counterparts. Indeed, the threshold temperatures for respiration, activity, feeding, development and emergence have long been shown to be very low in many arthropod species of northern origin (Downes, 1965; Danks, 1981). One more goal of our study was, therefore, to examine if this could hold also for *Myrmica* ants which are rather common and numerous in boreal habitats (Holgersen, 1942).

Ants of the genus *Myrmica* employ the strategy of prolonged brood-rearing which means that their colonies overwinter with larvae in diapause (Kipyatkov, 2001). In spring queens begin to lay eggs: however, only a part of the larvae which develop from these eggs, pupate during the same summer. These are the so-called *rapid* or *summer brood* (Brian, 1951, 1957). A large proportion of the larvae continue to grow slowly in autumn, overwinter in diapause and pupate during the next summer; these are usually called *slow* or *winter brood* (Brian, 1951, 1957). In late summer queens enter diapause and stop laying.

Larvae can only diapause in the third (final) instar, any eggs and young larvae that fail to reach the final instar before winter die so that all overwintering brood consists of third instar larvae (Brian, 1951; Elmes & Thomas, 1987; Elmes, 1991).

The duration of *Myrmica* colony's annual cycle of brood-rearing is controlled both by an endogenous timer and by external ecological factors - temperature and photoperiod. The environmental factors adjust the date of diapause onset in queens and larvae to the climatic characteristics of a given year. In late summer the lower temperature and short days induce the diapause thus curtailing the period of development (Kipyatkov, 1974, 1977, 1993, 2001). The winter diapause is, however, obligatory at a colony level and possible period of non-diapause development is strongly limited by endogenous factors in most temperate and especially boreal ants (including the genus *Myrmica*): In laboratory experiments, even at long days and optimal temperatures, diapause ensues and brood-rearing ceases sooner or later as a result of an internal timing effect (Kipyatkov, 1993, 1995, 2001). *Myrmica* populations adapt to distinct local climates by changing the period of rapid brood rearing and the amount of pupae produced which leads to a definite latitudinal variation of these parameters. This is controlled mainly by innate endogenous mechanisms: The length of *Myrmica* colony's intrinsic cycle of brood-rearing was found to be shorter in more northerly populations of the same species even if colonies were reared in common garden conditions (Kipyatkov & Lopatina, 1997).

MATERIALS AND METHODS

Stock colonies of *Myrmica rubra* L., *M. ruginodis* Nylander and *M. scabrinodis* Nylander were collected at the end of summer in four geographic regions: Kiev, Ukraine (50.5°N, 30.5°E – first two species), Vladimir, Russia (Yurievets, 56.2°N, 40.4°E – only last species), St. Petersburg, Russia (Vyritsa, 59.3°N, 30.3°E – all three species) and Chupa, Murmansk prov., Russia (66.3°N, 33.7°E – last two species). All sites were at low altitudes. In Kiev and St. Petersburg regions *M. rubra* and *M. ruginodis* lived together in the same habitat: near Kiev in deciduous oak forest nesting mainly in rotten wood and near St. Petersburg in coniferous pine woodland mostly in moss hillocks. *M. scabrinodis* lived mostly in soil mounds on grass meadows and clearings in deciduous woodland near Vladimir and in moss hillocks in the bogs near St. Petersburg. Near Chupa both *M. ruginodis* and *M. scabrinodis* occurred mainly in the bogs nesting in moss hillocks.

Before the experiments stock colonies were subjected to artificial overwintering in a refrigerator at 3–5°C for 4 months. Thus, they were physiologically in early spring state, just at the beginning of annual cycle of brood-rearing (Brian, 1955; Kipyatkov, 1993, 2001). Following the overwintering colonies were kept at 10°C and at 15°C (for a week at each temperature), and after that the experimental cultures consisted of 150 workers and one queen were established (all overwintered larvae were removed from colonies). From 11 to 18 stock colonies of each species from each site were used, which were both monogynous and polygynous. Each monogynous colony gave rise to one experimental culture. Polygynous colonies were used to establish from 2 to 8 experimental cultures each. In the latter case

cultures originating from the same stock colony were evenly distributed among experimental regimes.

Ant cultures were maintained in plastic laboratory nests with approximately 100% humidity and food (cockroaches *Nauphoeta cinerea* cut into pieces and 15% sucrose solution) added twice a week in photo thermostatic chambers (photothermostats). Six constant temperatures (16 ± 0.2°C, 18 ± 0.2°C, 20 ± 0.2°C, 22 ± 0.2°C, 24 ± 0.2°C and 26 ± 0.2°C) all at long-day photoperiod 22L : 2D were used, except for *M. scabrinodis* from Chupa where the temperature of 16°C was not used. From 3 to 7 (usually 5–6) cultures from each population were used in each experimental temperature.

Queens began to lay eggs soon after the start of the experiment. The workers reared these into rapid brood pupae and diapause larvae. Twice a week cultures were examined and all prepupae and pupae produced during the preceding week were removed and counted (they were not returned to nests). The presence of eggs and early instars larvae was also checked. When pupation stopped, eggs and early instars larvae disappeared, all the remaining third instar diapause larvae were counted in each culture. During these manipulations with ants they were anaesthetised by a short (up to 30 seconds) exposure to carbon-dioxide which is known to have no negative effect on brood rearing (Wardlaw, 1995). Worker mortality was not excessive (on average < 20%) and not enough to affect brood-rearing significantly.

From data obtained the following parameters were calculated for each group: the period of rapid brood pupation (the interval between the appearance of the first and the last pupa), the number of rapid brood pupae reared, the number of diapause larvae reared, the total number of brood produced (rapid plus diapause brood). The time of development (D) from egg to prepupa was also calculated for each culture by determining the period elapsed between the appearance of the first eggs and the first prepupae for which purpose their presence in ant cultures were checked each 1–2 days. The rate of development at a given temperature (T) were calculated for each culture as $R_T = 1/D$.

The relationship between development rate and temperature in insects and many other poikilotherms is curvilinear at extreme temperatures, but at moderate temperature it is approximately linear, which feature allows to calculate so-called lower developmental threshold, or else thermal threshold for development (TTD) – the theoretical minimum temperature at which development will proceed assuming a linear relationship between development rate and temperature and the sum of effective temperatures (SET), or else the thermal requirement for development, i.e. the number of day-degrees above thermal threshold needed to complete development (Campbell et al., 1974; Ratte, 1985). The TTD and SET are widely used as important life-history traits, especially in comparative studies, usually to examine and illustrate the adaptations of insect populations to local environmental conditions (Campbell et al., 1974; Lamb et al., 1987; Tauber et al., 1987, 1988; Honěk & Kocourek, 1990; Honěk, 1996a, b). This is why we also used linear regression analysis in our study.

Assuming a linear relationship between development rate and temperature in a restricted temperature range (16–24°C) two coefficients of linear equation were estimated using regression analysis:

$$R_T = a + b \times T$$

where a – intercept, b – slope (i.e. the coefficient of linear regression of development rate on temperature). The value of TTD was estimated by extrapolating the regression line to $R_T = 0$, thus $TTD = -a/b$. SET was calculated as the reciprocal value of the slope: $SET = 1/b$. The standard errors (SE) of intercept

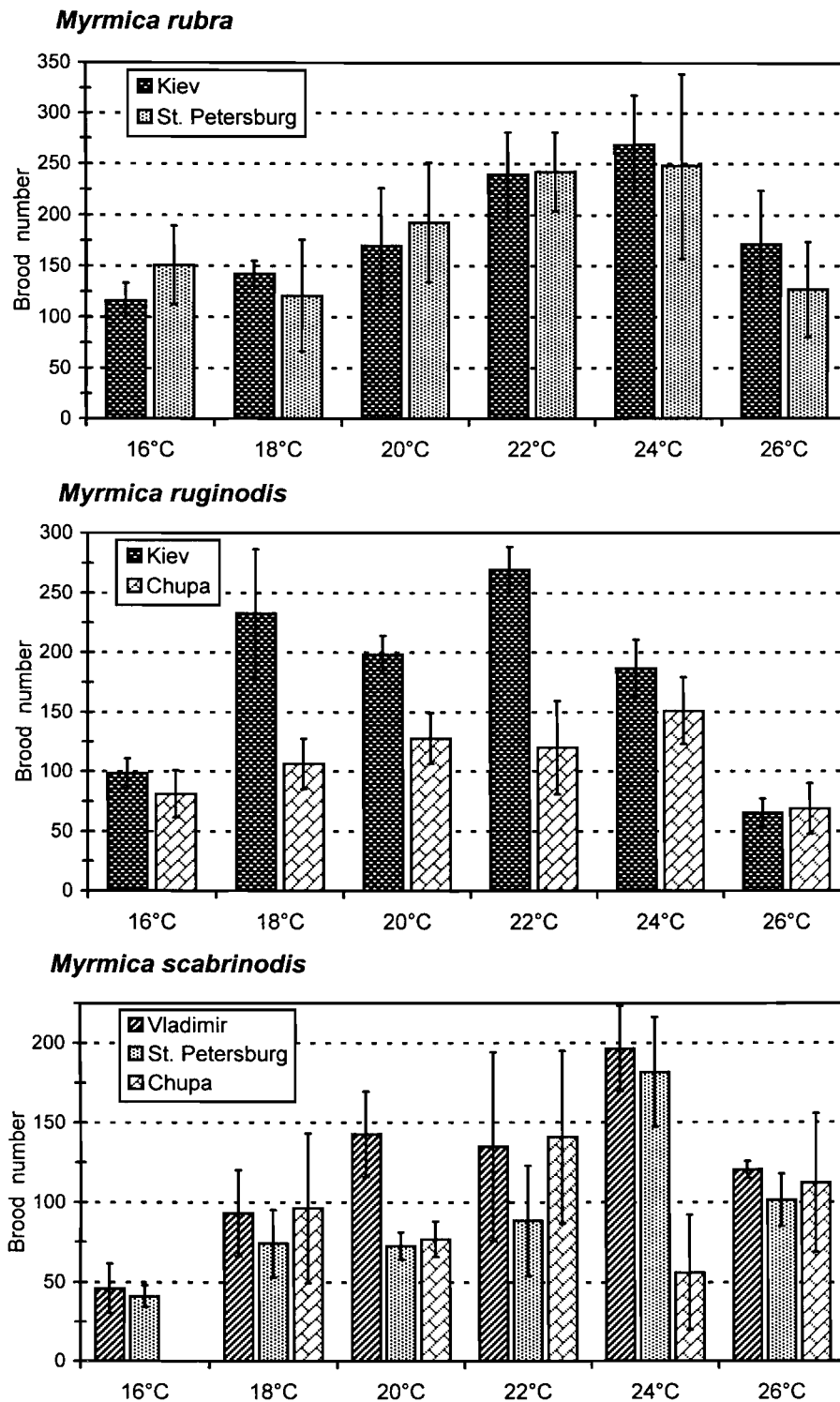


Fig. 1. Mean total brood production at six constant temperatures by experimental cultures of three *Myrmica* species from different geographic regions. Vertical bars – standard errors of means.

and slope were obtained from regression analysis, the SE values for TTD and SET were calculated using formulas given by Campbell et al. (1974).

Data were analysed by ANOVA using Statistica 4.1 package. Development times were more or less normally distributed and there were no significant correlations between means and variances. The reverse was true for other data which were very overdispersed in many experimental variants. Consequently we used data log transformation which apparently improved nor-

mality and eliminated correlation between means and variances in most such cases. Tukey HSD test was used for *post hoc* comparison of means.

RESULTS

Brood production

The total production of brood (rapid brood pupae plus diapause larvae) by ant cultures (Fig. 1) was evidently

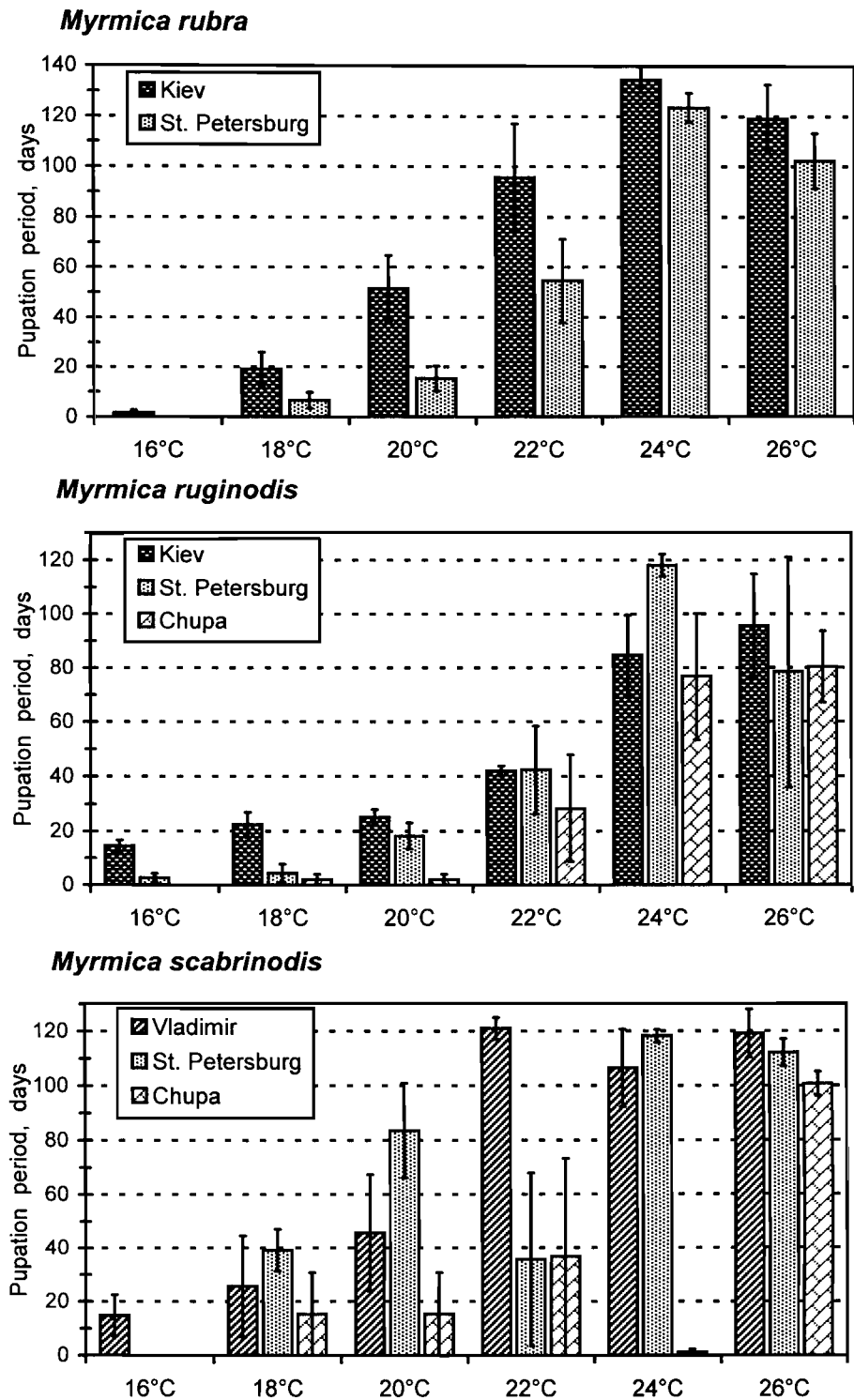


Fig. 2. Mean period of rapid brood pupation at six constant temperatures in experimental cultures of three *Myrmica* species from different geographic regions. Vertical bars – standard errors of means.

affected by temperature which influence appeared significant for all three species (*M. rubra* – $F_{5,58} = 2.8, p < 0.024$; *M. ruginodis* – $F_{5,59} = 8.6, p < 0.001$; *M. scabrinodis* – $F_{5,56} = 3.3, p < 0.012$). The highest brood production was observed at 22–24°C depending on species and population; the temperature of 26°C apparently suppressed brood rearing (Fig. 1). Two populations of *M. rubra* did not differ significantly in mean number of

brood reared. In the case of St. Petersburg population of *M. ruginodis* the diapause larvae were not counted for technical reasons. But *M. ruginodis* cultures from Kiev produced significantly more brood at all temperatures except 26°C in comparison with those from Chupa ($F_{1,59} = 21.1, p < 0.001$). The differences in total brood production between *M. scabrinodis* populations did not appear significant mainly due to greater variation of this

parameter (Fig. 1). A significant effect of site x temperature interaction ($F_{5,59} = 3.0, p < 0.017$) was found only for *M. ruginodis*.

The mean period during which rapid brood larvae pupated in ant cultures (Fig. 2) was significantly influenced by temperature in all three species (*M. rubra* – $F_{5,52} = 40.0, p < 0.001$; *M. ruginodis* – $F_{5,78} = 42.8, p < 0.001$; *M. scabrinodis* – $F_{4,40} = 10.0, p < 0.001$). *M. rubra* cultures from St. Petersburg produced pupae during shorter time than cultures from Kiev at all temperatures ($F_{1,52} = 8.9, p < 0.005$), these differences being much more marked at lower temperatures of 16–22°C. The influence of site on the mean period of rapid brood pupation in *M. ruginodis* cultures was significant both by ANOVA ($F_{2,78} = 32.9, p < 0.036$) and by Tukey HSD test ($p < 0.002$). Again the differences between sites were greater at lower temperature range (16–20°C). *M. scabrinodis* cultures from Vladimir and St. Petersburg appeared rather similar in the mean duration of pupation period but both differed significantly ($p < 0.002$) from Chupa cultures which produced pupae during shorter period. Only one out of three *M. scabrinodis* cultures from Chupa kept at 24°C reared 2 pupae, others did not produced pupae at all. This was obviously due to greater variation of rapid brood production observed among *M. scabrinodis* colonies (and also individual queens) some of which did not rear rapid brood even in optimal conditions. Cultures from 3 such colonies were placed at 24°C regime simply by chance which explained the unusually low value of pupation period obtained at 24°C (Fig. 2). A significant effect of site x temperature interaction ($F_{8,40} = 3.2, p < 0.007$) was found only for *M. scabrinodis*.

The differences between populations in temperature effects on the production of rapid brood pupae appeared even more pronounced and instructive (Fig. 3). The total production of pupae by ant cultures was clearly and significantly influenced by temperature in all species (*M. rubra* – $F_{5,52} = 21.0, p < 0.0001$; *M. ruginodis* – $F_{5,78} = 46.0, p < 0.0001$; *M. scabrinodis* – $F_{4,40} = 8.5, p < 0.001$). The maximum pupae production was observed at 24°C except *M. ruginodis* from Kiev which probably had a maximum at 22–23°C and *M. scabrinodis* from Chupa which did not produce rapid brood at 24°C by chance (see above). The temperature of 26°C apparently suppressed rapid brood production in *M. rubra* and *M. ruginodis* (Fig. 3). The influence of site on pupae production appeared significant in all species (*M. rubra* – $F_{1,52} = 10.2, p < 0.003$; *M. ruginodis* – $F_{2,78} = 50.1, p < 0.0001$; *M. scabrinodis* – $F_{2,40} = 11.5, p < 0.0002$). The effects of site x temperature interaction appeared significant for *M. ruginodis* ($F_{10,78} = 2.7, p < 0.007$) and *M. scabrinodis* ($F_{8,40} = 2.7, p < 0.018$). All populations within each species differed quite significantly in pupae production, except between *M. scabrinodis* from Vladimir and St. Petersburg (Tukey HSD test: $p < 0.002$ for *M. rubra*; $p < 0.007$ for *M. ruginodis*; $p < 0.005$ for *M. scabrinodis*). Almost invariably more northern populations produced less rapid brood pupae in comparison with southern populations of the same species. These differences were much

more pronounced at lower temperatures of 16–22°C (Fig. 3).

The effects of temperature on number of diapause larvae reared by ant cultures (Fig. 4) were significant both in *M. rubra* ($F_{5,52} = 3.5, p < 0.009$) and *M. ruginodis* ($F_{5,59} = 10.9, p < 0.0001$). The influence of site appeared, however, significant only in *M. ruginodis* ($F_{1,59} = 8.3, p < 0.006$): the cultures of this species from Kiev reared more diapause larvae in comparison with those from Chupa. The interaction between site and temperature was insignificant in this case. The effects of both temperature and site on the production of diapause larvae in *M. scabrinodis* seemed uncertain (Fig. 4) and were found to be insignificant.

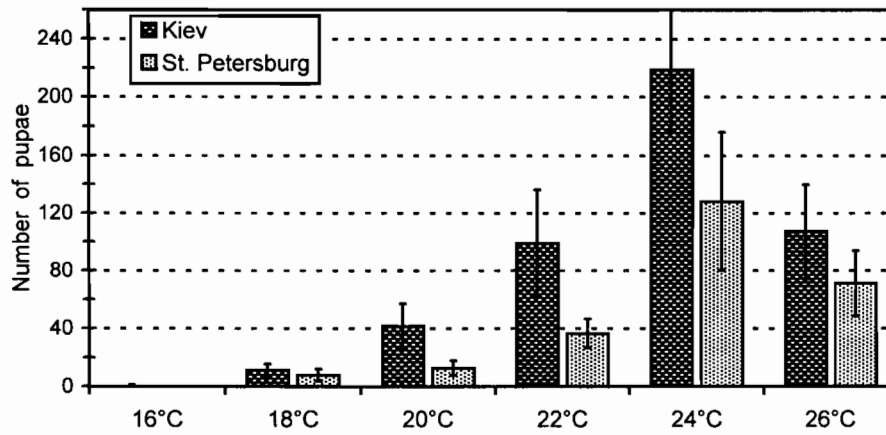
Rate of development

The increase of temperature invariably shortened the time of development from egg to prepupa in all species and populations (Fig. 5). The temperature of 26°C that has been shown above to be unfavourable for brood rearing clearly slowed down the development. This temperature was, therefore, excluded from further analysis. The influence of temperature from 16 to 24°C on the development time was highly significant in all species and populations (*M. rubra* – $F_{4,55} = 20.8, p < 0.0001$; *M. ruginodis* – $F_{3,53} = 54.6, p < 0.0001$; *M. scabrinodis* – $F_{4,50} = 100.5, p < 0.0001$).

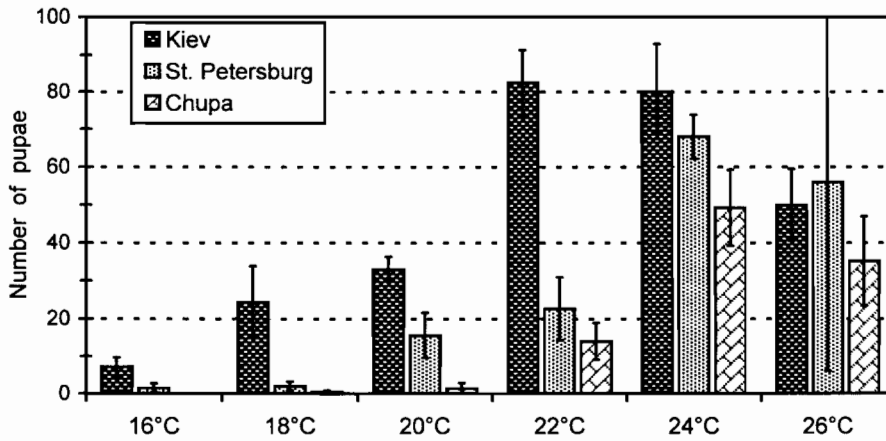
Whereas the influence of temperature on the development time is rather trivial, the effects of site deserve much more attention. These effects appeared significant in all species (*M. rubra* – $F_{1,55} = 9.6, p < 0.003$; *M. ruginodis* – $F_{2,53} = 8.3, p < 0.0008$; *M. scabrinodis* – $F_{2,50} = 4.3, p < 0.019$). Almost invariably the development times of brood from more northern populations were a bit shorter in comparison with values obtained for southern populations of the same species, these differences being usually greater at higher temperatures 20–24°C (Fig. 5). Thus, eggs and larvae from more northern sites developed faster than southern brood. These differences appeared quite significant (Tukey HSD test) for *M. rubra* ($p < 0.001$) and *M. ruginodis* ($p = 0.0004–0.023$), except between St. Petersburg and Chupa populations which did not differ significantly. In *M. scabrinodis* the differences between populations were not so definite and only St. Petersburg and Chupa populations differed significantly ($p = 0.034$). No significant effects of interaction between site and temperature were found by ANOVA.

Parameters of linear regression of development rate on temperature, the values of the thermal threshold for development and of the sum of effective temperatures calculated for species and populations studied are given in Table 1, and the resulted regression lines are depicted in Fig. 6. The values of slope and SET differed significantly (t -test: $p < 0.05$) only between two populations of *M. rubra*. The coefficients of linear regression equation appeared very similar for St. Petersburg and Chupa populations of *M. ruginodis* and for Vladimir and St. Petersburg populations of *M. scabrinodis*. Nevertheless, the overall trend observed seems to be quite apparent: The slope of the regression line of development rate on tem-

Myrmica rubra



Myrmica ruginodis



Myrmica scabrinodis

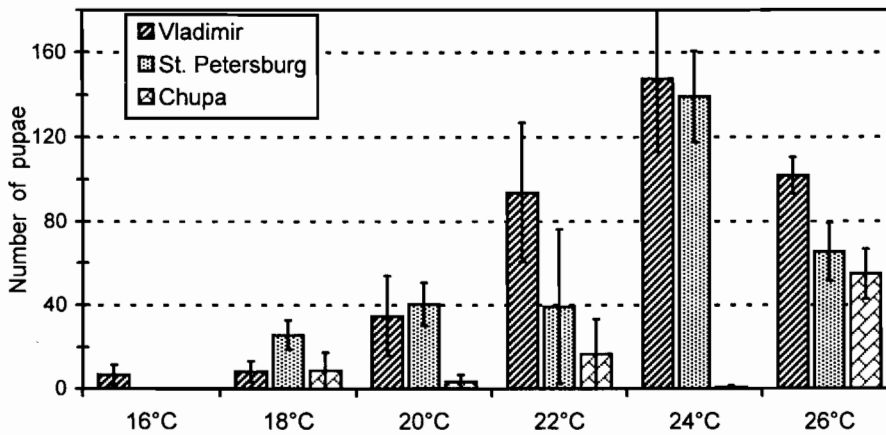


Fig. 3. Mean total production of rapid brood pupae at six constant temperatures by experimental cultures of three *Myrmica* species from different geographic regions. Vertical bars – standard errors of means.

perature and the value of thermal threshold increased in more northern populations. It is also worth to note that the sum of effective temperatures which is the reciprocal value of the slope decreased with the advance to the North. All this means that rapid brood development was more temperature dependent in northern *Myrmica* populations, the rates of development being a bit greater within

higher temperature range (above 16–18°C) but lesser at lower temperatures.

Species comparison

Apparent differences between species in the mean period of rapid brood pupation and the numbers of pupae reared were found (Figs 2–3). The overall influence of species appeared significant for pupation period ($F_{2,66} =$

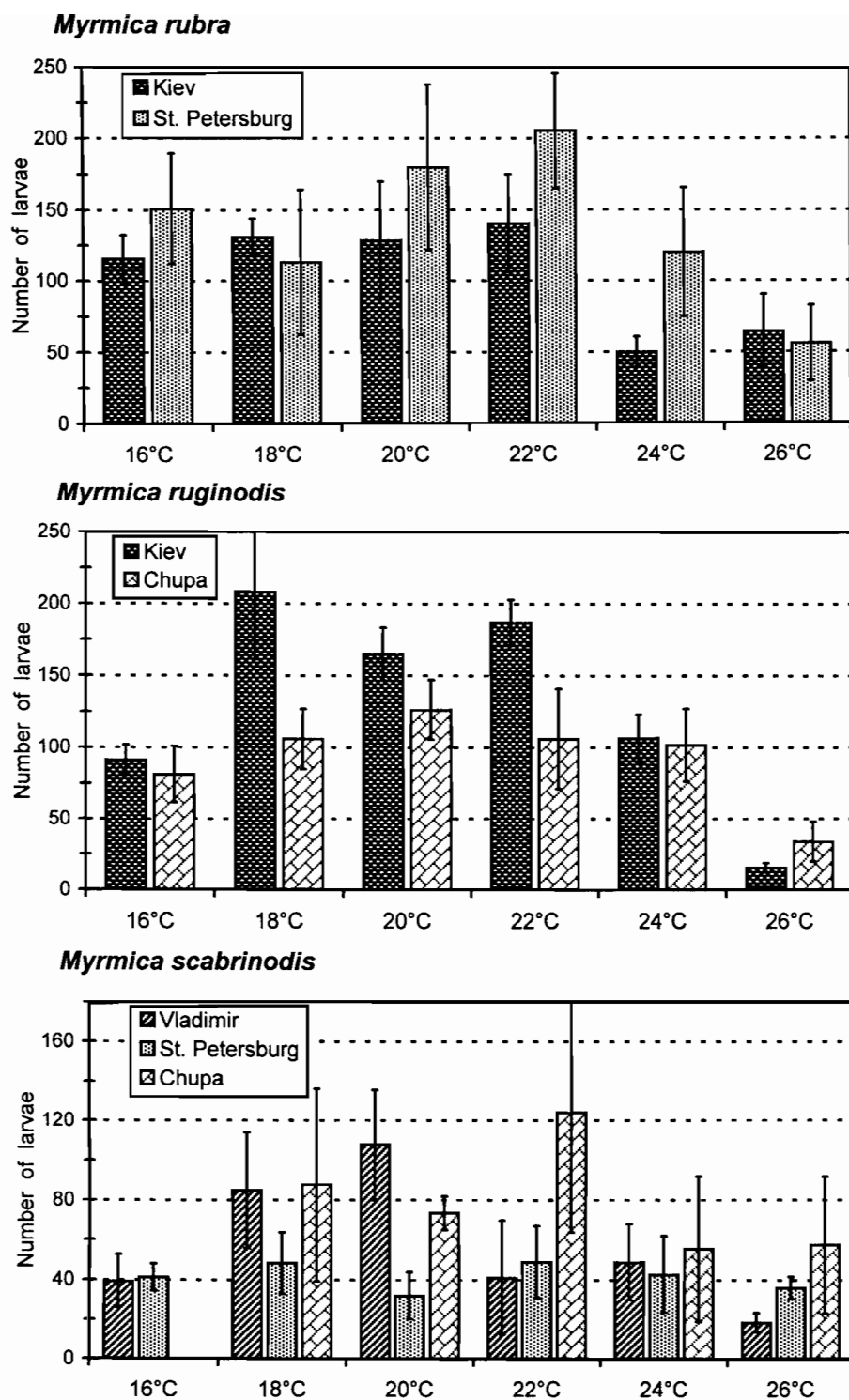


Fig. 4. Mean total production of diapause larvae at six constant temperatures by experimental cultures of three *Myrmica* species from different geographic regions. Vertical bars – standard errors of means.

3.9, $p < 0.03$; for interaction species \times temperature $F_{10,66} = 2.0$, $p < 0.042$) but not for number of pupae. The period of pupation was usually longer and more pupae were produced in *M. rubra* as compared to *M. ruginodis*. The effect of species on these variables was significant (for periods: $F_{1,100} = 9.5$, $p < 0.0027$; for numbers: $F_{1,100} = 13.6$, $p < 0.0004$), the species differences, however, appeared significant at *post hoc* comparison only between

sympatric populations in Kiev ($p < 0.001$). A significant interaction effect was found only between species and temperature and only for pupae number ($F_{5,100} = 6.2$, $p < 0.00005$). *M. ruginodis* and *M. scabrinodis* differed significantly in the periods of pupation only in St. Petersburg ($p < 0.0194$) but not in Chupa. Nevertheless, the mean numbers of pupae produced by *M. scabrinodis* cultures were usually greater than in *M. ruginodis* from sympatric

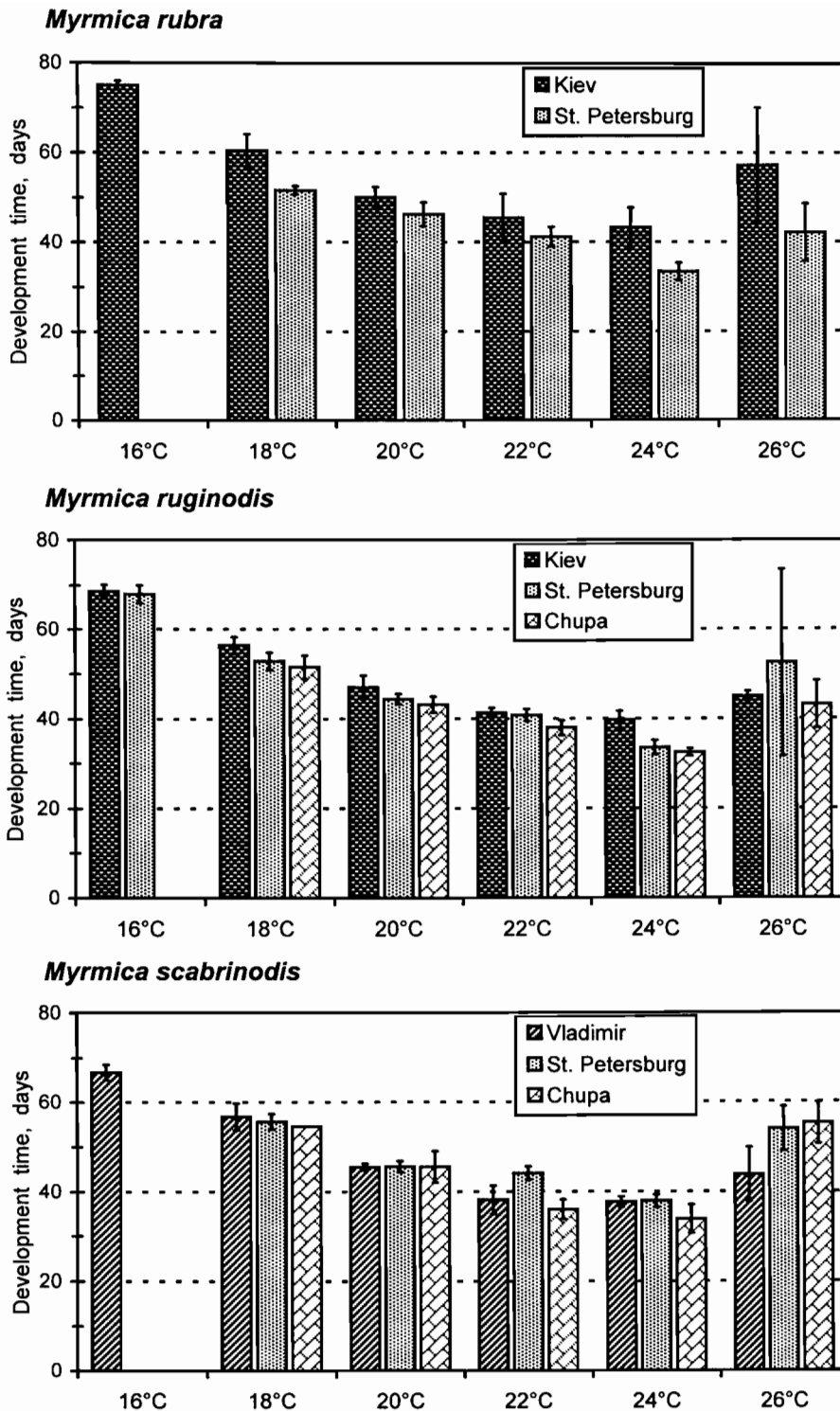


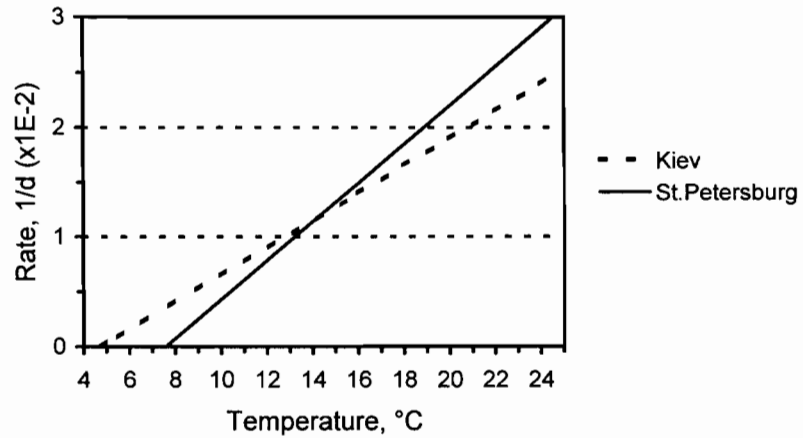
Fig. 5. Mean times of development from egg to prepupa at six constant temperatures in experimental cultures of three *Myrmica* species from different geographic regions. Vertical bars – standard errors of means.

populations (Fig. 2); these differences were significant both by ANOVA ($F_{1,64} = 6.2, p < 0.0154$) and Tukey HSD test ($p < 0.0129$). There were significant effects of interactions species \times site ($F_{1,64} = 9.7, p < 0.0027$) and site \times temperature ($F_{4,64} = 5.9, p < 0.0004$). The cultures of *M. scabrinodis* from St. Petersburg reared on average just the same number of pupae as *M. rubra* cultures from sym-

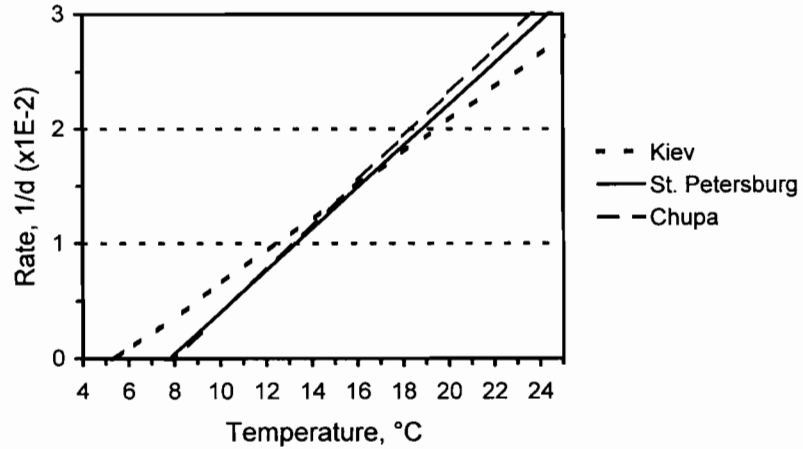
patric population at higher temperatures (24–26°C) but significantly more pupae at lower temperature range (16–22°C).

The effect of species on the development time from egg to prepupa appeared significant ($F_{2,85} = 5.6, p < 0.0126$) in St. Petersburg region, with no significant interaction species \times temperature. Sympatric *M. rubra* and *M. ruginodis*

Myrmica rubra



Myrmica ruginodis



Myrmica scabrinodis

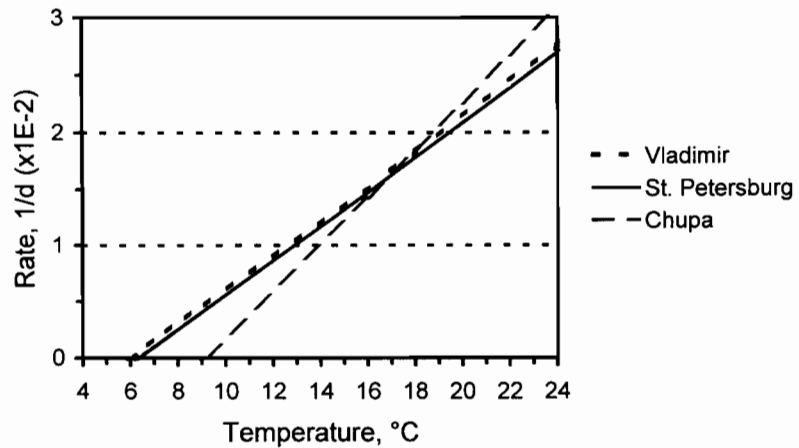


Fig. 6. The lines of linear regression of development rate on temperature for three *Myrmica* species from different geographic regions.

populations did not, however, differ significantly at *post hoc* comparison. These two species were evidently very similar both in Kiev and St. Petersburg regions in their development times (Fig. 5) and thermal requirements for development (similar values of slopes, intercepts, TTD and SET), although *M. ruginodis* seems to have a bit higher TTD and a bit lower SET in Kiev (Table 1, Fig. 6).

On the contrary, *M. scabrinodis* differed significantly both from *M. rubra* (in St. Petersburg; Tukey HSD: $p < 0.0092$) and from *M. ruginodis* (in St. Petersburg and Chupa; ANOVA: $F_{1,67} = 4.7, p < 0.0333$; Tukey HSD: $p < 0.0256$; no significant effects of interactions species \times site, species \times temperature and site \times temperature were found). However, whereas the development of *M. scabri-*

TABLE 1. Thermal requirements for rapid brood development from egg to prepupa in species and populations studied.

Species	Place	Number of temperatures used	Number of observations	Parameters of linear regression of development rate on temperature ($\times 10^{-2}$)				TTD ($^{\circ}\text{C}$)	SE of TTD ($^{\circ}\text{C}$)	SET (dd)	SE of SET (dd)
				Intercept	SE of intercept	Slope	SE of slope				
<i>Myrmica rubra</i>	Kiev	5	22	-0.60 ^A	0.090	0.13 ^A	0.014	4.8	2.26	802 ^A	91.5
	St. Petersburg	5	43	-1.34 ^A	0.105	0.18 ^A	0.024	7.8	1.76	547 ^A	72.6
<i>Myrmica ruginodis</i>	Kiev	5	30	-0.77 ^{BC}	0.210	0.14	0.013	5.4	1.36	703	64.8
	St. Petersburg	5	22	-1.40 ^B	0.228	0.18	0.020	7.8	1.45	553	60.4
	Chupa	4	22	-1.52 ^C	0.246	0.19	0.025	7.9	1.85	521	68.1
<i>Myrmica scabrinodis</i>	Vladimir	5	18	-0.95 ^D	0.219	0.15	0.019	6.1	1.74	648	77.6
	St. Petersburg	5	35	-0.97 ^E	0.239	0.15	0.015	6.4	1.44	655	65.6
	Chupa	5	12	-1.91 ^{DE}	0.300	0.21	0.030	9.2	1.67	480	70.2

TTD – Thermal threshold for development ($^{\circ}\text{C}$); SET (dd) – sum of effective temperatures (day-degrees).

The values of intercept, slope and SET marked with the same letters differ significantly (t -test: $p < 0.05$) within the same species.

nodis brood was clearly less temperature dependent (lesser slopes and TTD and greater SET) compared to sympatric *M. rubra* and *M. ruginodis* in St. Petersburg, it appeared even more temperature dependent compared to sympatric *M. ruginodis* population in Chupa (Tab. 1, Fig. 6). The calculations showed that in St. Petersburg *M. scabrinodis* brood would need the temperature of 23.5 $^{\circ}\text{C}$ to develop at the same rate as sympatric *M. rubra* or *M. ruginodis* brood at 22 $^{\circ}\text{C}$, whereas in Chupa it would need only 21.7 $^{\circ}\text{C}$. This difference in thermal requirement for development between *M. scabrinodis* and *M. ruginodis* was shown to be much greater (2–3 $^{\circ}\text{C}$) in Southern England by Elmes & Wardlaw (1983).

CONCLUSIONS AND DISCUSSION

This study shows the distinct latitudinal variation in the temperature effects on rapid brood rearing and in the thermal requirements for brood development in three *Myrmica* species.

First, the period during which new rapid brood pupae appear in ant cultures is found to be longer and the total number of pupae produced to be greater in ants from more southern populations in most experimental variants. The number of diapause larvae reared by ant cultures was also usually greater in ants from southern sites. These results are in good agreement with our previous studies which have revealed the same latitudinal differences in the length of colony's intrinsic seasonal cycle of rapid brood rearing and in the number of pupae produced with the use of *M. rubra* and *M. ruginodis* populations from two geographical region - Belgorod and St. Petersburg (Kipyatkov & Lopatina, 1997).

Much more interesting is, however, the finding that low temperatures reduce the period of rapid brood production and the number of pupae reared to a greater degree in ants from northern populations. The differences in these two parameters observed between experimental cultures kept at relatively low (16–18 $^{\circ}\text{C}$) and relatively high (20–24 $^{\circ}\text{C}$) temperatures always appeared much more pronounced in ants from northern sites. It means that northern *Myrmica* colonies rear rapid brood under lower temperatures evi-

dently worse in comparison with ants from southern regions.

Besides that eggs and larvae from more northern sites appear to develop faster than southern brood at temperatures above 16–18 $^{\circ}\text{C}$. This is because brood development in northern populations is more temperature dependent, i.e. is characterised by higher slopes of regression lines of development rate on temperature. In other words the sum of effective temperatures (thermal requirement for development), which is the reciprocal value of the slope, decreases with the advance to the North. It is also worth to note that the higher slopes of regression lines are always associated with higher thermal thresholds for development (Fig. 6). Although the causes of such a correlation are still open to question (e.g. Groeters, 1992; Trudgill & Perry, 1994; Trudgill, 1995) its existence has been recently confirmed by the thorough analysis of published data both at interspecific (i.e. between species) and intraspecific (i.e. between populations of a species) levels (Honěk & Kocourek, 1990; Honěk, 1996a,b).

We conclude from this that the reaction norm of *Myrmica* colonies, in response to temperature, changes according to the local climate in such a way that brood rearing, growth and development of individuals become more temperature dependent in more severe environments with colder and shorter summers. This lead to the increase of the physiological and developmental responses at higher temperatures at the expense of a decrease within lower temperature range. These adaptive changes in the reaction norm to temperature are best illustrated by the differences in the slopes of regression lines of the development rates on temperatures found between *Myrmica* populations living at different latitudes (Fig. 6). Earlier, the similar change in the reaction norm to temperature was demonstrated in respiration studies using the same three *Myrmica* species: populations from higher latitudes had higher Q10s, i.e. their metabolism was more intensive than that of southern populations at higher temperatures but less intensive at lower temperatures (Elmes et al., 1999; Nielsen et al., 1999). Thus, the respiratory metabolism in individual ants from northern populations also appears more dependent on temperature. Such

changes of the reaction norms to temperature allow northern *Myrmica* colonies "to live faster" and to respond more quickly to occasionally favourable temperatures.

In fact *Myrmica* colonies from northern populations need on average higher temperatures in their nests for successful production of new adults as compared to southern ants. Our unpublished data on nest microclimate confirm this conclusion suggesting that northern *Myrmica* colonies really rear their brood even at higher average temperatures than southern ants owing to the adaptive changes in habitat preferences and the improvements of the thermal characteristics of the nests.

It is rather surprising that ants, contrary to a lot of other arthropods, adapt to boreal environments by increasing their thermophily, i.e. by relying upon higher temperatures for more rapid development and productive brood rearing. This unusual trait is undoubtedly related to the fact that originally thermophilic ants manage to exist in boreal regions only owing to special construction of their nests destined to collect sunshine and to rise the temperature inside (Brian, 1983). All these phenomena are evidently worth further study.

ACKNOWLEDGEMENTS. We are very much grateful to Dr. Alexander Radchenko and Dr. Vadim Fomenko for their invaluable help in collecting ant colonies in Kiev and Vladimir. We are also much obliged to two anonymous reviewers for their important advice and comments on the manuscript. This work was supported by Russian Foundation of Basic Research (grant No 00-04-49003), as well as by The Council for Grants from the President of Russian Federation and for State Support of Leading Scientific Schools (grant No 00-15-97934).

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Received December 12, 2001; revised April 17, 2002; accepted April 18, 2002