

## Duration and thermal reaction norms of development are significantly different in winter and summer brood pupae of the ants *Myrmica rubra* LINNAEUS, 1758 and *M. ruginodis* NYLANDER, 1846 (Hymenoptera: Formicidae)

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### Abstract

Seasonal variation of the duration and temperature dependence of development was discovered for the first time using pupae of two ant species of the genus *Myrmica*. Worker pupae produced at the beginning of summer from overwintered larvae (so-called *winter brood*) developed significantly slower and their development rate was less dependent on temperature in comparison with worker pupae produced later in the season from *summer brood* from newly laid eggs. The differences between mean development times of winter and summer brood pupae amounted to 7 - 12 % in *M. ruginodis* from St. Petersburg (Russia), 9 - 11 % in *M. rubra* from St. Petersburg and 2 - 5 % in *M. rubra* from Belgorod (Russia). The lines of regression of development rate on temperature had greater slopes in summer brood pupae as compared to winter brood pupae. The differences between winter and summer brood pupae appeared greater in northern populations of both species (St. Petersburg region) compared to the southern population of *M. rubra* (Belgorod region), both in development times and in temperature dependence of development. Summer brood pupae were found to be smaller and developed significantly faster compared to winter brood pupae. The mean head width of *M. rubra* (Belgorod region) workers produced from summer brood was almost the same at 20 - 24 °C but substantially decreased at 18 and 16 °C. Thus, larvae developing at low temperatures pupate at smaller size in order to finish their development in time before the autumn cold weather. Summer brood workers from St. Petersburg *M. rubra* population were significantly smaller than those from Belgorod population. Size differences between summer brood workers were greater in St. Petersburg population compared to the Belgorod region. We suggest that the smaller size of summer brood workers is an adaptation which allows northern ant populations to rear summer brood faster and to produce some adults from summer brood in spite of cooler and shorter summer season.

**Key words:** Insecta, Formicidae, ants, *Myrmica*, seasonal variation, thermal reaction norms, brood rearing, worker size, temperature, development time, thermal threshold

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### Introduction

Temperate and boreal ants use two main seasonal strategies: the strategy of *concentrated* brood-rearing and the strategy of *prolonged* brood-rearing, the latter being the most widespread among them (KIPYATKOV 2001, in press). The strategy of prolonged brood-rearing is distinguished by the following features:

1. Larvae are able to fall in diapause which is facultative and controlled by environmental (temperature, photoperiods) and social (worker care, queen influence, pheromones etc.) factors.

2. Only some larvae develop from egg to pupa within the same summer season without overwintering. This is so-called *rapid* or *summer brood* (BRIAN 1951, 1957) that yields only workers.

3. A large proportion of larvae delay their development, continue to grow in autumn, overwinter in diapause and pupate during the next summer. This is so-called *slow* or *winter brood* (BRIAN 1951, 1957) that yields alates and workers.

The strategy of prolonged brood-rearing has evident advantages important for adaptation to temperate and boreal climates (KIPYATKOV 1993): (1) the larvae can be reared from early spring up to late autumn thus utilizing the whole warm period of a year; (2) the quantity of rapid brood can be changed to adapt to long-term and short-term climatic variations and to the duration of the warm season.

In the first theoretical study of life history evolution in social insects OSTER & WILSON (1978) predicted the "bang-bang" strategy for a perennial colony, which maximizes colony's fitness by alternation ergonomic and reproductive phases within each year. The ergonomic phase, in which the colony grows by producing more workers, should be as long as possible within each year so that more workers are available to raise the largest number of sexuals during the second part of the year. For a perennial colony living in temperate climatic zone this strategy demands that the colony's annual brood-rearing cycle should be organized in a way to maximize the quantity of pupae (i.e., new wor-

kers) and diapause larvae produced by the end of each summer season. These new workers will facilitate colony's winter survival and will rear alate females and males from overwintered larvae or from eggs next spring. For this purpose the brood-rearing should start in spring as early as possible and continue as long as possible (KIPYATKOV 1993, 2001, in press).

Another way to produce more brood within the same summer season is to accelerate the development of eggs, larvae and pupae. This might be especially important for ant colonies living in northern regions with shorter summers. Indeed, a distinct latitudinal variation of the duration and temperature dependence of brood development has been revealed in our previous studies carried out using four species of *Myrmica* and *Lasius* (KIPYATKOV & LOPATINA 2002, LOPATINA & al. 2002, KIPYATKOV & al. 2004). It was found that brood development in northern ant populations was more temperature dependent, i.e., characterised by higher slopes of regression lines of development rate on temperature.

Eggs, larvae and pupae from more northern sites appeared to develop faster than southern brood at temperatures above 16 - 18 °C, i.e., under optimal thermal conditions. We concluded that the reaction norms of ant colonies, in response to temperature, change 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 leads to the increase of the physiological and developmental responses at higher temperatures at the expense of a decrease within lower temperature range.

The acceleration of development might be especially important for summer brood rearing because pupae produced in late summer, being incapable to overwinter, should necessarily finish their development before autumn cold weather. In fact, the increase of development rates of individuals from northern populations in comparison with southern insects appeared more pronounced exactly for summer brood rearing (KIPYATKOV & LOPATINA 2002).

However, nobody has yet compared the duration and temperature dependence of development in winter and summer broods directly. It is useful promising to compare thermal reaction norms of development in winter and summer brood pupae because the latter must particularly hasten their development in order to become adults and thus survive the forthcoming winter. This is the goal of the work reported here.

## Materials and methods

Stock colonies of *Myrmica rubra* LINNAEUS, 1758 and *M. ruginodis* NYLANDER, 1846 were collected at the end of summer near Borisovka, Belgorod prov. (50°36'N, 36°00'E) and near Martyshkino, St. Petersburg region (59°53'N, 29°48'E). Both sites were at low altitudes. In Belgorod and St. Petersburg regions *M. rubra* and *M. ruginodis* lived together in the same habitat: near Borisovka in deciduous oak forest nesting mainly in rotten wood and near St. Petersburg in coniferous pine woodland mostly in moss hillocks.

Before the experiments stock colonies were subjected to artificial overwintering in a refrigerator at 3 - 5 °C for 4 - 5 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 8 - 10 °C and then at 13 - 15 °C (for a week at each temperature). Experimental groups were then set up with 150 workers, one queen and 30 - 50 overwintered larvae using randomly chosen individuals from the stock colonies. Unfortunately, *M. ruginodis* stock colonies from Borisovka were lost during the overwintering due to technical problems. So we had three populations for comparison: *M. ruginodis* from St. Petersburg region and *M. rubra* from both sites. Sixteen to 26 stock colonies from each population were used, including both monogyne and polygyne colonies. Each monogyne colony gave rise to one experimental group. Polygyne colonies were used to establish from 2 to 25 (usually 5 - 10) experimental groups each. In the latter case, groups originating from the same stock colony were evenly distributed among experimental regimes.

Each ant group was kept in a plastic laboratory nest consisting of a dark and wet (approx. 100 % rel. humidity) brood chamber and two illuminated and relatively dry foraging chambers where food (cockroaches *Nauphoeta cinerea* (OLIVIER, 1789) cut into pieces and 15 % sucrose solution) was added twice a week. Laboratory nests with experimental ant groups were maintained in photo-thermostatic chambers (photothermostats). Six constant temperatures (14 ± 0.5 °C, 16 ± 0.5 °C, 18 ± 0.5 °C, 20 ± 0.5 °C, 22 ± 0.5 °C and 24 ± 0.5 °C), all at long-day (22 h) photoperiod, were used for *M. rubra* from Belgorod and four of them (18 - 24 °C) for both species from St. Petersburg. Some groups perished over time. As a result, the experimental data on winter brood were obtained from 9 to 19 groups from each population in each temperature, and the data on summer brood – from 2 to 17 groups.

Overwintered larvae developed and began to pupate at rates depending on their initial size and experimental temperature. After the first 10 - 15 larvae had pupated, all of the smaller overwintered larvae were removed from this experimental group in order that they would not be confused later with summer brood larvae developing from newly laid eggs. Queens began to lay eggs soon after the start of the experiment. The workers reared these into summer brood pupae and diapausing larvae. Worker groups of both species from the St. Petersburg region which were destined to rear summer brood were kept initially under 24 °C and were transferred to the ultimate temperature only after the appearance of the first summer brood prepupae. This is because northern *Myrmica* colonies produce only a few or even no rapid brood pupae at low temperatures (KIPYATKOV & LOPATINA 1997, LOPATINA & KIPYATKOV 1997, KIPYATKOV 2001, KIPYATKOV & LOPATINA 2002).

The first winter and summer brood pupae were observed in order to determine their development time. For that purpose experimental groups were checked once a day. The development time (*D*) of each pupa was calculated by measuring the period (in days) elapsed between the pupa's appearance after a molt from prepupa and the e-closure of a callow worker from this pupa. It appeared possible to measure the development time of up to 15 pupae from the winter brood and as many pupae from the summer brood in each experimental group. All additional pupae were removed from experimental groups in order that they were not a hindrance to the observations of the first ones.

Tab. 1: Parameters of linear regression of development rate on temperature and the values of thermal threshold for development calculated for three ant populations. TTD – Thermal threshold for development (°C). The values of intercept, slope and TTD calculated for winter and summer broods differ significantly (*t*-test) within the same population if are marked with asterisks: \* – *p* < 0.05; \*\*\* – *p* < 0.01.

Species	Population	Brood	Number of temperatures used	Sample size	Parameters of linear regression of development rate on temperature ( $\times 10^{-2}$ )				TTD	SE of TTD
					Intercept	SE of intercept	Slope	SE of slope		
<i>M. ruginodis</i>	St. Petersburg	Winter	4	536	-5.16*	0.316	0.478***	0.0063	10.8	0.15
		Summer	4	147	-6.57*	0.512	0.573***	0.0206	11.5	0.39
<i>M. rubra</i>	St. Petersburg	Winter	4	621	-4.93	0.333	0.463	0.0062	10.7	0.14
		Summer	4	80	-5.62	0.848	0.521	0.0479	10.8	1.11
	Belgorod	Winter	5	673	-5.16	0.416	0.479***	0.0061	10.8*	0.13
		Summer	5	802	-5.94	0.553	0.524***	0.0094	11.3*	0.19

Tab. 2: Mean values of head width of worker ants eclosed in experiments from winter and summer brood pupae in three *Myrmica* populations. The mean head widths of workers eclosed from winter and summer brood pupae differed significantly (*t*-test: *p* << 0.01) within each population (not marked in the table). The mean head widths of *M. rubra* workers eclosed from summer brood differed significantly (*t*-test: *p* << 0.01) between St. Petersburg and Belgorod populations (marked with an asterisk).

Species	Population	Brood	Sample size	Head width, mm			
				Min	Max	Mean	SE
<i>M. ruginodis</i>	St. Petersburg	Winter	119	0.89	1.21	1.04	0.006
		Summer	85	0.76	1.11	0.95	0.009
<i>M. rubra</i>	St. Petersburg	Winter	66	0.86	1.21	0.97	0.009
		Summer	64	0.77	1.00	0.88*	0.006
	Belgorod	Winter	157	0.77	1.11	0.97	0.005
		Summer	391	0.71	1.16	0.94*	0.003

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 1991). Worker mortality was not excessive (on average < 25 %) and not enough to affect brood-rearing significantly. Callow workers were taken out of groups each day and the width of their heads were measured with the use of a binocular microscope with an ocular-micrometer (magnification 56 $\times$ ).

In total, development time was measured for several tens of pupae in each of most temperature regimes for each population. The sample size range was 65 - 190 pupae for winter brood and 7 - 280 pupae, i.e., much greater, for summer brood. This is because the production of rapid brood pupae is under strong temperature influence in *Myrmica* (BRIAN 1963) and other ants (KIPYATKOV 2001) and decreases significantly in northern *Myrmica* populations (KIPYATKOV & LOPATINA 1997, LOPATINA & KIPYATKOV 1997, KIPYATKOV 2001, KIPYATKOV & LOPATINA 2002). Consequently, only few rapid brood pupae were raised in each experimental group under 16 - 18 °C, especially in groups from St. Petersburg populations, and some groups even failed to produce rapid brood at all.

The data were analysed on the computer using "Quattro Pro 7.0" (© 1996 Corel Corporation Ltd). The rate of development at a given temperature (*T*) was calculated for each pupa 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. This feature allowed us to calculate the coefficient of linear regression of development rate on temperature (the slope of the regression line), the 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 & 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 species and populations to local environmental conditions (CAMPBELL & al. 1974, LAMB & al. 1987, TAUBER & 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:

$$R_T = a + bT$$

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  $TTD = -a / b$ . The standard errors (SE) of intercept and slope were obtained from regression analysis, the SE values for TTD were calculated using a formula given by CAMPBELL & al. (1974).

Statistical analysis was carried out with the use of "Statistica 5.5" (© 1984 - 1999 by StatSoft, Inc.). Development times of winter and summer brood pupae from different populations were compared by ANOVA. In some experimental variants, the development times were more or less normally distributed and there were no significant correlations between means and variances. The reverse was true for other experimental variants in which the data were overdispersed. Consequently we used a log-transformation which improved normality and eliminated correlation between means and variances in many such cases. However, we invariably used nonparametric statistics (Kruskal-Wallis ANOVA by Ranks test) for all comparisons simultaneously with parametric ANOVA. Tukey HSD for unequal  $N$  (Spjøtvoll / Stolene) test was used for post hoc comparison of means after ANOVA. The  $t$ -test for independent samples was used for comparison of regression coefficients, intercepts, TTD and mean head widths.

## Results

### Duration of pupal development

The increase of temperature invariably shortened developmental time in all species and populations (Fig. 1). This influence was highly significant (ANOVA: *M. rubra* –  $F_{3,2086} = 2634.8$ ,  $p \ll 0.001$ ; *M. ruginodis* –  $F_{3,675} = 1766.0$ ,  $p \ll 0.001$ ). Because the influence of temperature on the development time is already well documented, the seasonal effects deserve more attention. The summer brood pupae from all populations developed faster compared to winter brood pupae at all temperatures (Fig. 1). This effect appeared quite significant for both species (*M. rubra* – ANOVA:  $F_{3,2086} = 36.6$ ,  $p \ll 0.001$ , Tukey HSD:  $p \ll 0.001$ ; *M. ruginodis* – Kruskal-Wallis:  $H[1, N = 683] = 57.3$ ,  $p \ll 0.001$ ) and for both *M. rubra* populations (Kruskal-Wallis: Belgorod –  $H[1, N = 1475] = 87.8$ ,  $p \ll 0.001$ ; St. Petersburg –  $H[1, N = 701] = 88.3$ ,  $p \ll 0.001$ ).

### Thermal reaction norms

Parameters of linear regression of development rate on temperature and the values of TTD calculated for three populations studied are given in Table 1, and the resulted regression lines are depicted in Fig. 2. It is obvious from these graphs that the development of summer brood pupae is more dependent on temperature compared to that of winter brood pupae. The slopes of the regression lines of development rate against temperature for summer brood are substantially greater than for winter brood in all three populations. These differences are highly significant ( $t$ -test:  $p \ll 0.01$ ) for two populations (*M. ruginodis*, St. Petersburg and *M. rubra*, Belgorod), but non-significant for *M. rubra* from St. Petersburg, probably due to smaller sample size resulting in a higher SE of slope for this population (Tab. 1).

The values of TTD for summer brood pupae were slightly higher than for winter brood pupae for *M. ruginodis* from St. Petersburg and *M. rubra* from Belgorod, but very similar for both pupae types in *M. rubra* from St. Petersburg. This difference is, however, significant ( $t$ -test:  $p < 0.05$ ) only for *M. rubra* from Belgorod (Tab. 1).

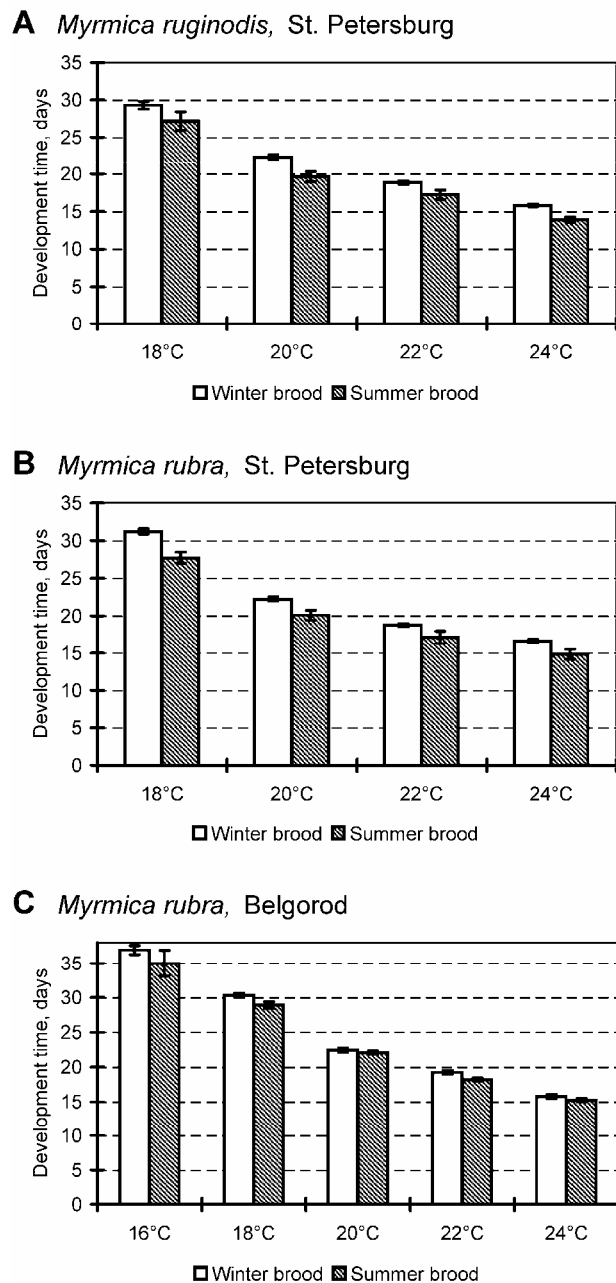


Fig. 1: Comparison of mean development times of winter and summer brood pupae in three *Myrmica* populations at different experimental temperatures. Vertical bars denote confidence interval values calculated for  $p = 0.99$  (i.e., for a 99 % chance that the true mean falls within this interval).

### Worker size

The effects of species / population and brood type factors on the head width of workers eclosed from experimental pupae were highly significant (ANOVA: species / population –  $F_{2,876} = 45.3$ ,  $p \ll 0.001$ ; brood type –  $F_{1,876} = 174.7$ ,  $p \ll 0.001$ ). The workers eclosed from winter brood pupae were substantially bigger on average compared to those produced from summer brood (Tab. 2). These differences of the means were highly significant both on the whole (Tukey HSD:  $p \ll 0.001$ ; Kruskal-Wallis:  $H[1, N = 882] = 139.9$ ,  $p \ll 0.001$ ) and in each of three populations studied (Tab. 2).

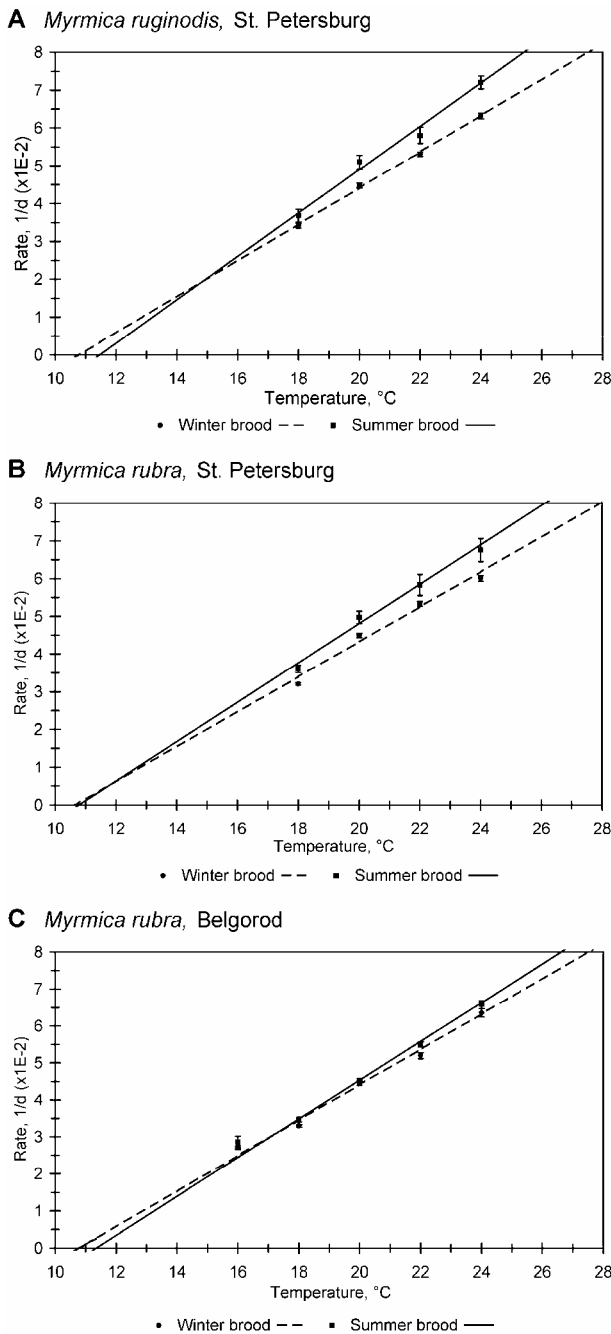


Fig. 2: Thermal reaction norms of development for winter and summer brood pupae in three *Myrmica* populations. The regression lines of development rate on temperature for winter and summer brood pupae are depicted. Vertical bars denote confidence interval values calculated for  $p = 0.99$ .

In experimental groups of *M. rubra* from Belgorod in which summer brood developed at different temperatures the size of workers produced was significantly influenced by temperature (Kruskal-Wallis:  $H [4, N = 391] = 22.3, p < 0.0002$ ). The workers raised under 16 and 18 °C were significantly smaller compared to individuals produced under 20 - 24 °C (Fig. 3A). The size differences between the latter was not significant (Kruskal-Wallis:  $H [2, N = 343] = 0.36, p = 0.83$ ). On the contrary, the size of workers produced from winter brood was unaffected by temperature (Fig. 3B) (Kruskal-Wallis:  $H [4, N = 157] = 0.96, p = 0.92$ ).

## Discussion and conclusions

This study is the first demonstration of the differences in duration and temperature dependence of development between winter and summer broods in ants. The mean development times of summer brood pupae appeared significantly shorter than those of winter brood pupae in all species and populations studied at all experimental temperatures (Fig. 1). These differences between mean development times amount to 7 - 12 % in *M. ruginodis* from St. Petersburg, 9 - 11 % in *M. rubra* from St. Petersburg and 2 - 5 % in *M. rubra* from Belgorod. BRIAN (1951, 1957) coined the term "rapid" or "fast" brood to designate those *Myrmica* larvae which developed from egg to adult within one summer compared to "slow" brood larvae whose development was interrupted by the winter. Now we can add that summer brood is also "rapid" in a sense that its pupae have higher development rates compared to winter brood pupae under the same temperature conditions. Summer brood pupae apparently hasten their development in order to complete it before the winter comes. The adaptive benefits of such a feature of summer brood physiology, especially for northern ant populations, is obvious.

Unfortunately, it is impossible in principle to compare the development times of summer and winter brood larvae because the latter fall into an obligatory diapause. It is, however, possible for eggs. We expect to make such a comparison in the near future.

No less important is our finding that the thermal reaction norms of development of winter and summer brood pupae are significantly different. Properly speaking this is in fact the proximate (i.e., physiological) cause of the differences between development times discussed above. The development of summer brood pupae is more temperature dependent, i.e., characterised by higher slopes of regression lines of development rate on temperature (Fig. 2). This seasonal variation is exactly analogous to the latitudinal variation of the thermal reaction norms of brood development which was revealed in our previous research on ants (KIPYATKOV & LOPATINA 2002, LOPATINA & al. 2002, KIPYATKOV & al. 2004; see Introduction for details). It is also worthwhile to note that the higher slopes of regression lines are usually associated with a higher TTD. The data reported here confirm this pattern (Fig. 2, Tab. 1). Although the causes of such a correlation are still open to questions (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).

The differences between winter and summer brood pupae were greater in northern populations of both species (St. Petersburg region) compared to the southern population of *M. rubra* (Belgorod region), both in development times (compare per cent values given in the first paragraph of Discussion and conclusions) and in temperature dependence of development (compare slopes of regression lines in Fig. 2 and Tab. 1). Thus, summer brood become still faster in comparison with winter brood in northern *Myrmica* populations, which is evidently an adaptation attained in evolution by northern ant populations.

In the course of his famous study on caste differentiation in *Myrmica*, BRIAN (1955) found that the development

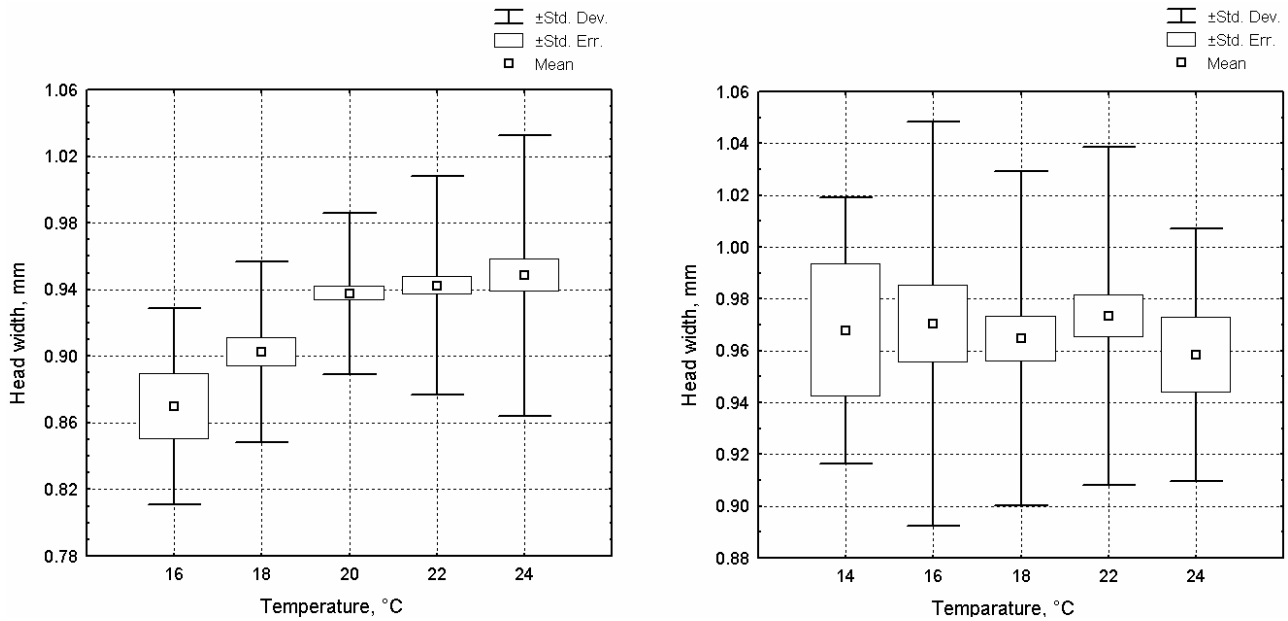


Fig. 3: Mean values of head width of *Myrmica rubra* worker ants developed from winter and summer brood at different experimental temperatures. (A) Workers eclosed from summer brood pupae. (B) Workers eclosed from winter brood pupae.

of rapid brood larvae was characterised by earlier departure from queen's ontogeny and premature metamorphosis as compared to winter brood larvae finishing their development after the winter. As a result rapid brood larvae pupated at lower weight and yielded smaller workers than winter brood larvae. Our results are fully consistent with his conclusions: workers raised from winter brood were significantly bigger than those eclosed from summer brood pupae (Tab. 2). One can suppose that smaller size of summer brood workers is related to their higher development rates in the larval stage. Unfortunately, it is impossible to test this hypothesis because, as we should repeat, there are no methods to compare directly the development times of summer and winter brood larvae.

In most insect species, faster development at higher temperatures results in smaller size of adults produced (RATTE 1985, DANKS 1994). In particular, summer adults of many species are smaller than individuals developed when the weather is cooler, especially imagoes of overwintering generation (e.g., LEPRINCE & BIGRAS-POULIN 1988, ROWE & BERRILL 1989, other references in DANKS 1994). These effects are evidently related to faster development at larval, not at pupal stages. PORTER (1988) found that in the fire ant *Solenopsis invicta* BUREN, 1972 miniature nanitic worker pupae reared by nest-founding queens developed 10 % faster than minor worker pupae reared in mature colonies, and even greater female sexual pupae took about 27 % longer. As far as we know this work was the first demonstration of a relation between size and development time in insect pupae. PORTER (1988) reasonably suggested that faster development of the nanitic worker brood should accelerate the growth of incipient colonies and thus improve colony fitness. The adaptive value of nanitic workers in newly founded red imported fire ant colonies was also experimentally confirmed by PORTER & TSCHINKEL (1986).

In our experiments we have also found that summer brood pupae, which were in fact smaller than winter brood pupae, developed significantly faster compared to the latter. Similarly to the situation studied by PORTER (1988) in the fire ant, this difference is evidently adaptive and improves colony fitness. We realize, however, that the correlation between pupal size and development time revealed in our experiments does not yet prove the causal relationship between these two parameters in itself. Consequently, further experiments on the influence of the size on development rate of pupae are needed.

The size of *M. rubra* workers from Belgorod population produced from winter brood pupae was unaffected by temperature (Fig. 3B). This might be due to the fact they have spent only a smaller part of their larval lives at the experimental temperatures. Contrary to winter brood workers the size of summer brood workers was significantly influenced by temperature: the mean head width of workers was almost the same at 20 - 24 °C but substantially decreased at 18 and 16 °C (Fig. 3A). Regardless of the fact that in most insects the increase of temperature leads to the decrease of size of imagoes developed, there are other species characterized by the absence of any temperature effects or even by the opposite relation between size and temperature (RATTE 1985, DANKS 1994). In *M. rubra* from Belgorod population one meets just with the latter situation. We suppose that smaller size of summer brood workers at lower temperatures might be an adaptation for completing larval development in time. The optimal temperatures for brood development in *M. rubra* are 20 - 22 °C (BRIAN 1973; our own observations). Consequently, summer brood larvae developing at optimal temperatures or above may attain approximately the same size and yield full sized workers, whereas larvae developing at lower temperatures should pupate at small-

ler size in order to finish their development in time before the winter.

While *M. rubra* workers from Belgorod and St. Petersburg regions produced winter brood pupae that were virtually identical in size, the summer brood workers from St. Petersburg population were significantly smaller than summer brood workers from Belgorod population (Tab. 2). Thus, the size difference between the workers produced from summer brood was greater in the St. Petersburg population as compared to the Belgorod region. We suggest that the smaller size of summer brood workers is also an adaptation attained by northern ant populations in order to rear summer brood faster and to produce some adults from summer brood in spite of cooler and shorter summer season.

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### Zusammenfassung

Saisonale Variation der Entwicklungsdauer und Temperaturabhängigkeit der Entwicklung wurden erstmals, bei Puppen zweier Ameisenarten der Gattung *Myrmica*, festgestellt. Zu Beginn des Sommers aus überwinterten Larven (Winterbrut) entstandene Arbeiterinnenpuppen entwickelten sich signifikant schneller, und ihre Entwicklungsgeschwindigkeit war weniger temperaturabhängig – verglichen mit später im Sommer aus Sommerbrut von neu gelegten Eiern entstandenen Arbeiterinnenpuppen. Die Unterschiede zwischen durchschnittlicher Entwicklungsdauer von Puppen aus Winter- und Sommerbrut betragen 7 - 12 % bei *M. ruginodis* aus St. Petersburg (Russland), 9 - 11 % bei *M. rubra* aus St. Petersburg und 2 - 5 % bei *M. rubra* aus Belgorod (Russland). Die Regressionsgeraden der Temperaturabhängigkeit der Entwicklungsgeschwindigkeit hatten größeren Anstieg bei Puppen von Sommer- als von Winterbrut. Die Unterschiede zwischen Puppen aus Winter- und Sommerbrut waren in den nördlichen Populationen (St. Petersburg) beider Arten größer als in der südlichen Population von *M. rubra* (Belgorod), sowohl hinsichtlich Entwicklungsdauer als auch hinsichtlich Temperaturabhängigkeit der Entwicklung. Puppen aus Sommerbrut waren kleiner und entwickelten sich signifikant schneller als Puppen aus Winterbrut. Die durchschnittliche Kopfbreite von aus Sommerbrut (Belgorod) entstandenen Arbeiterinnen von *M. rubra* war nahezu konstant zwischen 20 und 24 °C, nahm aber bei 18 und 16 °C deutlich ab. Dies bedeutet, daß Larven, die sich bei niedrigeren Temperaturen entwickelten, mit kleinerer Körpergröße verpuppen, um ihre Entwicklung rechtzeitig vor der kalten Herbstwitterung abzuschließen. *M. rubra* Arbeiterinnen aus Sommerbrut aus St. Petersburg waren signifikant kleiner als jene aus Belgorod. Größenunterschiede zwischen Sommerbrut-Arbeiterinnen aus St. Petersburg

waren größer als zwischen jenen aus Belgorod. Wir nehmen an, dass die geringere Größe von Arbeiterinnen aus Sommerbrut eine Anpassung ist, die es nördlichen Ameisenpopulationen erlaubt, Sommerbrut rascher aufzuziehen und somit trotz des kühleren und kürzeren Sommers zumindest einige Adulte aus Sommerbrut zu produzieren.

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