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Research article

Experimental study of seasonal cycle of rapid brood production in the ants *Myrmica rubra* L. and *M. ruginodis* Nyl. from two different latitudes

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Abstract – *The period of pupation of larvae which develop from eggs laid during the same summer season (so-called rapid brood), is much shorter in Myrmica colonies in St. Petersburg (near Vyritsa, 59.25°N) than in Belgorod (near Borisovka, 50.5°N). Thus, in Belgorod rapid brood pupae are always abundant whereas in St. Petersburg only a few such pupae are produced. One could suggest that this important difference is due to direct influence of very different local climatic conditions on brood development in ant colonies. To investigate this assumption experimentally we used natural colonies of both Myrmica rubra and M. ruginodis collected near Borisovka and near Vyritsa, in spring before the commencement of oviposition. Experimental cultures consisted of 150 workers and one queen. They were maintained in photo thermostatic chambers at long (20 h light) days (LD) or short (12 h) days (SD) and 17, 20 or 25°C. and the workers were allowed to rear the eggs laid by queens, into either rapid brood pupae or diapausing larvae (slow brood). Both queen oviposition and brood pupation eventually ceased under all regimes, but SD and low temperature significantly reduced the periods of oviposition and pupation, and consequently the numbers of rapid brood. The effects of photoperiod appeared to be less clear-cut at 17°C in comparison to higher temperatures, for both species. The most pronounced temperature effects on the duration of oviposition and rapid brood production were observed at LD. In addition, St. Petersburg colonies differed from those from Belgorod by having far shorter oviposition and pupation periods, and much weaker rapid brood production, at the same temperature and photoperiod. Thus, we conclude that the dramatic differences in the colony life cycles between Belgorod and St. Petersburg Myrmica populations, are not only the results of responses to distinct local climates, but is also due to local adaptation of the innate endogenous mechanisms which exist in ant colonies. Some interspecific differences were also found: in contrast to M. rubra, the cultures of M. ruginodis from St. Petersburg only produced rapid brood at 25° LD, and at all other regimes all larvae entered diapause. M. rubra from Belgorod, laid eggs and produced rapid brood for longer at 17 and 20°C than sympatric M. ruginodis, but at 25°C the situation was reversed: the M. ruginodis cultures reared rapid brood for much longer at LD, and oviposition was prolonged at both photoperiods compared to in M. rubra.*

Keywords: Formicidae, *Myrmica*, seasonal cycle, phenology, oviposition, rapid brood, pupation, diapause, photoperiod, temperature, control, biogeography.

Introduction

Ants of the genus *Myrmica* employ the strategy of prolonged development in their annual cycle (Kipyatkov and Lopatina, 1995, 1996a,b). This means that their colonies hibernate with diapausing larvae (Jezhikov, 1929; Eidmann, 1943; Talbot, 1945; Brian, 1950, 1951; Cammaerts, 1977). In spring queens begin to lay eggs: however, only a proportion 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, hibernate 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 hibernating brood consists of third instar larvae (Brian, 1951; Elmes and Thomas, 1987; Elmes, 1991). Thus, the duration of the seasonal cycle of development in *Myrmica* depends upon the time when diapause is triggered in larvae and queens, in late summer (Kipyatkov, 1993).

It is well known that photoperiod is one of the most important environmental cues which control the seasonal life cycles and dormancy in terrestrial arthropods (Danilevski, 1965; Danilevsky et al., 1970; Beck, 1980; Zaslavski, 1988; Behrens, 1985; Tauber et al., 1986; Danks, 1987). Hence it was rather surprising that the photoperiodic responses play only a modest role in ant seasonality (Kipyatkov, 1993). For example, Brian neglected photoperiod as a factor that could control seasonality in ants for a long time (Brian, 1977, 1983) because his experiments revealed no effects of day-length on the production of rapid brood and only insignificant influence on the duration of queen oviposition in *M. ruginodis* from Southern England (Brian, 1963; Brian and Hibble, 1964; Brian and Kelly, 1967).

However, the importance of photoperiodism in the control of ant seasonal cycles was demonstrated for the first time by Kipyatkov (1972, 1974) who used colonies of *M. rubra* and *M. ruginodis* from the middle of European Russia (Belgorod region). It has been shown that the diapause induction in *M. rubra* larvae and queens was due to the influence of natural photoperiods during the second half of summer (Kipyatkov, 1974, 1977a, 1979). When ant colonies in the autumn state were subjected to long-day photoperiods, it resulted in a quick termination of diapause both in queens and larvae (Kipyatkov, 1977b). Subsequently the existence of photoperiodic responses in *M. rubra* was confirmed by Hand (1983) in experiments on worker egg-laying and by Brian (1986) who studied the larval care by young workers at three photoperiods.

Nevertheless, the following extensive experimental studies by Kipyatkov and his co-workers on the seasonal cycle control in temperate ant species, demonstrated that only some used day-length as an environmental cue inducing the state of dormancy. Most ants rely upon the internal clocks as well as on the ambient temperature in triggering the onset of diapause (see a review in Kipyatkov, 1993). The genus *Myrmica* thus represents a rather curious exception among temperate ants since all its species studied so far, possess clear-cut photoperiodic responses controlling the induction and termination of diapause (Kipyatkov, 1972, 1993; Kipyatkov and Lopatina, 1997, 1998a,b; Kipyatkov et al., 1998).

It was also found that in most temperate and especially boreal ants including the genus *Myrmica*, winter diapause was obligatory at a colony level and the seasonal cycle was controlled mainly by endogenous factors. Even at long days and optimal temperature the development in colonies ceases sooner or later as a result of an internal timing effect. Thus the duration of colony's annual cycle of development is controlled both by an endogenous timer and by external ecological factors – temperature and photoperiod. The environmental factors adjust the date of diapause onset 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 and Shenderova, 1990; Kipyatkov, 1993, 1995; Kipyatkov and Lopatina, 1996a,b).

Our pilot studies (Kipyatkov and Lopatina, 1996a) showed that the phenology of *Myrmica* brood development in the north is fairly different from that in the middle of European Russia (Fig. 1). The first rapid brood pupae appear in June or early in July in Belgorod populations and only in late July or even at the beginning of August in St. Petersburg. Despite this, pupation ceases almost at the same time in both regions, in the middle or in the second part of August depending on the weather. Consequently in Belgorod rapid brood is always abundant whereas in St. Petersburg only a few rapid brood pupae are produced. Thus, the seasonal cycle of rapid brood production in *Myrmica* colonies is much shorter in St. Petersburg than in Belgorod.

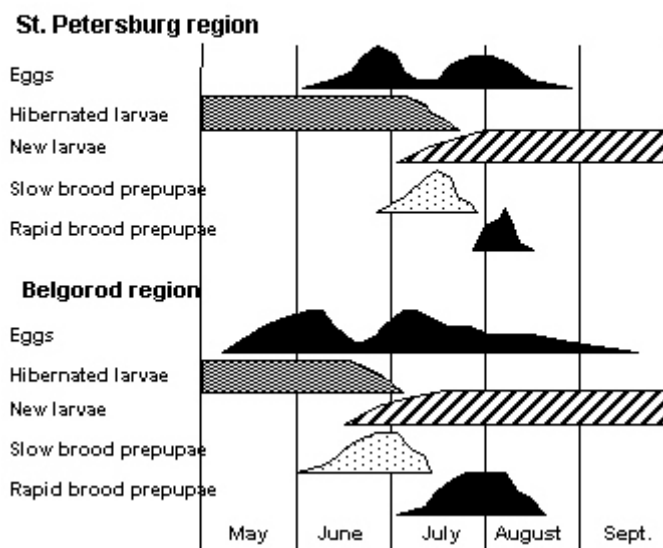


Figure 1. Phenology of brood development in *Myrmica* colonies in two latitudinally remote regions.

One hypothesis is that this important difference between *Myrmica* populations from two distant regions is due to direct responses to the very different climatic conditions. In which case, if we placed *Myrmica* colonies from St. Petersburg into the climatic regime of the Belgorod region they should rear numerous rapid brood and vice versa with the opposite transposition. An alternative hypothesis is that colonies in northern population really have shorter innate cycles of development in comparison to southern populations. The main goal of this work was to test and to compare both hypothesis.

Materials and methods

Stock nests were excavated in spring before the appearance of eggs in two regions: near Borisovka (Belgorod region, 50.5°N) in early April and near Vyritsa (St. Petersburg region, 59.25°N) at the end of May. In the first region both species live under the canopy of oak deciduous forest nesting mainly in rotting dead wood. The site in the second region was in the coniferous pine woodland where ants build nests mostly in moss hillocks and very rarely in dead wood. Both sites were at low altitudes.

Experimental cultures were established a few days after the collection, each consisting of 150 workers and one queen. These were maintained in plastic laboratory nests with approximately 100% humidity and ample food (cockroaches *Nauphoeta cinerea* cut into pieces and 15% sucrose

solution) in photo thermostatic chambers (photothermostats). Six experimental regimes were used: three temperatures: $17\pm 1^\circ\text{C}$, $20\pm 1^\circ\text{C}$ and $25\pm 1^\circ\text{C}$, each at two photoperiods: long (20 h) days (LD) and short (12 h) days (SD). Ant groups were kept under the same regime throughout the experiment.

Queens began to lay eggs at the start of the experiment. The workers reared these into rapid brood pupae and diapausing larvae. Once per week or sometimes per two weeks, cultures were examined and all pupae produced during the preceding period 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 diapausing 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).

From data obtained the following parameters were calculated for each group: the period for which eggs were present (interval between the start of experiment and the disappearance of eggs), the duration of rapid brood production (the period between the production of the first and last pupae), the number of rapid brood pupae reared, the number of diapause larvae reared, the total number of brood produced (rapid brood plus diapause larvae), the share (per cent) of the rapid brood in the total brood produced.

Results

Rapid brood production

Rapid brood pupae were reared at all experimental regimes and by each ant group with the exception of *M. ruginodis* cultures from St. Petersburg population kept at all regimes but 25°C LD (to be discussed below). The pupation began a bit later at lower temperatures but apparently without any dependence on photoperiodic conditions (Fig. 2–4). *M. rubra* from Belgorod had slightly slower development and the first pupae, therefore, appeared in its groups a week later than in St. Petersburg groups at all regimes.

The influence of photoperiods on the dynamics and the duration of pupation was evident. Under SD conditions, a rapid decline followed the first peak of pupation and pupation soon ceased (Fig. 2–4). The mean duration of pupation period was significantly shorter at SD than at LD under all temperature regimes (Tab. 1–3). The temperature effects on the period of pupation appeared to be dependent on photoperiodic conditions. Under LD, pupation generally stopped sooner with lower temperatures. However, under SD the duration of pupation was much shorter and not so dependent on temperature (Tab. 1–3).

The quantity of rapid brood pupae produced was affected both by photoperiod and temperature, both factors again interacting to some extent (Tab. 1–3). The influence of SD significantly reduced the mean number and share of rapid brood pupae as compared to LD both at 25°C and 20°C , but at 17°C the differences between SD and LD appeared to be small and ambiguous. Similarly, under LD the mean number and share of pupae were clearly the less the lower was the temperature (with the exception of pupae number in *M. rubra* from Belgorod at 20°C), but at SD the dependence of rapid brood quantity on temperature was not so regular (eg. Tab. 1, 3) and sometimes insignificant (eg. Tab. 2).

However, the comparison of rapid brood production patterns characteristic to different geographical populations of the same species appears more interesting. Obviously, the duration of rapid brood pupation was significantly longer and the number and the share of pupae produced were significantly higher in *M. rubra* cultures from Belgorod population as compared to the same species groups from St. Petersburg region under all temperature and photoperiodic regimes (Fig. 2, Tab. 1, 2). As regards to *M. ruginodis* these differences appeared even more distinct since ants from St. Petersburg reared rapid brood only under 25°C LD (see Fig. 3) whereas the Belgorod population of this species, produced rapid brood pupae for rather long periods and in significant quantities at all regimes (Fig. 3, 4; Tab. 3).

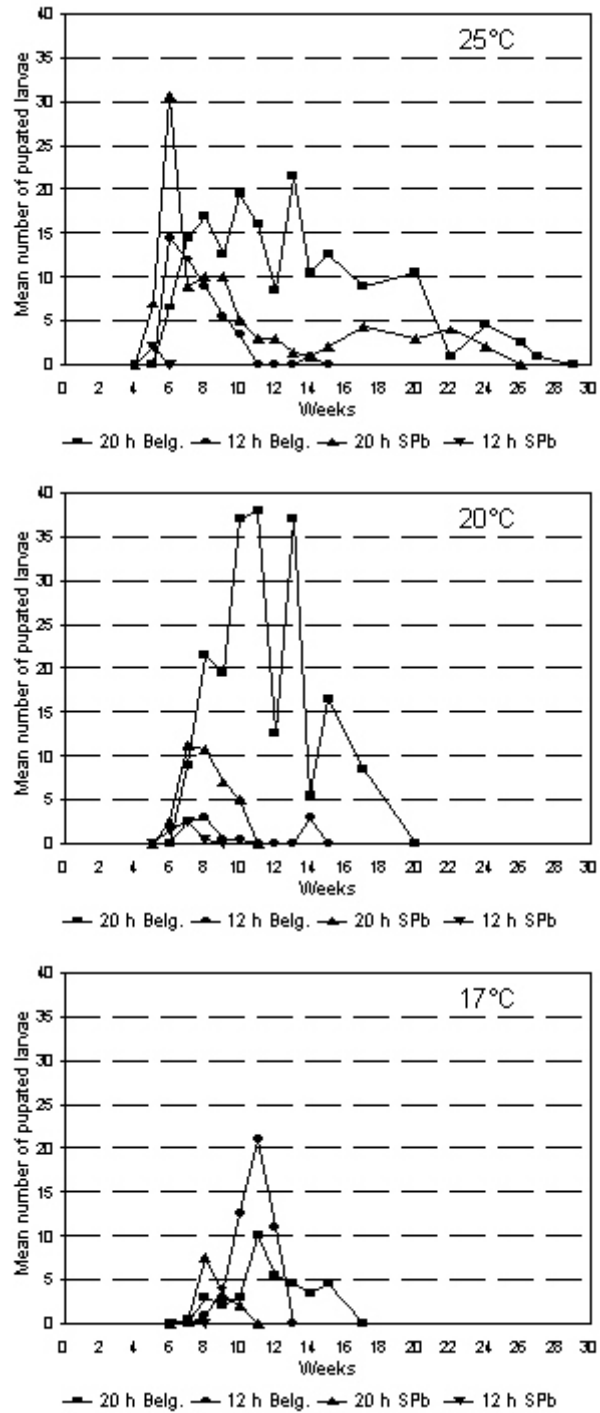


Figure 2. Rapid brood pupation per culture per week in *Myrmica rubra* under three temperatures and two photoperiods. Belg. – Belgorod population; SPb – St. Petersburg.

St. Petersburg cultures of *M. ruginodis* kept at 25°C LD produced rapid brood pupae between 98–129 days (average 113), rearing 79 to 116 pupae (average 98) that formed 68–100% (average 84%) of the total brood production. Thus, for *M. ruginodis* similarly to *M. rubra* the duration of rapid brood pupation was significantly shorter and the number and the share of pupae produced were significantly less in St. Petersburg cultures compared with the same species groups from Belgorod kept under the same regime (25°C LD).

Table 1. Duration of seasonal cycle and number of rapid brood produced in cultures of *Myrmica rubra* from Belgorod population under three temperatures and two photoperiods.

Experimental regimes and parameters		Period until eggs disappearance (days)	Rapid brood pupation			Number of larvae in diapause	Total number of brood produced
			duration (days)	number	share (%)		
25°C 20 h n = 2	min	203	151	134	90	15	149
	max	214	161	201	93	15	216
	mean	208	156	168	92	15	183
25°C 12 h n = 2	min	97	41	52	34	26	65
	max	102	41	39	60	102	154
	mean	100	41	46	47	64	110
20°C 20 h n = 2	min	140	82	186	49	173	358
	max	140	91	224	52	234	458
	mean	140	87	205	50	204	409
20°C 12 h n = 2	min	104	18	5	2	204	218
	max	104	32	14	6	285	290
	mean	104	25	10	4	245	254
17°C 20 h n = 2	min	115	49	32	15	93	133
	max	115	60	40	30	188	220
	mean	115	55	36	22	141	177
17°C 12 h n = 2	min	103	29	59	28	151	193
	max	115	36	40	29	153	210
	mean	109	32	50	29	152	202

Duration of oviposition

The periods until eggs disappeared in our experimental ant cultures were obviously longer than the real duration of oviposition, since eggs are present in nests for a short period after queen oviposition ceases. The difference between these two parameters should be greater at lower temperature due to slower development rates. Unfortunately, the data are insufficient to calculate the mean values of egg developmental time at each temperature for each species and population. Also it is emphasized, that our method of calculation might underestimate the duration of oviposition because the last eggs laid by queens at the end of seasonal cycle might be cannibalized by workers and larvae and thus disappear prematurely, as has been shown for *Formica* species (Kipyatkov and Shenderova, 1989; Kipyatkov and Lopatina, 1993).

The mean period of egg presence (Tab. 1–3) showed clear dependence on both photoperiod and temperature. The influence of SD led to significant reduction of this parameter in comparison to LD, although the difference became less at lower temperatures. The period until egg disappearance decreased at lower temperature, and this effect was more pronounced at LD than at SD. It is important to note that in *M. rubra* cultures from Belgorod, the mean period until eggs disappearance was significantly longer in comparison with the same species groups from St.

Petersburg region under all temperature and photoperiodic regimes except at 20°C SD (Tab. 1, 2, 4). It is also very interesting that in most *M. ruginodis* cultures kept at 25°C egg-laying did not cease until the end of experiment, i.e. queens oviposited for more than 300 days (Tab. 3).

Table 2. Duration of seasonal cycle and number of rapid brood produced in cultures of *Myrmica rubra* from St. Petersburg population under three temperatures and two photoperiods.

Experimental regimes and parameters		Period until eggs disappearance (days)	Rapid brood pupation			Number of larvae in diapause	Total number of brood produced
			duration (days)	number	share (%)		
25°C	min	109	90	39	49	35	74
20 h	max	240	124	172	76	66	227
n = 3	mean	161	105	91	59	52	143
25°C	min	71	7	2	2	55	57
12 h	max	77	7	2	4	106	108
n = 2	mean	74	7	2	3	81	83
20°C	min	84	28	19	17	60	79
20 h	max	105	42	48	31	257	308
n = 4	mean	98	38	37	23	133	170
20°C	min	95	7	1	1	115	116
12 h	max	109	14	8	4	196	204
n = 2	mean	102	10	5	2	156	160
17°C	min	95	23	10	5	154	173
20 h	max	95	38	23	13	200	210
n = 3	mean	95	31	17	9	172	189
17°C	min	71	0	0	0	183	184
12 h	max	71	6	1	1	193	193
n = 2	mean	71	3	<1	<1	188	189

Total brood production

Both the number of slow brood larvae and the total number of larvae reared were dependent on temperature and photoperiod (Tab. 1–3). It was not surprising that in *M. rubra* the dependance of diapausing larvae number on the day-length appeared to be inverse to that described above for the number of rapid brood pupae: the slow brood quantity was less at LD than at SD apparently because more larvae had the possibility to pupate at LD than at SD (Tab. 1, 2). The influence of photoperiod became less clear at 17°C. It is however, more difficult to explain the opposite results obtained for *M. ruginodis* cultures where the number of diapausing larvae reared was on the average less at SD than at LD (Tab. 3). It might be partially due to shorter duration of oviposition and thus lower total egg production in *M. ruginodis* cultures at 17 and 20°C in comparison to *M. rubra* ones (cf. Tab. 1 and 3).

The total number of larvae reared was on average significantly greater under LD than under SD except in cultures kept at 17°C where the influence of day-length seemed to be entirely absent (Tab. 1–3). This effect of photoperiod was probably due to much shorter duration of oviposition under short days (discussed above) which resulted in lower total egg production and hence in lower numbers of larvae reared. Two *M. ruginodis* cultures kept at 25°C SD clearly differed from the others by having extremely low brood production despite very long oviposition by their queens (Tab. 3), this might be a result of abnormally high mortality from unknown causes.

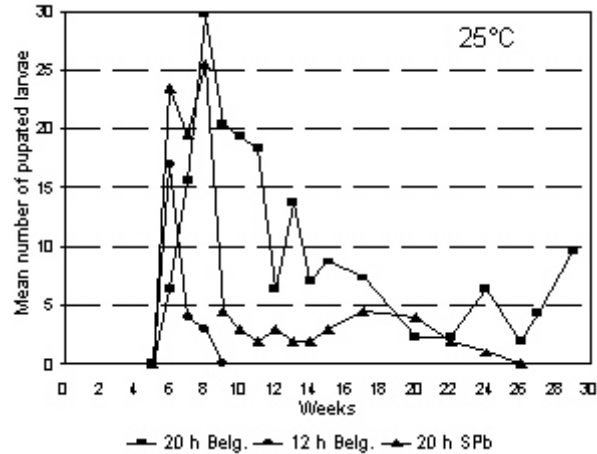


Figure 3. Rapid brood pupation per culture per week in *Myrmica ruginodis* under 25°C and two photoperiods. Belg. – Belgorod population; SPb – St. Petersburg population.

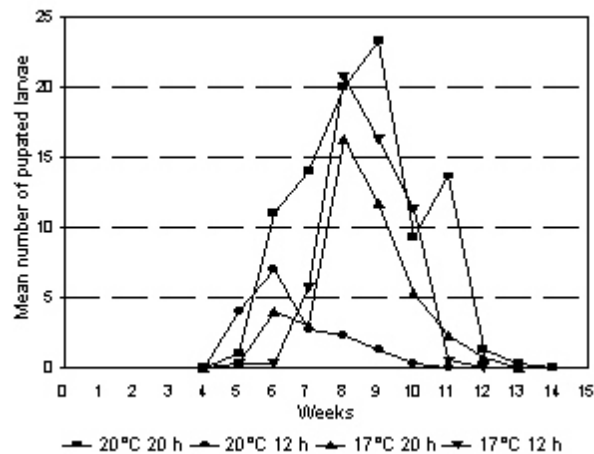


Figure 4. Rapid brood pupation per culture per week in *Myrmica ruginodis* from Belgorod population under two temperatures and two photoperiods.

The influence of temperature on the total brood production seems to be better revealed at LD than at SD. Considering only the data obtained under LD, it is very interesting to note that on average, cultures from the Belgorod populations of both species produced maximum numbers of larvae at 20°C whereas in *M. rubra* from St. Petersburg the maximum were reared at 17°C (cf. Tab. 1, 3 and Tab. 2). From this it might be deduced that the temperature optimum for brood rearing of *Myrmica* larvae from Belgorod is a little higher compared to St. Petersburg colonies.

Comparison of species

Differences between populations of the two species inhabiting the same regions are evident.

Under 17 and 20°C, the mean durations of oviposition and rapid brood pupation of the Belgorod populations were generally greater in *M. rubra* compared to *M. ruginodis*, the only two

exceptions when the values were very similar, were pupation at 17 and 20°C SD (Tab. 1, 3). The interspecific differences were greatest at 20°C (i.e. near optimal temperature) and LD. It is also worthy to note that at 20°C *M. rubra* cultures produced significantly more larvae than *M. ruginodis*. However, a temperature of 25°C caused longer pupation at LD and extremely prolonged oviposition (see above) at both photoperiods in *M. ruginodis* groups from Belgorod in comparison with *M. rubra* cultures from the same site. At St. Petersburg, interspecific differences were no less pronounced. *M. ruginodis* cultures did not produce rapid brood at any regime except 25°C LD (Fig. 3), whereas *M. rubra* ants reared pupae in all treatments (Tab. 2). The mean duration of rapid brood pupation under 25°C LD did not differ significantly between species: 105 days in *M. rubra* and 113 days in *M. ruginodis*.

Table 3. Duration of seasonal cycle and number of rapid brood produced in cultures of *Myrmica ruginodis* from Belgorod population under three temperatures and two photoperiods.

Experimental regimes and parameters	Period until eggs disappearance (days)	Rapid brood pupation			Number of larvae in diapause	Total number of brood produced	
		duration (days)	number	share (%)			
25°C	min	217	169	147	79	35	187
20 h	max	>300	234	231	87	40	266
n = 3	mean	—	193	180	83	38	227
25°C	min	—	5	9	75	3	12
12 h	max	—	32	24	77	7	31
n = 2	mean	>300	18	17	76	5	22
20°C	min	104	41	59	36	85	144
20 h	max	104	59	134	42	235	369
n = 3	mean	104	49	94	40	148	242
20°C	min	63	14	2	9	60	72
12 h	max	104	46	44	27	132	166
n = 3	mean	83	29	18	17	105	127
17°C	min	104	34	18	11	141	159
20 h	max	112	56	63	31	143	193
n = 3	mean	109	45	44	23	142	185
17°C	min	91	21	21	15	90	141
12 h	max	104	43	85	49	148	231
n = 4	mean	97	32	55	29	126	181

Discussion

The results from this experiment provide good evidence in favour of the hypothesis that the seasonal development of *Myrmica* colonies is under external environmental control. Both day-length and temperature exert an influence on the onset of the diapause in queens and larvae and so control the duration of the seasonal cycle of oviposition, and the development and the quantity of rapid and slow brood produced. It is worth noting that the photoperiodic responses of both species appeared to be less pronounced at 17°C than at higher temperatures, which is probably due to the well-known phenomenon of thermal optimum of photoperiodic responses in insects (Danilevski, 1965; Danilevsky et al., 1970; Beck, 1980; Zaslavski, 1988; Behrens, 1985; Tauber et al., 1986; Danks, 1987) which has also been demonstrated for *Myrmica* (Kipyatkov, 1977a).

Our data also confirms the second hypothesis of the existence of an internal control for the seasonal cycle of oviposition and development in *Myrmica* colonies. The egg-laying and pupation in experimental cultures ceased eventually under any treatment, which suggests endogenous controls. The most prolonged development was obtained under long-day conditions. It is not surprising, therefore, that we observed the most pronounced temperature effects on the duration of oviposition and rapid brood production at long days

However, the most fascinating result of our experiment is the latitudinal variation of the length of *Myrmica* colony's intrinsic cycle of development, which is shorter when in more northerly populations of the same species. From this we can speculate that the northernmost *Myrmica* populations should produce no rapid brood at all even at optimal conditions, because of the extremely short intrinsic cycle of development. The first results obtained in our pilot study of five *Myrmica* species in the Polar Circle region give good confirmation for this speculation (Kipyatkov and Lopatina, 1997– pp. 277–286 of this volume). Thus, the dramatic difference between Belgorod and St. Petersburg *Myrmica* populations in the duration of seasonal cycle of development and in rapid brood quantity, which is an adaptation to really distinct local climates, is not simply due to the direct influence of temperature and photoperiod but is controlled by innate endogenous mechanisms.

We now believe that if we transplanted *Myrmica* colonies from St. Petersburg to the Belgorod region, they would still rear considerably less rapid brood pupae in comparison to native colonies. We also can predict that ant colonies from Belgorod placed into St. Petersburg region would probably produce a little more rapid brood than local colonies, but less than colonies remaining in Belgorod because of the shorter warm season in St. Petersburg.

Thus we conclude that while the second hypothesis – that *Myrmica* colonies in northern population have shorter innate cycle of development in comparison to southern ones – is correct, the response to environmental factors also plays an important role. The interrelations between these two mechanisms should be the subject of further studies.

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