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Research article

Seasonal cycle and winter diapause induction in ants of the genus *Myrmica* in the Polar Circle region

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Abstract – Stock colonies of five species, *Myrmica lobicornis*, *M. rubra*, *M. ruginodis*, *M. scabrinodis*, and *M. sulcinodis*, were collected near Poyakonda (Murmansk district, just on the Polar Circle latitude) at the end of June. Experimental cultures each consisting of 150 workers, one queen and about 100 overwintered larvae were established and maintained in photothermodynamic chambers at two temperature regimes – 22.5 or 25°C and three day-lengths – mid-summer photoperiod (24 h), late-August photoperiod (17 h) and autumn photoperiod (12 h). All or almost all larvae pupated regardless of photoperiod and temperature. New larvae emerging from the eggs laid by queens developed up to the third (final) instar and fell in diapause independently of the day-length and temperature. No larvae pupated except for a few in one culture of *M. scabrinodis*. Thus generally, *Myrmica* cultures failed to produce so-called rapid brood (i.e. larvae pupated during their first summer) even under long days and optimal temperature. The lack of the photoperiodic control of larval development in the ant populations studied is evidently a consequence of the absence of rapid brood in the colonies. Nevertheless, the photoperiods appeared to control the duration of oviposition and the time of queen onset of diapause in experiments. It is, however, questionable that August photoperiods alone could induce queen diapause in subarctic populations of *M. ruginodis* in real time. We suppose that queen diapause arises mainly due to the influence of inferior temperature in August. The possibility of photoperiodic termination of diapause in both queens and larvae in autumn is revealed in all species studied. From this we formulate a new hypothesis of “vestigial photoperiodic responses” in *Myrmica* populations inhabiting the subarctic regions.

Keywords: seasonal cycle, oviposition, rapid brood, pupation, diapause, photoperiod, temperature, control.

Introduction

Seasonal cycle of colony development in ants of the genus *Myrmica* was studied for the first time by Jezhikov (1929) and later by some other authors (Eidmann, 1943; Talbot, 1945; Brian, 1950, 1951; Cammaerts, 1977). It has been shown that all *Myrmica* species hibernate with diapausing larvae. It means that *Myrmica* ants as well as a lot of other ant species employ the strategy of prolonged development in their annual cycle, i.e. they extend the development of larvae for two summer seasons (Kipyatkov and Lopatina, 1995, 1996a,b). In spring queens lay eggs from which new larvae emerge. Only a proportion of these larvae develop into pupae within the same summer season without hibernation; they are called *rapid* or *summer brood*. The remaining larvae enter diapause, continue to grow slowly in autumn, hibernate and finish their

development during the next summer; these larvae represent so-called *slow* or *winter brood* (Brian, 1951, 1957). In late summer queens stop egg-laying because of the onset of diapause. All hibernating brood consists of third instar larvae only (Brian, 1951; Elmes and Thomas, 1987; Elmes, 1991) and any brood which does not attain the final instar by the onset of winter dies.

Thus, the duration of seasonal cycle of oviposition and development in *Myrmica* colonies is determined by the time of diapause induction in queens and larvae in late summer, this process being controlled both by external and internal factors (Kipyatkov, 1993). Among the environmental factors controlling the diapause induction in terrestrial arthropods photoperiod and temperature are known to be most important (Danilevski, 1965; Beck, 1980; Behrens, 1985; Tauber et al., 1986; Danks, 1987; Zaslavski, 1988). The significant role of photoperiodism in the control of seasonal cycles in *Myrmica* ants was demonstrated for the first time by Kipyatkov (1972, 1974) who used for the experiments colonies of *M. rubra* and *M. ruginodis* from the middle of European Russia (Belgorod region). He has 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). The action of long-day photoperiods on ant colonies in autumn state resulted in rather quick termination of diapause (so-cold photoperiodic reactivation) both in queens and larvae (Kipyatkov, 1977b). Several years later 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.

Subsequent studies by Kipyatkov and his colleagues demonstrated that only some ant species use day-length as an environmental cue inducing diapause. Most rely upon internal clocks and on the environmental temperature in the timing of onset of diapause (see a review in Kipyatkov, 1993). The genus *Myrmica* represents an unusual exception among ants since all *Myrmica* species studied so far possess clear-cut photoperiodic responses controlling the induction and termination of diapause (Kipyatkov, 1972, 1993; Kipyatkov and Lopatina, 1998a,b; Kipyatkov et al., 1998).

Winter diapause was found to be obligatory at a colony level in most temperate and especially boreal ants, their seasonal cycle being controlled mainly by endogenous factors. This was confirmed by the observation that even at long days and optimal temperature, the development in colonies ceases sooner or later as a result of an internal timer effect. Thus, the colony's annual cycle of development is controlled by an endogenous timer along with external cues – temperature and photoperiod. These factors adjust the date of onset of diapause according to the weather - prevailing during the late summer: short days together with lower temperature, hasten the diapause induction thus diminishing the period of development; on the contrary, when the weather is warmer, diapause would occur later in the season (Kipyatkov and Shenderova, 1990; Kipyatkov, 1993, 1995; Kipyatkov and Lopatina, 1996a,b). This basic scheme of seasonal development control is relevant for *Myrmica* species.

Since all field and experimental studies of *Myrmica* seasonal cycles have been carried out in the regions with temperate or warm temperate climates nothing was known about seasonality and diapause control of these ants living in boreal and subarctic zones. Our first research in this field (Zhigul'skaya et al., 1992) was done on a population of *Myrmica kamtschatica* Kupianskaya in the upper Kolyma River (Magadan district in the Far North-East of Russia). All or almost all overwintered larvae in colonies of this species were found to pupate during the very short summer, but all the larvae emerging from the eggs only reached the final instar and hibernated in diapause. The rapid brood was entirely absent in *M. kamtschatica*, but nothing was known about the nature of the factors that control the obligate larval diapause of this species.

As part of a joint international project aimed to study the social organisation and physiological regulation of *Myrmica* ants adapted to living in variable seasonal climates, we have carried out this experimental study of five species of *Myrmica* from a region situated just on the Polar Circle on the Western coast of the White Sea. The main aim was to test whether the colony life cycle observed for *M. kamtschatica* applies generally to boreal *Myrmica*.

Materials and methods

Ant colonies were collected at the end of June 1996 in the vicinity of the White Sea Biological Station of Moscow State University (Cape Kindo, near Poyakonda, Murmanskaya oblast, 66° 33' N), at low altitudes. *M. ruginodis* Nyl., the most abundant *Myrmica* species in this region, lives in coniferous (spruce and pine) forests (northern taiga) where ants prefer clearings or less dense places with mainly southern exposure, and also in the bogs. Nests are mostly constructed in moss hillocks and very rarely in dead wood. Numerous nests of this species can also be found in driftwood and logs on the sea shores and in moss or soil hillocks along the edges of forest roads. *M. scabrinodis* Nyl. is less abundant and found almost exclusively in bogs, nesting in moss hillocks or occasionally in the most sunny and warm sites in the forest and in driftwood. Nest sites of *M. sulcinodis* Nyl. are in the warmest places, necessarily with southern exposure and having sandy soil, in clearings or on the roads and tracks in the forest. Here the ants build their nests in soil, normally under stones, without any above-ground structures. Despite intensive search only two colonies of *M. rubra* L. and one of *M. lobicornis* Nyl. were found, all in the driftwood on the extremely wet and marshy sea coast, having a southern exposure. At the time of collection, the first eggs were present in only few nests but some of the overwintered larvae have grown sufficiently to pupate in colonies of all species. Five to seven days after collection experimental cultures were established, each consisting of 150 workers, one queen and about 100 overwintered larvae of various sizes or 30–50 medium and large larvae, depending on the experimental design (see below). Altogether the following numbers of cultures were used: 53 of *M. ruginodis*, 40 of *M. scabrinodis*, 17 of *M. sulcinodis*, 8 of *M. rubra* and 4 of *M. lobicornis*.

The cultures were maintained in plastic laboratory nests with approximately 100% humidity and ample food (cockroaches *Nauphoeta cinerea* cut into pieces and 15% sucrose solution) in photothermostatic chambers at 22–23°C and 24 h day-length until the middle of July when they were transferred to different experimental regimes. Two temperature regimes were used – 22.5±1 and 25±1°C, and three day-lengths – *Mid-summer photoperiod*, i.e. constant light (24 h) corresponding to natural conditions during the Polar day, *August photoperiod* (17 h) corresponding to natural conditions in the region of ant collection at the end of August and *Autumn photoperiod* (12 h) observed in nature at the end of September, i.e. in late autumn.

Three experimental layouts were employed. First we discriminated cultures that contained only big and medium sized overwintered larvae from those containing a mixture of sizes. Then: (1) In half of the cultures with larvae of various sizes all the eggs laid by queen were removed and counted each one or sometimes two weeks, thus measuring the dynamics and the length of oviposition. Besides that in the absence of any new larvae originating from the eggs it was easy to observe the fate of all overwintered ones. (2) In the remaining half of cultures with larvae of various sizes we did not remove eggs allowing them to develop. These cultures were given food with neutral red – a vital dye that accumulated in the fat body of overwintered larvae allowing to distinguish them from new larvae subsequently hatching from the eggs. Thus, it appeared possible to see if these new larvae pupated or not, i.e. to uncover the presence or absence of the rapid brood. (3) In cultures with large and medium larvae the eggs were not removed because all overwintered larvae pupated before new larvae grew sufficiently to become confused with them. The cultures from both 2nd and 3rd layouts were observed until queens stopped laying and all the eggs and early instar larvae disappeared. Thus, the interval between the start of experiment and the disappearance of eggs, i.e. the period of egg presence, was determined. For *M. ruginodis* and *M. scabrinodis* we used all three layouts, but for *M. sulcinodis* – only the 2nd and the 3rd, and for *M. lobicornis* and *M. rubra* – only the 3rd layouts were employed.

In mid-October when the eggs disappeared and the pupation stopped in all ant groups an additional experiment on photoperiodic reactivation was done, using cultures of all five species. The cultures with diapausing larvae and non-laying (i.e. diapausing) queens were transferred from 12 h 22.5°C to 22 h 22.5°C, the control cultures being kept at 12 h 22.5°C as before.

While removing eggs or pupae the ants were anaesthetised by a short (up to 30 seconds) exposure to carbon-dioxide which is known to have no negative effects on brood rearing (Wardlaw, 1995).

Results

Development of overwintered larvae

All or almost all overwintered larvae that survived and developed in the cultures of all the five species pupated regardless of temperature and photoperiods at which they were reared. Only a few such larvae still remained in two cultures of *M. ruginodis* and two cultures of *M. scabrinodis* in the middle of August when the pupation had stopped in all experimental groups. Most overwintered larvae developed into workers and some into males. Presumably the presence of queens affected the development of larvae inhibiting the rearing of sexual brood (Brian, 1983; Elmes, 1991), although occasionally a few alate queens were reared by some groups.

Table 1. The influence of day-length on the time of onset of diapause in queens of *Myrmica ruginodis* in cultures kept at 22.5°C (the start of experiment on 24 July).

| Day-length | Parameters | Period of eggs presence (P) or oviposition (O), days | | |
|------------|--------------------|--|------------------------|-----------|
| | | Set 1 (P) | Set 2 (P) | Set 3 (O) |
| 24 h | Number of cultures | 7 | 5 | 3 |
| | Min | – | 46 | 46 |
| | Max | *** 84 | * 84 | * 81 |
| | Mean | ^s 84 | ^s 70 | 67 |
| | SD | 0.0 | 16.8 | 18.7 |
| | 17 h | Number of cultures | – | 4 |
| | Min | – | 25 | – |
| | Max | – | * 84 | ** 81 |
| | Mean | – | 42 | 81 |
| | SD | – | 28.4 | 0.0 |
| 12 h | Number of cultures | 7 | 4 | 4 |
| | Min | 17 | 17 | 12 |
| | Max | 53 | 36 | 69 |
| | Mean | ^s 28 | ^s 25 | 48 |
| | SD | 13.5 | 7.6 | 25.4 |

The letter “S” denotes the means that are significantly ($p \leq 0.05$) different in each column.

* In one ** two or *** all 7 cultures eggs were still present at the end of experiment. Thus, both the mean and the maximum values were underestimated.

Development of new brood

In all experimental cultures queens laid eggs that developed into larvae. However, none of these new larvae completed their development with the exception of only in one culture of *M. scabrinodis* kept under 24 h 25°C, in which nine rapid brood pupae appeared by the end of

August. Although some new larvae became quite large, no others had pupated by the end of experiment in mid-October. All had entered diapause regardless of the photoperiodic treatments. It was noted that in all cultures of *M. lobicornis*, *M. rubra*, *M. ruginodis* and in some cultures of *M. scabrinodis* kept at 25°C, there was a rather high mortality of new brood with only a few larvae surviving, whereas at 22.5°C the development of new brood proceeded well and without excess mortality.

Table 2. The influence of day-length on the time of onset of diapause in queens of *Myrmica scabrinodis* in cultures kept at 25 or 22.5°C (the start of experiment on 24 July).

| Day-length | Parameters | Period of eggs presence (P) or oviposition (O), days | | | |
|------------|--------------------|--|------------------------|------------------------|---------------------|
| | | Set 1 (P) 25°C | Set 2 (P) 25°C | Set 3 (P) 22.5°C | Set 4 (O) 22.5°C |
| 24 h | Number of cultures | 4 | 4 | 3 | 4 |
| | Min | 36 | 25 | 74 | 75 |
| | Max | 46 | 35 | ** 84 | *** 81 |
| | Mean | ^s 38 | ^s 30 | ^s 81 | 79 |
| | SD | 5.0 | 6.4 | 6.1 | 3.0 |
| 17 h | Number of cultures | – | 4 | – | 3 |
| | Min | – | 17 | – | 53 |
| | Max | – | 35 | – | * 81 |
| | Mean | – | 25 | – | 65 |
| | SD | – | 7.6 | – | 14.4 |
| 12 h | Number of cultures | 4 | 4 | 4 | 4 |
| | Min | 17 | 17 | 25 | 25 |
| | Max | 25 | 25 | 35 | * 81 |
| | Mean | ^s 21 | ^s 19 | ^s 33 | 57 |
| | SD | 4.3 | 3.8 | 5.5 | 23.3 |

The letter “S” denotes the means that are significantly ($p \leq 0.05$) different in each column.

* In one ** two or *** three cultures eggs were still present at the end of experiment. Thus, both the mean and the maximum values were underestimated.

Queen oviposition and diapause

The mean period of egg presence in cultures of both *M. ruginodis* (Tab. 1) and *M. scabrinodis* (Tab. 2) appeared to be strongly dependent on day-length conditions. Under short days, i.e. autumn photoperiods, the eggs disappeared significantly sooner in comparison to cultures kept at mid-summer (24 h) and even at August (17 h) photoperiods. Moreover, at 24 h queens in many cultures did not enter a diapause state and were still laying in mid-October when the experiment was terminated. The mean periods of egg presence under August (17 h) photoperiods were intermediate to the 24 h and 12 h treatments in both species. Eggs disappeared much sooner (i.e. oviposition ceased) in cultures of *M. scabrinodis* kept at 25°C than at 22.5°C irrespectively of the day-length (Tab. 2).

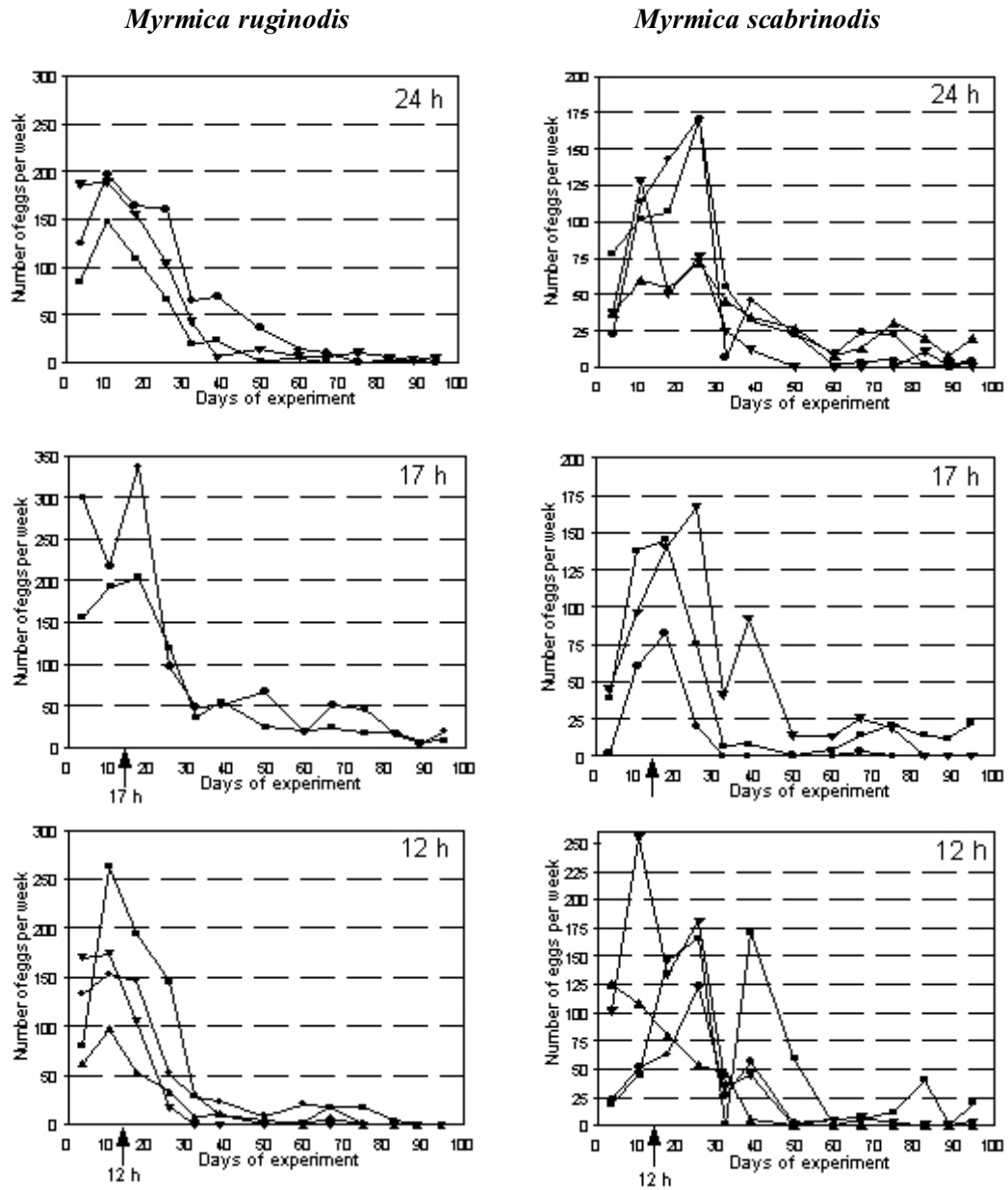


Figure 1. Oviposition of *Myrmica ruginodis* and *M. scabrinodis* queens in cultures kept at 22.5°C and different day-lengths. Each line – oviposition of one queen in a separate culture. An arrow denotes the moment (24 July) when cultures were transferred from 24 h to 17 h or 12 h.

It is also very interesting to compare these data with the results obtained in cultures where eggs laid by queens were regularly removed. The dynamics of oviposition in these cultures

(Fig. 1) was not so clearly dependent on photoperiodic conditions. Some queens at 12 h stopped laying significantly earlier (as soon as in 12 days in *M. ruginodis* and in 25 days in *M. scabrinodis*) than those kept at 24 h, but others laid eggs much longer and one *M. scabrinodis* queen was still ovipositing in mid-October when the experiment was finished. Nevertheless, on the average the oviposition ceased earlier at 12 h than at 24 h although the differences were not statistically significant (Tab. 1, Set 3; Tab. 2, Set 4).

The effect of August photoperiods in experiments where eggs were removed seemed to be indistinguishable from that of mid-summer long days. Both *M. ruginodis* queens and one *M. scabrinodis* queen out of three which survived, in cultures kept at 17 h were still laying at the end of experiment (Fig. 1, Tab. 1, 2). The mean duration of oviposition in *M. scabrinodis* at 17 h appeared intermediate between the values obtained at 12 h and 24 h but only a bit lower than at mid-summer photoperiods (Tab. 2).

Nevertheless, the periods of oviposition observed in experiment, even under autumn short days, were significantly longer than the possible duration of egg-laying in nature. In fact under 12 h queens stopped laying on the average on 10 September in *M. ruginodis* and on 19 September in *M. scabrinodis* whereas according to our (later) field observations in the White Sea region the eggs in colonies of both species usually disappear at the end of August (unpublished). We suppose that such an abnormally long oviposition might be an experimental effect due to the absence of brood in cultures where all overwintered larvae pupated but new ones did not appear because the eggs were periodically removed. The absence of larvae and the removing of eggs might stimulate queens to lay more eggs and not enter diapause despite environmental cues. This hypothesis should be tested in future experiments.

Photoperiodic termination of diapause

When the ant cultures with diapausing larvae and non-laying (i.e. diapausing) queens were transferred from 12 h to 22 h in mid-October a strong diapause terminating effect was observed. Queens began to lay eggs in one-two weeks; their productivity first reached a peak and then gradually declined for several weeks until the queens reenter diapause again (Fig. 2). At the same time in control cultures remaining at 12 h queens did not lay any eggs. In cultures of *M. lobicornis*, *M. rubra* and *M. sulcinodis* the long days also caused the termination of queen diapause but the numbers produced were not recorded.

The diapausing larvae began to pupate in one-two weeks after the transfer to long-day photoperiods (Fig. 2). There was also a peak and a subsequent decline in the rate of pupation. In some cultures almost all larvae pupated, in others – only a part of them did so. However in control cultures remaining at 12 h not one larva pupated. In cultures of *M. lobicornis* and *M. rubra* the long days also caused the termination of larval diapause but we did not remove and count the pupae produced. In general the photoperiodic termination of diapause appeared quite similar to that described earlier for *M. rubra* and *M. ruginodis* from Belgorod region (Kipyatkov, 1972, 1977b).

Discussion

The most important result of this study is the absence of the rapid brood in cultures of all five *Myrmica* species in all experimental conditions, even under long summer days and rather high temperature. We can, therefore, predict that in natural *Myrmica* colonies living in the subarctic zone all or most of overwintered larvae should finish their development during the summer and not hibernate a second winter, but almost all new larvae hatching from the eggs laid by queens, will enter diapause and hibernate pupating the following summer. Only a very few new larvae will pupate if the conditions are extremely favourable. This results accords with the previous study of one species in Kolyma region (Zhigul'skaya et al., 1992) and our preliminary observations on *M. ruginodis* phenology in the Polar Circle region (unpublished).

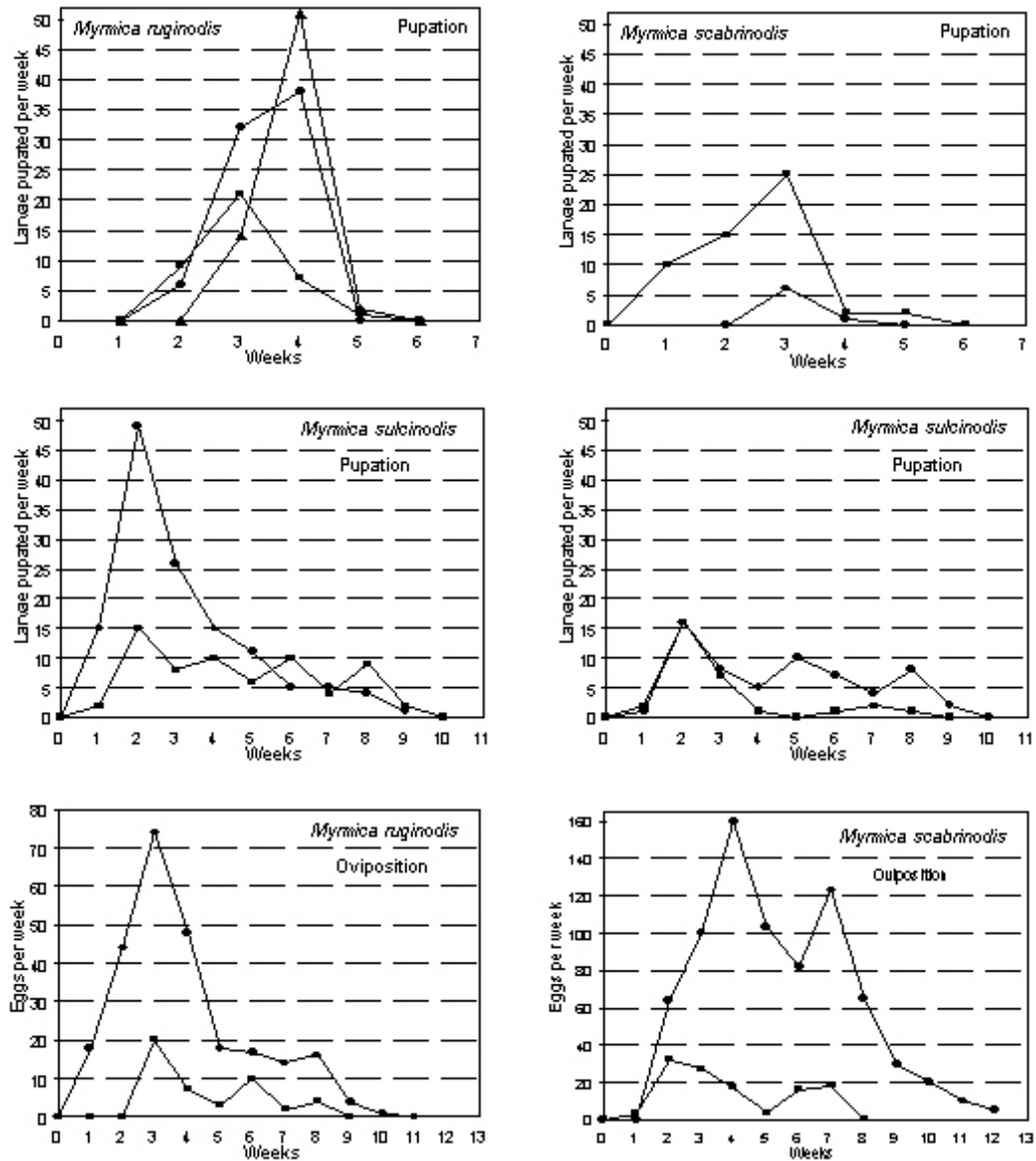


Figure 2. Photoperiodic termination of queen and larval diapause in cultures of three *Myrmica* species transferred from 12 h to 22 h at 22.5°C in October. Each line – oviposition of one queen or pupation of larvae in a separate culture. In control cultures kept at 12 h oviposition and pupation did not occur.

According to our results photoperiods control neither the development of overwintered larvae nor the diapause induction in new larvae in natural *Myrmica* colonies in the Polar Circle region. In fact the diapause appears to be obligate for all larvae originating from the eggs during summer. This might be one of the important traits distinguishing subarctic *Myrmica* populations from those living in more southern regions. However, day-length exerted a distinct effect upon the

length of oviposition and the time of onset of diapause in queens of both *M. ruginodis* and *M. scabrinodis*. Autumn short-day photoperiods (12 h) caused significantly earlier queen diapause induction and disappearance of eggs in comparison with mid-summer ones (24 h). However, such short days cannot be really encountered by natural ant colonies in the period of queen diapause induction which takes place in August.

Therefore, the results obtained in our experiments for August photoperiods deserve special attention. However, it should be emphasized that the mean period of oviposition at August photoperiods in our experiment was much longer in comparison with its possible duration in nature, e.g. when *M. ruginodis* cultures were kept at late August day-length (17 h) from 24 July the eggs disappeared on the average on 4 September (Tab. 1) but in nature ants could encounter such day-length only in late August. However, according to our phenological observations in the Polar Circle region eggs in natural ant nests disappear before the end of August, thus we question whether August photoperiods alone could induce diapause in real time. We suppose, therefore, that queen diapause in subarctic populations of *M. ruginodis* arises mainly due to the influence of inferior temperature in August.

From this we formulate a new hypothesis of "vestigial photoperiodic responses" in *Myrmica* populations inhabiting the subarctic regions. We suppose that these northern populations have originated from southern ancestors which possessed the photoperiodic control of seasonal cycle but in new environment where the summer was too short and the days were too long the photoperiodic responses became unnecessary and were entirely replaced by a mixture of endogenous controls and temperature cues. But photoperiodic responses still remain in these populations in the form of redundant physiological reactions. For example, although day-length does not control the induction of larval diapause, the influence of long days in autumn results in diapause termination by larvae, a process that can easily be observed in an experiment but can never be realized in nature.

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