7. Rele, M. V., Bansod, S. M. and Srinivasan, M. C., US Patent 5534429, 1996.
8. Bansod, S. M., Dutta-Choudhary, M. D., Srinivasan, M.C. and Rele, M. V., *Biotechnol. Lett.*, 1993, **15**, 965–970.
9. Srinivasan, M. C. and Rele, M. V., *Indian J. Microbiol.*, 1995, **35**, 93–101.
10. Balakrishnan, H., Srinivasan, M. C. and Rele, M. V., *Biotechnol. Lett.*, 1997, 19, 599–601.
11. Ikura, Y. and Horikoshi, K., *Agric. Biol. Chem.*, 1987, **51**, 3143–3145.
12. Reese, E. T. and Maguire, A., *Appl. Microbiol.*, 1969, **17**, 242–245.
13. Pazlarova, J. and Vortruba, J., *Appl. Microbiol. Biotechnol.*, 1996, **45**, 314–318.
14. Breck, D. W., in *Zeolite Molecular Sieves*, Wiley, New York, 1974, pp. 83–88.

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Vestigial photoperiodic response in subarctic *Myrmica* ants

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Studies carried out on the effects of day-length on the development of the arctic insects are probably less because the Polar day does not provide strong photoperiodic cues. In arthropods living in the subarctic zone, where photoperiodic signals are relatively more distinct, the role of day-length in the control of seasonal life cycles has been studied only by a few workers. We performed experiments on two species of *Myrmica* ants from two populations in the Polar Circle region, which revealed a clear-cut photoperiodic response that appeared to be 'vestigial', i.e. non-adaptive and unfit to induce diapause in proper time under natural photoperiodic conditions.

IN spite of the very extensive studies on insect dormancy[1–3] relatively less is known about the control of seasonal life cycles in arctic and subarctic arthropods[4–6]. The effects of day-length on the development of insects living in the high arctic have not been studied probably because the photoperiodic cues are virtually absent during most of the summer season[5,6]. Nevertheless, such effects might exist, especially in species and populations from the subarctic zone where photoperiodic cues are a little more pronounced in summer. Ferenz[7] and Thiele[8] found that the photoperiodic response in the carabid beetle *Pterostichus nigrita* from a subarctic population differed from that of a temperate population and was clearly adaptive, i.e. had critical photoperiod corresponding to natural day-lengths characteristic of the proper season in the subarctic.

We have done experiments on two species of *Myrmica* ants from the subarctic regions. *Myrmica* colonies have 'split' brood cycles: larvae from eggs laid in summer either pupate and eclose the same summer or enter diapause, hibernate and complete their development during the following spring[9]. It has been shown earlier[10–13] that temperate populations of *Myrmica* use external ecological factors such as photoperiods and temperature together with an 'endogenous clock' to regulate the onset of diapause in larvae and the cessation of oviposition by the queens. Our preliminary experiments on subarctic *Myrmica* populations[14] showed that the development of their larvae is not influenced by photoperiods. The main aim of the present study was to test whether the day-length could influence the duration of the queen oviposition and whether onset of the queen diapause could be really controlled by natural photoperiods in subarctic populations.

Colonies of *M. ruginodis* and *M. scabrinodis* were collected in June on the Western coast of the White Sea just on the Polar Circle, near Poyakonda (66°33′N) and near Chupa (66°15′N). The cultures, each consisting of 150 workers, one queen and 30–50 overwintered larvae, were maintained in photothermostatic chambers at an optimal temperature (22.5 ± 1°C or 12-h daily thermoperiod 15/25°C) and long-day photoperiods (23 or 24 h light per day depending on the experimental set-up) until the middle of July. Then they were transferred to three photoperiodic regimes (under the same temperature): *Mid-summer day-length* (23 or 24 h), simulating the situation in nature during the Polar day, *August day-length* (18 or 17 h), corresponding to natural conditions in the middle or at the end of August, and *Late-autumn day-length* (12 h) observed in the Polar Circle region at the beginning of October.

Almost all overwintered larvae pupated regardless of the photoperiod. However, no new larvae hatching from the eggs laid by the queens completed their development – all of them entered diapause. Thus, photoperiods control neither the development of overwintered larvae nor the induction of diapause in new ones. In fact diapause appears to be obligatory for all larvae originating from eggs deposited during summer. This is in accordance with our preliminary results[14] and might be one important trait distinguishing subarctic *Myrmica* populations from those living in more southern regions.

The day-length exerted a distinct effect upon the duration of oviposition and the time of onset of diapause in the queens of both species (see examples in Figure 1). Late-

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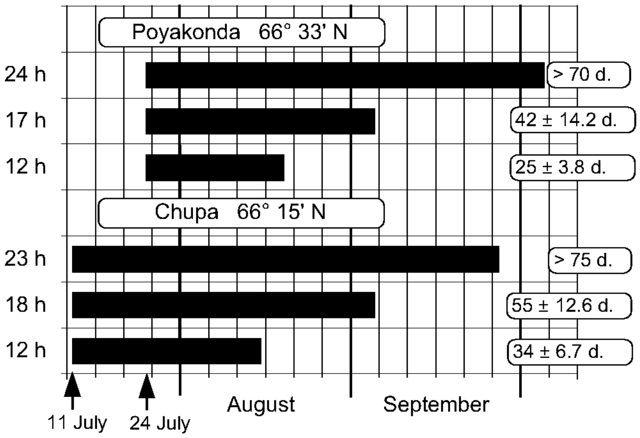

Figure 1. Influence of day-length on the time of onset of queen ant diapause in experimental cultures of *Myrmica ruginodis* collected in June in two locations on the Western coast of the White Sea just on the Polar Circle. Ant cultures were maintained at an optimal temperature (22.5 ± 1°C or 12-h daily thermoperiod 15/25°C) and 23 or 24 h day-length until the middle of July when they were transferred to three photoperiodic regimes (under the same temperature). After a queen ceased to lay eggs as a result of the onset of diapause, all the eggs present developed into larvae and hence disappeared in that culture. Thus, the period until the eggs developed into larvae which was recorded for each culture, was longer than the period of the queen's egg-laying. The mean intervals (in days) between the start of the experiment (indicated by an arrow) and the disappearance of eggs are shown by black horizontal bars. The values of the mean ± 1 standard error are given for each day-length. Five cultures were used in each photoperiod. Under mid-summer photoperiods (23–24 h) in one (for Poyakonda) or two (for Chupa) cultures, eggs were still present at the end of the experiment; thus the mean values were underestimated.

autumn photoperiods caused significantly earlier cessation of oviposition and subsequent disappearance of eggs in comparison with mid-summer ones. However, such short days would not be encountered by natural ant colonies until October when ants are already in a diapause state. According to our field phenological observations in the Polar Circle region, the queens in *Myrmica* nests cease to lay eggs (the onset of diapause) in the first half of August and the eggs then disappear (or rather develop into larvae) well before the end of August. Since the diapause induction in the queens takes place in August, this should be due to the influence of natural day-lengths characteristic for that season.

Therefore, the results obtained in experiments for August photoperiods deserve special attention. It should be emphasized, however, that the mean period of oviposition for August photoperiods in all experiments was much longer in comparison with its possible duration in nature. For example, when *M. ruginodis* cultures were kept in cultures at 18 h from 11 July, the eggs disappeared as a consequence of the diapause onset in queens in 55 days on an average, i.e. on 4 September (Figure 1). Similarly, in the experiment started on 24 July in cultures kept at 17 h, eggs disappeared in 42 days on an average, again on 4 September, i.e. significantly later than in nature. Thus, we question whether August photoperiods alone could induce diapause in real time. We suppose, therefore, that queen diapause in subarctic populations of *Myrmica* ants arises mainly due to the influence of low temperature in August.

Thus we formulate a new hypothesis of 'vestigial photoperiodic responses' in *Myrmica* populations inhabiting the subarctic regions. We assume that these northern populations have originated from southern ancestors which possessed photoperiodic control of the seasonal cycle, but in a new environment where days were excessively long during most of summer and not useful for control of the life cycle, the photoperiodic response has lost its former role and was replaced by a mixture of endogenous control and induction by temperature cues. Similar transition was first demonstrated by shift in the controlling factor for daily periodicities from photoperiod to temperature in some high arctic Chironomidae[15]. But photoperiodic responses still remain in the subarctic *Myrmica* populations in the form of redundant physiological reactions. For example, although in our experiments day-length did not control the induction of larval diapause, the influence of long days on autumn ant colonies resulted in diapause termination by the larvae (and also by the queens), a process that can easily be observed in an experiment but can never be realized in nature.

The phenomenon discovered in *Myrmica* ants needs further investigation. But it is also worth studying whether vestigial photoperiodic responses exist in arctic and subarctic arthropods other than ants.

1. Saunders, D. S., *Insect Clocks*, Pergamon Press, Oxford, 1976, 280 p.
2. Beck, S. D., *Insect Photoperiodism*, Academic Press, New York, 1980, 2nd edn, 387 pp.
3. Danks, H. V., *Insect Dormancy: An Ecological Perspective*, Biological Survey of Canada (Terrestrial Arthropods), Ottawa, 1987, p. 439.
4. Downes, J. A., *Annu. Rev. Entomol.*, 1965, **10**, 257–274.
5. Danks, H. V., *Arctic Arthropods: A Review of Systematics and Ecology with Particular Reference to the North American Fauna*, Entomological Society of Canada, Ottawa, 1981, p. 608.
6. Danks, H. V., *Eur. J. Entomol.*, 1999, **96**, 83–102.
7. Ferenz, H.-J., *Oecologia*, 1975, **19**, 49–57.
8. Thiele, H. U., *Oecologia*, 1977, **30**, 349–365.
9. Elmes, G. W., *Actes Colloq. Ins. Soc.*, 1991, **7**, 17–34.
10. Kipyatkov, V. E., *Entomol. Rev.*, 1974, **53**, 35–41.
11. Kipyatkov, V. E., *Vestn. Leningr. Univ.*, 1977, **3**, 14–21.
12. Kipyatkov, V. E., *Entomol. Rev.*, 1979, **58**, 10–19.
13. Kipyatkov, V. E., in Proceedings of the Colloquia on Social Insects (ed. Kipyatkov, V. E.), Russian-speaking Section of the IUSSI, Socium, St. Petersburg, 1993, vol. 2, pp. 25–48.
14. Kipyatkov, V. E. and Lopatina, E. B., in Proceedings of the International Colloquia on Social Insects (ed. Kipyatkov, V. E.), Russian Language Section of the IUSSI, Socium, St. Petersburg, 1997, vol. 3–4, pp. 277–286.
15. Danks, H. V. and Oliver, D. R., *Can. Entomol.*, 1972, **104**, 903–916.

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