

**Photo-thermoperiodic responses in some species of lacewings
(Neuroptera: Chrysopidae): Their role in diapause induction**

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**Photoperiod, temperature, thermoperiod, cryophase, thermophase, diapause, seasonal cycle,
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Abstract. The effects of combinations of photoperiod and temperature on diapause induction in six species of lacewings (Chrysopidae) from the forest-steppe zone (Russia, 50°N) were examined. Diapause induction in the short day was temperature-independent in all species, with exception of *Chrysopa phyllochroma*. In this species the incidence of diapause decreased within the range from 25 to 33°C. The long day prevented diapause only within particular temperature limits, which were species specific. In species with typical long-day photoperiodic response (*C. perla*, *C. septempunctata* and *Chrysoperla carnea*) daily temperature fluctuations were less favourable to diapause induction than constant mean temperature. In *C. phyllochroma* and *C. abbreviata* the similar high incidence of diapausing prepupae was induced both by daily natural thermoperiods and constant mean temperature. In experiments carried out under 12-h thermophase: 12-h cryophase conditions it was revealed that photo-thermoperiodic responses of *C. phyllochroma* were significantly dependent on cryophase temperature, whereas diapause of *C. perla* was determined mainly by photoperiod. The diversity of seasonal cycles in *Chrysopa* species and the role of photoperiod and thermoperiod in the development and diapause control in nature are discussed.

INTRODUCTION

Diapause is rightly considered to be essential for seasonal cycles of insects, for survival of unfavourable conditions and synchronization of development with favourable period of the year (Danilevsky, 1961). Determination of seasonal developmental pattern (with or without diapause) by photoperiod has been described for the wide range of insects. However, photoperiodic response may be modified significantly by other environmental factors, for example, by temperature (Danilevsky, 1961; Saunders, 1982; Tauber et al., 1986; Danks, 1987).

Most experimental studies of photoperiodism are conducted under constant temperature conditions, and results obtained from such experiments usually provide the basis for an analysis of phenology and seasonal development which occur in nature. However, wild populations of insects are exposed to daily temperature fluctuations. Therefore, it is important to study the complex effects of light and temperature rhythms.

The pioneering study was performed by Lees (1955) on *Metatetranychus ulmi* Koch (Acarina: Tetranychidae). Then the photo-thermoperiodic induction of diapause was investigated in detail in some species of insects and mites (Beck, 1962, 1983, 1987; Goryshin, 1964; Geispitz et al., 1972; Chippendale et al., 1976; Zinovieva, 1976, 1991; Bradshaw, 1980; Goryshin et al., 1980; Goryshin et al., 1988; van Houten et al., 1988; Lenga et al., 1991; Numata et al., 1993). Mainly the physiological mechanism of photo-thermoperiod interaction or its ecological content were studied. Unfortunately, in some

cases there are difficulties in interpretation of published data due, mainly to response specificity in insect species and the difference between methodological approaches.

Thus, comparative studies of related insect species using the same method are preferred. This allowed us to assess common features as well as specific (for particular groups) photoperiod-thermoperiod interactions. Six related species of lacewings (Chrysopidae) were selected to study the effects of combinations of photoperiod and temperature on diapause determination.

Diapause determination in *Chrysoperla carnea* Stephens (McLeod, 1967; Tauber & Tauber, 1970, 1972) and *Chrysopa perla* L. (Hinke, 1975; Canard, 1976) was studied earlier, while reports on ecology of other species are very scarce and papers on ecophysiological mechanisms of diapause are lacking.

The present paper aims to study the influence of constant and fluctuating (daily thermoperiods) temperature on the photoperiodic determination of diapause and to investigate the role of natural temperature fluctuations in the regulation of insect seasonal development.

MATERIAL AND METHODS

The following species of lacewings were used in experiments: *Chrysopa perla* L., *C. septempunctata* Wesmael, *C. abbreviata* Curtis, *C. phyllochroma* Wesmael diapausing as prepupae within the cocoon, *Mallada prasinus* Burmeister diapausing as larvae of second instar, and *Chrysoperla carnea* Stephens with imaginal diapause. Prepupae, pupae and adult in *C. carnea* or larvae in other lacewings are the stages sensitive to day length.

Adult lacewings were collected from natural populations in the reserve Forest on the River Vorskla, which is located in the forest-steppe zone in Belgorod region, Russia (50°N, 36°E). Insects were reared as described earlier (Volkovich, 1987; Volkovich & Arapov, 1993).

Experiments were performed in chambers in which both temperature and photoperiod were controlled.

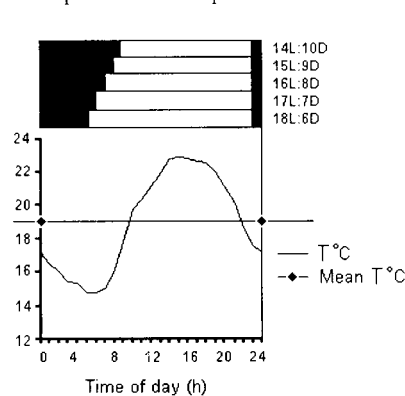


Fig. 1. The scheme of combination of photoperiodic regimes with daily fluctuations of temperature in outdoor experiments. Black bars – scotophase, open bars – photophase. The curve given as an example corresponds with real daily dynamics of temperature which took place in experiments with *C. phyllochroma* from 7 to 28 July 1993.

The light intensity in the boxes ranged between 180 and 250 Lx and was supplied by 20 W fluorescent lamps. The deviation from the set temperatures was not more than 1°C. Humidity fluctuated between 45% and 80%.

Only ecologically significant photoperiodic regimes (those which occur in natural conditions) were used: from 14L : 10D (photophase 14 h – scotophase 10 h) or 12L : 12D (in one experiment) to 18L : 6D. The longest photophase corresponds to the maximum daylength (including civil twilight) on the latitude of the reserve.

Diapause induction was studied in two series of experiments. In the first one the insects were exposed to five different constant photoperiods under outdoor conditions. Lamp DRL-500W was used to increase the illumination in the twilight. Experiments were carried out during favourable season (from mid June to late August) under combinations of photoperiods and natural fluctuations of temperature (Fig. 1). Control insects were reared in the same photoperiods but at constant temperature equivalent to the mean temperature of daily thermoperiod during the period of sensitive stages in each species.

In second series of experiments a square-wave type of thermoperiod was made by transferring insects between different temperatures every day at 9:00 and 21:00. Thus, the

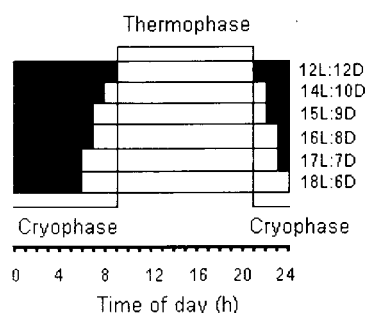


Fig. 2. The combinations of thermophase and photophase used in the experiments. Black bars – scotophase, open bars – photophase in 24-h cycles.

thermophase. The combinations of thermo- and photoperiods used in these experiments are shown in Fig. 2.

Each experiment under thermoperiodic conditions had three controls at constant temperatures which were equivalent to: (1) the mean temperature of the thermoperiod, (2) the thermophase temperature and (3) the cryophase temperature (as possible). Final number of insects varied in experiments between 20 and 77 (mean 38). Statistical analysis was performed according to Terentiev & Rostova (1977).

RESULTS

The first set of experiments examined the influence of various constant temperatures from 13 up to 33°C on diapause induction in the short day (14L : 10D) and in the long day (18L : 6D).

The short day (open squares in Fig. 3) induced diapause independently of temperature in all species with exception of *C. phyllochroma*. If the larvae of the species were exposed to temperatures 25–33°C, 10–45% of prepupae did not enter diapause. All larvae of *C. phyllochroma* became diapausing prepupae in the range 15–20°C.

In the long day the incidence of diapause (black squares in Fig. 3) was temperature dependent in all species. Only *C. septempunctata* developed virtually without diapause in the temperature range 16.5–28°C (lower temperatures were not tested). Diapause was averted over wide temperature range in *C. perla* (20 to 27–28°C) and *C. carnea* (22–30°C), as well. Temperatures below 16°C suppressed the effect of long day completely, although larvae of *C. perla* survived at temperature 12–13°C.

Active development of *C. phyllochroma* prepupae was limited by temperature range 24–27°C, while in *C. abbreviata* only at 32°C all prepupae were nondiapausing (higher temperatures were not tested). In spite of long-day conditions only about 60% larvae of *M. prasinus* developed without diapause at 25–26°C and the rest entered diapause in the larvae of second instar. The number of diapausing insects increased up to 100% at both lower (20°C) and higher (32°C) temperatures.

Diapausing insects at high temperature under the long day were found not only in *M. prasinus*, but also in *C. perla* and *C. phyllochroma*. In the last two species the incidence of diapause achieved 24–40% at 31–33°C (Fig. 3). It was certainly winter diapause, because it was terminated only by the cold treatment.

In the next experiment, lacewings were reared under outdoor conditions to examine the effect of natural thermoperiods on photoperiodic determination of diapause. Five photoperiods were synchronized with a daily fluctuation of temperature as shown in Fig. 2. *C. carnea*, *C. septempunctata* and *C. perla* manifested typical long-day photoperiodic responses (PhPR) (Fig. 4). There was a great number of nondiapausing insects in photoperiods 16L : 8D, 17L : 7D and 18L : 6D, even at comparatively low temperatures 17–18°C, whereas short days were fully inductive (100% diapause). In other species curves of PhPR were characterised by high incidence of diapause in all photoperiods except 18L : 6D.

Curves of PhPR obtained under fluctuating temperatures (black squares in Fig. 4) were compared with those obtained at constant temperatures relatively close to the mean

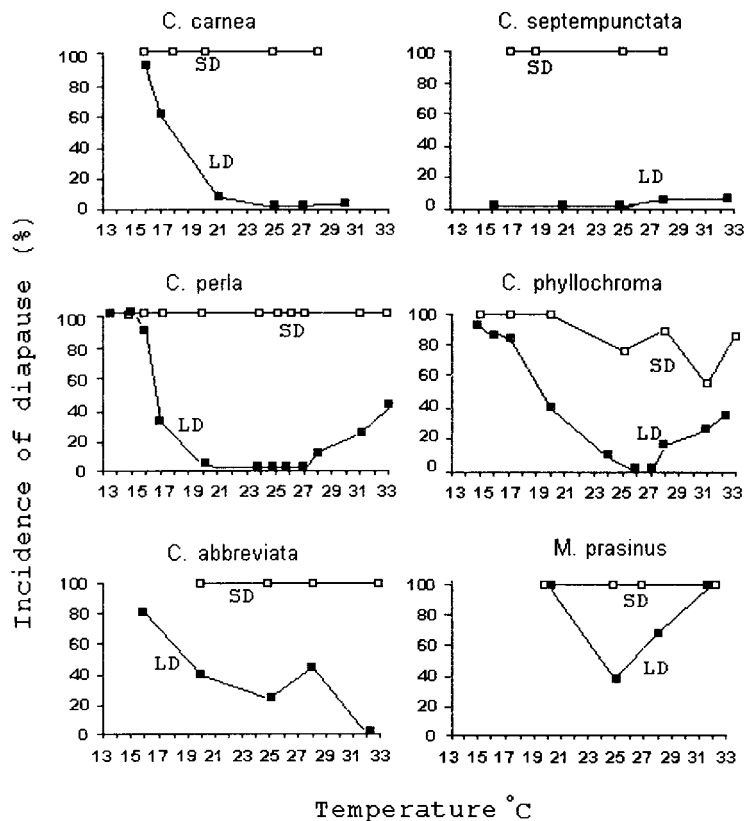


Fig. 3. Dependence of diapause incidence under long and short days on temperature in some Chrysopidae species. Short day (open squares) – 14L : 10D, or 15L : 9D (for *C. septempunctata* at 16.5°C and *C. phyllochroma* at 15°C); long day (black squares) – 18L : 6D.

temperatures of thermoperiods (open squares in Fig. 4). In *C. carnea*, *C. septempunctata* and *C. perla* the incidence of diapause was reduced significantly ($P < 0.01$) as an effect of temperature fluctuations in photoperiods 16L : 8D and 17L : 7D. Furthermore, in *C. carnea* the pre-oviposition period was significantly shorter in females reared under outdoor conditions (11.5 ± 1.0 day in 16L : 8D and 11.1 ± 0.97 day in 17L : 7D) than in those reared at a constant 17°C (25.0 ± 4.12 day). At higher mean temperature, the difference was recorded in *C. perla* in the threshold photoperiod 16L : 8D ($P < 0.01$) only. The threshold of PhPR in *C. perla* did not diminish when the mean temperature rose from 18.6 to 21.4°C.

In *M. prasinus* the proportion of diapausing larvae was lower under natural thermoperiods with a mean temperature of 18.4°C than at a constant of 20°C ($P < 0.01$), but tendency to enter diapause was very strong.

The curves of PhPR obtained under fluctuating temperatures were similar to those at constant temperatures 19–20°C in *C. phyllochroma* and *C. abbreviata*, although the

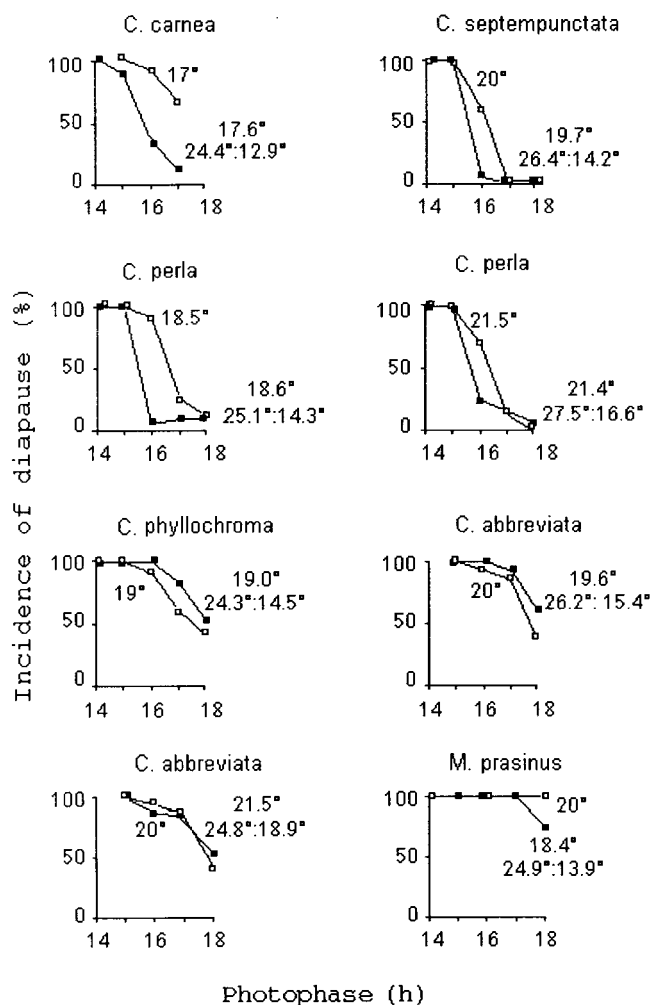


Fig. 4. Photoperiodic responses in some Chrysopidae species in outdoor experiments. Black squares indicate diapause incidence at fluctuating temperatures (scheme of experiments – see Fig. 1). Mean temperature and its amplitude for the period of season when sensitive stages developed are indicated near the curves. Open squares – diapause incidence in the laboratory experiments at constant temperatures equivalent to the mean temperatures of natural thermoperiods obtained by daily temperature summation.

development threshold (LDT) of about 12°C for *C. phyllochroma* and 8.5°C for *C. perla* (Clo); (c) equal to the LDT (Ct); (d) lower than LDT (Clt).

At lower cryophase temperature, more prepupae of *C. phyllochroma* entered diapause (Fig. 5A). There was high negative correlation between the cryophase temperature and the

incidence of diapause slightly increased under 16L : 8D and 17L : 7D in *C. phyllochroma* and under 18L : 6D in *C. abbreviata* ($0.01 < P < 0.05$). In the last species the number of diapausing prepupae slightly diminished when the mean temperature of thermoperiod rose from 19.6 to 21.5°C.

The square-wave type of thermoperiods (Fig. 2) were used to find the influence of cryophase and thermophase temperatures on the photoperiodic induction of diapause. *C. phyllochroma* and *C. perla* were chosen as model subjects because the temperature effects on PhPR of these species were different (Figs 3–4). In accordance with the results of the constant temperature experiments (see Fig. 3) the thermoperiods were composed of: (1) the thermophase temperature (a) equal to the optimum for the long-day response manifestation (T_o); (b) higher than T_o (T_h) and (2) the cryophase temperature (a) equal to the optimum for the long-day response manifestation (C_o); (b) lower than C_o , but higher than the low

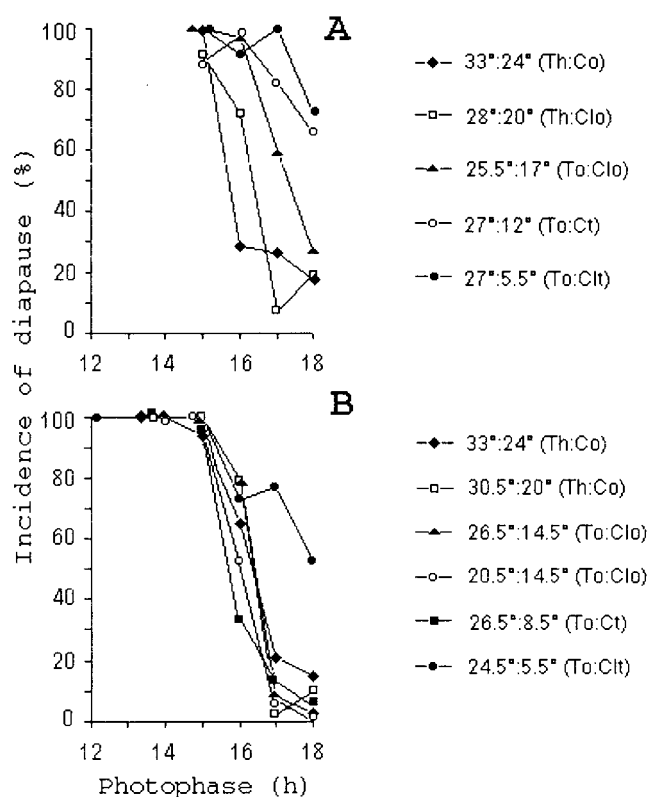


Fig. 5A–B. Photoperiodic response for the induction of prepupae diapause under thermoperiodic conditions with different temperatures of thermophase and cryophase (scheme of experiments – see Fig. 2). A – *C. phyllochroma*; B – *C. perla*. To and Co – thermophase and cryophase temperatures are equal to the optimum for long-day response manifestation; Th – thermophase temperature higher than To; Clo – cryophase temperature lower than Co, but higher than LDT; Ct – equal to LDT; Clt – lower than LDT.

In *C. perla*, the curves of PhPR were similar despite different thermoperiodic conditions (Fig. 5B). The critical day length for diapause induction varied between 15 h 40 min (26.5 : 8.5°C) and 16 h 24 min (26.5 : 20°C) independently on thermo- and cryophase temperatures. The higher incidence of diapause in photoperiods 18L : 6D and 17L : 7D was observed under 33 : 24°C and 24.5 : 5.5°C conditions only. In the last case the cryophase temperature was below the LDT in this species. The short day (12L : 12D) was fully inductive, but the long day (18L : 6D) prevented diapause only in about 50% prepupae.

incidence of diapause in photoperiodic conditions 17L : 7D ($r = -0.92$) and in 18L : 6D ($r = -0.96$). Thermophase temperature had insignificant effect on diapause induction ($r = -0.45$ for photoperiods 17L : 7D and 18L : 6D and $r = -0.47$ for 16L : 8D).

However, only PhPR under 33 : 24°C coincided with that obtained at 24.5°C, which was equivalent to the cryophase temperature of the preceding conditions. Under 28 : 20°C and 25.5 : 17°C the proportion of diapausing prepupae was significantly lower in comparison with that at constant 20.5°C or 17°C (Table 1).

In general, photothermoperiodic responses in *C. phyllochroma* were similar to those obtained at constant temperatures relatively close to the mean temperature of thermoperiods, as well as in the natural experiment. However, the incidence of diapause was a little higher occasionally (Table 1).

TABLE 1. Photoperiodic diapause induction in prepupae of *Chrysopa phyllochroma* under thermoperiodic conditions and at constant temperatures.

Photoperiods (h)	Thermoperiods		Controls at constant temperatures similar to:					
			thermophase		cryophase		means	
	%	N	%	N	%	N	%	N
	33 : 24°C		32.5°C		24.5°C		28°C	
15L : 9D	100	47	77.8*	36	83.3*	30	61.5*	26
16L : 8D	28.9	38	30.4	23	40	55	18.5	27
17L : 7D	26.8	41			9.1	22	4.9*	41
18L : 6D	17.4	46	36.0	25	6.7	30	16.7	42
	28 : 20°C		28°C		20.5°C		24.5°C	
15L : 9D	91.5	35	61.5*	26	100	24	83.3	30
16L : 8D	71.9	32	18.5*	27	92.7*	41	40.0*	55
17L : 7D	7.3	41	4.9	41	45.7*	35	9.1	22
18L : 6D	18.9	37	16.7	42	40.5*	37	6.7	30
	25.5 : 17°C				17 °C		20.5 °C	
15L : 9D	100	38			100	30	100	24
16L : 8D	97.4	39			100	26	92.7	41
17L : 7D	60	45			100*	31	45.7	35
18L : 6D	27.5	48			85.7*	23	40.5	37

* The difference between data obtained under thermoperiod and control data is significant (P = 0.01); N – number of prepupae in experiment.

DISCUSSION

The comparative study of six related Chrysopidae species elucidated both general and specific properties. All investigated species were from the forest-steppe zone of Russia and had facultative diapause induced by the short-day and prevented by the long-day signals. However, long-day responses were manifested in particular temperature limits which were species specific. Two main groups of lacewings were distinguished according to their temperature reaction. One consisted of species (*C. carnea*, *C. septempunctata* and *C. perla*), which had shown typical long-day PhPR over a wide range of temperatures. As for the other (*C. phyllochroma*, *C. abbreviata* and *M. prasinus*), their active development was restricted by a narrow range of relatively high temperatures. In outdoor experiments these species displayed slighter or stronger tendencies to enter diapause according to closeness of the ambient temperature to the optimum of nondiapause development.

As it was found, fluctuating temperatures in comparison to those constant provoked the diapause-preventing effect in all lacewings of the first group. The same was found in the laboratory in *C. perla* under thermoperiodic conditions with cryophase temperatures of 8 to 14°C (Volkovich & Arapov, 1994) and in *C. carnea* under 27 : 12°C conditions (unpublished). Thus, the active development was at lower temperatures.

An adaptive significance of this feature is quite clear. It ensures the bivoltine developmental pathway even in cold seasons. The daily mean temperatures in May-June often drop to 14–16°C. It could be expected that a high proportion of insects enter diapause

under such conditions in spite of long days. However, most *C. perla* prepupae and *C. carnea* adults of the first generations usually develop without diapause despite low ambient temperature (Volkovich, 1988; Volkovich & Arapov, 1993, 1994).

Such a response is relatively rare among insects (Geispitz et al., 1972; Volkovich et al., 1990). The enhancement of the photoperiodic induction of diapause in long-day insects by natural fluctuations of temperature has been described more often (Danilevsky & Kuznetsova, 1968; Chippendale et al., 1976; Bradshaw, 1980; Saulitch et al., 1983 etc.).

In the forest-steppe zone 70–95% prepupal diapause was recorded in the first generations of *C. phyllochroma* and *C. abbreviata*. This is not surprising because, in these species, the incidence of diapause rises sharply when temperature drops below 20°C. Daily fluctuations in temperature appear to promote diapause induction, as well. Thus, the realisation of bivoltine developmental pathway in *C. phyllochroma* and *C. abbreviata* is strongly restricted by temperature.

In *C. phyllochroma* the cryophase temperature significantly influenced the photoperiodic induction of diapause. It is probable that the high proportion of diapausing prepupae in nature depended on the low night and dawn temperatures.

In *C. perla*, on the contrary, photoperiod was the main factor in diapause determination, whereas temperature had an effect at extreme values only. An inadequate response (diapause under long-day conditions) was induced by both very high thermophase (30–33°C) and very low cryophase (5.5°C), while the causes apparently were different.

Our results confirm Becks (1987) standpoint that scotophase and photophase temperatures are significant for diapause determination. It should be noted that photophases extended into the cryophase in the scheme employed in our experiments. Therefore, the light reaction of biological clock system must start already at low temperature (in the last hours of cryophase) and a similar situation takes place in nature. It is probable that photo-thermoperiodic response may coincide with PhPR at constant temperature equivalent to that at scotophase, as postulated earlier (Danilevsky, 1961; Goryshin, 1964; Beck, 1983; Tauber et al., 1986), only if the cryophase temperature permits both dark and light reactions. The results obtained under thermoperiods with 24°C cryophase in *C. phyllochroma* (Table 1) and 20°C cryophase in *C. perla* (Volkovich & Arapov, 1994) confirm this assumption.

The effects of thermoperiods with cryophase below LDT were unexpected. Diapause was induced under thermoperiods 24.5 : 5.5°C and 27 : 5.5°C if they were combined with short day, although in accordance with Beck's (1987) hypothesis, cryophase temperature below LDT should have prevented diapause by checking or slowing the biological clock system. It is probable that there are various types of photo-thermoperiod interactions in different insect species. More thorough studies of the problem are needed.

Chrysopidae proved to be very appropriate objects for comprehensive studies of photo-thermoperiodic interactions, both in ecological (formation of various seasonal strategies in related species) and in the physiological aspects (mechanisms of timing in biological clocks).

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