

Photoperiodic Control of Seasonal Development in Bugs (Heteroptera)

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Abstract—In the review, results of an experimental research on photoperiodic responses (PhPRs) and their role in the control of seasonal development in the Heteroptera are analyzed. Day-length controls some qualitative (appearance of seasonal morphs, diapause induction) and quantitative characters (wing length, body coloration, diapause duration, rates of nymph growth, etc.). Various bug species and their responses are given as examples. The role of different PhPRs in the control of seasonal development of six bug species is revealed. In *Coreus marginatus* (Coreidae) and *Palomena prasina* (Pentatomidae) reproductive diapause is obligatory, but photoperiodic conditions regulate rates of nymph growth and synchronize adult emergence with optimal terms for diapause formation. In *Graphosoma lineatum* and *Arma custos* (Pentatomidae) reproductive diapause is facultative, but the species produce one generation per year in the region investigated owing to the peculiarities of their response to day-length and sensitive stage. In *Pyrrhocoris apterus* (Pyrrhocoridae) PhPR determines the parallel existence of uni- and bivoltine fractions, whose values are controlled by temperature conditions of the given season. The seasonal cycle of *Picromerus bidens* (Pentatomidae) includes not only an obligatory egg diapause, but also aestivation, induced and terminated by day-length. Two types of dormancy (facultative aestivation and obligatory hibernation) lead to univoltinism in the species. The adaptive significance of various PhPRs is discussed.

It is a common knowledge that the photoperiodic responses can control two categories of character, qualitative and quantitative. The origin and mechanisms of these two types of appropriate responses have not yet got a unified and widely accepted interpretation (Tyshchenko, 1976, 1977, 1981; Zaslavskii, 1975, 1984). It is clear, however, that in the case of qualitative characters, the photoperiodic response changes the direction of morphogenetic processes, determining the course of development through a choice of one of two possible alternative states (e.g., diapause vs. active development), while in the case of quantitative characters, the photoperiodic response controls growth processes and morphometric features, and regulates the intensity of biological and physiological processes, while not changing their principal directions.

PHOTOPERIODIC CONTROL OF QUALITATIVE CHARACTERS

By now, photoperiodic control of qualitative characters has been studied in ample detail in a large number of insect species. Induction and termination of diapause, seasonal polymorphism and aphid cyclomorphosis are the most important and widespread examples of this type of photoperiodic response.

The seasonal polymorphism (or, more correctly, dimorphism in the case when only two morphs are possible) is not uncommon among Heter-

optera. Usually, it is connected with wing dimorphism and color forms.

The wing (alary) polymorphism is well investigated in such water bugs as *Gerris odontogaster* (Vepsäläinen, 1971, 1978), *Microvelia douglasi* (Muraji *et al.*, 1989), *Limnoporus canaliculatus* (Zera and Tiebel, 1991), *Aquarius paludum* (Harada and Taneda, 1989; Harada, 1993). For example, in *Gerris odontogaster* (Gerridae) macropterous adults hibernate; their progeny is dimorphic: in the first half of summer the majority of emerged adults have short wings, in the second half macropterous forms prevail in the population. These macropterous bugs fly to hibernation places and overwinter there (Fig. 1). In *Pyrrhocoris apterus* (Pyrrhocoridae) two wing forms are usually distinguished: common (micropterous) and a more rare one (macropterous). Although the wing length is a genetically determined feature, long day and high temperature increase the fraction of macropterous individuals, while short day and low temperature reduce it (Honek, 1976).

Alternative seasonal color forms are also known among Heteroptera. *Notostira elongata* (Miridae) can be considered an example. In this species long-day summer bugs have green coloration, while short-day autumn bugs are brown (Dolling, 1973). Two seasonal forms of *Euschistus tristigmus tristigmus* (Pentatomidae) differ morphologically and in abdomen pig-

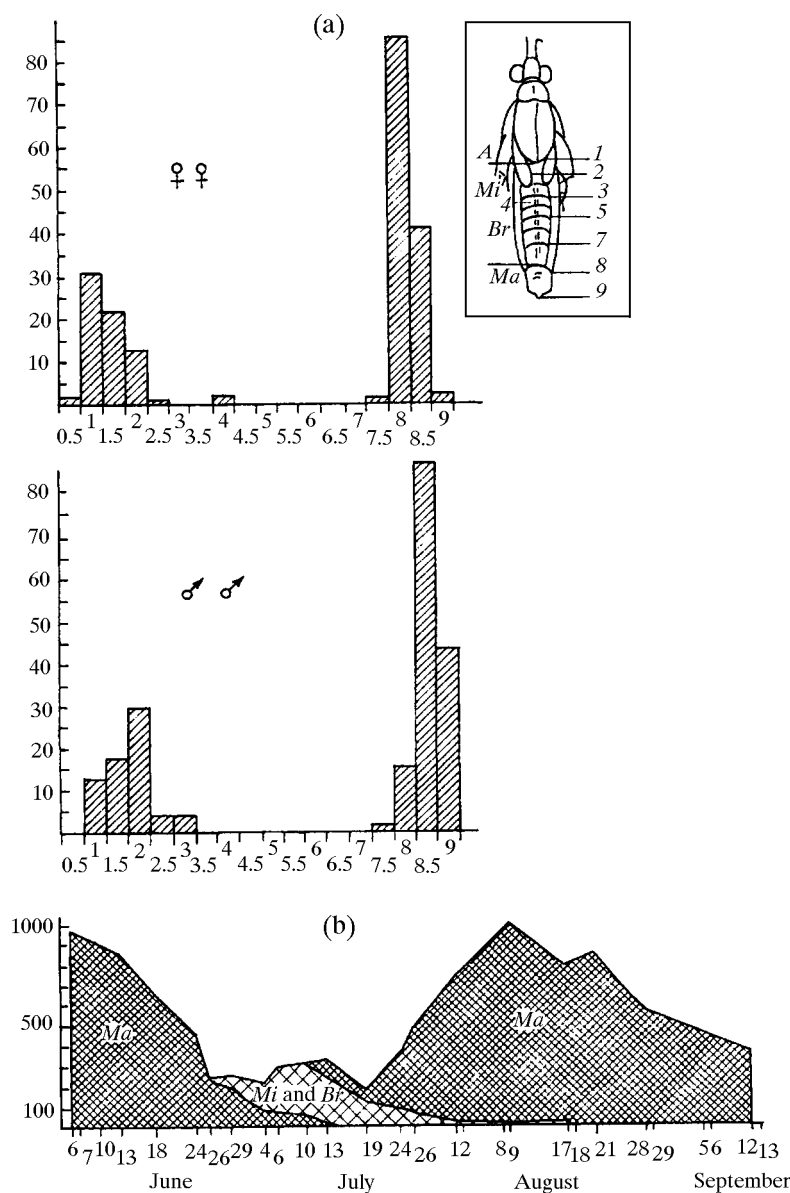


Fig. 1. Alary dimorphism in *Gerris odontogaster* (after Vepsäläinen, 1971). (a) Distribution of wing length within different wing classes (combined data for three populations, July 28–August 12, 1967). *Abscissa*—wing indexes (see insert); *ordinate*—number of individuals. *In the insert*—accepted wing classes [(A) apterous, (Mi) micropterous, (Br) brachypterous, (Ma) macropterous]. (b) Seasonal pattern of wing class abundance in the population: long-winged (Ma) and short-winged (Mi and Br). *Ordinate*—estimated size of the population.

mentation, because of which they were considered two independent species (McPherson, 1974, 1975). All color variants mentioned here could be easily induced in laboratory experiments by rearing insects under alternative photoperiodic conditions.

Induction of diapause is one of the most shining and biologically important examples of photoperiodic control over qualitative characters. It is peculiar to all species with heterodynamic polyvoltine seasonal development.

Heteroptera are known to have all types of diapause common to *Hemimetabola*. The majority of temperate zone bug species hibernate as adults. The nymphal diapause is much more rare. As examples of bugs with nymphal diapause, *Odontoscelis fuliginosa* (Scutelleridae), *Coptosoma scutellatum* (Plataspidae), and *Pentatoma rufipes* (Pentatomidae) can be mentioned. An egg stage hibernation can be found more often and is typical of damsel bugs (Nabidae) and capsid bugs (Miridae). Among Pentatomidae an embryonic dia-

pause is known only in *Picromerus bidens*, and among Alydidae—in *Alydus calcaratus*. Because the diapause may be obligatory or facultative in different species, and the life cycle of some species may exceed one year or include more than one period of rest, it is clear that the seasonal cycles in Heteroptera are quite diverse.

Photoperiodic responses (PhPRs) of four bug species are shown in Fig. 2. These species are characterized by adult diapause, and the onset of this physiological state was judged from the absence of reproduction. All the known heteropteran species with facultative winter diapause (hibernation) have PhPRs of long-day type, namely, long day exceeding in duration the photoperiodic threshold determines active development (and reproduction in species with adult diapause), and short day, on the contrary, prevents reproduction and induces the onset of diapause.

The dependence on temperature is one of the most important properties of PhPR. In the majority of species with long-day type response a decrease of temperature causes an increase in critical day-length (the photoperiod which induces diapause in 50% of individuals). As shown for many insect species, a 5°C change in temperature corresponds a 1–1.5 hour shift in PhPR threshold (Danilevskii, 1961). In true bugs investigated in our laboratory, well pronounced temperature dependence of PhPR was found in Belgorod populations of *Pyrrhocoris apterus* (Numata *et al.*, 1993; Saulich *et al.*, 1993) and *Graphosoma lineatum* (Pentatomidae) (Musolin and Saulich, 1995) (Fig. 2).

At the same time, a thermally stable photoperiodic threshold has been previously considered a more unusual event. But, as shown by further investigations, it can be often met in all insects, and rather often among heteropterans. For example, the PhPR thresholds are essentially independent of temperature in *Arma custos* (Pentatomidae) (Volkovich and Saulich, 1994) and *Riptortus clavatus* (Alydidae) (Numata, 1985) (Fig. 2).

In *Podisus maculiventris* (Pentatomidae), the influence of temperature manifested itself not only in a shift of the threshold, but also in a slackening tendency to diapause: at higher temperature even a short day induced a decrease in the fraction of diapausing bugs (Goryshin *et al.*, 1988) (Fig. 3).

While discussing the “work” of PhPR, which controls qualitative characteristics, it is necessary to touch on such its parameters as the sensitive stage and pack-

age of photoperiodic information (required number of days). When complicated seasonal cycles are studied in nature, it is rather difficult to understand how PhPR works without a knowledge of the stage in which the species perceives photoperiodic information and also of the number of short or long days necessary and sufficient to determine the pathway of further development. Unfortunately, such experiments are carried out very seldom. That is why the information about these parameters in Heteroptera is scarce.

Sensitive stage. Based on data available, in the case of facultative adult diapause photoperiodic signals are perceived by nymphs of the last (V) or two last (IV and V) instars and by adults in the majority of heteropteran species. This was shown directly or indirectly by experiments with *Dolycoris baccarum* (Pentatomidae) (Perepelitsa, 1971), *Pyrrhocoris apterus* (Volkovich and Goryshin, 1978), *Anasa tristis* (Coreidae) (Nechols, 1988), *Eysarcoris lewisi* (Pentatomidae) (Hori and Kimura, 1993), *Riptortus clavatus* (Kobayashi and Numata, 1993), and in some others. However in some species, e.g., in *Arma custos*, the photoperiodic sensitivity is related to adult stage only (Saulich and Volkovich, 1996). In *Podisus maculiventris*, the final response is determined by the day-length at which nymphs developed beginning with III instar (Volkovich *et al.*, 1991). In *Oncopeltus fasciatus* (Lygaeidae), only last instar nymphs or very young adults are sensitive to day-length (Dingle, 1974). In *Graphosoma lineatum*, because of the sensitivity to photoperiod at adult stage, it was possible to induce and terminate the diapause repeatedly under experimental conditions.

The package of photoperiodic information, describing the duration of induction of alternative physiological states (diapause or active development), is of great importance in studying the phenology of insects. An analysis of the accumulation of photoperiodic information has revealed species-specific peculiarities of this process. In some insects, for example, in *Mamestra brassicae* (Noctuidae), the photoperiodic response is determined by the number of short-day impulses received at a sensitive stage only. The long-day impulses are inefficient (Goryshin and Tyshchenko, 1973). In other species both the short-day and long-day information is perceived, the final response being determined by which package (short-day or long-day, respectively) is accumulated last. This principle of perceiving the photoperiodic information seems to be used by *Pyrrhocoris apterus* (Volkovich

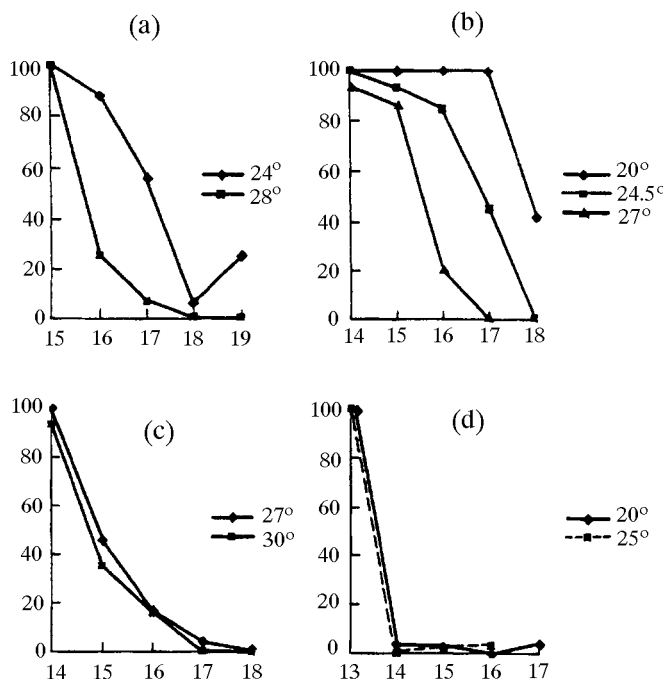


Fig. 2. Temperature variability of photoperiodic responses in (a) *Graphosoma lineatum* (Musolin and Saulich, 1995), (b) *Pyrrhocoris apterus* (Numata *et al.*, 1993), (c) *Arma custos* (Volkovich and Saulich, 1994) and (d) *Riptortus clavatus* (Numata, 1985 [25°C] and original [20°C]). *Abscissa*—photoperiod, h; *ordinate*—incidence of diapause, %.

and Goryshin, 1978), *Podisus maculiventris* (Volkovich *et al.*, 1991), and *Riptortus clavatus* (Numata, 1985).

PHOTOPERIODIC CONTROL OF QUANTITATIVE CHARACTERS

The photoperiodic responses of the second type—those controlling quantitative characters and many smoothly varying biological parameters—turned out to be no less diverse and ecologically important.

To demonstrate this we shall recall that the day-length controls such quantitative characters as duration and intensity of winter or summer diapauses, e.g., in *Telleogryllus emma* (Gryllidae, Orthoptera) (Masaki, 1965, 1972), *Chrysopa downesi* (Chrysopidae, Neuroptera) (Tauber *et al.*, 1986), *Luehdorfia japonica* (Papilionidae, Lepidoptera) (Ishii and Hidaka, 1982), *Calliphora vicina* (Calliphoridae, Diptera) (Vinogradova, 1978, 1991), some *Drosophila* species (Drosophilidae, Diptera) (Kimura, 1990), *Elcysma westwoodii* (Zygaenidae, Lepidoptera) (Gomi and Takeda, 1992), and others. The photoperiod influences the pupa weight in some *Lepidoptera* species (Tyshchenko and Gasanov, 1983), rate of female maturation in

Chrysopa carnea (Chrysopidae, Neuroptera) (Volkovich, 1987), size and body proportions in some leafhoppers (Homoptera) (Müller, 1979), fecundity in *Plutella maculipennis* (Plutellidae, Lepidoptera) (Atwal, 1955) and *Locusta migratoria* (Acrididae, Orthoptera) (Perez *et al.*, 1971), and quite a number of various other parameters.

The quantitative characters controlled by photoperiodic conditions have been found in Heteroptera as well.

Photoperiodic control of wing length. As previously mentioned, the day-length can be a principal environmental factor which determines the appearance of macropterous and micropterous individuals in the case of alary dimorphism. However, at least some species have not only two extreme wing forms, but some intermediate ones as well. This is most evident in those cases when absolute or relative wing indexes are used to define the wing-length. These indexes are usually applied to divide all individuals into two groups, macro- and micropterous, but the quantitative data sometimes indicate the opposite. As an example we can refer to the data presented in papers on *Cavelerius saccharivorus* (Lygaeidae)

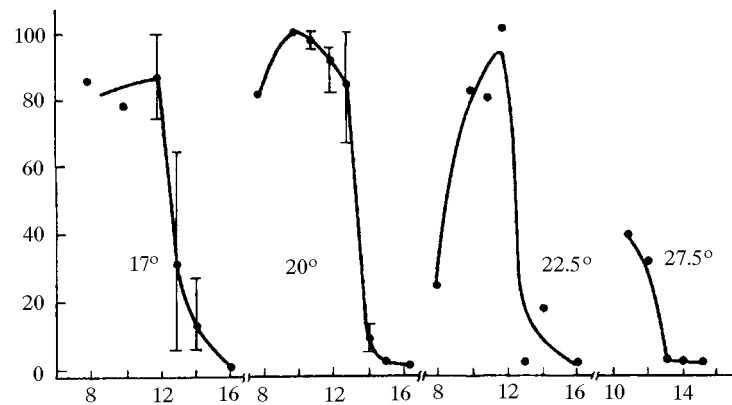


Fig. 3. Photoperiodic response in *Podisus maculiventris* at different temperatures (Goryshin *et al.*, 1988). *Abscissa*—photoperiod, h; *ordinate*—incidence of diapause, %.

(Fujisaki, 1989, 1993). The wing index (“relative wing length”) was defined as the number of abdominal segments overlapped by the forewings. This index varied in the species from 2.5 to 5.5. In the experiment the bugs were reared under natural conditions. As shown in Fig. 4, individuals with different wing length occurred in the nature practically in any season, and during autumn bugs with shorter wings gradually replaced those with longer wings. It is known that in this species the wing-length depends on photoperiod to a greater extent than on temperature or crowding (Oshiro, 1981; Fujisaki, 1989).

This and some other examples of wing length control by external factors suggest that difference in wing length is not always a result of alary dimorphism with only two alternate wing forms possible.

Among other factors, the incidence of all forms (both extreme and intermediate) can also be determined by day-length. The PhPR which demonstrates the relation between wing length and photoperiodic conditions may be of both threshold and gradual types, which will reflect the presence in nature or experiment of two extreme forms only or of a whole spectrum of intermediate ones. In many cases the complexity of analysis of data published by other researchers is related to the gradation of wing length accepted by the author.

Photoperiodic control of coloration. There is much evidence that insect coloration is controlled by photoperiodic conditions. As stated above, in the case of seasonal dimorphism (controlled by “qualitative” PhPR), only two morphs strongly differing in color are possible in the nature and experiment.

This was observed, for example, in some butterflies, namely, *Peronia lubricana—fimbriana* (Tortricidae) (Kuznetsov, 1955), *Arashnia levana—prorsa* (Nymphalidae) (Danilevskii, 1961), or *Polygonia c-aureum* (Nymphalidae) (Endo *et al.*, 1992). But sometimes it is possible to recognize with more or less confidence several distinct intermediate grades (forms). For example, in bean bug, *Riptortus clavatus* (Alydidae) all males were classified into 5 grades, and females into 3 grades on the basis of lateral metathorax coloration (Kobayashi and Numata, 1993, 1995). It should be noted, that the incidence of these forms changed gradually along the photoperiodic scale. The adaptive significance of these intermediate forms in this species is not quite clear.

The photoperiodic conditions determine nymphal body coloration in *Plautia stali* (Pentatomidae) (Numata and Kobayashi, 1994). The coloration of the final instar nymphs in the species varied continuously between green and dark brown which allowed all nymphs to be classified into 6 color grades in the experiment (Fig. 5). It is easy to see that as duration of photophase increases, so does the portion of light-colored nymphs.

Photoperiodic control of coloration was also found in *Arma custos* (Volkovich and Saulich, 1994). Last instar nymphs, reared under controlled conditions, differed significantly in degree of head, pronotum, scutellum, and wing rudiment punctation. Two morphological forms were recognized. In one of them the indicated parts of the body were thickly strewn with black punctures passing frequently into continuous black stains that imparted the nymphs a bright metallic

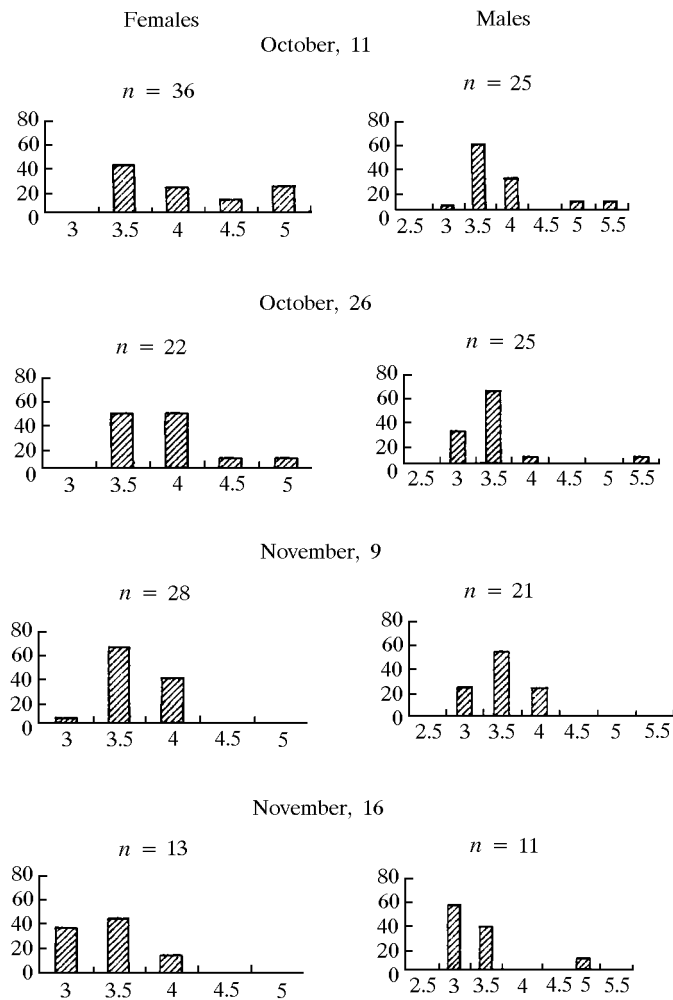


Fig. 4. Changes in the frequency of relative wing length in *Cavalerius saccharivorus* during autumn (data from Fujisaki, 1993). *Ab-scissa*—relative wing length (number of abdominal segments overlapped by the forewings); *ordinate*—incidence, %. *n*—total number of individuals.

glitter; in another form the black punctures on yellow background were considerably weaker and those nymphs never had a metal glitter. The appearance of the dark form was stimulated by short day conditions and lower temperature (Fig. 6), which suggests an adaptive significance of that character and its participation in thermoregulation.

Photoperiodic control of diapause parameters. It is well known, that some diapause parameters can be controlled by photoperiodic conditions as well. In *Podisus maculiventris*, the day-length determined duration of spontaneous reactivation, and the diapause induced under 12L : 12D photoperiodic regime had the shortest duration (Fig. 7, data of Dr. T.A. Volkovich).

Photoperiodic control of nymphal development duration. A great body of examples illustrates the possibility of photoperiodic control over other quantitative parameters such as duration and rate of nymphal development. H.V. Danks (1987) lists 80 species from all the largest orders of insects in which such a control is known. And in all groups there are species whose nymphal development is accelerated by long-day and retarded by short-day conditions, and those for which opposite effects are known.

Only in several heteropterans, PhPR and/or environmental control of seasonal development have been studied more or less thoroughly. By now, information is available on nymphal growth duration under different photoperiodic conditions for 15 species of bugs.

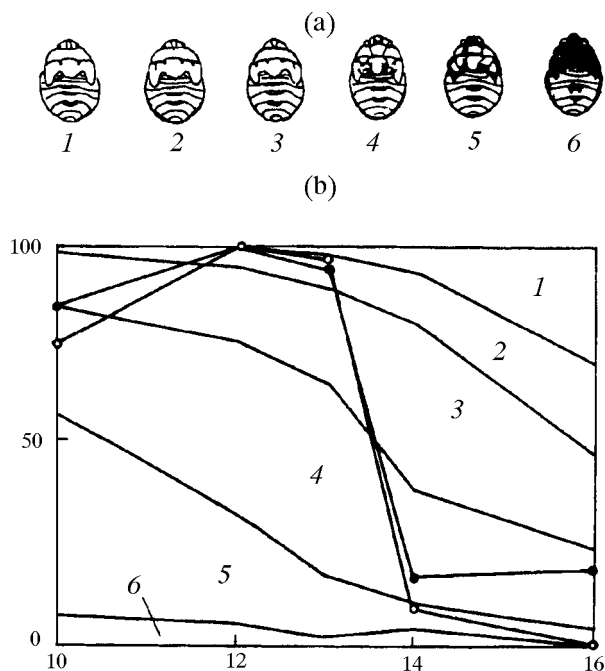


Fig. 5. Photoperiodic control over coloration in the fifth instar nymphs of *Plautia stali* (Numata and Kobayashi, 1994). (a) Grades of body coloration in the fifth instar nymphs. (b) PhPR curves for the induction of adult diapause (thick lines) and determination of nymphal body coloration (thin lines) at 25°C. Closed circles, males; open circles, females. Numerals on the graph indicate grades of body coloration. *Abscissa*—photoperiod, h; *ordinate*—number of individuals, %.

Analysis of these data showed that in 8 species retardation of nymphal development had been observed in long-day regimes and in 3 species—in the short-day part of the photoperiodic scale. In 4 other species the day-length did not influence nymphal development duration (Musolin and Saulich, 1997).

Nymphs of *Nezara viridula* (Pentatomidae) grew longer under short- than under long-day conditions (Ali and Ewiess, 1977). At 25°C the retardation reached 20% as compared with the nymphal development under long-day conditions (Fig. 8). It is interesting that this tendency was observed over a wide range of temperatures. The authors of the research assumed that the long photophase provided a longer feeding period which in turn enhanced metabolic functions and accelerated the development.

The role of day-length in the control of nymphal development duration was much more pronounced in *Carbula humerigera* (Pentatomidae) (Fig. 9). The observed 30–40-day retardation in growth under short-day conditions was considered a facultative nymphal winter diapause (Kiritani, 1985).

The species discussed above are characterized by a long-day type of nymphal development acceleration.

However, in a considerably greater number of species the acceleration of nymphal development appeared to

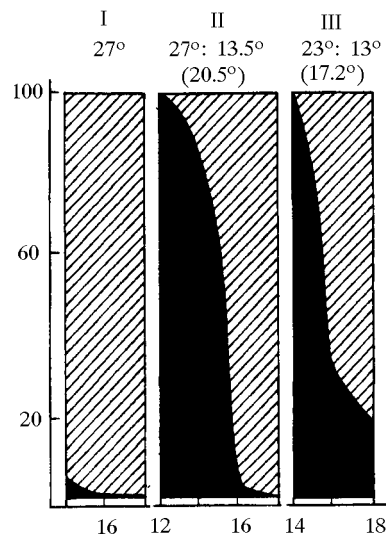


Fig. 6. Influence of temperature and photoperiod on the percentage of two morphological forms in *Arma custos* (Volkovich and Saulich, 1994). Black fields—nymphs of the dark form, shaded fields—nymphs of the light form (see the text for explanation); I–III—temperature regimes (constant temperature and thermorhythm). *Abscissa*—photoperiod, h; *ordinate*—number of nymphs, %.

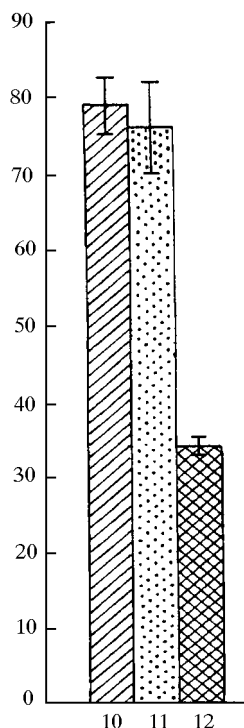


Fig. 7. Duration of spontaneous reactivation in *Podisus maculiventris* under short-day conditions at 24°C (from the data of Volkovich). *Abscissa*—photoperiod, h; *ordinate*—days, $m \pm S.E.$

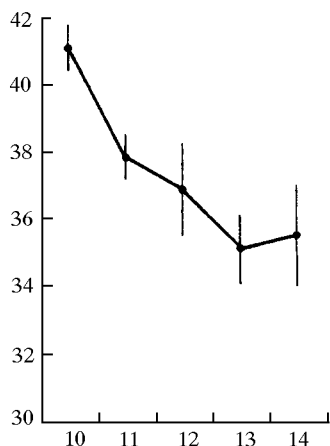


Fig. 8. Duration of nymphal development in *Nezara viridula* at 25°C (data from Ali and Ewiess, 1977). *Abscissa*—photoperiod, h; *ordinate*—days, $m \pm S.E.$

be related not to long-day conditions, but to short-day ones. For instance, in *Graphosoma lineatum* and *Coreus marginatus* such acceleration was not well pronounced and amounted to 10–15% as compared to the longest nymphal development. Nymphs of pentatomids *Arma custos* (Volkovich and Saulich, 1994),

Eurydema oleracea (Fasulati, 1976) and *Eysarcoris lewisi* (Hori and Inamura, 1991) also grew almost 15–20% faster under short-day than under long-day conditions. The effect of short-day photoperiodic conditions on acceleration of nymphal development was particularly strong in *Palomena prasina* (Pentatomidae) (Saulich and Musolin, 1995): at 20°C the acceleration amounted to 25% (Fig. 10). The nymphs of a closely related Japanese species *Palomena angulosa* developed 1.36 times longer under short-day conditions (15L : 9D) than in the long-day case (Hori, 1988).

The most comprehensive data on duration of nymphal development are available for *Pyrrhocoris apterus*. The species was studied both at constant temperature, and under conditions of natural and laboratory thermorhythms (Numata *et al.*, 1993; Saulich *et al.*, 1993). For example, as duration of photophase increased from 15 to 17 h at 20°C, so did the duration of nymphal development (Fig. 11). The tendency was also observed under many other temperature regimes.

As evident from these data, there is a lot of examples of photoperiodically induced retardation of nymphal development among heteropterans. It turned to be possible to reveal some common features of this phenomenon.

The last (fifth) instar was the longest stage of the whole nymphal development in all the investigated species and in all variants. It accounted for about one third of the whole period of nymphal growth. The most pronounced retardation of nymphal development fell just on that instar.

It is well known that any physiological response has its own temperature optimum and limits of manifestation. Experimental results showed, that acceleration of nymphal development was mostly pronounced at lower temperatures and was much weaker or sometimes absolutely disappeared at higher temperatures. At constant temperatures this was observed, for example, in experiments with *Graphosoma lineatum*, *Eurydema oleracea*, *Pyrrhocoris apterus*, and *Palomena prasina*. Under conditions of laboratory thermorhythm increasing the average temperature of the rhythm suppressed the reaction in *Pyrrhocoris apterus*.

In nature insects develop on a background of seasonal changes of day-length, rather than under conditions of constant photoperiods. In experiments the influence of changing the day-length was studied in two bug species.

In *Palomena angulosa* (Pentatomidae), the gradually decreasing photoperiod accelerated nymphal development. The shorter the average photoperiod, the faster nymphs grew (Hori, 1986). In the case of *Carbula humerigera* (Pentatomidae), the transfer of nymphs from short-day to longer photoperiod conditions was more effective for synchronization of adult emergence rather than for acceleration of nymphal development (Kiritani, 1985).

ROLE OF PHOTOPERIODIC RESPONSES IN SEASONAL DEVELOPMENT IN HETEROPTERA

The seasonal development of a species or a local population is a more complex phenomenon than it seems to be at first sight. It is not merely a recurrent change of developmental stages or even phenology. The seasonal development, its dynamics and, eventually, its success depend on the whole complex of information and energy relationships in the ecosystem. If any of these relationships are broken, a population may become vulnerable to adverse environmental conditions, which can result in death of separate individuals or even of the whole local population.

Analysis of all information and energy relationships between the population and its environment is a very complicated task. We shall try to consider only one its aspect, namely, the signaling role of photoperiodic conditions in the control over seasonal development in some heteropterans.

An obligatory formation of adult diapause in univoltine seasonal cycle was observed in *Coreus marginatus* and *Palomena prasina*. The seasonal development of these two species in the forest-steppe zone of Russia is the following: adults hibernate, in spring or at the beginning of summer after a short feeding period they begin reproduction, which may last for a month or more; the hatching nymphs feed, grow slowly and by early August they moult to adults; after pre-diapause feeding period the bugs enter imaginal diapause and hibernate (Fig. 12). None of the tested provoking conditions could induce reproduction before diapause. The second generation of these bugs has not been recorded throughout the species' area.

Quantitative photoperiodic response which controls the rate (duration) of nymphal development in *P. prasina* plays an important role in synchronizing the diapausing stage with the period optimal for dormancy beginning.

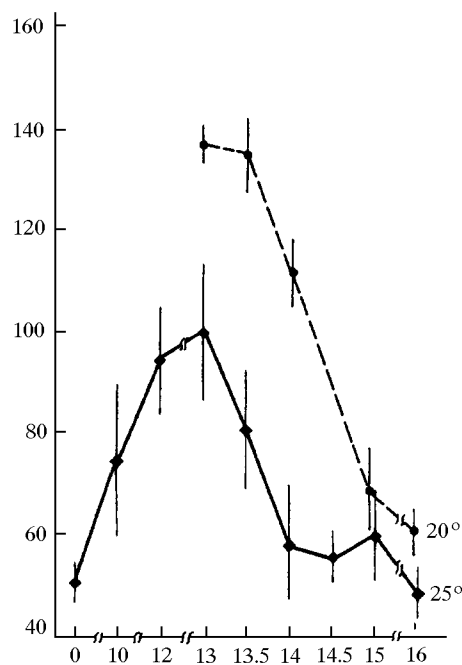


Fig. 9. Duration of nymphal development in *Carbula humerigera* (data from Kiritani, 1985). Abscissa—photoperiod, h; ordinate—days, $m \pm S. E.$

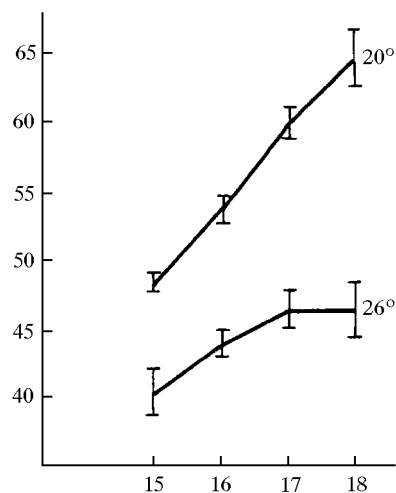


Fig. 10. Duration of nymphal development in *Palomena prasina* under different photoperiodic and temperature regimes. Abscissa—photoperiod, h; ordinate—days, $m \pm S. E.$

In the experiments the greatest accelerating effect at 20°C was recorded under short-day photoperiodic conditions (15L : 9D). In the region of investigations (50°N, 36°E), such a day-length, including half civil twilight, occurs in mid-August (Fig. 12). The acceleration of nymphal development under these conditions undoubtedly has an adaptive significance, be-

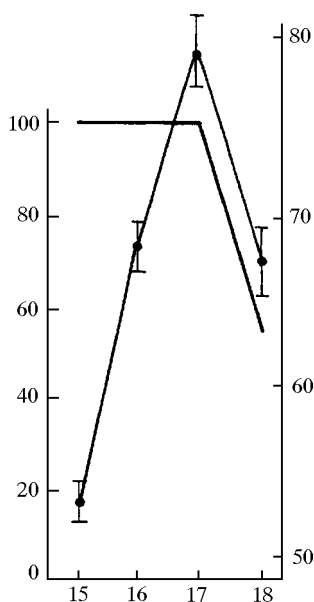


Fig. 11. PhPR and duration of nymphal development in *Pyrrhocoris apterus* under different photoperiodic conditions at 20°C (Saulich *et al.*, 1993). *Abscissa*—photoperiod, h; *left ordinate*—incidence of diapausing females (thick line), %; *right ordinate*—duration of nymphal development, days (thin line), $m \pm S. E.$

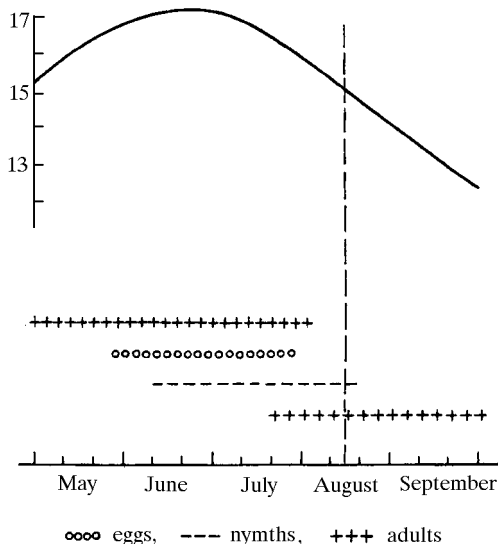


Fig. 12. Phenology of *Palomena prasina* and *Coreus marginatus* in the forest-steppe zone of Russia. *Vertical axis*—natural day-length at latitude 50°N (h) including half civil twilight (after Sharonov, 1945). *Vertical line*—day-length 15 h.

cause it increases chances for later nymphs to reach the diapausing stage before the beginning of the autumn lowering of temperature.

Retardation of nymphal growth under long-day conditions (in June–July) delays early emergence of adults and formation of diapause.

Facultative adult diapause is an important element of the life cycle of many heteropterans in the temperate zone. The pentatomid bug *Graphosoma lineatum* is a common species of the central part of Russia and is widely spread in the Palearctic. Throughout the species' area the number of generation per season varies along the geographical latitude. It was found that in Southern Sweden the population of *G. lineatum* is univoltine (Larsson, 1989), in the Ukraine and Kazakhstan the species produces 1 or 2 generations during the summer season (Puchkov, 1961; Asanova and Iskakov, 1977), while in the Crimea and Toulouse (Southern France) it produces 2 generations (Arnoldi, 1948; Nguyen Ban, 1964). This testifies that the seasonal development of *G. lineatum* is controlled by external (environmental) conditions.

The sum of effective temperatures, required for successful development of full species generation, is approximately 325 degree-days (Musolin and Saulich, 1995). This allowed for an *a priori* assumption that development of two generations per a season is possible in the forest-steppe zone of Russia. To verify the assumption in the experiment carried out in the warm season of 1995, series (batches) of first instar nymphs were placed into a specially equipped meteorological booth every 10 days (from June 10 to July 20) and reared there under quasi-natural conditions. More than 400 bugs successfully completed their nymphal development and winged in 5 series of the field experiment (Fig. 13). However none of the females began oviposition. All bugs entered diapause after a short feeding period. The bugs from the earliest series emerged in mid-July. At this time the natural day-length in the region, including half civil twilight, is about 16 h 30 min, which, according to the data of laboratory research, induces diapause in 75% of females even at a constant temperature of 24°C (Musolin and Saulich, 1995). The lower average daily temperature in the nature (down to 20°C) and the sensitivity of adults to photoperiod determined diapause induction in 100% of bugs.

The temperature conditions under which preimaginal development and female maturation occurred are also of primary importance in determining the structure of the seasonal pattern (and also possible appearance of a second generation). A warmer spring might

shift the beginning, and hence, the completion of the first generation development, and a higher temperature after adults' emergence might promote a decrease of the photoperiodic threshold. This would result in an increase of the female fraction determined to develop actively and capable of producing a second generation of *G. lineatum* in nature. However, this assumption requires additional experimental testing by means of artificial shift of the seasonal development periods of the species.

A similar regulation of seasonal development in the forest-steppe zone is found in *Arma custos* (Volkovich and Saulich, 1994). This species has facultative adult diapause, but all emerged bugs are determined to diapause. This is caused by the appearance of adults (the only stage sensitive to photoperiod in this species) no sooner than the second half of July. This means that the adults live at a day-length shorter than that critical for the species.

By shifting artificially the time of adult emergence from the end of July to the end of June it turned out to be possible to induce reproduction in 37% of females in a field experiment (Saulich and Volkovich, 1996). This proved the role of photoperiod in the control over the species seasonal development.

The importance of photoperiodic response in the control of seasonal development was even more evident in the linden bug *Pyrrhocoris apterus* (Saulich *et al.*, 1993; Saulich *et al.*, 1994).

In warm years, all females who wing up by mid-July, are determined to reproduce but later since the end of the month, all bugs enter diapause. During the second half of July both fractions (reproducing and diapausing) can be found. In cool years the temperature resources provide for development of only one generation, and all bugs diapause.

Females of *P. apterus* live over a long period and lay eggs during six weeks or more. As a result, nymphs of all instars and adults may be encountered simultaneously in the population (Fig. 14). Nymphs emerged from late eggs grow under short-day conditions, hence new adults enter diapause even in the first generation. Nymphs hatched from eggs that had been laid earlier in the season (from the end of April to the beginning of May) develop under long-day conditions, and this induces reproduction. Usually, both types of development are realized at the same year. Warmer seasons increase the bivoltine fraction, while cooler seasons promote univoltinism.

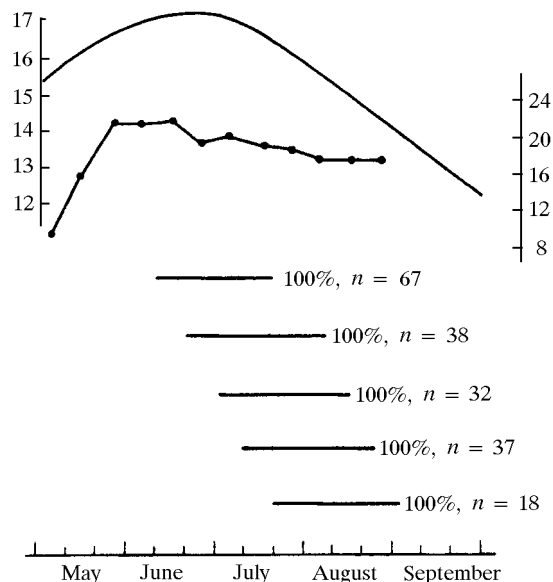


Fig. 13. Induction of adult diapause in *Graphosoma lineatum* in field experiments. *Horizontal lines*—nymphal development, *numerals at lines*—incidence of diapause (%) and number of diapausing females (*n*). *Left vertical axis*—natural day-length at 50°N (h) including half civil twilight (after Sharonov, 1945). *Right vertical axis*—temperature for ten days, °C.

When sensitive stages occur under intermediate conditions, both active and diapausing fractions may be found among insects. In this situation the weather conditions become the principal factor which controls the values of these fractions.

From the above scheme of the species seasonal development it is easy to appreciate the ecological significance of photoperiodic control over nymphal development rates. Those individuals which develop according to bivoltine seasonal scheme meet with short-day conditions twice a season, namely, in spring and in autumn. This stimulates a significant acceleration of growth and increases the chances of successful completion of active development and entering diapause before the autumn lowering of temperature. It is worth noting that the shorter the day-length, the faster the nymphal growth. This is essential in the autumn period, when the heat resources are at a critical level.

Bugs from later eggs develop according to a univoltine seasonal pattern. Their nymphs grow under long-day conditions which result in significant retardation of their development. Owing to this regulation, the emergence of adults is delayed until later, when the conditions become more favorable for diapause formation.

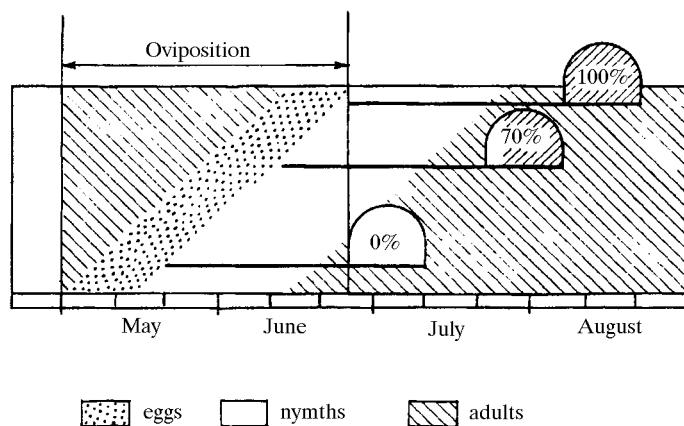


Fig. 14. Phenology and mechanism of formation of uni- and bivoltine fractions in *Pyrrhocoris apterus* in the forest-steppe zone of Russia (Saulich and Volkovich, 1996). *Horizontal lines*—nymphal development, *numerals near lines*—incidence of diapause, %.

In the species with stable polyvoltine seasonal cycle, PhPR ensures reproduction during the part of season favorable for activity and induces diapause just before the beginning of adverse environmental conditions. This was evident from the experiments with *Riptortus clavatus* (Alydidae). Within its natural area in Japan the species produces two generations per year (Numata, 1985). In the experiments carried out in the forest-steppe zone of Russia in 1995, the series of the first instar nymphs of *R. clavatus* were placed into a special meteorological booth every 10 days (from June 1 to July 30) and reared there under quasi-natural conditions. In the first five series of the experiment all females were determined to reproduce and in 10–15 days after emergence they began ovi-

position. According to the parameters of PhPR, the diapause was formed only for bugs winged at the end of August, when the day-length approached the threshold.

The examples discussed above concerned the species which have only one period of dormancy, namely, winter diapause (hibernation), in their seasonal cycles. It may be obligatory in some species or be induced by external cues in others, but also on a strictly species-specific stage. However, there are species among Heteroptera with more complicated seasonal schemes.

A seasonal cycle with two periods of physiological rest was found in a predatory bug, *Picromerus bidens* (Pentatomidae).

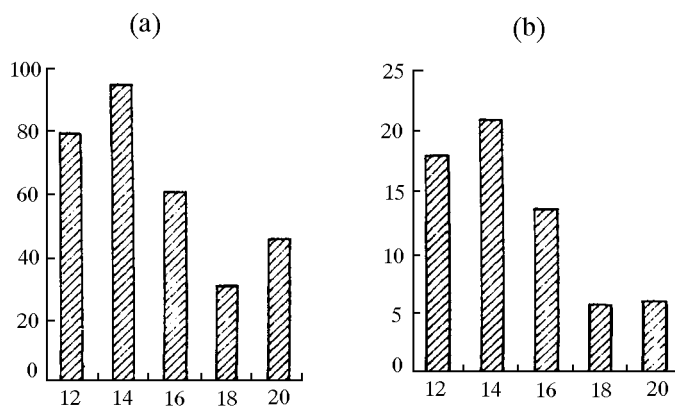


Fig. 15. Spontaneous reactivation and hatching without cold treatment of nymphs of *Picromerus bidens* within 60 days after oviposition at 25°C. *Abscissa*—photoperiodic regimes (h) under which parents and egg-batches were reared and kept. *Ordinate*—(a) portion of batches with reactivated eggs, ($n = 13-29$), (b) portion of reactivated eggs, % ($n = 281-996$).

The seasonal development of this species is usually considered univoltine with an obligatory egg diapause (Leston, 1955; Southwood and Leston, 1959; Puchkov, 1961). In spring, nymphs hatch from the hibernated eggs and grow during the summer. Emerged adults couple at the end of summer, and females begin to lay diapausing eggs in autumn. It seems that the simplicity of this unusual for pentatomids seasonal cycle does not make room for photoperiodic control over seasonal development.

According to the literature, there have been several registrations of individual adults in spring, rather than in autumn (see Leston, 1955). In the collection of the Zoological Institute, Russian Academy of Sciences (St. Petersburg) we found 9 individuals caught in field from April to June in different years. Moreover, M.-C. Larivier and A. Laroche (1989) supposed the existence in nature of a "secondary" seasonal cycle with hibernation of adults that had not been reproductively active and with egg development without cold exposure. The questions now arise as to what special biological features allow some individuals to overwinter successfully, and what kind of eggs will females lay after hibernation (whether they will be diapausing or active, not requiring a cold treatment)?

In the experimental conditions the response to day-length showed itself during the reproduction period (Musolin, 1996). In short-day regimes female began to lay eggs very synchronously, and the preoviposition period averaged between 11 and 19 days. In long-day regimes (18L : 6D and 20L : 4D) the first egg-batches appeared considerably later; and in the 18L : 6D regime the average preoviposition period amounted to 53 days.

The long-day-induced delay of reproduction was considered an aestivation (summer diapause). The results of a laboratory research allow us to assert that this state is induced and terminated by photoperiodic conditions.

The obligatory embryonic diapause is common to insects and, as a rule, it would require a cold treatment for its completion. It was precisely this phenomenon that was expected in *P. bidens*. To test this assumption, the eggs laid by females in the experiment were kept at +25°C for two months. 30 days after oviposition nymphs began to hatch from individual eggs. From 30 to 94% of batches contained eggs from which nymphs reactivated spontaneously and hatched within 60 days after oviposition (Fig. 15a). The fraction of

these batches was much higher in the short-day regimes than in the long-day ones. Moreover, the fraction of reactivated eggs was 14–20% in the short-day regimes, being significantly less (5–6%) in long-day ones (Fig. 15b). Hence, under short-day conditions both reactivated eggs and the batches which contained them constituted a higher fraction.

Facultative adult aestivation and spontaneous embryonic reactivation found in *P. bidens* give grounds for a new approach to the species seasonal cycle. As indicated by the material obtained, *P. bidens* has a labile embryonic diapause. Therefore, if the first batches were laid at the end of June, nymphs would hatch at least from some eggs at the same season even without cold treatment. This would result in death of nymphs and adults unprepared for overwintering. To prevent occurrence of a second generation, the photoperiodic response which induces aestivation in early winged adults had developed. Under June–August long-day conditions most bugs aestivate and begin oviposition only in September. Late-autumn low temperature prevents embryogenesis. Hence, there are two mechanisms, namely, facultative adult aestivation and obligatory egg hibernation, which successfully provide univoltinism of the species.

In conclusion it is necessary to note that the seasonal adaptations and role of photoperiodic responses in heteropterans' seasonal development control are still poorly understood. But even the data discussed here reveal the diversity of seasonal strategies of these insects and the complexity of controlling mechanisms.

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