Univoltinism and its regulation in some temperate true bugs (Heteroptera)

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Abstract. Various types of univoltine life cycle and its regulation were studied in Heteroptera. Very often, univoltinism was ensured by obligatory diapause in the species-specific stage. Obligatory egg diapause has been known in mirids *Leptopterna dolobrata* and *Calocoris roseomaculatus*. Obligatory nymphal diapause was investigated in *Coptosoma scutellatum* and obligatory adult diapause with quantitative photoperiodic regulation of nymphal growth was found in *Coreus marginatus* and *Palomena prasina*. Univoltinism occurs also in polyvoltine species. For example, in *Arma custos* and *Pyrrhocoris apterus* the univoltine development is regulated by environmental factors. Three peculiarities of the photoperiodic response in *A. custos* (high thermal optimum and threshold and adult photoperiodic sensitivity only) determine diapause induction in each generation throughout the temperate zone. *P. apterus* has facultative diapause and both univoltine and bivoltine life cycle in the forest-steppe zone. Usually both pathways may occur in the same vegetative season. In cool years, environmental conditions promote increase in univoltinism, whilst, in those warmer, bivoltinism prevails. The univoltine cycle, including summer and winter diapauses, was found in *Picromerus bidens*. It is concluded that univoltinism may promote spreading of the species area by the use of natural resources during limited periods of year.

INTRODUCTION

Univoltine seasonal development is characterised by only one generation a year, i.e., diapause or another form of dormancy is formed in each ontogenetic cycle.

The problem of insect univoltinism has been studied by many researchers (Geispits, 1953; Geispits & Zarankina, 1963; Danilevskii, 1961; Danilevskii et al., 1970; Masaki, 1980; Tyshchenko, 1983; Tauber et al., 1986), and it has been observed that many seasonal cycles appear similar to univoltinism. Mechanisms providing this type of seasonal strategies are more diverse and complicated than those in bi- and multivoltinism.

Univoltinism is found in insects in all climatic zones and is found throughout the Insecta, including many species of Heteroptera.

True bugs are thermophiles which have high temperature thresholds and require a large sum of effective temperature to complete their development. Only orthopterans surpass them in temperature requirements (Honěk & Kocourek, 1990). In some bug species, thermophily alone reduces the number of generations to one throughout the temperate zone. In other univoltine bugs, the temperature requirements permit bivoltine or multivoltine development in some regions, but only one generation a year is the standard.

Undoubtedly, a special ecophysiological mechanism controlling induction of diapause in the species-specific stage must exist since it stops further active development and synchronises the resistant stage with the beginning of an unfavourable season.

The present study examines the seasonal cycles of some temperate heteropteran insects and investigates the diversity of seasonal schemes based on the univoltine strategy and the mechanisms underlying occurrence of these patterns.

MATERIAL AND METHODS

The research was performed in the reservation Forest on the River Vorskla (forest-steppe zone, 50°N, 36°E, Belgorod region, Russia) on local populations of true bugs, including observations of phenology, laboratory experiments and field experiments.

Observations of phenology included registration of the occurrence of all stages of bugs and determination of their physiological state (diapause – active development).

In laboratory experiments several ecological characteristics were tested including temperature requirements of different stages, lower development thresholds (LDT), sum of effective temperatures (SET) (necessary for the development of particular stages and the generation in whole), parameters of photoperiodic responses (PhPR) at different temperatures, photoperiodically sensitive stage(s), package of photoperiodic information (i.e., the number of days required for diapause induction) and some others.

In field experiments, insect seasonal development was studied under natural or quasi-natural conditions. They permitted not only to simulate the species' phenology, but also to create unusual environments. For example, it is possible to advance or retard photoperiodically sensitive stages in order that they would develop under conditions of longer or shorter daylength. This permits a potential multivoltine development or induces diapause.

Peculiarities of experimental techniques have been described (Numata et al., 1993; Saulich & Volkovich, 1994; Saulich et al., 1994; Volkovich & Saulich, 1994).

All data obtained enable the determination of the character of seasonal cycle and the evaluation of the role of external and internal factors in its regulation.

RESULTS

INTERNAL REGULATION OF UNIVOLTINE CYCLE

In many cases univoltinism is a consequence of obligatory diapause and the active development is arrested in a certain species-specific stage. As a rule, diapause is completed after cold treatment, though photoperiodic or spontaneous termination is possible too.

The obligatory univoltinism may be found in true bugs with embryonic, larval or adult diapause.

Obligatory embryonic diapause

Obligatory embryonic diapause has been studied in detail in the mirids, *Leptopterna dolobrata* L. and *Calocoris roseomaculatus* Deg. (Braune, 1971, 1980). In those experiments the obligatory diapause was formed in all combinations of environmental factors. The development resumed only after the low temperature exposition.

The present phenological observations showed all the active development of these species (growth, feeding, maturation and oviposition) is connected with the end of spring and the beginning of summer and, usually, lasts only 1 or 1.5 months. Egg dormancy occurs in the remainder of the year. Seasonal development of *L. dolobrata* in forest-steppe zone is shown in Fig. 1.

Obligatory nymphal diapause

This was investigated in *Coptosoma scutellatum* Geoffroy (Plataspidae). This species overwinters as 3rd or 4th instar nymphs. In the spring these resume feeding and adults emerge early in the season, usually, in mid-June. However, in some years with very warm
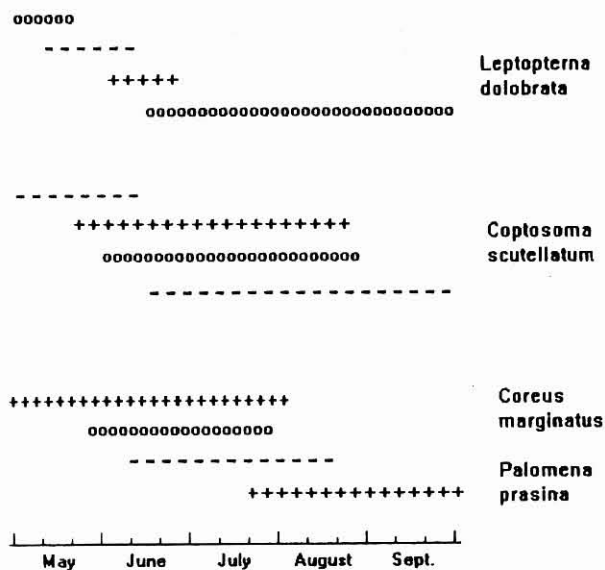
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oooooo
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    +++++                          Leptopterna
        ooooooooooooooooooooooooooooooooo   dolobrata

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      ++++++++++++++++++          Coptosoma
        oooooooooooooooooooooo    scutellatum
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+++++++++++++++++++++++          Coreus
     ooooooooooooooooo           marginatus
        --------------           Palomena
             +++++++++++++++     prasina

  May    June    July   August   Sept.
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Fig. 1. The phenology of some true bugs in forest-steppe zone. 0, eggs; –, nymphs; +, adults.

springs (for example, 1995), ovipositing adults may be found from the end of May. They continue reproduction until mid-August. New nymphs emerge in several days, feed, slowly grow and enter nymphal diapause in the beginning or mid-August (Fig. 1).

This seasonal cycle appears to be extremely unusual, because it is not well adapted to the conditions of forest-steppe zone. Diapause occurs early in the season (in the beginning to middle of July), and diapausing insects spend a lot of time under unfavourable conditions, which are inadequate to the requirements of the overwintering stage. In addition, the majority of insect strategies are oriented to use the entire energy resources of the vegetative season.

Preliminary experiments showed that nymphal diapause in *C. scutellatum* commenced independently of temperature or photoperiodic conditions. Puchkov (1961) reported, that nymphs of this species were very sensitive to humidity, but it is unlikely that this factor is the main regulator in the induction of diapause. This is uncommon in insects from the temperate zone. At the same time it is possible that noticeable diminution of adult numbers in the middle of summer results from imaginal aestivation under the conditions of low moisture. Studies of the absence of external regulation of life cycle in the species are in progress.

Obligatory adult diapause

Univoltinism, as a result of obligatory adult diapause, was studied in *Coreus marginatus* L. (Coreidae) and *Palomena prasina* L. (Pentatomidae). Their seasonal cycle in forest-steppe zone is: adult overwintering followed by a brief feeding period and then reproduction. Oviposition period may last for a month or more. Nymphs from early eclosions are found from the first week of June. They feed, grow slowly, and new adults emerge in mid-August. After pre-diapause feeding adults enter reproductive diapause (Fig. 1). Any combination of temperature and photoperiod does not induce reproduction at that time. The second generation has not been recorded throughout the species' area (Puchkov, 1973).

In the laboratory, nymphs of *P. prasina* grew more rapidly under short-day conditions (15 L : 9 D) than under those of long-day (17 L : 7 D and 18 L : 6 D). It was recorded at all temperature regimes (20, 26 and 30°C), but reached the maximum value (34%) at 20°C (Fig. 2).

During field investigations short-day conditions (15 h, including civil twilight) occur at the beginning of September. The acceleration of nymphal development is of adaptive significance, because it increases the chance of later nymphs reaching diapause before the onset of colder conditions in autumn. Retardation of nymphal development under long-day conditions (in June–July) delays the early emergence of adults. Hence, such a quantitative
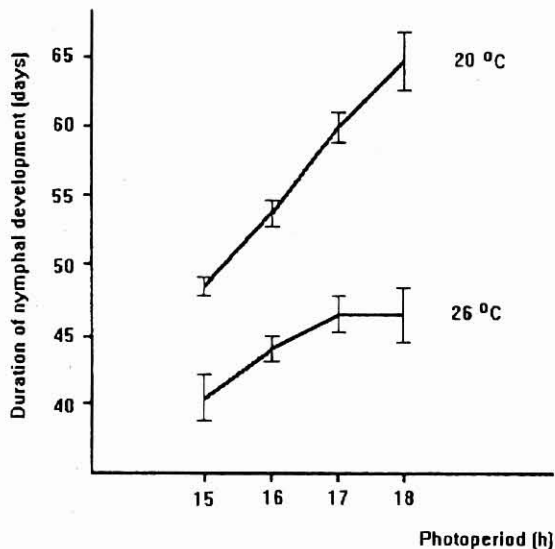
Fig. 2. Effect of photoperiod on the duration of nymphal development in *Palomena prasina* at constant (20 and 26°C) temperatures. Vertical bars show standard error.
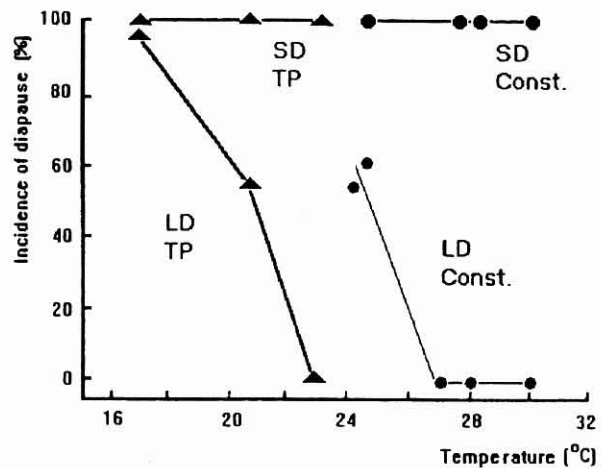
Fig. 3. Temperature optimum of the PhPR in *Arma custos*. PhPR under long- (18L : 6D) and short- (14L : 10D) day conditions, at constant temperature and under thermoperiodic conditions (12 h thermophase-12 h cryophase). Points indicate the mean value of the thermoperiod.

PhPR, regulating the rate of nymphal development, was important in the synchronization of the diapausing stage with an optimal period for dormancy beginning.

In C. *marginatus* such acceleration under short-day was not so significant (11.6%) as that in *P. prasina*.

Similar quantitative PhPR regulation of the rate of nymphal growth was described by Hori (1988) in *Palomena angulosa* from Japan. The retardation under long-day conditions reached 50–60%. The earlier the nymphs emerged in the season, the slower their growth.

EXTERNAL REGULATION OF UNIVOLTINE CYCLE

Arma custos

The predatory bug *A. custos* F. (Pentatomidae) was studied in detail in laboratory and field experiments (Saulich & Volkovich, 1994; Volkovich & Saulich, 1994). This species has facultative adult diapause, controlled by qualitative PhPR of long-day type. The critical day length for diapause induction was about 15 h at 29–30°C. A decrease in temperature down to 24°C caused an increase of diapause incidence in females. A lower temperature (20°C) caused nymph mortality, so it was impossible to obtain a PhPR curve below this temperature.

Alternating temperatures (33 : 14°C and 27 : 13.5°C) were more favourable to development of *A. custos*. A square-wave type of thermorhythm was made by transferring rearing dishes between temperatures at 9.00 and 21.00 every day. Cryophase and thermophase lasted 12 h each.

Data showing the extent of PhPR of *A. custos* under constant and alternating temperatures in laboratory experiments are shown on Fig. 3. It is evident that active development even under long-day conditions was possible only at temperatures higher than 27°C. The temperature range of PhPR manifestation was slightly greater under thermoperiodic conditions, but about 60% of females diapaused under long-day conditions (average temperature
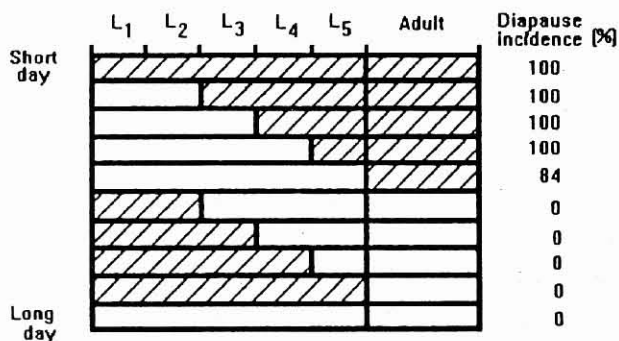
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Fig. 4. Sensitivity of different stages of *Arma custos* to short-day (14 L : 10 D) and long-day (18 L : 6 D) conditions, 28.5°C.

of the thermorhythm was 20.5°C). The data obtained indicate that the PhPR of *A. custos* population from forest-steppe zone has a high temperature optimum. Only adults were sensitive to photoperiod (Fig. 4). Sixteen short-day impulses are necessary to initiate diapause at 28°C.

In laboratory and field experiments it was found that *A. custos* required about 400 day-degrees above 13°C to complete one full generation. In the Belgorod region, where the present experiments took place, about 720 day-degrees were available for insects with such a development threshold (Karausheva, 1980). Thus *A. custos* can produce two generations per year at warmer summer in the forest-steppe zone. But in this region the second brood was never recorded irrespective of the length of observations. Irrespective of adult emergence dates, all summer bugs enter diapause.
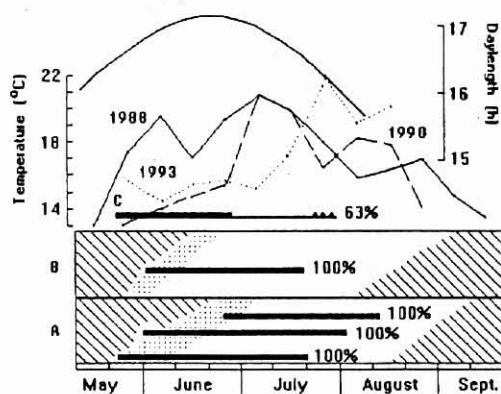
Usually, such a seasonal cycle is caused by obligatory arrest of development. In *A. custos*, as mentioned above, facultative diapause is controlled by qualitative PhPR. Thus, it is probable that there is an ecophysiological mechanism ensuring univoltinism in *A. custos* in the forest-steppe zone.

The results of phenological observations and field experiments are presented in Fig. 5. All insects entered diapause. Induction of reproduction in bugs was possible only by an artificial shift of the adult emergence (sensitive stage) from the end of July (as in nature) to the end of June. Even under these conditions only 37% of females laid eggs. However, according to our observation, it never occurs in nature. Even in the warmest years the first adults of the new generation do not appear before the end of July, when active development is not possible due to the photoperiodic and temperature conditions. The fact that adults only possess photoperiodic sensitivity increases the certainty of entering diapause.

It may be concluded, that a univoltine life cycle in *A. custos* in forest-steppe zone is determined by the peculiarities of its PhPR.

It should be stated that the bug has one generation not only in the region of the present investigations, but also much further south – in South Ukraine and Kirghizia (Puchkov, 1961, 1965) and in Bulgaria (Iosiphov, 1981). Unfortunately, more southerly populations of *A. custos* have not been studied.

Fig. 5. The seasonal cycle of *Arma custos* in the forest-steppe zone. Phenology and results of the field experiments 1990 (A), 1988 (B) and 1993 (C). Above: Natural daylength including 1/2 civil twilight at 50°N and temperature for ten days. Each horizontal line shows period of nymphal development from the hatching of the nymphs to adult moulting. Thick line, nymphs; thin line, adults. In 1993 (C) 4th instar nymphs were used in the experiments. Numbers, incidence of diapause, %. 1, adults; 2, eggs; 3, nymphs.

Univoltinism in the linden bug, *P. apterus* L. (Pyrrhocoridae), is maintained by external factors as well, but is based on a quite different principle.

As was shown before, facultative adult diapause in *P. apterus* is controlled by PhPR of long-day type (Hodek, 1968; Volkovich & Goryshin, 1978; Saunders, 1983).

In laboratory experiments (Numata et al., 1993) it was suggested that about 500 day-degrees (from 380 up to 590 day-degrees in different variants) were required to complete one generation and LDT is about 12–13°C. During the vegetative season SET, above the level of this LDT, is near 800 day-degrees in the region of the present investigations (Karausheva, 1980). Both the natural temperature conditions as well as the facultative diapause in *P. apterus* create the possibility of a multivoltine seasonal cycle in the local population.

However, a univoltine life cycle has been observed in populations from Paris, France (Pouvreau, 1963) and Bohemia (Hodek, 1968). Puchkov (1973) and Asanova & Iskakov (1977) suggested the possibility of a partially bivoltine life cycle in the Ukraine and Kazakhstan. But, until recently, no reliable evidence has been shown of the type of voltinism in *P. apterus*. There are some indications that *P. apterus* may not be strictly univoltine in Southern Bohemia (Honěk & Šrámková, 1976; Socha & Šula, 1992; Socha, 1993). A second generation arises from eggs laid by females emerging between June and the beginning of August. Adults that emerge later, enter diapause without having laid eggs (Socha & Šula, 1992; Socha, 1993). Honěk & Šrámková (1976) considered the occurrence of a partial second generation in Bohemia in warmer conditions as a rather unfavourable modification of its life strategy, due to damage to the population caused by total mortality of second generation nymphs.

According to many years of observations, in the forest-steppe zone, overwintering bugs become active since the end of April. On warm sunny days mating and oviposition may be observed. Thereafter, both nymphs and adults occur until late autumn.

It was difficult to separate generations by field observation only, because adults lived and continued to lay eggs for a long period. To determine the actual time of development of each generation, fifth (final) instar nymphs were collected and kept in cages on the soil's surface. After adult emergence, their diapause status was examined (Table 1).

TABLE 1. Incidence of adult diapause in *Pyrrhocoris apterus* collected as fifth instar nymphs in 1991.

Dates of collection	No. of nymphs collected	Dates of adult emergence	No. of adult pairs	Incidence of diapause (%)
07.06	46	09–14.06	20	0
02.07	35	04–06.07	22	0
12.07	20	14–18.07	18	0
12.07	12	21.07	6	33.3
22.07	40	30.07–02.08	19	84.2
22.07	30	06.08	15	75.0

Nymphs collected on 7th June 1991 moulted from 9th to 14th June. Thus, it corresponded to the first emergence of new adults in nature. They all were non-diapausing and began to lay eggs in late June. On 21st July, the first diapausing adults emerged and, thereafter, diapausing bugs prevailed in the samples. Results of phenological observations
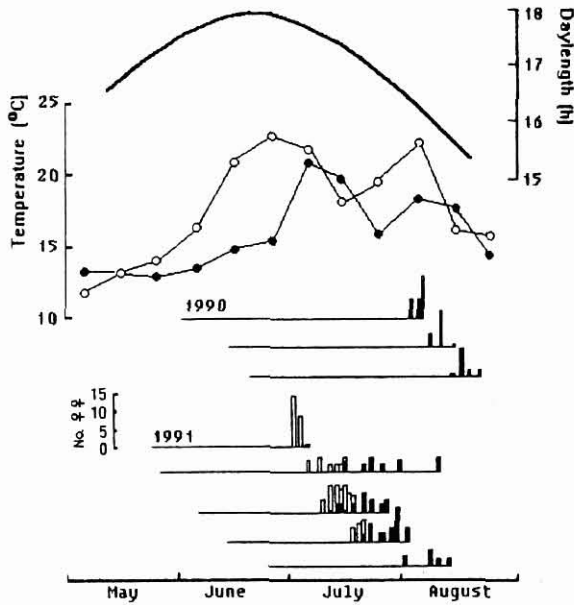
Fig. 6. Induction of adult diapause in *Pyrrhocoris apterus* under quasi-natural conditions in 1990 and 1991. Each horizontal line shows an experimental series. The outset corresponds to the hatching of nymphs. Date of adults emergence and number of females are shown at the end of line as histograms (black, diapause; white, reproductive). Circles show the mean temperatures for ten days in the cage used for the experiments in 1990 (closed) and in 1991 (open). Solid line, natural daylength including twilight at 50°N.

suggest the possibility of a two-generation life-cycle of this species in the forest-steppe zone.

The most reliable information about real number of generations and terms of diapause induction were obtained from field experiments conducted in 1990 and 1991 (Fig. 6).

In 1991, first instar nymphs were placed in an experimental cage on 23rd and 27th May (Saulich et al., 1994). New adults first emerged on 2nd July. All females that emerged before 10th July were active and laid eggs. From 12th to 21st July, both reproducting and diapausing females were registered, and all females that moulted after 22nd July entered diapause. This regularity was noted for first four variants of the experiment in 1991. In later experimental series in 1991, and in all series during the cool summer of 1990, all females entered diapause.

From the present data it is concluded that there are two alternatives (univoltine and bivoltine) in the life cycle of the local population of *P. apterus* (Fig. 7).

Females of *P. apterus* are characterised by a very long period of oviposition, which may last up to six weeks. Nymphs of all instars and adults may be encountered together in the population throughout the summer. Nymphs emerging from late eggs grow under short-day conditions, hence new adults enter diapause. Nymphs hatching from eggs laid earlier in the season (end of April to beginning of May) develop under long-day conditions, and this induces reproduction.

Usually, both types of development are realised at the same year. Warmer seasons increase the bivoltine fraction and cooler seasons promote univoltinism. When sensitive
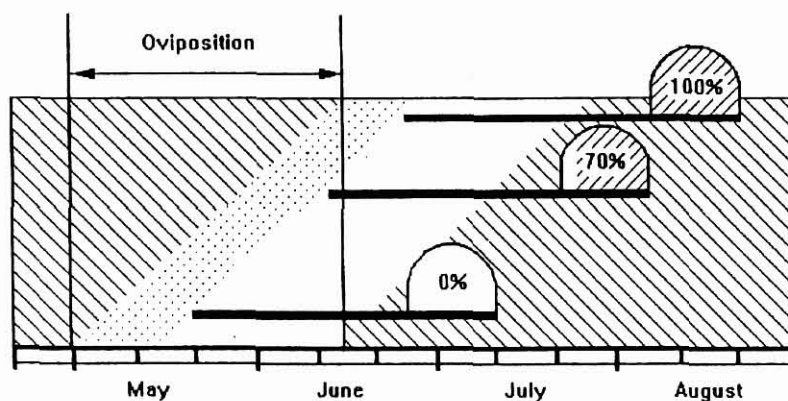

Fig. 7. The phenology and mechanism of formation of the univoltine fraction in *Pyrrhocoris apterus* in the forest-steppe zone. See explanation to Fig. 5.
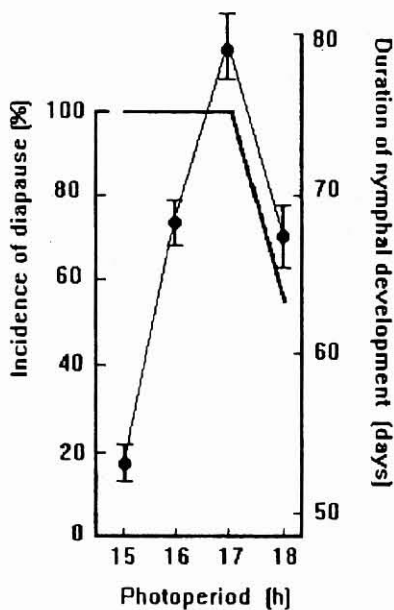
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Fig. 8. Effect of photoperiod on the development period in *Pyrrhocoris apterus* (20°C). Fine line – development duration, thick line – the photoperiodic response curve. Vertical bars show standard errors.

stages occur under intermediate conditions, both active and diapausing fractions may be found among insects and then the weather conditions become the principal factor controlling the values of these fractions.

Taking into consideration the scheme of seasonal development of the species it is easy to understand the ecological significance of photoperiodical regulation of nymphal development rate.

Retardation of nymphal growth

Retardation of nymphal growth near critical threshold as a quantitative effect of photoperiodism was described in the linden bug from Central Bohemia by Saunders (1983). In the Belgorod population of *P. apterus* this effect was found at all constant and alternating temperature regimes (Numata et al., 1993) and attained its maximum value at 20°C (Fig. 8).

In nature, nymphs of the bivoltine fraction meet with short-day conditions twice in a season – in spring and autumn. This stimulates strong acceleration of growth and increases the chances of successful completion of active development and the entering of diapause before the autumn fall of temperature.

Bugs from later spring eggs develop according to a univoltine seasonal pattern. Nymphs grow under long-day conditions which cause strong retardation of their development. Due to this regulation, emergence of adults is delayed until conditions are more favourable for diapause.

Thus, it was established in phenological observations, laboratory and field experiments that *P. apterus* may produce one or two generations a year in the forest-steppe zone (Russia, 50°N) and that the seasonal cycle is regulated by the qualitative and quantitative PhPRs.

UNIVOLTINISM AS A RESULT OF TWO FORMS OF DORMANCY

A peculiar type of univoltinism regulation by external environmental factors was noted in *Carbula humerigera* (Pentatomidae) (Kiritani, 1985). The seasonal cycle of the species includes two facultative diapauses: winter nymphal and summer adult ones. Winter diapause is induced by short and decreasing daylength and manifests itself as a prolonged (30–40 days) retardation of nymphal growth. Diapause development is completed in December, but further morphogenesis is arrested by low temperature. The increase of temperature and daylength in spring induces facultative diapause in newly emerged adults and, as a result, the species produces only one generation a year even in the subtropical climate of Japan.

Some similar traits in univoltine regulation were found in *Picromerus bidens* L. (Pentatomidae), under laboratory conditions (Musolin, unpubl.). The annual cycle of the species is characterised by two periods of physiological resting. Embryonal diapause is obligatory

and summer reproductive diapause (aestivation) is induced by long-day conditions and may last up to two months. Retardation of females' maturation under short day was not observed. After a short period of feeding, females began oviposition, and all eggs were determined as diapausing.

These results clarify the interpretation of *P. bidens* life history, as suggested by Larivière & Larochelle (1989). Based upon literature and their own observations, the authors suggested a parallel coexistence of two life cycles of the species in nature; a primary cycle in which insects overwinter in the egg stage and, less frequently, a secondary cycle, in which some adults overwinter.

In fact, prolonged reproductive diapause induced by long-day conditions creates preconditions for favourable overwintering not only in embryo stage, but also in that imaginal. This seasonal pattern is confirmed indirectly by captures of adults in the early spring, which would be impossible if the species should overwinter in embryo stage only.

DISCUSSION

The data obtained testify that univoltinism among true bugs is caused by different mechanisms. As noted earlier (Saulich & Volkovich, 1996) the same mechanisms may be employed in the maintenance of univoltine development in different groups. However, various mechanisms may be found in a certain group.

The most simple and widespread method of maintaining univoltinism in Heteroptera is an obligatory diapause in each generation. As mentioned above, seasonal development with obligatory egg diapause was studied in detail in mirids *Leptopterna dolobrata* and *Calocoris roseomaculatus* (Braune, 1971). Life cycles of the same kind have been described in some moths, e.g. *Tortrix viridana* L. (Lepidoptera: Tortricidae) (Danilevskii & Bei-Bienko, 1958) and gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae) (Leonard, 1968; Tauber et al., 1990) and others.

Obligatory nymphal diapause has been studied in *Coptosoma scutellatum*. This kind of univoltinism is known in many species of orders other than Heteroptera, for example, in *Aporia crataegi* L. (Lepidoptera: Pieridae) (Danilevskii, 1961). In bugs it is rather unusual.

Obligatory adult diapause combined with the quantitative PhPR determines univoltine seasonal cycle in *Palomena prasina* and *Coreus marginatus*.

Quantitative PhPRs, controlling the rate of nymphal growth and having significance in insect life-cycle regulation, were discovered in *Dasychira pudibunda* L. (Lepidoptera: Orgyidae) by Geispits & Zarankina (1963). Such responses were later studied in many other species. Danks (1987) lists more than 80 species, from the 9 largest orders of insects, in which photoperiodic control of nymphal growth was recorded.

These responses have not been well documented in heteropteran insects. However, the known examples suggest that this type of life-cycle regulation may be widespread among true bugs (Saunders, 1983; Kiritani, 1985; Hori, 1988).

External life cycle regulation was studied in *Arma custos* and *Pyrrhocoris apterus*. Qualitative and quantitative PhPRs are included into the regulation of seasonal cycles of many insects. Univoltine development of potentially multivoltine species may enable their expansion into high latitudes and montane habitats. Examples of this strategy may be found in northern and montane populations of many insects: *Acronycta rumicis* L. and

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Mamestra brassicae L. (Lepidoptera: Noctuidae) (Danilevskii, 1961), *Polychrosis botrana* Schiff. (Lepidoptera: Tortricidae) (Komarova, 1954), *Chrysopa perla* L. (Neuroptera: Chrysopidae) (Gepp, 1975) and others.

A life cycle with two periods of prospective rest (winter and summer diapauses) in the same ontogenetic cycle is also a widespread pattern of univoltinism in insects (Falkovich, 1979; Masaki, 1980; Ushatinskaya, 1987). Among true bugs, such a life-cycle regulation has been described from the pentatomid *Carbula humerigera* (Kiritani, 1985) only. Results of our preliminary experiments suggest two diapauses in *Picromerus bidens*.

Extremely complex ways of univoltinism maintenance on the base of two-step responses, found in staphylinids (Lipkow, 1966; Topp, 1986), carabids (Thiele, 1977) and chrysopids (Tauber & Tauber, 1976; Grimal, 1988), have never been described in true bugs, but it is possible that similar mechanisms will be found among Heteroptera as well.

CONCLUSION

Univoltine seasonal cycles and complex mechanisms of its regulation among Insecta as whole, and Heteroptera in particular, are widespread. However, sometimes it is difficult to understand the adaptive significance of the reduction of generation number per annum in locations where temperature conditions permit the development of more than one generation. It is probable that the choice of this seasonal pathway is dictated by the need of adaptations to extreme environments. Thus univoltinism is more frequent in species living in "risk zones" (e.g., high latitudes, montane, arid and semi-arid climates), where some environmental resources are limited. Univoltinism in predators, parasitoids, phytophagous (mono- and oligophagous) insects may be connected with the seasonality of food.

In general, univoltinism promotes enlargement of the species' area, by the use of natural resources during limited periods of the year.

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