

Summer dormancy ensures univoltinism in the predatory bug *Picromerus bidens*

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Abstract

The seasonal cycle of *Picromerus bidens* L. (Heteroptera: Pentatomidae) is usually considered to be univoltine with an obligatory winter egg diapause. Seasonal adaptations of the species were studied in the laboratory and in field experiments. When reared under short-day photoperiodic conditions (L12:D12 and L14:D10), all females began to lay eggs synchronously soon after their emergence. However, in the females reared under long-day conditions (L18:D6 and L20:D4) and outdoors in June–July, oviposition was significantly delayed. This delay in reproduction induced by photoperiodic conditions and then spontaneously terminated was considered to be aestivation. Egg batches laid by females in the laboratory and in the field were kept at 25 °C for two months. From 30.8 to 93.8% of batches contained eggs which hatched without cold treatment between day 14 and 60 after oviposition. The proportion of eggs hatched was 17.7 to 20.9% in the short-day regimes, while it was significantly less (5.7 to 6.0%) under long-day conditions. It is concluded that in some eggs diapause is of low intensity and that if under natural conditions the first batches had been laid at the end of June, nymphs would have hatched at least from some eggs during the same season even without cold treatment. Such untimely hatching would have resulted in the death of nymphs and adults unprepared for overwintering. A photoperiodic response which induces aestivation in the early emerging adults in June–August may prevent early oviposition and occurrence of a second generation and thus maintains univoltinism in *P. bidens*.

Introduction

Picromerus bidens L. (Heteroptera: Pentatomidae) is a predatory polyphagous true bug. The geographic distribution of this species is very wide: in the Palearctic from 64° N to northern Africa, and from Ireland to Siberia and China (Southwood & Leston, 1959; Puchkov, 1961; Larivière & Larochelle, 1989; Vinokurov & Kanukova, 1995). In the Nearctic, this species has been recorded from more than 180 locations in North America (Larivière & Larochelle, 1989). It is believed that *P. bidens* was accidentally, and probably more than once, introduced into North America where the species became successfully ac-

climatized (Jawahery, 1986). Throughout its natural range and in North America, the species occupies mainly shaded and humid forests, although it can also inhabit open forest edges, meadows, and gardens (Puchkov, 1961; Jawahery, 1986; Larivière & Larochelle, 1989).

Animal food is indispensable from the 2nd or 3rd nymphal instars (Mayné & Breny, 1948). *Picromerus bidens* is a highly polyphagous bug that preys on larvae and sometimes adults or even pupae of more than 250 species from several insect orders (Puchkov, 1961; Larivière & Larochelle, 1989). Some of its potential prey are agricultural or forest pests.

The seasonal cycle of the species is usually considered to be univoltine with an obligatory winter egg diapause (e.g., Leston, 1955; Southwood & Leston, 1959; Puchkov, 1961; Javahery, 1986; Larivière & Laroche, 1989). In accordance with this seasonal scheme, nymphs hatch from the overwintered eggs in the spring (in May in the forest-steppe zone of Russia where our experiments were conducted; Puchkov, 1961). Nymphs feed intensively beginning at the 2nd instar and full nymphal development takes 30 to 60 days. In the southern regions, the first new adults may emerge at the beginning of June, although most of the bugs moult into adults by the middle of July. Young adults feed actively, but begin to mate not earlier than August. Females oviposit diapause eggs from the beginning of September. Bugs of both sexes die after about a month after the beginning of oviposition but egg-laying females have been recorded as late as the beginning of October (Puchkov, 1961). Eggs deposited during the autumn overwinter, and nymphs hatch the next spring.

However, the seasonal pattern of this species is not so clear. Thus, there are several records of active adults in the spring (Schumacher, 1910–1911; Butler, 1923; Leston, 1955; Musolin, 1996). These observations are contradictory to the traditionally accepted seasonal pattern presented above. It was supposed that some adults that had not been reproductively active could survive winter, mate in the spring or summer and produce eggs that hatch without exposure to cold during the same season (Schumacher, 1910–1911; Butler, 1923; Dupuis, 1949). Recently, Larivière & Laroche (1989) suggested that these two seasonal cycles may co-exist in nature and considered the seasonal pattern with overwintering of adults to be more rare and ‘secondary’.

Typical winter egg diapause requires cold exposure for termination (Danilevskii, 1961; Danks, 1987). If cold exposure is required for *P. bidens* (as suggested, for example, by Javahery, 1986, 1994), nymphs from the eggs laid by overwintered adults would not hatch during the same spring, but only after the next winter (after exposure to cold).

These characteristics of the seasonal pattern in this species prompted detailed laboratory and field experimental research aimed at understanding the mechanism controlling seasonal development of *P. bidens*. Diapause is usually strictly related to a species-specific stage, and photoperiod and temperature are the two most important factors controlling its induction in many insect species. The aim of the laboratory

experiments was to estimate the possibility of diapause induction at different stages (egg and adult), and to determine the conditions which can induce suppression of development (delay in nymph hatching in the case of egg diapause, and absence of oviposition in the case of adult diapause).

Materials and methods

Insects. The stock culture of *P. bidens* originated from Moscow province, Russia (56° N, 38° E) and was kept and partly renewed every year by Dr O. Volkov at the Institute of Plant Quarantine (Moscow). Egg batches were obtained from this culture. Nymphs that hatched after cold treatment from these batches were used in the experiments.

Laboratory experiment. Insects were kept in plastic Petri dishes 100 mm in diameter, the lids of which had openings 50 mm in diameter for aeration covered by gauze. Caterpillars of the wax moth *Galleria mellonella* L. and other lepidopterans and larvae in various instars of the Colorado potato beetle *Leptinotarsa decemlineata* Say were supplied as food for nymphs and adults. Propagules and leaves of the common burdock *Arctium lappa* L. and water-soaked cotton pads were always available. Fresh food, propagules, and water were added every second day. The density of the nymphs was kept at 20–30 per Petri dish for the 1st and 2nd instars and was gradually reduced to 4–5 for the final (5th) instar. Adults were kept in single male-female pairs in the same size Petri dishes. Zigzag-folded paper served as a substratum for egg-laying.

The laboratory experiment was performed in incubators in which both photoperiod and temperature were controlled automatically (Braun & Goryshin, 1978). The following constant photoperiodic regimes were used: L12:D12, L14:D10, L16:D8, L18:D6, and L20:D4. The light intensity in the incubators ranged between 180 and 250 lx and was supplied by 20W fluorescent lamps. The temperature was maintained at $24.5 \pm 1.0^{\circ}\text{C}$.

The appearance of adults and of new egg batches were recorded daily. The experiment ended when the last female died.

Field experiment. To observe development under conditions similar to those encountered in the field, one experimental series of bugs was reared from the

egg stage to the death of adults (from 4 June to 10 September, 1995) outdoors in the reserve 'Forest on the Vorskla River' (Belgorod region of Russia, forest-steppe zone, 50° N, 36° E). Insects in Petri dishes (as described above) were kept in a specially modified meteorological booth on a shelf about 130 cm above ground level. Only the northern side of the booth was open and the insects inside the booth were sheltered from direct sunlight and rain. The temperature in the booth was recorded daily with a thermograph and checked using minimum and maximum thermometers.

Egg hatching. To test the possibility of hatching of nymphs without cold treatment, the eggs laid in the experiments were kept for 60 days under embryogenesis stimulating conditions: the batches laid in the laboratory were kept at $25.0 \pm 1.0^\circ\text{C}$ and L16:D8 and those laid in the field experiment were kept outdoors until 10 September (day 10 to 40 after oviposition) and were also transferred to $25.0 \pm 1.0^\circ\text{C}$ and L16:D8. The batches were kept in individual plastic Petri dishes with water-soaked cotton pads. Hatching of nymphs was recorded every second day.

Results

Nymphal development. Nymphal development took approximately the same time in all laboratory regimes in both sexes with the exception of the L20:D4 regime, in which development lasted longer; the difference was small but significant (Tukey multiple comparison test; $P = 0.05$; Zar, 1996; Table 1). Development under outdoor conditions took longer because the temperature was lower (see footnotes in Table 1 for details). There was no difference in duration of nymphal period between the sexes (t -test, $P > 0.05$).

Induction and termination of adult aestivation. A pronounced response to daylength was observed during the reproductive period. Under short-day conditions (L12:D12 and L14:D10) all females began to lay eggs synchronously between day 11 and 19 after moulting to the adult stage, whereas in the long-day regimes oviposition was delayed despite active feeding and mobility.

As in the two short-day regimes all females laid their first batches by day 16 (L14:D10) and day 19 (L12:D12), it was decided that the physiological state of females (reproduction or dormancy) should be evaluated on day 20 after adult moulting (Figure 1). The

Table 1. Duration of nymphal period in *Picromerus bidens* under laboratory ($24.5 \pm 1.0^\circ\text{C}$) and field conditions

Regimes	Duration of nymphal period (days), mean \pm SE (n) ^a	
	Females	Males
L12:D12	24.69 ± 0.58 (13), c	24.74 ± 0.33 (19), c
L14:D10	25.67 ± 0.67 (12), bc	25.93 ± 0.32 (14), bc
L16L:D8	26.30 ± 0.47 (23), bc	25.80 ± 0.19 (30), bc
L18L:D6	25.77 ± 0.44 (13), bc	26.00 ± 0.48 (14), bc
L20L:D4	28.12 ± 0.40 (26), a	26.90 ± 0.29 (29), ab
Field ^b	35.68 ± 0.40 (19), d	35.85 ± 0.28 (26), d

^aMeans followed by the same letter are not significantly different (laboratory regimes, at $P = 0.05$ by Tukey multiple comparison test; field regime, by t -test, $P > 0.05$) (Zar, 1996).

^bNymphs grew in the field experiments from 4 June until 14 July, 1995; mean temperature for every five-day period varied between 16.2 and 20.9°C .

physiological state of females was evaluated not only on day 20, but also later (day 30, 40, etc.); the overall shape of the curve did not change significantly. The results of the field experiment are presented in the same figure.

After induction of diapause, the insects were kept under the same conditions. In the long-day laboratory and field regimes, females terminated diapause spontaneously and laid their first batches of eggs on average between day 30 and 53 after moulting to the adult stage (Figure 2).

Longevity. Some females died during the first few days after moulting, before the beginning of reproduction. In surviving females, the mean duration of adult life after the beginning of oviposition ranged in different regimes from 14.3 ± 4.8 to 27.0 ± 4.8 days (mean \pm SE; Figure 3). In females from the long-day laboratory regimes (L16:D8 and L18:D6) and from the field series, the preoviposition period (including aestivation) exceeded 50% of the total duration of adult life. Photoperiod did not directly affect the pattern of female mortality.

Quantitative characteristics of reproduction. After termination of summer diapause, females began oviposition in all experimental regimes. The average number of batches deposited per female (lifetime fecundity) ranged in different photoperiodic regimes from 1.9 ± 0.5 batch/female (L18:D6) to 4.0 ± 0.8 batch/female (L20:D4) (mean \pm SE), although the difference between conditions was not statistically significant (single-factor ANOVA at $\alpha = 0.05$). The average number of eggs deposited per female ranged from

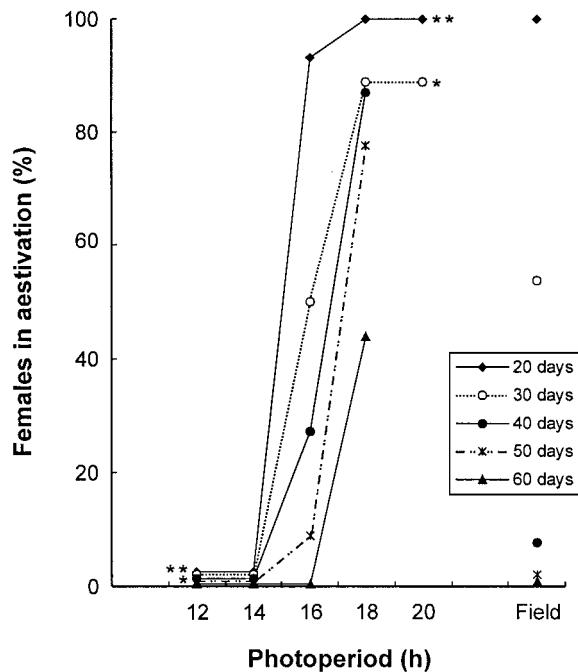


Figure 1. Photoperiodic induction of aestivation in *Picromerus bidens* in laboratory and field experiments. The set of curves represents the results of the laboratory experiments (% females in aestivation; at 24.5 °C); stars represent the results of a preliminary laboratory experiment (% females in aestivation; * on day 30 and ** on day 20; at 22.5–23.0 °C; Musolin, 1996). For the L20:D4 regime, data for day 20 and 30 only are presented, because later on some females from this regime were used for another experiment. Preoviposition period in the field experiment ('Field') was between 6 July and 23 August, 1995; mean temperature for every five-day period varied between 16.1 and 20.9 °C; $n = 6$ –21.

40.1 ± 13.7 eggs/female (L18:D6) to 131.0 ± 35.6 and 132.4 ± 24.3 eggs/female in the L14:D10 regime and in the outdoor series, respectively (difference was not significant; single-factor ANOVA at $\alpha = 0.05$). In general, the longer females lived after the commencement of reproduction, the more eggs and batches they deposited (although variation in each regime was high and the coefficient of correlation was only $r = 0.53$).

Termination of egg diapause without chilling. To test the assumption that cold is required for termination of winter egg diapause in this species, the eggs laid by females in the experiments were subjected to a temperature of 25.0 ± 1.0 °C. Soon nymphs began to hatch from some eggs: the beginning of this process ranged in different regimes between day 14 (eggs laid in the L12:D12 regime) and day 32 (those laid in the L16:D8 regime) (Figure 4).

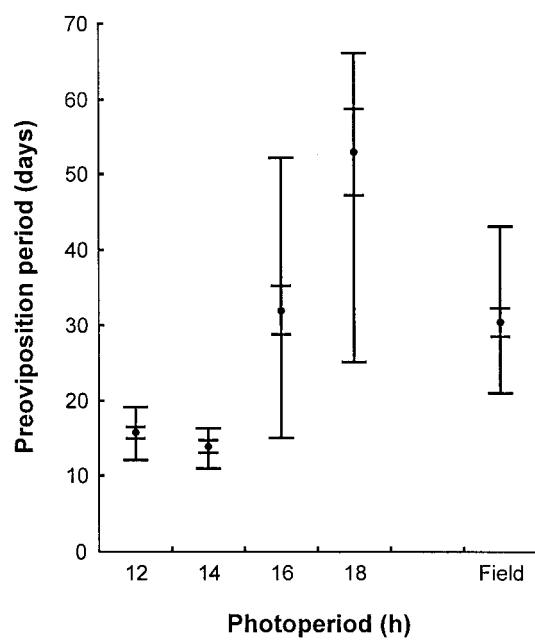


Figure 2. The preoviposition period in *Picromerus bidens* in the laboratory (24.5 °C) and field experiments. Mean values, SE and ranges of the preoviposition period in females are shown. Preoviposition period in the field experiment ('Field') was between 6 July and 23 August, 1995; mean temperature for every five-day period varied between 16.1 and 20.9 °C; $n = 6$ –13.

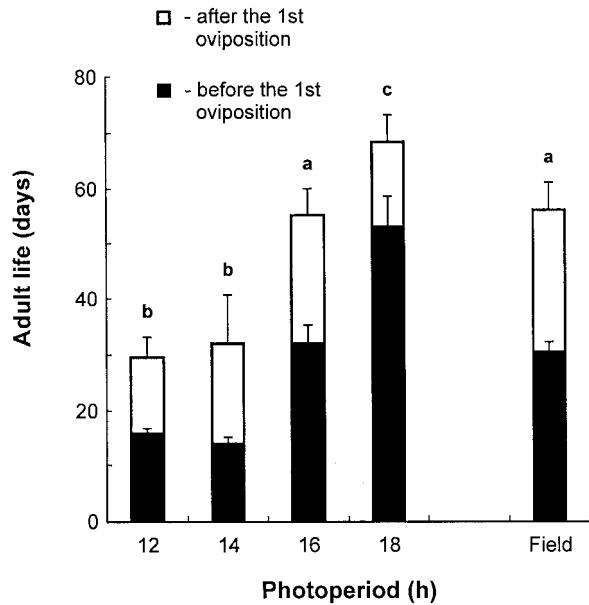
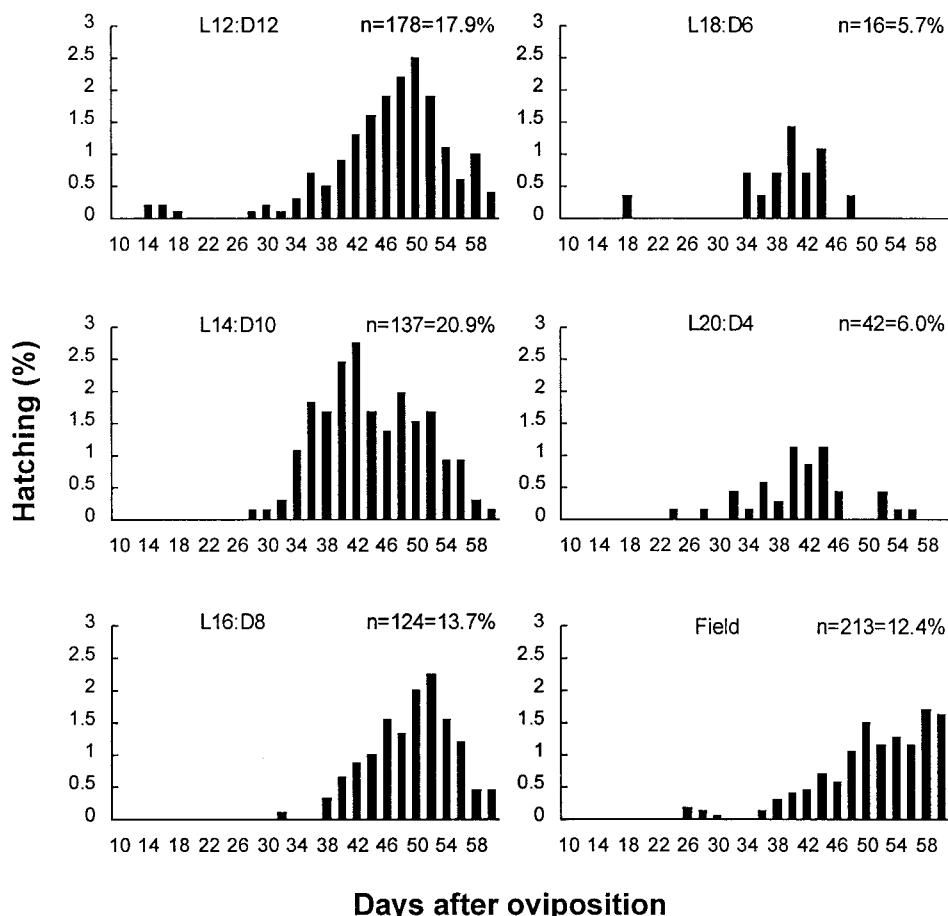


Figure 3. Duration of adult life in females of *Picromerus bidens* in the laboratory (24.5 °C) and field experiments. Duration of adult life after commencement of oviposition did not differ significantly at $P = 0.05$ by Tukey multiple comparison test (Zar, 1996); duration of preoviposition period (mean \pm SE) followed by the same letter are not significantly different by the same test; $n = 10$ –17.



Days after oviposition

Figure 4. Hatching of eggs of *Picromerus bidens* during the first 60 days after oviposition. Temperature in the laboratory series was $25.0 \pm 1.0^\circ\text{C}$. Egg batches of the field series were kept outdoors till 10 September (day 10 to 40 after oviposition) and were also transferred to $25.0 \pm 1.0^\circ\text{C}$ and L16:D8; n shows total number of nymphs hatched and percentage shows the proportion of eggs hatched (100% = all eggs deposited in the given regime).

From 30.8 to 93.8% of the batches contained some eggs from which nymphs terminated diapause and hatched within 60 days after oviposition (Figure 5A). These batches were significantly more numerous in the short-day regimes (L12:D12 and L14:D10) than in the long-day ones (L18:D6 and L20:D4) (Tukey-type multiple comparison test for proportions; $P = 0.05$). The overall percentage of eggs hatched was also significantly higher in the two short-day regimes (17.7 and 20.9%) than in the two long-day regimes (5.7 and 6.0%) (Figure 5B).

Discussion

Induction and termination of adult aestivation. The state of physiological rest of adult bugs revealed in

the experiments was considered to be a reproductive oligopause in terms of physiological classification of dormancy (*sensu* Mansingh, 1971 and Ushatinskaya, 1976) or aestivation, ‘a summer rest aimed at avoiding summer overheating and other associated adverse environmental conditions (water deficit, starvation, etc.)’ (Ushatinskaya, 1987). Aestivation is widely represented in different orders of insects in the tropics, as well as in the temperate and arid zones (Masaki, 1980; Ushatinskaya, 1987). However, among Heteroptera this kind of dormancy has been reported only in several species from warm regions. Thus, Brown (1962) supposed on field observations that dormancy in the univoltine scutellerid *Eurygaster integriceps* Put. consists of two phases: aestivation (followed by a short period of autumn migration) and hibernation. Noda (1984) showed that the start of oviposition in the

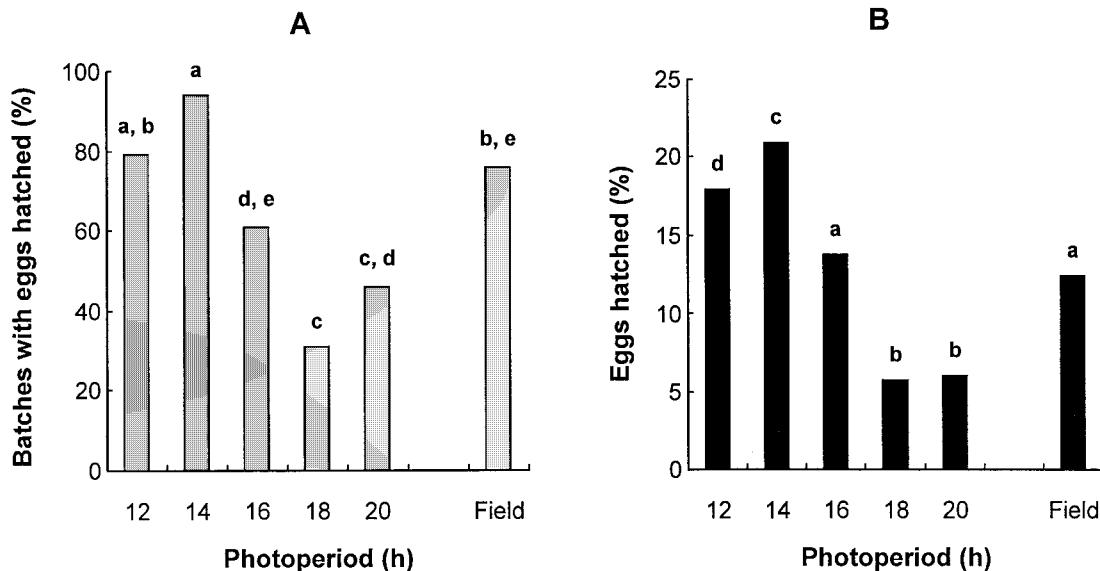


Figure 5. Hatching of eggs of *Picromerus bidens* without cold treatment within the first 60 days after oviposition under experimental conditions. A. Proportion of batches with eggs hatched ($n = 13\text{--}41$). B. Proportion of eggs hatched ($n = 281\text{--}1721$). Abscissa – regimes under which parents and batches were reared and kept. Values followed by the same letter are not significantly different at $P = 0.05$ by Tukey-type multiple comparison test for proportions (Zar, 1996).

pentatomid *Nezara antennata* Scott is under photoperiodic control. Photoperiodically induced retardation of oviposition was also found in another pentatomid *Carbula humerigera* Uhler and it was suggested that this response is more important in southern populations of the species than in northern ones (Kiritani, 1985a, 1987). In this study we report an example of a photoperiodically controlled aestivation in a population of *P. bidens* originated from the northern part of the temperate zone.

The two degree centigrade difference in the conditions between the laboratory experiment and our preliminary study (Musolin, 1996) did not significantly affect the induction of aestivation (L12:D12 and L20:D4 regimes at 22.5–23.0 °C and 24.5 °C; results of both experiments are shown in Figure 1). The results obtained outdoors were very similar to those in the laboratory experiment under the L16:D8 regime. The bugs from the field emerged as adults in the second half of July when the natural daylength decreased from 16 h 30 min to 16 h, and ambient temperature was lower than in the laboratory experiment. The preoviposition period in the outdoor series (30.3 ± 2.9 days; mean \pm SE) and in the laboratory under the L16:D8 regime (32.0 ± 3.4 days) did not differ significantly, but differed from those of the two laboratory short-day (L12:D12 and L14:D10) and long-day (L18:D6) regimes (Figure 3; Tukey multiple

comparison test; $P = 0.05$). These findings clearly showed that summer dormancy in *P. bidens* is controlled by daylength, and results obtained in the laboratory experiments can be used to analyse seasonal development of the species in the field.

Termination of egg diapause. The pattern of nymph hatching showed that the process of termination of diapause in eggs was not occasional, but had a regular character. For technical reasons, egg batches laid in the outdoor series were transferred to laboratory conditions on 10 September (day 10 to 40 after oviposition). The ambient temperature in the field was lower than that in the laboratory incubators, which probably explained why hatching of nymphs was slightly retarded in the outdoor series. However, the first eggs in this series hatched before transfer to the laboratory and this showed that early termination of egg diapause does take place outdoors. The proportions of eggs and batches from which nymphs hatched in the field experiment were similar to those from L16:D8 and the short-day series (Figure 5). In general, more eggs tended to hatch and more batches contained such eggs under short-day conditions. However, based on the data obtained, it is impossible to determine which developmental stage (adult or embryo) is sensitive to photoperiodic conditions.

When before the experiments egg batches were transferred in May from the cold treatment conditions to the laboratory temperature of 22–23 °C, it took 9 to 11 days to hatch and hatching was very synchronous. However, when the eggs laid in the experiment were kept at 25.0 ± 1.0 °C, very few hatched before day 22 and many hatched much later (Figure 4). These results suggested that all eggs entered diapause, but in part of the eggs diapause was much less intensive and unstable and was terminated even without a cold treatment.

A similar early hatching of eggs was reported in the gypsy moth *Lymantria dispar* (L.), a univoltine species with an aestival-autumnal-hibernal diapause (Leonard, 1968; Giese & Casagrande, 1981; Waggeron, 1984). A small but consistent proportion of larvae (8–15%) hatched before winter and without any chilling, although the hatched larvae do not survive winter in nature (Tauber et al., 1990). It was suggested that few eggs in egg masses did not enter diapause at all (Tauber et al., 1990). However, when egg masses were transferred to laboratory conditions in autumn, the time to first hatching in all samples exceeded that in the samples that overwintered outdoors and were transferred into the laboratory only in January or March. Moreover, the duration of the hatching period (calculated as the difference between time to first and last hatching) in some autumn samples extended 10 weeks and was much longer than in the samples transferred as the season progressed. These parameters of egg hatching might be interpreted as evidence of low-intensity diapause (rather than absence of diapause) and resembled our findings in *P. bidens*. It is clear that the variation in the initial intensity of diapause still remains an important but poorly understood issue in insect seasonality.

Seasonal development of P. bidens in the light of new experimental data. Facultative adult aestivation and termination of diapause in part of the eggs even without chilling found in *P. bidens* support a new understanding of the seasonal cycle in this species. As was shown, at least in some eggs of *P. bidens* diapause is unstable (or low-intensive): under favourable environmental conditions nymphs from these eggs hatch soon after oviposition and cold exposure is not required for termination of diapause in these eggs. Therefore, if the first egg batches had been laid at the end of June, nymphs would have hatched at least from some eggs during the same season even without a cold treatment. This would have resulted in the death of nymphs or

adults, because they are not physiologically prepared for overwintering. The occurrence of such a partial second generation and the death of non-diapause individuals during winter is prevented by the intervention of a photoperiodically induced aestival diapause in the adults that emerged early in the summer. Under the long-day conditions of June to August, most bugs aestivate and females begin oviposition only in September. Low temperatures during late autumn prevent untimely embryogenesis in the eggs with low-intensity diapause, and hatching occurs only in the spring of the next year. Hence, there are two periods of dormancy, facultative adult aestivation and obligatory egg winter diapause, which maintain univoltinism in this species (the 'primary life cycle' pattern in terms of Larivière & Laroche, 1989).

To date, no evidence has been reported that can convincingly explain the rare records of adults in spring and early summer mentioned above. Supposedly, some adults do not terminate aestivation and after sufficient feeding they may survive winter and reproduce next season (this overwintering of adults would correspond to the 'secondary life cycle' pattern in terms of Larivière & Laroche, 1989). However, further research is necessary to clarify these aspects of seasonal development in *P. bidens*.

Incorporation of two periods of dormancy into the annual seasonal cycle is not very rare among insects and might fulfil different functions (Geispits & Zarankina, 1963; Hidaka et al., 1971; Kimura, 1975; Ishii & Hidaka, 1982, 1983; Canard & Grimal, 1988; Grimal & Canard, 1996; for other examples see: Masaki, 1980; Danks, 1987 and Ushatinskaya, 1987). Thus, this seasonal strategy seems to be one of the most widespread and reliable ways of maintenance of univoltinism in insects (Saulich & Musolin, 1996; Saulich & Volkovich, 1996). Among Heteroptera, univoltine life cycles with two periods of dormancy (facultative winter diapause of nymphs and facultative adult eastivation) have been reported, for example, in the pentatomid *Carbula humerigera* Uhler (Kiritani, 1985a, b, 1987) and in the scutellerid *Poecilocoris lewisi* Distant (Tanaka et al., 1995; S.I. Tanaka, pers. comm.).

The special features of environmental control of seasonal development revealed in the predatory *P. bidens* (photoperiodically controlled summer diapause in adults and termination of diapause without chilling in some eggs) should be taken into consideration when discussing the possible use of this species as an agent for biological control. However, many

other aspects of the species' biology and seasonal development remain to be studied.

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References

- Braun, V. A. & N. I. Goryshin, 1978. Climate chambers with programming of photoperiodic and temperature rhythms for ecological research. *Vestnik Leningradskogo Gosudarstvennogo Universiteta* 3: 26–34 (in Russian, English Summary).
- Brown, E. S., 1962. Researches on the ecology and biology of *Eurygaster integriceps* Put. (Hemiptera, Scutelleridae) in Middle East countries, with special reference to the overwintering period. *Bulletin of Entomological Research* 53: 445–514.
- Butler, E. A., 1923. A Biology of British Hemiptera-Heteroptera. H.F. and G. Witherby, London.
- Canard, M. & A. Grimal, 1988. Insect photoperiodism: various ways of regulating univoltinism in lacewings (Planipennia: Chrysopidae). *Experientia* 44: 523–525.
- Danilevskii, A. S., 1961. Photoperiodism and Seasonal Development of Insects. Leningrad State University Press, Leningrad (in Russian) [translated from Russian into English by J. Johnson assisted by N. Waloff: 1965. Oliver & Boyd, Edinburgh].
- Danks, H. V., 1987. Insect Dormancy: An Ecological Perspective. Biological Survey of Canada, Ottawa.
- Dupuis, C., 1949. Les Asopinae de la faune française (Hemiptera: Pentatomidae). *Revue Française d'Entomologie* 16: 233–250.
- Geispits, K. F. & A. I. Zarankina, 1963. Some features of the photoperiodic reaction of *Dasychira pudibunda* L. (Lepidoptera, Oryctidae). *Entomologicheskoe Obozrenie* 42: 29–38 (in Russian, English Summary) [translation in *Entomological Review*. 1963. 42: 14–19].
- Giese, R. L. & R. A. Casagrande, 1981. Egg development and diapause. In: C. E. Doane & M. L. McManus (eds), *The Gypsy Moth: Research Towards Integrated Pest Management*. USDA Forest Service Science Education Administration Service Technical Bulletin # 1584, pp. 145–150.
- Grimal, A. & M. Canard, 1996. Preliminary observations on the effect of photoperiod on the life cycle of the green lacewing *Hypocharysa elegans* (Burmeister) (Insecta: Neuroptera: Chrysopidae: Nothochrysinae). In: M. Canard, H. Aspöck & M. W. Mansell (eds), *Pure and Applied Research in Neuropterology: Proceedings of the Fifth International Symposium on Neuropterology* [Cairo, Egypt, 1994]. Imprimerie Sacco, Toulouse, pp. 119–127.
- Hidaka, T., Y. Ishizuka & Y. Sakagami, 1971. Control of pupal diapause and adult differentiation in a univoltine papilionid butterfly, *Luehdorfia japonica*. *Journal of Insect Physiology* 17: 197–203.
- Ishii, M. & T. Hidaka, 1982. Characteristics of pupal diapause in the univoltine papilionid, *Luehdorfia japonica*. *Kontyû* 50: 610–620.
- Ishii, M. & T. Hidaka, 1983. The second pupal diapause in the univoltine papilionid, *Luehdorfia japonica* (Lepidoptera: Papilionidae) and its terminating factor. *Applied Entomology and Zoology* 18: 456–463.
- Javahery, M., 1986. Biology and ecology of *Picromerus bidens* (Hemiptera: Pentatomidae) in southeastern Canada. *Entomological News* 97: 87–98.
- Javahery, M., 1994. Development of eggs in some true bugs (Hemiptera–Heteroptera). Part I. Pentomoidea. *The Canadian Entomologist* 126: 401–433.
- Kimura, T., 1975. *Luehdorfia* butterflies waiting for emergence in spring. *Insectarium* 12: 76–79 (in Japanese).
- Kiritani, Y., 1985a. Timing of oviposition and nymphal diapause under the natural daylength in *Carbula humerigera* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology* 20: 252–256.
- Kiritani, Y., 1985b. Effect of stationary and changing photoperiods on nymphal development in *Carbula humerigera* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology* 20: 257–263.
- Kiritani, Y., 1987. Effect of stationary and changing photoperiods on oviposition in *Carbula humerigera* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology* 22: 29–34.
- Larivière, M.-C. & A. Larochelle, 1989. *Picromerus bidens* (Heteroptera: Pentatomidae) in North America, with a world review of distribution and bionomics. *Entomological News* 100: 133–146.
- Leonard, D. E., 1968. Diapause in the gypsy moth. *Journal of Economic Entomology* 61: 596–598.
- Leston, D., 1955. The life-cycle of *Picromerus bidens* (L.) (Hem., Pentatomidae) in Britain. *The Entomologist's Monthly Magazine* (L.) 91: 109.
- Mansingh, A., 1971. Physiological classification of dormancies in insects. *The Canadian Entomologist* 103: 983–1009.
- Masaki, S., 1980. Summer diapause. *Annual Review of Entomology* 25: 1–25.
- Mayné, R. & R. Breny, 1948. *Picromerus bidens* L.: Morphologie. Biologie. Détermination de sa valeur d'utilisation dans la lutte biologique contre le doryphore de la pomme de terre – La valeur économique antidoryphique des Asopines indigénées belges. *Parasitica* 4: 189–224.
- Musolin, D. L., 1996. Photoperiodic induction of aestivation in the stink bug *Picromerus bidens* (Heteroptera, Pentatomidae). A preliminary report. *Zoologicheskii Zhurnal* 75: 1901–1904 (in Russian, English Summary) [translation in *Entomological Review*. 1996. 76: 1058–1060].
- Noda, T., 1984. Short day photoperiod accelerates the oviposition in the oriental green stink bug, *Nezara antennata* Scott (Heteroptera: Pentatomidae). *Applied Entomology and Zoology* 19: 119–120.
- Puchkov, V. G., 1961. Stink Bugs. The Fauna of the Ukraine, Vol. 21(1). Institute of Zoology, the Academy of Sciences of the Ukrainian SSR, Kiev (in Ukrainian).

- Saulich, A. Kh. & D. L. Musolin, 1996. Univoltinism and its regulation in some temperate true bugs (Heteroptera). European Journal of Entomology 93: 507–518.
- Saulich, A. Kh. & T. A. Volkovich, 1996. Univoltinism and its control in insects. Entomologicheskoe Obozrenie 75: 244–258 (in Russian, English Summary). [translation in Entomological Review. 1996. 76: 205–217].
- Schumacher, F., 1910–1911. Beiträge zur Kenntnis der Biologie der Asopiden. Zeitschrift für wissenschaftliche Insectenbiologie 6: 263–266, 376–383, 430–437; 7: 40–47.
- Southwood, T. R. E. & D. Leston, 1959. Land and Water Bugs of the British Isles. Frederick Warne and Co., London.
- Tanaka, S. I., Y. Natuhara & C. Imai, 1995. Photoperiods inducing nymphal diapause accelerate oviposition in *Poecilocoris levisi* Distant (Heteroptera: Scutelleridae). In: Proceedings of 55th Meeting of Entomological Society of Japan and 39th Meeting of Japanese Society of Applied Entomology and Zoology [Obihiro, August 25–28, 1995]: 134 (in Japanese).
- Tauber, M. J., C. A. Tauber, J. R. Ruberson, A. J. Tauber & L. P. Abrahamson, 1990. Dormancy in *Lymantria dispar* (Lepidoptera: Lymantriidae): analysis of photoperiodic and thermal responses. Annals of the Entomological Society of America 83: 494–503.
- Ushatinskaya, R. S., 1976. Insect dormancy and its classification. Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere 103: 76–97.
- Ushatinskaya, R. S., 1987. Summer diapause (aestivation) in insects. In: R. S. Ushatinskaya (ed), Problems of Ecological Physiology of Insects. Nauka, Moscow, pp. 140–173 (in Russian).
- Vinokurov, N. N. & E. V. Kanukova, 1995. True Bugs (Heteroptera) of Siberia. Nauka, Novosibirsk (in Russian).
- Waggoner, P. E., 1984. The hatching of gypsy moth eggs, a phenological model. Agricultural and Forest Meteorology 33: 53–65.
- Zar, J. H., 1996. Biostatistical Analysis, 3rd edition. Prentice Hall, New Jersey.