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Seasonal Development of Plant Bugs (Heteroptera, Miridae): Subfamily Bryocorinae

A. Kh. Saulich[a]* and D. L. Musolin[b]**

[a]Saint Petersburg State University, St. Petersburg, 199034 Russia
*e-mail: 325mik40@gmail.com
[b]Saint Petersburg State Forest Technical University, St. Petersburg, 194021 Russia
**e-mail: musolin@gmail.com

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Abstract—Data on seasonal development of plant bugs from subfamily Bryocorinae (Miridae) are reviewed and analyzed. All of the species of bryocorines whose seasonal development has been studied so far belong to the tribe Dicyphini, owing to the latter's economic importance as agents of biological control in greenhouses. *Macrolophus melanotoma*, *M. pygmaeus*, and *Nesidiocoris tenuis* have homodynamic seasonal development and the lower developmental threshold of about 8–9°C. If food is available, they can remain active all year round and produce annually a varying number of generations, depending on the local climatic conditions. To survive adverse low-temperature winter conditions these species use various natural protected microhabitats and can overwinter at different developmental stages. The other two bryocorines studied (*Dicyphus errans* and *D. hesperus*) exhibit heterodynamic seasonal development and overwinter in the state of adult diapause. Induction of this diapause is controlled by a long day-type photoperiodic response. Also, the nymphal growth rate of *D. errans* is affected by day length and this quantitative photoperiodic response ensures that nymphs of this species reach the diapausing stage (adult) in appropriate time, which is crucial for successful overwintering. The threshold photoperiod for induction of winter adult diapause varies with latitude in *D. hesperus*, only nymphs being sensitive to day length in this species. Pilot experimental studies should precede any planned introduction of a biocontrol agent, as these may reduce the risk of invasions. During the early stages of settling in a new area, it is seasonal adaptations controlling development of bug populations in their natural environments that are particularly important. In greenhouses, higher efficiency of biocontrol measures can be achieved with southern multivoltine populations of homodynamic species, especially if these grow rapidly as immatures, have high reproduction rates at the adult stage, and easily switch to novel prey. Under field conditions, polyphagous heterodynamic univoltine species and populations with deep obligate diapause are more likely to naturalize successfully.

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The seasonal development of insects is immensely diverse. Every species has a unique seasonal cycle that differs from the cycles of other species, even those taxonomically related or sharing the same habitat. Oftentimes even individual populations exhibit complexes of seasonal adaptations with significantly divergent features (Saulich and Musolin, 2018). Research on patterns of insect seasonal development is one of the oldest branches of entomological science. However, it was not until the mid-XX century that knowledge of insect photoperiodism, significantly furthered by Professor A.S. Danilevskii and his colleagues at Leningrad State University, provided entomologists with a scientifically grounded method that enabled them to carry out a cause-and-effect analysis of insect phenology. This ecophysiological method incorporated the theory of temperature control of developmental rate in poikilothermic animals and the notion of the leading role of photoperiodic responses in the control of seasonal development of insects and other living organisms. Early research on photoperiodism mostly dealt with the Lepidoptera (Danilevskii, 1961), Diptera, in particular bloodsucking mosquitoes (Vinogradova, 1960), and Homoptera (Lees, 1955). Later on, interest in photoperiodism and seasonal development of insects grew dramatically, which widened the range of taxa studied and culminated in seminal monographs (Masaki, 1980; Tauber et al., 1986; Danks, 1987, etc.). The results of works devoted to this problem testify to its major significance for both basic biology and practical applications.

There exists abundant literature dealing with phenological observations on selected insect populations in nature or presenting experimental data. This body of evidence contributes to our understanding of regulatory mechanisms underlying the expression of particular adaptive phenological patterns and the plasticity and conservatism of these patterns, which either facilitate or impede insect dispersal, naturalization in new areas, and changes in distribution ranges. Unfortunately, this precious material is scattered in numerous and often hard-to-obtain papers, whereas specialized reviews only address the problem in general, using materials on individual species as mere examples.

Our current knowledge of the diversity of insect seasonal cycles still has to be organized. This idea was first brought forth by Professor V.P. Tyshchenko (Leningrad State University), who suggested that an "Encyclopedia of Seasonal Adaptations of Insects" should be compiled. This major project was commenced under his guidance and with his direct involvement in 1985–1986. It was based on experimental data mostly obtained on lepidopterans at the Laboratory of Entomology (Biological Institute, Leningrad State University). Unfortunately, the Encyclopedia was not completed.

This article is the first in a series of papers devoted to the seasonal adaptations of plant bugs (Miridae). We review and analyze data on seasonal development of species from subfamily Bryocorinae. This short review continues the series of previous generalizing works devoted to various heteropteran families: aquatic bugs (Saulich and Musolin, 2007), Anthocoridae (Saulich and Musolin, 2009), Plataspidae (Saulich and Musolin, 2014), and Pentatomidae (Musolin and Saulich, 2018; Saulich and Musolin, 2014, 2018), which can be regarded as a contribution to the elaboration of the ideas of A.S. Danilevskii and V.P. Tyshchenko.

Plant bugs are the largest family of true bugs (Heteroptera) and include over 11,000 species (Cassis and Schuh, 2012; Henry, 2017). The family is divided into 8 subfamilies, about 50 tribes, and over 1500 genera (Cassis and Schuh, 2012; Namyatova et al., 2016; Henry, 2017; Konstantinov et al., 2018). Plant bugs are predominantly phytophagous insects with broad or narrow host plant preferences. However, there are quite a few specialized predaceous, zoophytophagous, and phytozoophagous species. Many plant bugs are pests of agriculture, but some are used in biological control as natural enemies of other pests (Schaefer and Panizzi, 2000; Wheeler, 2001; Perez-Hedo and Urbaneja, 2015; Namyatova et al., 2016).

Bryocorinae is among the largest plant bug subfamilies. It comprises over 1000 mainly tropical and subtropical species from 200 genera arranged in 5 tribes: Bryocorini, Dicyphini, Eccritotarsini, Felisacini, and Monaloniini (Namyatova et al., 2016; Konstantinov et al., 2018). However, only several bryocorine species have been experimentally studied in terms of seasonal adaptations. These are mostly representatives of the tribe Dicyphini that are used in biological control against agricultural pests. Data on the control of seasonal development in these species are analyzed below.

Dicyphus errans (Wolff, 1804) is widely distributed in Europe from the south of Scandinavia to the Mediterranean; it is also reported from Transcaucasia and Turkey (Kerzhner and Josifov, 1999; Aukema and Hermes, 2014). This plant bug is a predator of thrips, aphids, and mites, but its preferable prey is whiteflies. It also makes use of over 150 plant species as sources of moisture (Voigt, 2005; Ingegno et al., 2017). Owing to its long legs and a number of morphological and behavioral adaptations, *D. errans* can colonize densely pubescent plants, which makes this species a unique biocontrol agent because many other predatory insects tend to avoid plants with pubescent surface (Southwood, 1986; Voigt, 2005; Voigt et al., 2007). This species is successfully being used against aphids in greenhouses in Italy (Schaefer and Panizzi, 2000). In France, a combination of *D. errans* with aphid parasitoids allowed successful and pesticide-free management of homopteran pests of tomatoes (Lyon, 1986; Malausa and Trottin-Caudal, 1996). *Dicyphus errans* is also recommended for use against the tomato leaf miner *Tuta absoluta* (Meyrick, 1917) (Lepidoptera, Gelechiidae), which is a serious invasive pest (Ingegno et al., 2017).

In Krasnodar Territory of Russia, *D. errans* is used in greenhouses for the control of pests of cucumber and summer squash. One generation is completed in 30–40 days. The bugs can be easily reared on fresh and cryopreserved eggs of the Angoumois grain moth *Sitotroga cerealella* (Olivier, 1789) (Lepidoptera: Gelechiidae) (Izhevsky et al., 1999).

On the British Isles, *D. errans* completes two generations a year and overwinters at the adult stage. Bugs visit various plants and differ in this respect from other *Dicyphus* species, which are monophagous. Adults are usually long-winged (f. *macroptera*) and occur from June till October. Females of the short-winged morph (f. *brachyptera*) are very rare and were only found in September. In Germany, bugs were encountered in greenhouses during winter where they probably overwintered and then, in spring, laid eggs in petioles of bloody crane's-bill (Butler, 1923; Southwood and Leston, 1959).

Under laboratory conditions (Pazyuk et al., 2018), the effects of photoperiod and temperature on the duration of immature development and the induction of facultative winter adult diapause were studied. The laboratory strain descended from two dozen individuals collected in 2013 in the environs of Rome (Tivoli: 41°58′N, 12°48′E and Ostia Antica: 41°45′N, 12°18′E). The experimental culture was kept at 22–25°C under a 16L : 8D photoperiod in cages with tobacco plants (*Nicotiana tabacum* cv. 'Virginia'). Eggs of the Angoumois grain moth *Sitotroga cerealella* and flower pollen were provided as food ad libitum.

The duration of immature development in *D. errans* at 20°C significantly depended on photoperiod (Fig. 1). Females reached the adult stage on average 1.3 d later than males did, but photoperiod affected development time of both sexes in the same manner. The duration of male and female immature development was minimal under short-day conditions (10–12 h of light per day), reached a maximum under 14-h light, but was also reduced under a 15-h photoperiod. Under the longest photophase used (16 h), the immature period was as short as that under short-day conditions.

In addition, female *D. errans* exhibited a well-defined long day-type photoperiodic response of the induction of adult diapause. Under short-day conditions (10 to 14 h of light per day) practically all the females entered diapause, whereas long-day conditions (15 and 16 h of light) promoted maturation and oviposition in about 90% of females. The threshold for this response was close to 14 h 30 min (Fig. 2). The photoperiodic response was not sensitive to temperature as the percentage of diapausing females in the near-threshold region practically coincided at 20 and 25°C.

Thus, two complementary photoperiodic responses were experimentally discovered in *D. errans*: one modifying the nymphal developmental rate and the other one controlling the induction of adult diapause. The presence of two photoperiodic responses is arguably adaptive. In Central Europe, *D. errans* populations are multivoltine with two or three generations being completed during the favorable season (Voigt, 2005) and overwinter as adults. Furthermore, it is possible that only mated females survive the winter while males perish as early as during the fall: Wachmann et al., 2004). As the photoperiodic induction of diapause is independent of temperature, winter quiescence always commences at the same time of the year regardless of weather conditions (first of all, temperature). However, under natural conditions, reproduction and immature development of insects are often protracted: individuals from early-season clutches usually have enough time for feeding and preparing for winter, whereas their late-season counterparts may be unable to molt to the adult stage in proper time and enter deep diapause before winter. The photoperiodic control of the nymphal developmental rate under short-day conditions of the fall (10–12 h of light) increases the chances that late-season nymphs successfully molt to the adult stage and proceed to the winter diapause state, even during the seasonal decrease in temperature.

Whether one analyzes the seasonal development of *D. errans* or develops methods for its mass rearing under artificial conditions, the experimental data need to be taken into account. Rearing the bug culture under long-day conditions (e.g., 16 h of light) would result in reproductively active females, whereas short-day conditions would induce diapause in nearly all of the females but accelerate nymphal development. Under near-threshold regimens (e.g., 14 and 15 h of light), immature development would be slower than under short-day conditions and many individuals would not enter diapause or it would be a shallower one. It should also be borne in mind that other geographic populations of *D. errans* may differ in their ecophysiological traits.

Dicyphus hesperus Knight, 1943 is a polyphagous predatory Nearctic plant bug that inhabits the west of North America from Canada to New Mexico (Henry and Wheeler, 1988). It is a promising biocontrol agent for

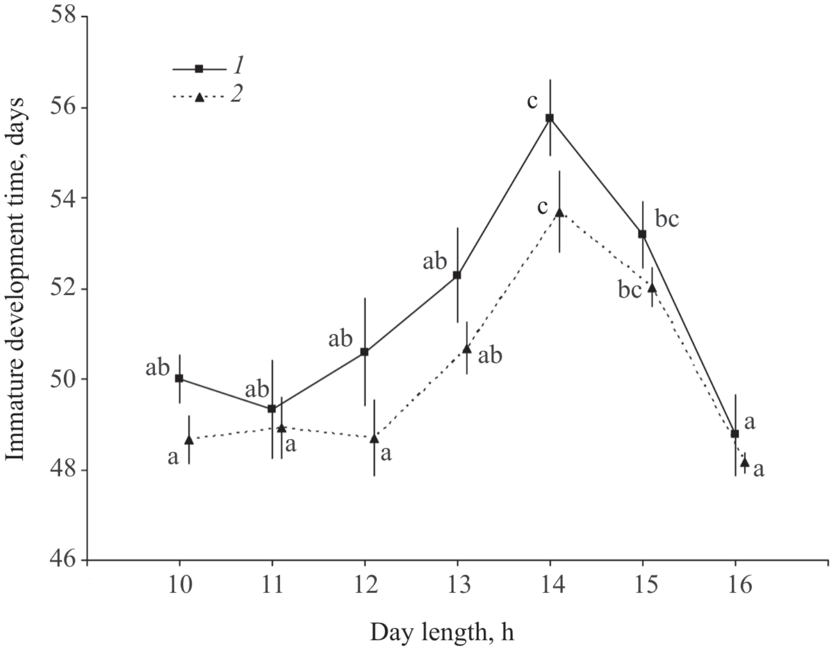

Fig. 1. The effect of photoperiod on the duration of immature development in *Dicyphus errans* (Wolff) at 20°C (after: Pazyuk et al., 2018). Immature development time, mean ± SE: (*1*) females, (*2*) males. Different letters denote significant differences (Tukey HSD test, $P < 0.05$) within sexes. Total sample size in the experiment was 774 females and 952 males, at least 99 individuals of either sex under each combination of temperature and photoperiod.

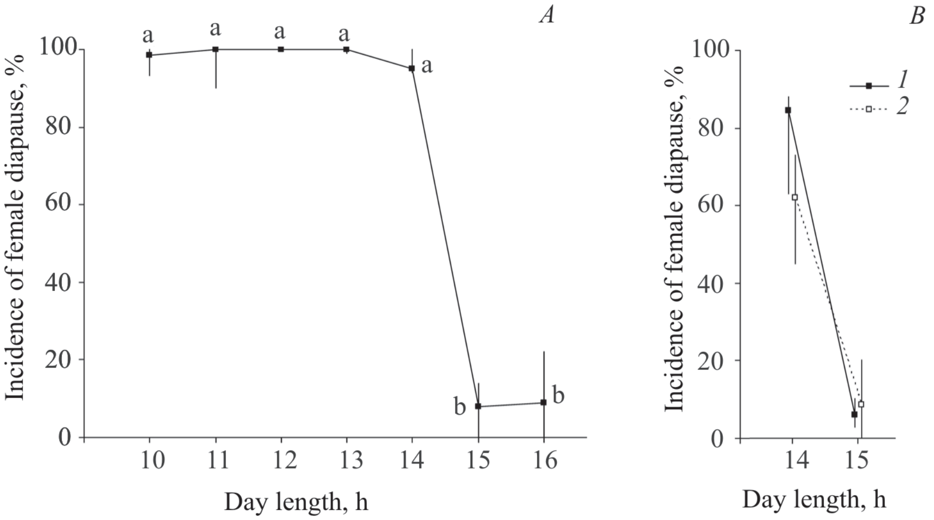

Fig. 2. The effects of photoperiod and temperature on the induction of adult diapause in female *Dicyphus errans* (Wolff) (after: Pazyuk et al., 2018). The number of diapausing females is expressed as median values across experimental series, bars denote quartiles. (*A*) at 20°C, (*B*) at 25°C. The number of cohorts was $n = 42$ (*a* and *b*, line *1*) and $n = 20$ (*b*, line *2*); the number of females was $n = 651$ (*A* and *B*, line *1*) and $n = 352$ (*B*, line *2*).

greenhouses and conservatories (van Lenteren, 2000), which is successfully used together with parasitoids *Encarsia formosa* Gahan, 1924 (Hymenoptera, Aphelinidae) and *Eretmocerus eremicus* (Rose et Zolnerowich, 1997) (Hymenoptera, Aphelinidae) for the control of tomato pests (Lambert et al., 2003). Also, methods for introduction of banker plants are currently being developed that would allow more rapid colonization of vegetable crops in greenhouses (Lambert et al., 2003; Sanchez et al., 2003). In the Netherlands, this plant bug is widely used against whiteflies that damage eggplants (Hatherly et al., 2008).

Dicyphus hesperus is a multivoltine species. Populations from Canada (British Columbia, 49°36′N, 119°40′W) and the USA (California, 35°43′N, 116°49′W) have been studied in quite sufficient detail (Gillespie et al., 2000, 2004; Gillespie and Quiring, 2005). Overwintering takes place at the adult stage; adults enter the state of diapause but diapausing females still feed and differ from reproductively active females in having a green, not black, abdomen (Gillespie and Quiring, 2005).

The thermal reaction norms for immature development do not significantly differ between the two *D. hesperus* populations mentioned above. This is also shown in Table 1 where data on nymphal development times from hatching to adult emergence are given after Gillespie et al. (2004).

The lower temperature threshold for development does not differ between these populations either and is close to 8°C. Such a relatively low value makes it possible for *D. hesperus* to be active all year round in many parts of California where long-term average temperatures never fall below the threshold value for this species even in winter. In that region, active females can be encountered as early as in January. These feed on aphids and are ready to reproduce (Gillespie et al., 2004). Similar to some other plant bugs, such as representatives of the genus *Lygus* (Beards and Strong, 1966), there is a brief adult diapause in *D. hesperus* that likely plays a synchronizing role and rather ensures the homogeneity of the age structure of the population than enhances winter survival.

The threshold for the photoperiodic induction of winter adult diapause in the Canadian population was 15.5 h at 23°C and remained similar under a thermoperiod of 23°C : 8°C (day : night). This threshold in the Californian population was only measured under the same thermoperiod and equaled approximately 13.5 h (Gillespie and Quiring, 2005). Adult diapause could only occur after the whole nymphal development had taken place under short-day conditions. Nymphs were shown to be highly sensitive to light levels and perceive civil twilight as daytime. Keeping eggs, nymphs of individual instars or adults under short-day conditions did not induce adult diapause (Gillespie et al., 2000).

In order to decide which of the two populations studied was more promising as agents of biological control for protected agriculture under seminatural conditions (without additional illumination) in Canada at the 49°N latitude, groups of individuals from different hatching dates were put in greenhouses. During the experiments, adult emergence times and the percentage of individuals entering diapause were recorded. Besides that, natural day length, both absolute and that including civil twilight, was accurately measured along with developmental temperature (Gillespie and Quiring, 2005).

The percentage of diapausing females under seminatural conditions in the greenhouse in British Columbia changed in accordance with experimentally determined thresholds for the photoperiodic responses in each population. In the Canadian population, most of the females in the group that emerged after August 25th (96%) entered diapause. For that group, day length including civil twilight decreased from 16.5 h at hatching to 14.9 h at adult emergence and the average developmental temperature was 21.9°C. A maximum incidence of diapause in the Californian population was observed for individuals that emerged after September 26th. Nymphal

Table 1. Temperature-dependent nymphal development times in two populations of *Dicyphus hesperus* Knight (after Gillespie et al., 2004)

Temperature, °C	Nymphal development time, days (mean ± SE; numbers in brackets show sample size)			
	males		females	
	population from British Columbia	population from California	population from British Columbia	population from California
14	51.0 ± 0.82 (23)	49.5 ± 0.69 (25)	48.3 ± 0.85 (24)	47.7 ± 0.52 (23)
19	29.0 ± 0.58 (17)	27.8 ± 0.43 (18)	29.4 ± 0.29 (27)	27.6 ± 0.32 (29)
22	21.5 ± 0.30 (26)	19.8 ± 0.17 (24)	20.3 ± 0.33 (21)	20.1 ± 0.25 (23)
27	16.3 ± 0.34 (18)	15.3 ± 0.10 (23)	16.2 ± 0.21 (24)	15.9 ± 0.17 (26)
35	14.9 ± 0.45 (15)	14.0 ± 0.38 (7)	13.3 ± 0.42 (16)	15.7 ± 0.47 (10)

development in that group took place under a day length decreasing from 14.3 to 13 h and at an average temperature of 20.6°C. Thus, Californian *D. hesperus* females delayed the onset of diapause almost by one month, as compared with females from the Canadian population, which quite well agrees with the geographic variation in the photoperiodic response revealed under experimental conditions.

Even though the incidence of diapause reached almost 100% in the experimental females from the Canadian population and over 60% in those from California, it decreased in the groups of individuals that emerged still later in the season. For example, half of Canadian *D. hesperus* females started laying eggs after 6 weeks and half of Californian ones after only 2 weeks (Fig. 3).

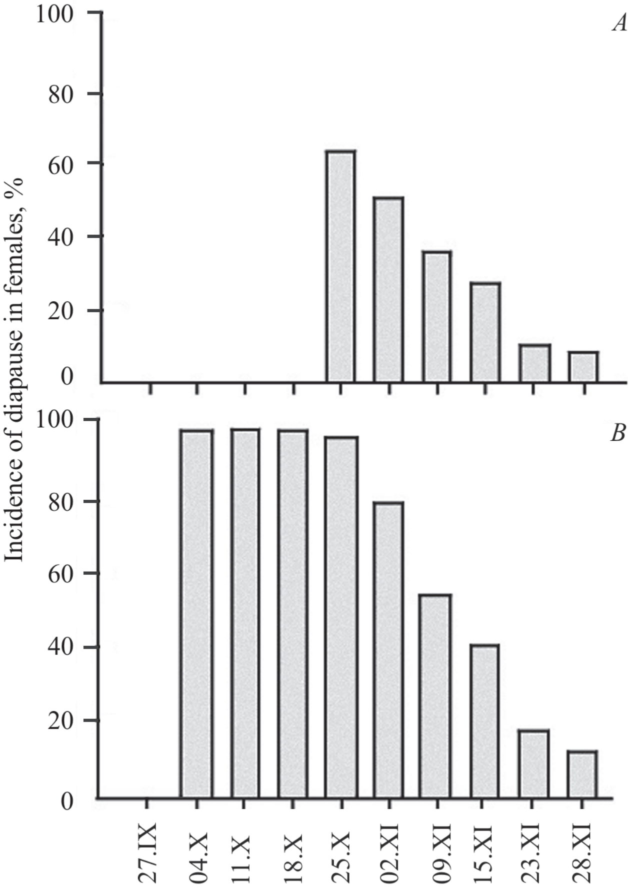

Fig. 3. The percentage of diapausing (not reproducing) females of *Dicyphus hesperus* Knight in an experiment with populations from (*A*) California and (*B*) British Columbia. Data are only shown for groups of individuals that emerged after October 18th or November 27th (see the *x*-axis) (after: Gillespie and Quiring, 2005). Sample size (the number of females): (*A*) $n = 34$, (*B*) $n = 46$.

In general, these results suggest that Californian *D. hesperus* is a more promising candidate for biocontrol in greenhouses because, under seminatural conditions, fewer females from this southern population enter diapause, the timing of this diapause is shifted to later dates, and postdiapause reproduction begins considerably earlier (Gillespie and Quiring, 2005).

Elevation of the habitat was shown to exert a weak effect on the percentage of diapausing individuals across three populations from California. Bugs collected at different elevations (2000 m a.s.l., about 500 m a.s.l., and at the bottom of the mountains) showed photoperiodic responses with a threshold between 13 and 14 h (Gillespie et al., 2000).

The results of studies with North American populations of *D. hesperus* and the successful use of this predator in Canadian greenhouses (in British Columbia, Ontario, and Quebec) suggest that *D. hesperus* might be used in other countries and on other continents. Therefore, survivorship of different developmental stages of *D. hesperus* was assessed under climatic conditions of northern Europe (Birmingham, Great Britain: 52°29′N, 1°54′W). This was done by measuring the supercooling point in different developmental stages and calculating mortality rates following long-term storage at various temperatures. The experiments were carried out with the Californian population (Hatherly et al., 2008).

Nymphs, active (non-diapausing) adults, and diapausing adults all had a supercooling point of about –20°C. The lower lethal temperatures resulting in 10, 50, and 90% mortality (LT_{10}, LT_{50}, and LT_{90}) were found to be –15.0, –17.6, and –21.0°C in *D. hesperus* nymphs; –15.0, –17.6, and –20.7°C in non-diapausing adults; –17.9, –19.2, and –20.4°C in diapausing adults. Durations of low-temperature exposure that resulted in 10, 50 and 90% mortality are shown in Fig. 4 after Hatherly et al. (2008).

Simultaneously with the abovementioned tests, experiments under seminatural conditions were also carried out in Birmingham (Hatherly et al., 2008). When I instar nymphs of *D. hesperus* were transferred to winter conditions, all unfed individuals died after 70 d, whereas 5% of nymphs that had access to food survived till the end of winter (140 d) and molted to the adult stage upon subsequent return to laboratory conditions.

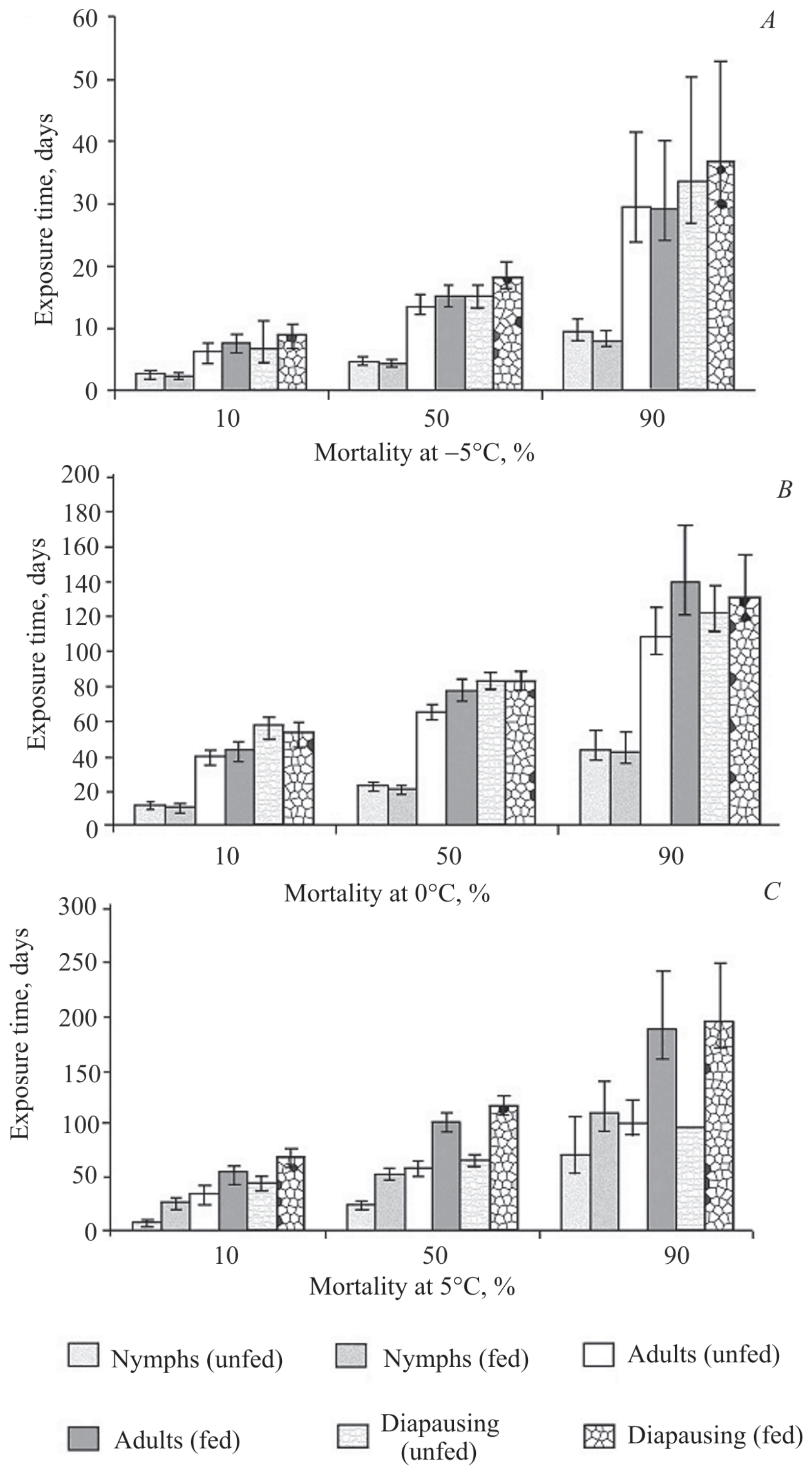

Fig. 4. The time to 10, 50, and 90% mortality (d, mean ± 95% CI) at a temperature of (*A*) –5°C, (*B*) 0°C or (*C*) 5°C among fed or unfed nymphs and diapausing or non-diapausing adults of *Dicyphus hesperus* Knight (after: Hatherly et al., 2008). The number of replicates per trial: $n = 4$ (10 ind. in each).

In a similar experiment with adult *D. hesperus*, all unfed diapausing individuals also died out during the 140-d exposure, but 50% of fed diapausing adults and 15% of fed non-diapausing adults survived. When returned to the laboratory after 5 months in the field, all the adults fed and mated and females gave rise to viable progeny, regardless of whether they spent the winter in diapause or in the active state.

Thus, field and laboratory experiments suggest that temperate winter temperatures do not pose a formidable obstacle for naturalization of *D. hesperus* across most of Europe, which holds even for the bugs from the southern population (California). Thus, it is hoped that this predator can be used in the biological control of insect pests all year round (Hatherly et al., 2008).

Macrolophus melanotoma (A. Costa, 1853) (= *M. caliginosus* Wagner, 1951)—is a Eurasian species (Schaefer and Panizzi, 2000) distributed in the south of Europe, in Western Asia (Turkey, Iraq, Iran, Cyprus, Israel, and Yemen), and in the north of Africa (Algeria, Tunisia, Canary Islands, Libya, and Morocco) (Kerzhner and Josifov, 1999; Aukema et al., 2013). This is a phytozoophagous species that feeds on small insects and mites. In nature, it is most commonly encountered on the Asteraceae and Solanaceae, in particular on tomatoes (Schaefer and Panizzi, 2000). This species is common in the Mediterranean region (Malausa and Trottin-Caudal, 1996), where it is widely used against arthropod pests in greenhouses.

To maintain a greenhouse population of *M. melanotoma* during periods of low prey density, it is recommended to supply the bug with eggs of the Angoumois grain moth (*S. cerealella*) or Mediterranean flour moth *Ephestia kuehniella* (Zeller, 1879) (Lepidoptera, Pyralidae). At high population density levels, *M. melanotoma* also feeds on plant fluids and inflicts noticeable damage. This is why this plant bug is not recommended for the management of *Gerbera* pests (Izhevskii et al., 1999).

Macrolophus melanotoma overwinters as nymphs of different instars. Under natural conditions of the western Peloponnese (Greece), early instar nymphs predominate in January and February, whereas adults emerge en masse as late as in June and July (Perdikis et al., 2007). In Spain, adults emerge after mid-March (Alomar et al., 1994).

In France (Carpentras, 44°03′21″N, 5°02′56″E), *M. melanotoma* has two generations per year and, provided that food is available, successfully overwinters on evergreen vegetation. Females have mature oocytes and oviposition was observed even in the middle of winter (Carayon, 1986), which indicates an absence of diapause.

Relatively recently *M. melanotoma* was introduced into the British Isles with the purpose of using it in greenhouses against the whitefly *Trialeurodes vaporariorum* Westwood, 1856 (Homoptera, Aleyrodidae), the aphid *Myzus persicae* (Sulzer, 1776) (Homoptera, Aphididae), and the spider mite *Tetranychus urticae* C.L. Koch, 1836 (Trombidiformes, Tetranychidae) (Foglar et al., 1990). However, the bugs were soon discovered outside greenhouses and conservatories. The potential for and possible consequences of naturalization of this species in Great Britain were yet to be determined.

Experiments were carried out with a population of *M. melanotoma* obtained from a Syngenta Bioline insect breeding facility at Little Clacton (Essex, UK) and the following parameters were measured: the duration of all immature stages in the temperature range from 11 to 26°C, ordinary and weighted regression coefficients for developmental rate in this range, as well as lower temperature thresholds and sums of degree-days for eggs, nymphs, and total immature development (Hart et al., 2002; Table 2).

As inferred from the experimentally obtained lower temperature threshold and sum of degree-days, *M. melanotoma* can complete two generations during the summer season in Great Britain (Hart et al., 2002).

The ability of *M. melanotoma* to survive British winter was tested by measuring cold-hardiness of different developmental stages of this species in the laboratory and by carrying out field trials in two geographic locations: Birmingham (52°28′53″N, 1°53′59″W) and York (53°57′27″N, 1°4′57″W).

Supercooling points measured by the thermoelectric cooling method were identical (around –20°C) in nymphs and adults of *M. melanotoma* regardless of prior acclimation at low temperatures (–5, 0 or +5°C) or lack thereof. The bugs were freeze-intolerant during any developmental stage (Hart et al., 2002).

Table 2. Lower temperature thresholds (LTT) and sums of degree-days (SDD) for different developmental stages of *Macrolophus melanotoma* (A. Costa, 1853) calculated using different methods* (after Hart et al., 2002).

Stage	Calculation method			
	ordinary linear regression		weighted linear regression	
	LTT, °C	SDD, °C×d	LTT, °C	SDD, °C×d
Egg	9.5	175.4	8.7	184.8
Nymph	8.1	279.3	7.2	270.3
Total immature	8.4	472.0	7.7	495.0

* There were 5–29 individuals of either sex at each of the 5 temperature regimens used.

The supercooling point is often interpreted as a criterion of cold hardiness. However, it merely mirrors the ability to withstand a short-term exposure to negative temperatures. To reveal actual tolerance to cold, experiments with chronic cold exposures were conducted. This part of the study was performed both in the laboratory and in the field (Fig. 5). Different experimental regimes showed that the availability of prey is of major importance for enhancing nymphal and adult cold hardiness (Hart et al., 2002).

The greatest cold hardiness was observed in adults provided with food, irrespective of prior low-temperature acclimation. Ninety percent of adults remained viable after 25 d at 5°C and 10% did so even after spending three months in the cold (Fig. 5; Hart et al., 2002).

Field experiments also showed that both nymphs and adults of *M. melanotoma* survived the winter and confirmed the importance of prey accessibility. Under field conditions, nymphs of this phytozoophagous bug turned out to be more cold tolerant as a minor fraction of these (3%) remained viable for almost 200 d (Hart et al., 2002).

Taking into account the fact that daily fluctuations in the environment (in particular, the diurnal rise in temperature) and a wide availability of suitable microhabitats have beneficial effects on insect fitness, it was conjectured that *M. melanotoma* was capable of naturalizing in the wild in Great Britain. Thus, an introduced species that lacked specific ecophysiological adaptations in the form of diapause or any other form of

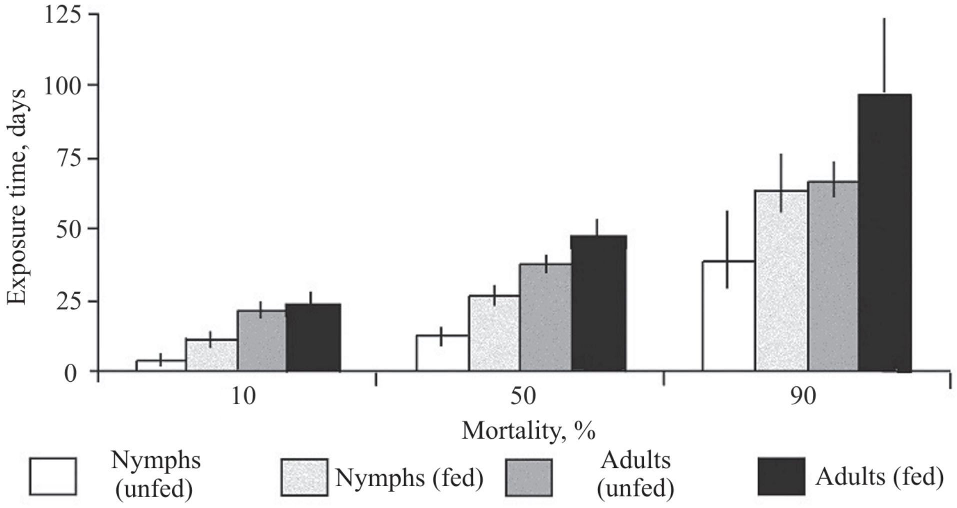

Fig. 5. The time to 10, 50, and 90% mortality (d, mean ± 95% CI) of acclimated and non-acclimated nymphs and adults of *Macrolophus melanotoma* of different categories at a temperature of 5°C under a 18-h photoperiod (after: Hart et al., 2002). The number of replicates per trial: $n = 5$ (10 ind. in each).

winter dormancy nevertheless turned out to have behavioral, ecological, and physiological traits that facilitated naturalization. This example is a telling illustration of how important it is to consider possible consequences of introduction of alien species to new territories even with the aim of limited use in greenhouses and conservatories.

Macrolophus pygmaeus (Rambur, 1839) is widely distributed across the Palaearctic from Finland to Algeria and from the Azores to Turkmenistan and Tajikistan (Puchkov, 1978; Kerzhner and Josifov, 1999; Aukema and Hermes, 2014), although some contemporary authors believe the Central Asian finds to be erroneously identified (Martinez-Cascales et al., 2006; Sanchez et al., 2012). In 2007, *M. pygmaeus* was first recorded in New Zealand (Eyles et al., 2008).

As a zoophytophagous insect, *M. pygmaeus* can consume both animal and plant matter (Perdikis and Lykouressis, 2000), sometimes causing damage to cultivated plants. However, the beneficial effect of the presence of these mirid bugs in agroecosystems considerably outweighs their usually insignificant damage. Thus, *M. pygmaeus* is successfully used against whiteflies, thrips, aphids, spider mites, and some other pests both in greenhouses and in the open field (Boyarin, 2000; Krasavina et al., 2010; Messelink and Janssen, 2014; Messelink et al., 2014). A peculiar feature of this zoophytophagous insect, besides its polyphagy, is the ability to complete the life cycle in the total absence of animal food, even though development slows down in this case (Perdikis and Lykouressis, 2002). The host plant species does not substantially affect developmental parameters (Perdikis and Lykouressis, 2004).

According to the data available, under natural conditions, *M. pygmaeus* overwinters as nymphs of various instars (Puchkov, 1978), but usually V instar, which is the final one (Cobben, 1968).

There is a study of the effects of day length on nymphal development and female maturation in two strains of *M. pygmaeus* that descend from individuals collected in the environs of Sochi (Krasnodar Territory, Russia, 43°54′N, 39°18′E) and in the environs of Rome (Italy, 41°45′N, 12°18′E and 41°57′N, 12°48′E) (Pazyuk and Reznik, 2016).

Experimental insects were kept at a constant temperature of 20°C under two photoperiods, 10 and 16 h of light per day. Nymphs and adults were fed on eggs of *S. cerealella*. Egg development took 18–20 d, nymphal development lasted 25–30 d, and females required 4–6 d to maturate. Under short-day conditions (10 h), male and female nymphs of both strains took 0.7–2.8 d longer to develop than under long-day conditions (16 h), and female maturation was also slower. Egg development was unaffected by day length. Under both photoperiods, males developed faster than females. Under short-day conditions, females of the Rome strain maturated noticeably faster than those originating from Sochi. The Sochi strain exhibited more rapid development at lower temperatures and a stronger tendency for delayed reproduction under short-day conditions, which is presumably explained by a more drastic decrease in temperatures during the fall in Sochi, as compared with Rome (Pazyuk and Reznik, 2016).

It is well known that short-day photoperiods often induce winter diapause (Danilevskii, 1961; Zaslavskii, 1984; Tauber et al., 1986; Saunders et al., 2002; Saulich and Volkovich, 2004). In adult *M. pygmaeus*, the effect of short days (at least at 20°C) was only manifested in a short-term delay in the maturation of females, as practically all individuals became mature by the 10th day (Pazyuk and Reznik, 2016).

Nesidiocoris tenuis (Reuter, 1895) is a cosmopolitan species (Vinokurov et al., 2010), native to the Old World, that dispersed to Palaearctic islands by air and widely colonized the Palaeotropical realm (Schaefer and Panizzi, 2000).

Some authors regard this species as a pest of crops, especially of tomatoes (El-Dessouki et al., 1976; Raman and Sanjayan, 1984; Raman et al., 1984; Sanchez, 2009), while others believe that the beneficial activity of *N. tenuis* as a predator far exceeds the damage it inflicts (Vacante and Tropea-Garzia, 1994; Carnero et al., 2000; Arnó et al., 2006). *Nesidiocoris tenuis* is currently successfully used in the biological control of many leaf-mining insects as well as openly feeding thrips, whiteflies, and spider mites in temperate climate greenhouses and outdoors in Europe and Asia (Wheeler, 2001; Urbaneja et al., 2005; Sanchez and Lacasa, 2008; Molla et al., 2011; Calvo et al., 2012; Xu et al., 2012; Perdikis et al., 2015; Shaltiel-Harpaz et al., 2016). Some authors mention that this species exhibits cannibalism as many other predatory insects do. In particular, nymphs and adults of *N. tenuis* prey upon conspecifics that are weakened for whatever reason or are in the process of molting (El-Dessouki et al., 1976).

Field observations on the development of *N. tenuis* in various regions as well as results of laboratory tests suggest that the populations from Morocco (Hughes et al., 2009), Spain (Sanchez et al., 2009), Armenia (Manukyan and Terlemezyan, 1984), Japan, and Korea (Pazyuk et al., 2014) lack a well-defined diapause. It can be assumed that bugs spend the winter either in a physiologically active state, hiding in various shelters, or in a quiescent state.

In Egypt (Cairo, 30°04′N, 31°15′E), where the average winter temperature is about +17°C and different developmental stages of *N. tenuis* can be encountered all year round, 6 generations are completed during the summer and 2 more during the winter (El-Dessouki et al., 1976). In Iraq (Baghdad, 33°20′N, 44°24′E) 3 summer generations were recorded (Al-Azawi and Al-Azawi, 1988).

In order to assess the possibilities for wider use of this beneficial zoophytophagous bug outside its native distribution range, experiments were carried out in different years with populations from the Mediterranean region, in particular, Morocco (Hughes et al., 2009; Hughes et al., 2010) and Iran (Tehran Province, 35°19′27″N, 51°38′45″E; Mirhosseini et al., 2018), and from the south of the Far East: Korea (Suwon, 37°16′N, 126°59′E) and Japan (Miyazaki, 31°55′N, 131°25′E) (Pazyuk, 2010; Pazyuk et al., 2014).

The Moroccan population of *N. tenuis* was studied in detail in terms of its thermal reaction norms for development (Hughes, 2010; Fig. 6).

The lower temperature threshold for immature development was found to be 12.9°C and the sum of degree-days, 278°C×d (Hughes et al., 2009). According to the estimated data across 1993–2007 for Birmingham (Great Britain, 52°29′N, 1°54′W), where the studies were carried out, the amount of heat is sufficient for the completion of only one generation per year. Only occasional warmer years may support a partial second generation. However, as experimental data show, all nymphs perish in the field early in November with the onset of cold weather (Hughes, 2010).

Supercooling points determined by the thermoelectric method in acclimated and non-acclimated adults and nymphs ranged from –17.6 to –21.5°C and the time to 50% mortality at 5°C varied from 6.1 d in nymphs to

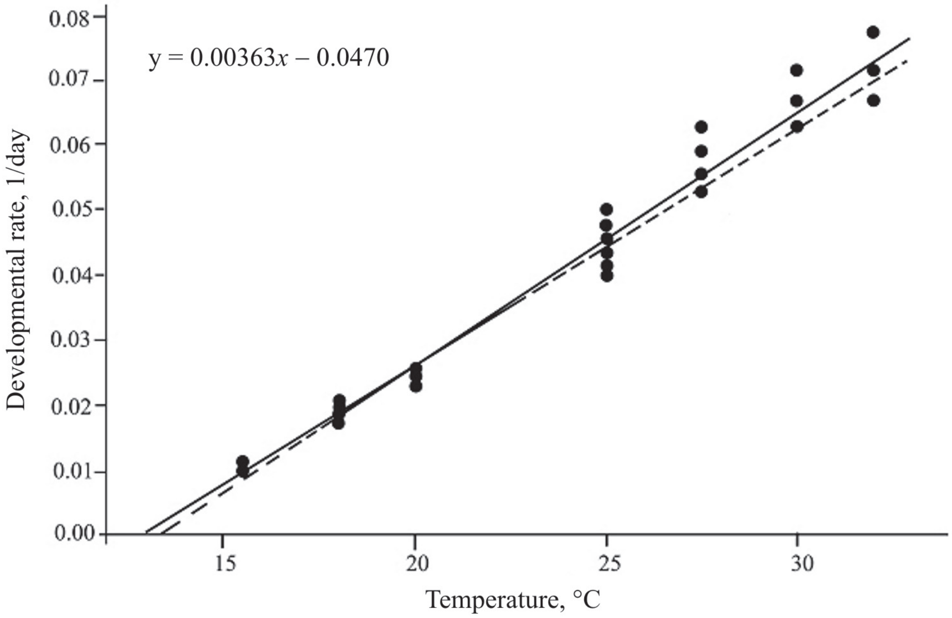

Fig. 6. Temperature-dependent immature developmental rate of *Nesidiocoris tenuis* under a 16-h photoperiod (after: Hughes et al., 2009; Hughes, 2010). Solid line: ordinary linear regression, dashed line: weighted linear regression. The intersection of the dashed regression line with the x-axis is the lower temperature threshold of 12.9°C. Sample size (ind./regimen): $n = 32\ldots72$.

8.9 d in adults. Under field conditions, 100% mortality during the winter was recorded after less than 4 weeks. In the absence of diapause, active individuals became immobilized at 4°C and entered chill coma at 0.3°C (Hughes et al., 2009)

In the Iranian population of *N. tenuis*, developmental rates of all stages were measured at temperatures from 14 to 34°C under a 16-h light regime. The lower temperature threshold and sum of degree-days obtained over the broad temperature range (10.94°C and 318.37°C×d, respectively: Mirhosseini et al., 2018) were similar to the developmental parameters for a Japanese population (10.28°C and 339.57°C×d: Ikemoto and Takai, 2000).

Far Eastern populations of *N. tenuis* also did not exhibit any state of diapause, akin to the population from Morocco. Their thermal reaction norms for immature development were also similar (Pazyuk et al., 2014). A comparison of thermal constants for the populations from the south of the Far East and one from Spain highlighted their similarity (Table 3).

However, a comparative study of temperature-sensitive traits (survivorship, nymphal developmental rate and adult maturation) between two Asian strains of *N. tenuis* (a northern one from Korea and a southern one from the subtropics of Japan) showed that the bugs retained the temperature responses of their ancestral populations, despite long-term maintenance in the laboratory. Southern bugs were better adapted to higher temperatures and northern ones, to lower temperatures. For example, nymphal survivorship in the northern strain of *N. tenuis* at a low temperature of 15°C was twice that in the southern strain. Therefore, it is recommended that bugs from more northerly populations should be used in cooler greenhouses (Pazyuk et al., 2014).

In general, results from different regions indicate that *N. tenuis* cannot naturalize even in Central Europe due to the absence of a specific physiological state for overwintering. It is a promising biocontrol agent for protected agriculture.

DISCUSSION

This communication summarizes the data for only 5 species from the speciose subfamily Bryocorinae (ca. 1000 species): *Dicyphus errans*, *D. hesperus*, *Macrolophus melanotoma*, *M. pygmaeus*, and *Nesidiocoris tenuis*. All of them belong to the tribe Dicyphini and were studied in particular detail due to their current or potential economic significance as biocontrol agents against arthropod pests in greenhouses. This is probably why the main focus of these studies was on thermal reaction norms and dietary preferences and not on other aspects of the bugs' seasonal cycles.

Nevertheless, even the limited data presented in this review show that seasonal adaptations of bryocorine plant bugs are quite diverse. Three of these species, *Macrolophus melanotoma, M. pygmaeus*, and *N. tenuis*, have homodynamic cycles at least in some parts of their distribution ranges. As their lower temperature thresholds for development are around 8–9°C, these species actively develop all year round, provided that the environmental conditions are favorable and food is available. Depending on the climatic zone and ambient temperature, these bugs produce from 2 to 6 and even more generations during the summer (like *N. tenuis* in Egypt). They spend the winter at different developmental stages, either in a physiologically active state, hiding in various shelters that protect them from low temperatures, or in a state of quiescence. Adults and nymphs continue actively feeding during the winter and females have mature oocytes. The possibility of such overwintering has

Table 3. Thermal constants for immature development in different populations of *Nesidiocoris tenuis* (Reuter)

Population	Nymphal SDD, °C×d	Total immature SDD, °C×d	LTT, °C	Source
Morocco	–	278	12.9	Hughes et al., 2009
Spain	182.3	–	11.7	Martinez-Garcia et al., 2016
Iran	–	318.37	10.94	Mirhosseini et al., 2018
Japan, Korea	174–189	–	12.8–13.0	Pazyuk et al., 2014
Japan	–	339.57	10.28–10.94	Ikemoto, Takai, 2000 (after: Mirhosseini et al., 2018)

been shown in many insects, including true bugs, that inhabit regions with mild winters (Richman and Mead, 1980; De Clercq and Degheele, 1993; Panizzi and Hirose, 1995; Wheeler, 2001).

Two other species, *Dicyphus errans* and *D. hesperus*, have heterodynamic seasonal cycles and spend the winter in a state of adult diapause, the onset of which is controlled by a long day-type photoperiodic response. In addition, *D. errans* exhibits photoperiodic control of nymphal developmental rate, a response that ensures a timely transition to the diapausing stage (in this case, adult), which is necessary for successful overwintering. In *D. hesperus,* the threshold for the photoperiodic induction of diapause shows geographic variation and only the nymphal stage is sensitive to photoperiod.

Bryocorines also have other seasonal adaptations, such as wing polymorphism (or polyphenism; in *D. errans*) and diapause-related changes in the body coloration (in *D. hesperus*). Mechanisms underlying these adaptations and their occurrence among plant bugs require further study. Whether or not the seasonal adaptations discovered in bryocorines are typical of the family as a whole is also yet to be found out.

The use of introduced heterodynamic natural enemies of pests in protected agriculture may have negative economic and ecological consequences. First, diapause decreases the period of activity of biocontrol agents as most of the species studied do not feed when in diapause. In this case, additional illumination is needed that would increase the length of daytime, prevent diapause, and extend the period of active predation. However, prolonged lighting may also stimulate non-diapause development, and, most importantly, feeding of phytophagous pests. Second, the presence of a long period of physiological inactivity in the seasonal cycle facilitates naturalization of introduced species on a novel territory outside the zones of protected agriculture. This is what already happened with *Macrolophus melanotoma* on the British Isles (Hart et al., 2002) and *Dicyphus hesperus* in the Netherlands, when a small number of bugs was discovered outside greenhouses (Hartherly et al., 2008). It turned out subsequently that the bugs survived all year round under rather harsh and unfamiliar conditions of northern latitudes. There should be more such examples but these are seldom mentioned in the literature.

Preliminary experimental studies of development in the species intended for introduction as biocontrol agents should reduce the risk of naturalization. During the early stages of establishing in a new area, it is seasonal adaptations controlling development of bug populations in their natural environments that are particularly important. In greenhouses, higher efficiency of biocontrol measures can be achieved with southern multivoltine populations of homodynamic species, especially if these require fewer degree-days as immatures, have high reproduction rates at the adult stage, and easily switch to novel prey. Under field conditions, polyphagous heterodynamic univoltine species with deep obligate diapause are more likely to naturalize successfully.

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