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Seasonal Development of Plant Bugs (Heteroptera, Miridae): Subfamily Mirinae, Tribe Mirini

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Abstract—The available data on seasonal development of plant bugs (Mirinae: Mirini) are reviewed, and the level of understanding of their seasonal adaptations is evaluated. The ecological responses involved in control of seasonal development of 14 species from 5 genera (*Adelphocoris*, *Apolygus*, *Lygus*, *Lygocoris*, and *Stenotus*) are analyzed in detail. All the studied species are broadly polyphagous and produce a varying number of annual generations in different climatic zones. The studied members of four genera, namely *Adelphocoris*, *Apolygus*, *Lygocoris*, and *Stenotus*, hibernate at the embryonic stage while bugs of the genus *Lygus* do so at the adult stage. Some species of the genera *Adelphocoris* and *Lygus*, in particular *Lygus pratensis*, have acquired a pronounced ability to fly over long distances, facilitating the search for flowering vegetation. However, unlike many insects that make distant migrations in the state of adult diapause, females of plant bugs of the genus *Adelphocoris* migrate with mature eggs in their oviducts. This feature allows *Adelphocoris* females to successfully colonize new areas even in the absence of males, since females do not need additional mating in the colonized area. For the majority of Mirini species experimentally studied in the laboratory, the temperature parameters of development and the sum of effective temperatures needed to complete the full generation were calculated. When combined with observations done under natural conditions, these data allowed us to determine the exact number of annual generations produced by the species or population. The role of day length in the control of seasonal development was analyzed in detail in three species of the genus *Adelphocoris*: *A. triannulatus*, *A. suturalis*, and *A. lineolatus*. The conditions inducing and terminating adult diapause were studied in detail in *Lygus hesperus* in the southern United States. The seasonal development of *Lygocoris pabulinus* is an unusual example of an obligate host plant change during the year. The diapausing eggs of this species overwinter in the tissues of woody plants but the nymphs then migrate onto herbaceous plants on which the summer generations develop. Such a seasonal strategy is more characteristic of aphids (Homoptera) than of true bugs (Heteroptera). On the whole, our analysis of the available data indicates that the control of seasonal development of plant bugs of the subfamily Mirinae is still poorly understood despite their high economic importance. Most reports deal with a small number of experimentally studied species and are limited to the data on temperature parameters of development. The important role of photoperiodic adaptations in the control of seasonal development has been demonstrated only for a few well-studied species (e.g., *Adelphocoris triannulatus*); such data are crucial for analysis and prediction of seasonal development and spread of harmful and beneficial insects, since the seasonal cycle of each population of a given species is strictly synchronized with the local conditions.

Keywords: adult diapause, biological control, day length, dormancy, seasonal development, photoperiod, photoperiodic response, plant protection, true bugs, voltinism

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The seasonal development of insects is highly diverse, and its various aspects are hard to classify. It is based on adaptations which facilitate the survival of local populations, the most efficient use of the available resources, and establishment of specific annual cycles under the conditions of pronounced seasonality of the climate. In our earlier works (Musolin and Saulich, 1999; Saulich and Musolin, 2007, 2018) we distinguished four main categories of phenomena determining the seasonal cycles in insects:

– *the active state* and the responses controlling active development, first of all its rate;

– *diapause* and the responses controlling induction, maintenance, and termination of physiological dormancy;

– *migrations* and the responses controlling active movements aimed at avoiding adverse conditions;

– *seasonal polyphenism* and the responses controlling the morphological and physiological traits (coloration, shape, size, and proportions of body parts, the degree of wing development, etc.) that are often closely linked to diapause or some other form of seasonal dormancy.

These seasonal adaptations, combined in various ways, form the basis for the diversity of seasonal patterns which are traditionally classified into several main types (Saulich and Musolin, 2014, 2018).

According to the recent assessment, the family of plant or capsid bugs (Miridae) is the largest family in the order of true bugs (Heteroptera). It comprises 8 subfamilies, about 50 tribes, over 1500 genera, and over 11 100 species (Cassis and Schuh, 2012; Namyatova et al., 2016; Henry, 2017; Konstantinov et al., 2018).

In the previous paper (Saulich and Musolin, 2019) we analyzed the seasonal adaptations and the corresponding phenological patterns in the subfamily Bryocorinae. This large taxon comprises about 1000 species of plant bugs, but seasonal adaptations have been characterized only for 5 species: *Dicyphus errans* (Wolff), *D. hesperus* Knight, *Macrolophus melanotoma* (A. Costa), *M. pygmaeus* (Rambur), and *Nesidiocoris tenuis* (Reuter), all of them belonging to the same tribe, Dicyphini. However, as shown in our previous review, even these scanty data demonstrate considerable diversity of the seasonal adaptations in Bryocorinae. In particular, three of the above species, namely *M. melanotoma*, *M. pygmaeus*, and *N. tenuis*, have a homodynamic seasonal cycle at least in some parts of their ranges. In different climate zones, depending on the temperature, these bugs produce from 2 to 6 and more generations during summer (e.g., *N. tenuis* in Egypt). They can overwinter at different developmental stages, either in a quiescent state or in a physiologically active state, using various shelters to escape low temperatures; both nymphs and adults actively feed in winter while egg maturation continues in the females. The two remaining species, *D. errans* and *D. hesperus*, have a heterodynamic seasonal cycle and form adult diapause that is induced by photoperiodic response (PhPR) of a long-day type. Besides, *D. errans* was found to possess photoperiodic control of the nymph growth rate, facilitating timely production of the diapausing stage (in this case, the adult), which is essential for successful overwintering. Geographic variation in the PhPR threshold was revealed in *D. hesperus*, with day length sensitivity being restricted to the nymphal stage. Other seasonal adaptations found in Bryocorinae include wing polymorphism or polyphenism in *D. errans* and changes in the body coloration linked to diapause in *D. hesperus* (Saulich and Musolin, 2019).

Here we consider the seasonal adaptations in one more plant bug subfamily, Mirinae Hahn, 1833, which comprises over 300 genera in 6 tribes: Herdoniini, Hyalopeplini, Mecistoscelidini, Mirini, Resthemini, and Stenodemini. Only 2 of these tribes, Mirini Hahn, 1833 (about 250 genera) and Stenodemini China, 1943 (about 35 genera), have cosmopolitan distribution while the other 4 tribes are represented in the tropical and subtropical areas (Schuh and Slater, 1995; Schuh and Weirauch, 2020). The Palaearctic fauna of Mirinae includes about 950 species from 126 genera (Kerzhner and Josifov, 1999). This review is focused on the data characterizing the seasonal adaptations in the tribe Mirini.

Genus ***Adelphocoris*** Reuter, 1896

Adelphocoris triannulatus (Stål, 1858)

This bug is distributed in the south of Siberia and the Russian Far East, in China, Korea, and Japan (Vinokurov et al., 2010). It inhabits grasslands and crop fields and mostly damages legumes, similar to many other *Adelphocoris* species (Vinokurov and Kanyukova, 1995).

The seasonal development of *A. triannulatus* was experimentally studied in Takanabe (Japan; 32.1°N, 131.5°E), where this bug was discovered in great numbers in sweet potato fields. There the species was also found to be phytozoophagous, although before that, animal diet had been considered uncharacteristic of *Adelphocoris* bugs. The temperature parameters of development of this species were determined in laboratory experiments at temperatures from 15 to 30°C, and the data were used to calculate the lower temperature thresh-

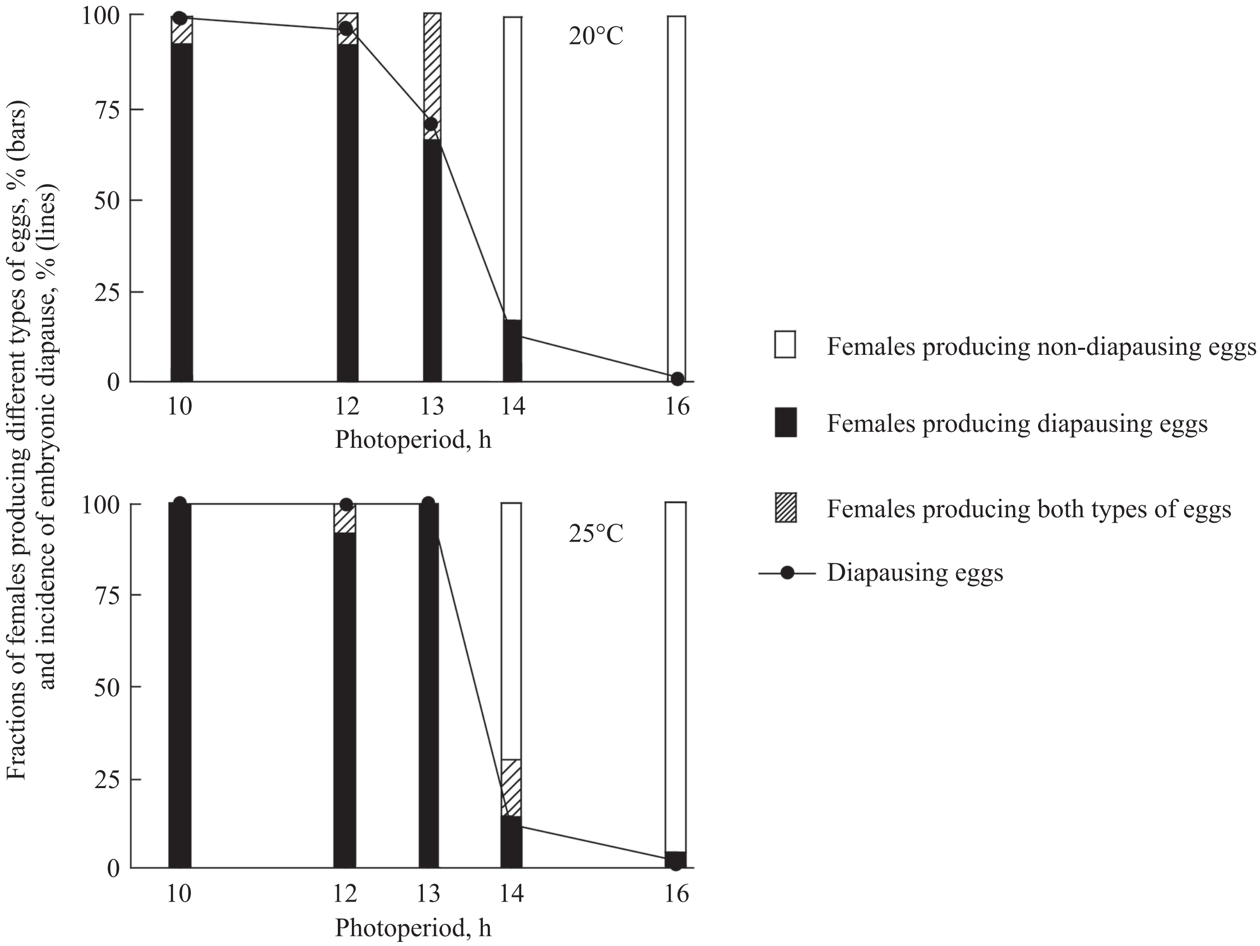

Fig. 1. The fraction of diapausing eggs laid by females of *Adelphocoris triannulatus* (Stål) which were kept at different photoperiods at 20°C or 25°C, and the fraction of females which laid non-diapausing eggs, diapausing eggs, and both types of eggs under the same conditions; population from Takanabe (Japan; 32.1°N, 131.5°E) (after Tajima et al., 2018).

olds (LTT) for development of eggs (10.0°C) and nymphs (12.7°C) and for maturation of females (13.5°C). The sum of effective temperatures (SET) required for completion of these developmental stages was 186.3, 184.8, and 67.5 degree-days, respectively, with a total of nearly 440 degree-days (Tajima et al., 2018).

The species overwinters at the egg stage. Laboratory experiments showed that the onset of winter embryonic diapause was controlled by the living conditions of females of the maternal generation. Under long-day conditions (16 h of light a day) the females produced actively developing eggs, whereas under short-day conditions (10 and 12 h of light) the great majority of the eggs diapaused. The PhPR threshold of embryonic diapause induction almost did not depend on the temperature: 13.4 h at 20°C and 13.7 h at 25°C (Tajima et al., 2018; Fig. 1).

Females of *A. triannulatus* can change the physiological status of the produced eggs in response to changes in the external photoperiodic conditions acting directly on the females. For instance, in an experiment 10 females reared at a long day (16 h) were transferred to short-day conditions (12 h; Fig. 2) on the day of their final molt. After the maturation period all the females started laying eggs that developed actively, i.e., did not diapause. Five of these females died a short time later (the lower part of Fig. 2), and the remaining 5 females gradually switched to producing diapausing eggs soon after the transfer to short-day conditions (Tajima et al., 2018).

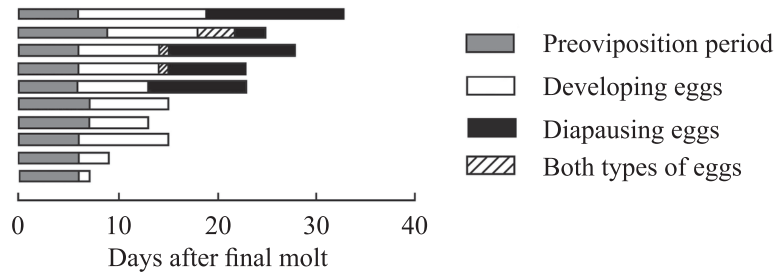

Fig. 2. The effect of changes in photoperiodic conditions on the physiological status of eggs produced by the females of *Adelphocoris triannulatus* (Stål) transferred from long-day conditions (16 h of light a day) to short-day ones (12 h) on the day of their final molt; population from Takanabe (Japan; 32.1°N, 131.5°E) (after Tajima et al., 2018). Data for each female (the types of eggs produced) are represented by a separate bar. Temperature 25°C.

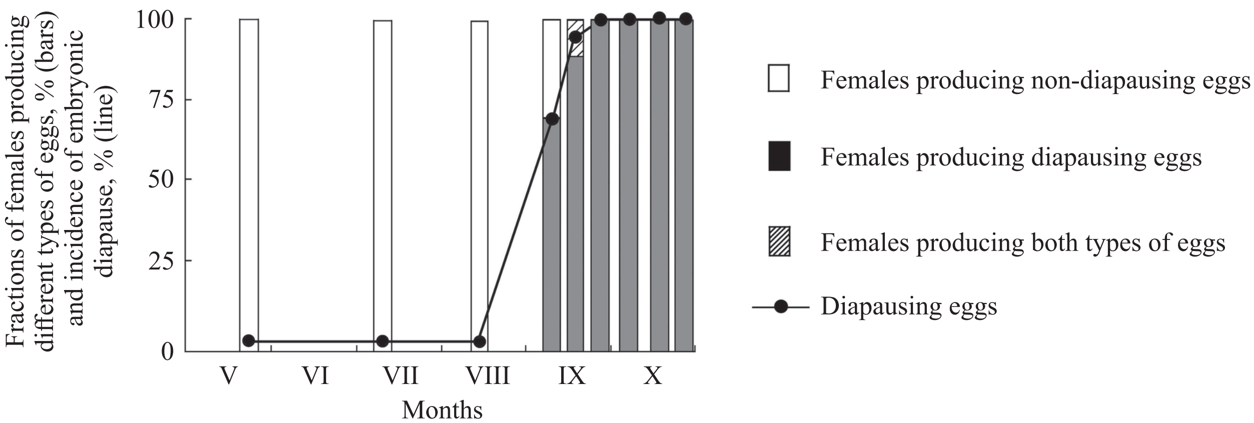

Fig. 3. Seasonal changes in the percentage of diapausing eggs laid by females of *Adelphocoris triannulatus* (Stål); population from Takanabe (Japan; 32.1°N, 131.5°E) (after Tajima et al., 2018). The females collected in nature from the end of May to the end of October were transferred to the long-day laboratory conditions (16 h of light, temperature 25°C); the physiological status of the eggs laid by these females during 3 days after transfer was determined, and the percentage of females that laid diapausing eggs, actively developing eggs, and both types of eggs was calculated.

Observations in the field showed that the earliest diapausing eggs of *A. triannulatus* were produced at the beginning of September (Fig. 3), when the air temperatures were still high enough and the day length corresponded to the PhPR threshold value determined in the laboratory (see Fig. 1).

Proceeding from the results of laboratory experiments and field observations, the cited authors supposed that under natural conditions, adults of the overwintered generation of *A. triannulatus* appeared from late April to early June. The adults recorded since the end of June and in July belonged to the I summer generation, and those active in August–September belonged to the II summer generation. The earlier females of the II generation first produced actively developing eggs which gave rise to the III generation; then, as the day length decreased below the critical value, these females started to lay diapausing eggs which overwintered. According to the results of laboratory experiments (Fig. 3), such females were not numerous in the II generation. However, their ability to switch to production of hibernating eggs allowed them to build up the overwintering reserve of the population. Nymphs hatched from the hibernating eggs only in the spring of the following year.

Thus, in the south of Japan *A. triannulatus* can complete 3 or even 4 generations during the vegetation season; however, the deteriorating trophic conditions and decreasing temperatures in late autumn reduce the chances of successful completion of the III generation, whose females would lay diapausing eggs. Since hibernation occurs at a certain late embryonic stage, the developing embryos require some time to reach it. The cited authors (Tajima et al., 2018) never found any nymphs of this species in nature in October and November. In view of all this, the ability of females of the II generation to switch from laying actively developing eggs to production of hibernating eggs is very important, since there is no guarantee that the following (III) generation will be able to form a sufficient overwintering population reserve.

Adelphocoris lineolatus (Goeze, 1778) (alfalfa plant bug)

This is a trans-Palaearctic species distributed in Western Europe, the north of Africa (Algeria, Tunisia), West Asia, Afghanistan, Pakistan, Mongolia, China, Korea, and Japan. In the early XX century this bug was inadvertently introduced to North America, namely Iowa in the USA and Nova Scotia in Canada, wherefrom it subsequently spread as far southwards as South Carolina and as far westwards as Alberta in Canada (Wheeler and Henry, 1992; Kerzhner and Josifov, 1999; Vinokurov et al., 2010). *Adelphocoris lineolatus* is a polyphagous bug with a clear preference for legumes; it damages alfalfa, sainfoin, less frequently melilot, clover, lupin, and other legumes, sporadically also cotton, ground nut, chickpea, lentil, soybean, kidney bean, and sunflower. Bugs of the II generation may also damage sugar beet seed plantations (Puchkov, 1966).

The species hibernates at the egg stage. The eggs overwinter in plant stems, as is typical of plant bugs with embryonic diapause (Puchkov, 1966; Schaefer and Panizzi, 2000; Wheeler, 2001). Diapause is induced by the long-day PhPR. The day-length sensitive stage in *A. lineolatus*, namely adults of the maternal generation, starting with the 5–6th day after the final molt, was determined by studying the activity of neurosecretory cells in females from the North American populations (Ewen, 1966).

In different zones within its native range, *A. lineolatus* completes from 1 to 3 or 4, and in the south, even up to 5 generations a year (Puchkov, 1966). In North America, it produces only 1 annual generation in Saskatchewan (Canada) and 2 incomplete generations in the more southern territory of Minnesota (USA); in the latter case all the hibernating eggs were laid by females of the I generation. Establishment of the univoltine seasonal cycle was probably a way of adaptation of such alien species to the new conditions of northern territories. Since no bugs of the II generation can reach maturity, individuals with a genetically determined shorter PhPR threshold do not participate in reproduction and are gradually eliminated from the population, as a result of which the PhPR threshold gradually increases, enhancing the univoltine trend in the population (Craig, 1963; Ewen, 1966). In Wisconsin (USA) the species produces two complete annual generations (Wipfli et al., 1989; Wheeler, 2001).

According to the data for Ukraine, the lower temperature threshold of *A. lineolatus* development is about 11.5°C. The sum of effective temperatures required for completion of the nymphal stage is about 250 degree-days (Puchkov, 1966).

At the beginning of the XXI century, after the introduction of transgenic Bt cotton (with the inserted gene from the bacterium *Bacillus thuringiensis* increasing its resistance to lepidopteran phytophages), several plant bugs of the genus *Adelphocoris*, previously regarded as minor pests in China, were elevated to the status of serious cotton pests (Lu et al., 2008, 2009b, 2010a). They were, in particular, *A. lineolatus*, *A. suturalis* (Jakovlev, 1882), and *A. fasciaticollis* Reuter, 1903. The three species strongly differ in geographic distribution: *A. lineolatus* has a wide range and is known from Europe, Asia, and North America (see above); *A. suturalis* is mostly distributed in the south of the Russian Far East, in China, Korea, and Japan (Kerzhner and Josifov, 1999; Vinokurov et al., 2010); *A. fasciaticollis* is known only from China and Korea (Kerzhner and Josifov, 1999). Their distribution within the territory of China is also different: *A. suturalis* mostly occurs in regions with a temperate climate while *A. lineolatus* and *A. fasciaticollis* prefer cooler climates. The species also differ in phenology, with *A. suturalis* producing 4–5 annual generations and the two other species, only 3–4 generations. The nymphs of *A. suturalis* hatch from overwintered eggs at the beginning of April, and the nymphs of the two other species do so in the middle and at the end of April (Lu et al., 2009b). In an attempt to explain the observed differences, Lu and co-authors (2009b) studied the effect of temperatures within a range from 10 to 35°C on the developmental time and survival of immature stages of these three species co-occurring in cotton fields in China (Henan Province; 35.5°N, 113.9°E) (Table 1).

Table 1. The developmental time and temperature thresholds of development of immature stages in three species of the genus *Adelphocoris* Reuter at a constant temperature, relative humidity 60 ± 5%, and a short day (14 h); populations from China (Henan Province; 35.5°N, 113.9°E) (after Lu et al., 2009b)

Species	Stage	Mean developmental time (± SE, days) at different temperatures, °C						Temperature threshold, °C	
		10	15	20	25	30	35	lower	upper
A. suturalis (Jakovlev)	Egg	–	20.0 ± 0.3	13.8 ± 0.1	9.8 ± 0.1	7.9 ± 0.1	8.4 ± 0.3	5.6	40.1
	Nymph	49.4 ± 0.6	41.0 ± 0.4	19.0 ± 0.2	14.9 ± 0.1	12.3 ± 0.2	14.0 ± 0.6	5.0	38.4
A. fasciaticollis Reuter	Egg	–	20.1 ± 0.4	14.5 ± 0.1	9.8 ± 0.1	7.8 ± 0.1	8.5 ± 0.1	6.3	39.0
	Nymph	47.9 ± 0.4	32.2 ± 0.3	22.9 ± 0.2	16.5 ± 0.4	13.6 ± 0.4	13.0 ± 0.1	3.0	41.9
A. lineolatus (Goeze)	Egg	–	24.5 ± 0.3	15.8 ± 0.1	12.3 ± 0.1	9.4 ± 0.1	9.1 ± 0.1	5.6	41.3
	Nymph	54.3 ± 0.7	45.8 ± 0.4	20.3 ± 0.2	15.3 ± 0.1	12.0 ± 0.2	12.8 ± 0.4	6.2	38.8

Using regression analysis, the SET values for egg and nymphal development were estimated at 189.9 and 308.8 for *A. suturalis*, 188.8 and 366.7 for *A. fasciaticollis*, and 231.7 and 291.6 degree-days for *A. lineolatus*, respectively (Lu et al., 2009b).

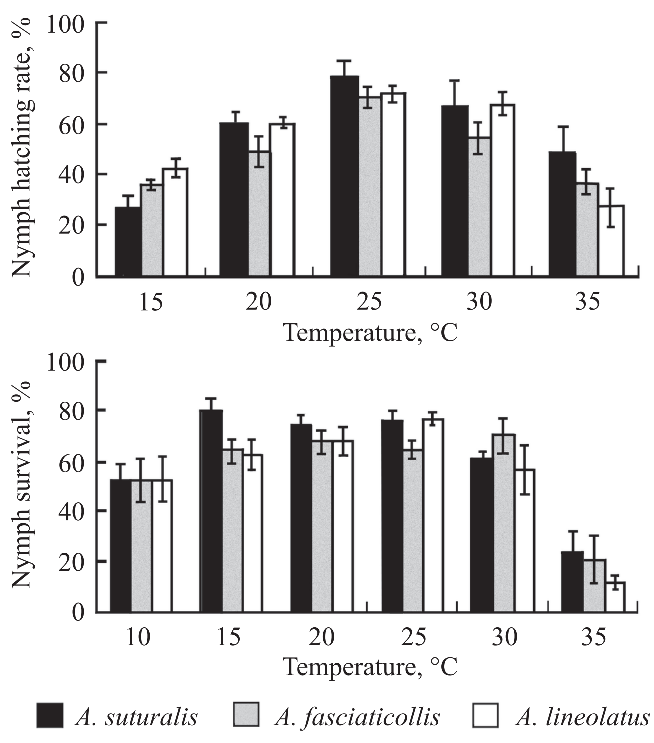

Fig. 4. Survival of eggs and nymphs of *Adelphocoris suturalis* (Jakovlev), *A. fasciaticollis* Reuter, and *A. lineolatus* (Goeze) at constant temperatures within a range from 10 to 35°C: mean values and standard errors. Populations from Henan Province (China; 35.5°N, 113.9°E) (after Lu et al., 2009b).

The egg hatching success and nymph survival significantly depended on the temperature in all the three species (Fig. 4).

Studies of the migration behavior of these bugs carried out in China (Lu et al., 2009a) showed that under the laboratory conditions (for experiment technique, see Beerwinkle et al., 1995; Cheng et al., 1997), fertilized females of *A. suturalis* and *A. fasciaticollis* could cover distances of up to 40 km in 8 h of continuous flight. Females of *A. lineolatus* demonstrated somewhat less pronounced flying abilities, but they could also fly for more than 5 h to a distance of about 30 km. Mature males of all the three species showed much lower endurance. The ability for prolonged flight depended not only on the sex but also on the age of bugs, reaching the maximum by the 10–13th day after the final molt and then gradually decreasing. The optimal air temperature for their flights was 20–23°C, at the relative air humidity of 64–68%.

All the three species overwinter in the state of embryonic diapause (Chen et al., 2010). The roles of temperature and photoperiod in winter diapause induction were studied only in *A. suturalis*. Experiments were carried out with bugs from Henan Province in the north of China (35.1°N, 113.5°E). Diapause was induced under short-day conditions (Feng et al., 2012). The critical day length remained practically the same (13 h 18 min) at temperatures varying from 17 to 26°C, indicating thermal stability of PhPR within this temperature range (Fig. 5, *A*).

In order to determine the day-length sensitive stage, nymphs of *A. suturalis* at a certain instar (from I to V), and also adults of this species were transferred from long-day conditions to short-day ones, with 8 or 10 h of

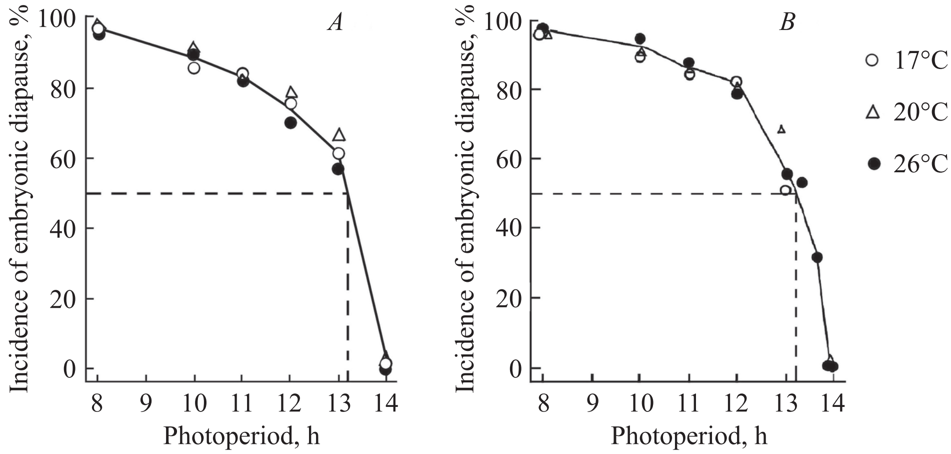

Fig. 5. Photoperiodic response of winter embryonic diapause induction in *Adelphocoris suturalis* (Jakovlev) (*A*) and *Apolygus lucorum* (Meyer-Dür) (*B*) at temperatures 17, 20, and 26°C. Populations from Henan Province (China; 35.1°N, 113.5°E) (after Feng et al., 2012). The PhPR threshold is indicated by the dashed line.

light a day, and then kept at a short photoperiod (Fig. 6). The greatest relative number of diapausing eggs was produced by females reared from the nymphs which were kept under short-day conditions since the I instar. The next cohort, in which the nymphs were kept under short day since the II instar, showed a smaller percentage of diapausing eggs. As the nymphal instar at the moment of transfer increased from III to V, the percentage of diapausing eggs in the females' progeny regularly decreased and dropped to zero in the cohort where only the adults experienced the short-day conditions. Thus, the day-length sensitivity was the highest in the I instar nymphs of the maternal generation. The level of photoperiodic sensitivity in all the nymphal instars of *A. suturalis* also depended on the day length: it was higher at a shorter day (in this case, 8 h of light a day) than at a longer day (10 h). The gradual decline of photoperiodic sensitivity from the I to the V instar took place synchronously at different photoperiodic regimes; in both short-day photoperiods the adult bugs could not perceive and evaluate the day length, and all the eggs produced by females in these experimental cohorts were non-diapausing (Feng et al., 2012).

Genus *Apolygus* China, 1941

Apolygus lucorum (Meyer-Dür, 1847) (green plant bug)

This is a trans-Eurasian species, also introduced to North America. Its records from Africa (Algeria and Egypt) are believed to be erroneous (Zhang and Zhao, 1996; Kerzhner and Josifov, 1999; Vinokurov et al., 2010).

Under the natural conditions of the Russian Far East and Japan this bug was earlier recorded on various species of wormwoods (*Artemisia*) (Vinokurov and Kanyukova, 1995; Watanabe et al., 1997); however, both its nymphs and adults were later shown to be broadly

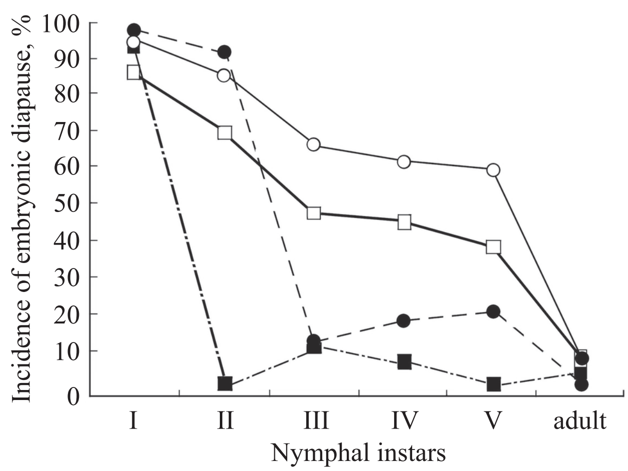

Fig. 6. Induction of winter embryonic diapause in the progeny of *Adelphocoris suturalis* (Jakovlev) (solid lines) and *Apolygus lucorum* (Meyer-Dür) (dashed lines) bugs which were reared under short-day conditions with 8 h (circles) or 10 h of light a day (squares), starting with a certain stage; populations from Henan Province (China; 35.1°N, 113.5°E) (after Feng et al., 2012). Abscissa: development stage of the maternal generation at which the bugs were transferred from long-day conditions to short-day ones. Temperature 26°C.

Table 2. The developmental time of immature stages of *Apolygus lucorum* (Meyer-Dür) at constant temperatures; population from Hebei Province (China; 39.5°N, 116.7°E) (after Lu et al., 2010b)

Stage	Mean developmental time (± SE, days) at different temperatures, °C					
	10	15	20	25	30	35
Egg	–	14.9 ± 0.3	11.0 ± 0.2	8.2 ± 0.1	6.7 ± 0.1	6.3 ± 0.1
I instar nymph	7.3 ± 0.4	5.6 ± 0.2	3.6 ± 0.1	3.0 ± 0.1	2.0 ± 0.1	2.6 ± 0.2
II instar nymph	5.9 ± 0.4	4.0 ± 0.2	2.8 ± 0.2	1.6 ± 0.1	1.6 ± 0.1	2.3 ± 0.4
III instar nymph	5.6 ± 0.5	4.4 ± 0.2	2.4 ± 0.1	2.2 ± 0.1	1.5 ± 0.1	1.7 ± 0.3
IV instar nymph	6.5 ± 0.4	4.5 ± 0.2	2.6 ± 0.1	1.8 ± 0.1	1.9 ± 0.1	2.1 ± 0.3
V instar nymph	12.9 ± 0.7	7.7 ± 0.2	4.1 ± 0.1	3.2 ± 0.1	3.0 ± 0.1	2.4 ± 0.3
I to V instar nymphs	38.2 ± 0.8	26.2 ± 0.2	15.5 ± 0.2	11.8 ± 0.2	10.2 ± 0.2	11.1 ± 0.6

Table 3. Thermal development parameters for immature stages of *Apolygus lucorum* (Meyer-Dür) and three species of the genus *Adelphocoris* Reuter feeding on cotton; populations from Hebei Province (China; 39.5°N, 116.7°E) (after Ting, 1963, cited after Lu et al., 2010b)

Species	Eggs		Nymphs	
	LTT, °C	SET, degree-days	LTT, °C	SET, degree-days
Apolygus lucorum	3.0	188	4.6	340
Adelphocoris suturalis (Jakovlev)	5.4	214	9.0	329
A. fasciaticollis Reuter	7.8	186	7.0	373
A. lineolatus (Goeze)	5.2	213	6.7	409

polyphagous. This feature manifested itself in full after the introduction of transgenic cotton, when *Apolygus lucorum*, similar to members of the genus *Adelphocoris* (see above), became the principal pest not only of cotton but of many other crops including cereal, vegetable, and orchard ones (Lu et al., 2008, 2010a; Lu and Wu, 2011; Pan et al., 2013).

Due to pronounced migration activity, *A. lucorum* can produce outbreaks over vast territories (Lu et al., 2007). The number of complete annual generations is difficult to determine in the field since adult bugs of this species have a long lifespan and the generations overlap. In view of this, the effect of constant temperatures on the pre-adult development of *A. lucorum* was studied in the laboratory (Lu et al., 2010b; Table 2).

The experimental data were processed using the linear regression model to determine the LTT and SET needed for completion of one generation. The calculated values were 3.2°C and 179.2 degree-days for the eggs and 3.7°C and 262.4 degree-days for the nymphs, respectively. Proceeding from these results, it was estimated that in the north of China *A. lucorum* could produce up to five complete generations a year (Lu et al., 2010b).

Comparison of the development parameters of immature stages in *Apolygus lucorum* and three *Adelphocoris* species (Lu et al., 2010b; Table 3) co-occurring in cotton fields shows that *A. lucorum* has lower LTT values for both eggs and nymphs and considerably lower SET values needed for completion of these stages. This difference explains the phenology of these species in northern China, where *Apolygus lucorum* usually completes 5 annual generations and species of the genus *Adelphocoris* have only 3 or 4 generations.

Similar to *Adelphocoris* bugs, members of the genus *Apolygus* overwinter in the state of embryonic diapause. The comparative significance of the temperature and photoperiod in winter diapause induction in *A. lucorum* (Feng et al., 2012) was studied in laboratory experiments using bugs from Henan Province (north of China; 35.1°N, 113.5°E).

Diapause in *A. lucorum* is induced by short-day conditions. The critical day length was found to be stable

(13 h 19 min) within a temperature range from 17 to 26°C and very close to that of *A. suturalis* (13 h 18 min; Figs. 5, *A* and *B*). At the same time, in a different population of *A. lucorum* occurring 3° of latitude farther northwards (Shandong Province, China), the photoperiodic threshold of diapause induction varied depending on the temperature: 13 h 10 min at 17°C, 12 h 58 min at 20°C, and 12 h 51 min at 23°C (Zhuo et al., 2011, cited after Feng et al., 2012).

Similar to *A. suturalis*, the highest day-length sensitivity of *A. lucorum* was observed in the I instar nymphs of the maternal generation; however, in *A. suturalis* it decreased gradually from the I to the V instar, whereas in *A. lucorum* the sensitivity decreased abruptly already in the II instar. In both cases, the dynamics of decline of day-length sensitivity depended on the photoperiod, with higher sensitivity at a shorter day (in this case, 8 h of light a day; see Fig. 6).

Genus ***Lygus*** Hahn, 1833

This is one of the largest genera in the subfamily Mirinae. It unites over 50 known species with cosmopolitan distribution. In particular, 34 species occur in North America, 19 in Europe, and 2 species are known from China. It is believed that none of the American species has become naturalized in Europe. At the same time, certain European species have been recorded in America (Kelton, 1975; Kerzhner and Josifov, 1999; Aglyamzyanov, 2009), where all of them are very rare, with the exception of *Lygus rugulipennis*.

Lygus rugulipennis Poppius, 1911 (European tarnished plant bug)

This bug has a Holarctic range: in the Palaearctic it is known from Great Britain and Spain to the Russian Far East and Japan (Kerzhner and Josifov, 1999; Vinokurov et al., 2010), and in North America, from Alaska to the north of California and the south of Colorado (Schwartz and Foottit, 1998). Of the 19 Palaearctic species of the genus *Lygus* (Aglyamzyanov, 2009), *L. rugulipennis* is not only the most widespread but also the most common and economically most important as a pest (Puchkov, 1966). Due to the difficult diagnostics of plant bugs, until recently this and some other species have been often misidentified. For instance, many records of *Lygus pratensis* L. from England and of *L. disponsi* Linnavuori from Japan actually refer to *L. rugulipennis* (Kerzhner and Josifov, 1999; Schaefer and Panizzi, 2000). The modern molecular diagnostic methods will hopefully eliminate such errors.

Lygus rugulipennis is a broadly polyphagous bug feeding on over 400 species of herbaceous plants and shrubs from 57 families (Holopainen and Varis, 1991; Schaefer and Panizzi, 2000; Wheeler, 2001). The bugs can consume all the soft parts of plants but prefer the reproductive organs; they damage many cultivated plants including legume, grain and orchard crops, ornamental and medicinal plants. For instance, nymphs and adults were recorded feeding on Scots pine seedlings; moreover, it was shown under the laboratory conditions that the species could successfully complete a generation on a diet consisting only of pine needles (Holopainen, 1986). In England *L. rugulipennis* strongly damages strawberry plantations (Easterbrook, 1997). A characteristic feature of all the generations of *L. rugulipennis* is high mobility: the bugs readily migrate from one host plant species to another and can easily cover distances of 1–2 km in search of succulent vegetation (Puchkov, 1966).

The species overwinters at the adult stage. Females of *L. rugulipennis* always hibernate with still underdeveloped ovaries, whereas males in autumn already have bright green gonads that externally look exactly as mature ones. Some bugs overwinter in the litter among the stubble remains of perennial herbs, while others migrate into shrub thickets, forest shelter belts, and forest edges up to several kilometers away. Overwintered females usually lay eggs in the stems and leafstalks of perennial herbaceous legumes (Puchkov, 1966).

In the north of Europe (Scotland, Sweden) *L. rugulipennis* has a univoltine seasonal cycle (Kullenberg, 1944; Stewart, 1969). The phenology of this species developing on sugar beet was studied in detail in the environs of Tikkurila (Finland; 60.3°N, 25.0°E; Vans, 1972, 1995), where it also completes only one generation a year (Fig. 7). The adults overwinter under the herbaceous and woody plant remains; winter mortality is usually very high, reaching 80% (Vans, 1972).

In the greatest part of the Palaearctic, *L. rugulipennis* produces two annual generations (Puchkov, 1966). In particular, such data are available for the Czech Republic (Sedivy and Honek, 1983), Romania (Cojocaru, 1997), and Hungary (Kocka, 1985). In England, according to the observations of Southwood and Leston (1959), this

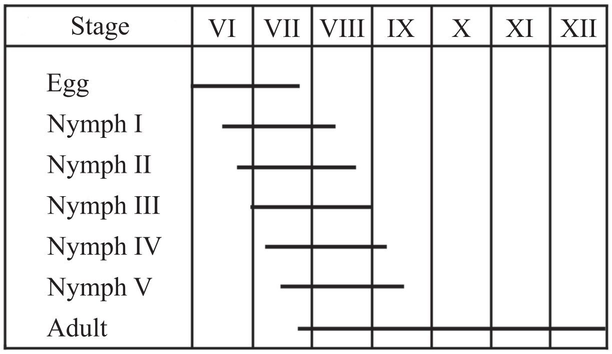

Fig. 7. Phenology of *Lygus rugulipennis* Poppius in the environs of Tikkurila (Finland; 60.3°N, 25.0°E; after Varis, 1972).

species also develops in two generations; after oviposition the overwintered females continue to live for a long time, which is not generally typical of true bugs. Some individuals survive till August, so that the natural populations may simultaneously contain not only bugs from two consecutive (maternal and filial) generations, but also “grandmothers” and their “grandchildren.” An interesting phenological feature of *L. rugulipennis* was observed in Poland: the bugs feeding on the blue lupin (*Lupinus* sp.) formed 1 annual generation while those feeding on the white and yellow lupins formed 2 generations (Gorski, 1996).

In the south of the Palaearctic *L. rugulipennis* produces up to 4 annual generations (Asanova and Iskakov, 1977); in particular, in Italy it has 3 or 4 generations (Tavella et al., 1994, 1997). In Japan the species is bi- or trivoltine (Hori and Hanada, 1970).

Research carried out in England (Kent; ~50°N, 0°E) was primarily focused on improving control measures against *L. rugulipennis* on everbearing strawberry varieties. It was found out that the bugs which had overwintered under the remains of wild vegetation formed the I generation which developed both on strawberries and on wild plants. Adults of this summer generation appeared in late June and early July. Some of them remained on wild plants and gave rise to the II generation there, but a greater part of the bugs migrated onto the everbearing strawberry plantations and gave rise to the II and sometimes also the III generation of the pest. The bug population on strawberries grew very rapidly due to the inflow of immigrants, and the nymphs significantly damaged the developing fruits (Easterbrook, 1997, 2000; Easterbrook et al., 2003; Xu et al., 2014). A model was proposed to predict *L. rugulipennis* development on late-season strawberry plantations and to determine the best time for insecticide treatment. In addition, recent observations in England showed that bugs of the I generation could colonize and damage many other crops, including early strawberry varieties, blackberry, raspberry, etc. (Xu et al., 2014).

Lygus pratensis (Linnaeus, 1758) (tarnished plant bug)

This species has a West-Central Palaearctic range covering almost the whole of Europe and also India (Kerzhner and Josifov, 1999; Vinokurov et al., 2010); it is relatively rare on the British Isles (Woodroffe, 1966), while its records from various regions of Siberia remain to be verified (Vinokurov et al., 2010).

Lygus pratensis is one of the commonest members of the genus. It is very close to *L. rugulipennis* both biologically and ecologically, has a very similar range, and often co-occurs with the latter in the fields, being somewhat less abundant, especially in Western Europe (Puchkov, 1966). This is a broadly polyphagous species that strongly damages legume, grain, vegetable, and orchard crops, in particular alfalfa, beet, maize, tobacco, cotton, pumpkin, potato, hemp, sunflower, grapevine, cucumber, raspberry, strawberry, and many other cultivated plants. In China the nymphs and adults of *L. pratensis* have been recorded on 52 plant species from 18 families (Lu and Wu, 2008). This bug is a vector of many plant pathogens, in particular the potato mottle, alfalfa virus, bacterial bean blight, tobacco and beet mosaic viruses (Puchkov, 1966). In Pamir this bug threatened the very possibility of growing potatoes (Asanova and Iskakov, 1977).

In the north of Russia the tarnished plant bug produces 1 annual generation, and in the south it may have up to 4 loosely delimited generations (Puchkov, 1966). One annual generation develops in the south of Finland (Helsinki, 60°N, 25°E) (Vans, 1997), 3 generations in Kazakhstan (Almaty, 43°N, 77°E) (Asanova and Iskakov, 1977), 4 generations in Spain (Douro, 41.8°N, 8.4°W) (Asensio de la Sierra, 1973), and up to 4 generations in the northwest of China (Xinjiang Uygur Autonomous Region, 41°N) (Yang and Yang, 2001). Adult bugs overwinter under the plant remains and migrate in spring onto vegetating plants for maturation feeding and reproduction.

Lygus pratensis has a pronounced ability for long-distance migrations. These bugs have been recorded in aerial plankton at altitudes of up to 915 m above sea level (Johnson and Southwood, 1949).

The biology and ecophysiology of *L. rugulipennis* is intensively studied in China, because this species is the main cotton and alfalfa pest in the northwest of the country, in Xinjiang Uygur Autonomous Region (Yang and Yang, 2001; Zhang et al., 2017). According to the observations carried out in the north of the region, overwintered adults emerge at the end of April; females lay eggs on weeds and orchard crops (pear, grapevine), on which the I generation of the bug develops. Adults of this generation migrate onto cotton fields in July and produce the II generation. The population reaches the maximum density due to individuals of the II and III generations which develop on cotton plants. Adults of the III generation appear at the end of August and migrate to their wintering places (Liu et al., 2015). In the south of Xinjiang, overwintered adults reactivate from diapause in March, and the local population has enough time to form four generations; bugs of the I and IV generations feed on cultivated woody plants, and those of the II and III generations feed on cotton plants (Yang et al., 2004).

According to the laboratory data for *L. pratensis* population from Korla (Xinjiang, China, 41.4°N, 85.5°E), the LTT for the development of eggs was 11.97°C, that for nymphs was 12.08°C. The SET required for completion of the embryonic stage was 131.6 degree-days, that for the nymphal stage was 208.3 degree-days. Pre-adult development was most favored by higher relative air humidity, about 75% (Liu et al., 2015).

Among the North American members of the genus *Lygus*, four species have been the best studied due to their considerable economic importance: *Lygus lineolaris*, *L. borealis*, *L. hesperus*, and *L. elisus* (Schwartz and Foottit, 1992; Gerber and Wise, 1995).

Lygus lineolaris (Palisot de Beauvois, 1818)
(tarnished plant bug)

This species is widely distributed over the whole North American continent, from Canada to Mexico, and is known as the principal pest of cotton, rape, and alfalfa. Nymphs and adults of *L. lineolaris* have been recorded on 328 plant species from 55 families (Young, 1986). The number of generations in the region varies from 1 in the north of Canada (60°N) to 4 and more overlapping generations in the south of the USA (33°N) (Strong et al., 1969; Kelton, 1975; Snodgrass et al., 1984). The bugs successfully develop on various plants, can easily migrate over large distances, and usually colonize different crops in different generations. They predominantly feed on plants but may also consume animal food; in particular, they attack the alfalfa bug *Adelphocoris lineolatus*, the potato leafhopper *Empoasca fabae* (Harris), eggs and larvae of the Colorado potato beetle *Leptinotarsa decemlineata* (Say), the alfalfa weevil *Hypera postica* (Gyllenhal), small lepidopteran larvae, and many other arthropods (Wheeler, 2001). The species overwinters at the adult stage (Guppy, 1958; Kelton, 1975).

In Manitoba (Winnipeg, south of Canada; 49.9°N, 97.1°W) *L. lineolaris* produces two overlapping annual generations (Gerber and Wise, 1995). The overwintered adults appear in April–May on alfalfa, strawberry, and other herbaceous plants and lay eggs during May–June. Nymphs of the I generation occur in nature until the end of July and turn into adults from the end of June to the beginning of August. Nymphs of the II generation complete development in autumn and turn into adults at the end of September. However, the earliest adults appear already in August, so that the two generations partly overlap during this month. The adults which appear in late autumn form winter diapause, and the females hibernate with still underdeveloped gonads (at the previtellogenesis phase). In some years, up to 20% of bugs of the I generation overwinter. The I generation usually develops on alfalfa, and the more abundant II generation, on rape; the migration of adults onto rape fields is strictly synchronized with rape flowering (Gerber and Wise, 1995).

In Asheville (North Carolina, USA; 35.5°N, 82.5°W) *L. lineolaris* produces 2 or 3 annual generations (Stewart and Khoury, 1976). The overwintered adults emerge in late March; adults of the summer generation appear from the end of May to August; those of the II generation appear at the end of August or in September and overwinter. One more generation may be formed in the middle of summer (McPherson et al., 1983).

In the south of the North American continent, the population of *L. lineolaris* from Stoneville (Mississippi, USA; 33.4°N, 90.9°W) was studied in detail. There the species produces 2 generations in regular years and

3 generations in warm years, and sometimes remains active all the year round (Bariola, 1969; Kelton, 1975; Snodgrass et al., 1984; Snodgrass, 2003; Villavaso and Snodgrass, 2004).

In laboratory experiments, rearing nymphs of *L. lineolaris* at constant temperatures of 21 and 27°C and short-day conditions with 12 and 12.5 h of light a day led to diapause induction in all the adults. When the diapausing adults were exposed to a higher temperature (27°C) and a longer photoperiod (13.5 h), all the individuals terminated diapause in 2 weeks and became reproductively active. If pre-adult development proceeded at 13 h of light a day, all the adults were active and capable of reproduction. These data indicated that at the studied temperatures, the PhPR threshold was between 12.5 and 13 h. Photoperiodic sensitivity was observed in both nymphs and adults (Bariola, 1969).

The subsequent research was focused on determining the role of the day length in diapause induction in the natural populations of *L. lineolaris* (Snodgrass, 2003). During three consecutive years, nymphs were collected in nature in different periods starting from August, and the incidence of diapause in the adults that developed from these nymphs was recorded. The critical day length inducing diapause in half the individuals, determined in the previous laboratory experiments (12.5 h), was reached in the study region on September 12–14 (Snodgrass, 2003). The series of nymphs collected in August yielded a small percentage of diapausing adults, no more than 7–8%. Then the incidence of diapause gradually increased and reached 100% for the nymphs collected in late October or early November.

An interesting feature of the annual cycle of *L. lineolaris* in the Mississippi delta was observed during a study of the timing of diapause termination in adults overwintering on different plants. In the bugs which overwintered on the blossoming common henbit *Lamium amplexicaule* L., diapause was terminated as early as in December. For instance, among the adults collected off this host plant at the end of December, no more than 9% were in diapause; over 90% of the females were reproductively active, and at least 50% of them already contained mature eggs (Snodgrass, 2003). By contrast, the bugs which overwintered on remains of other plants reactivated only in January, i.e., a month later. According to the cited authors (Snodgrass et al., 1984, 2012; Snodgrass, 2003), diapause termination in December was related to the presence of favorable food, namely the blossoming *L. amplexicaule* plants. This assumption was experimentally supported. Laboratory tests showed that at favorable temperatures and in the presence of blossoming plants, the bugs reactivated even under short-day conditions which normally maintained diapause. Due to early diapause termination in the south of North America, the local population of *L. lineolaris* has enough time to produce an additional spring generation, whose adults appear as early as in the second half of March.

Unfortunately, despite detailed experimental studies of the factors affecting *L. lineolaris* development both in the laboratory and under the natural conditions of the southern part of North America (Snodgrass et al., 2012), some aspects of seasonal development of the local populations remain obscure. In particular, it is unknown if there are independent populations overwintering on different host plants and, correspondingly, producing different numbers of annual generations; how the bugs are distributed over different plants before overwintering; why some bugs remain on the weeds that wither in late autumn, while others migrate onto the common henbit, which vegetates and blossoms in winter but makes an inferior host plant in spring; how the species got adapted to the common henbit (an invasive plant in North America) as the best host for winter feeding. These and some other questions require further research.

Lygus borealis (Kelton, 1955)

This is a typical inhabitant of the steppe (prairie) zone of Canada (Scudder, 2014). The seasonal development of the studied population in Manitoba resembles that of *L. lineolaris* (Gerber and Wise, 1995).

Lygus hesperus (Knight, 1917)
(western tarnished plant bug)

This bug is widely distributed over the whole west coast of North America (the Rocky Mountains region), from British Columbia in Canada to New Mexico in the USA, where it produces from 1 to 5 annual generations depending on the thermal parameters during the vegetation season. The seasonal development of *L. hesperus* was most thoroughly studied in Davis (California, USA; 38.6°N, 121.7°W), where from 3 to 5 annual generations can develop, depending on the local temperature conditions (Beards and Strong, 1966; Gillespie et al., 2003). The earliest diapausing females appear in the

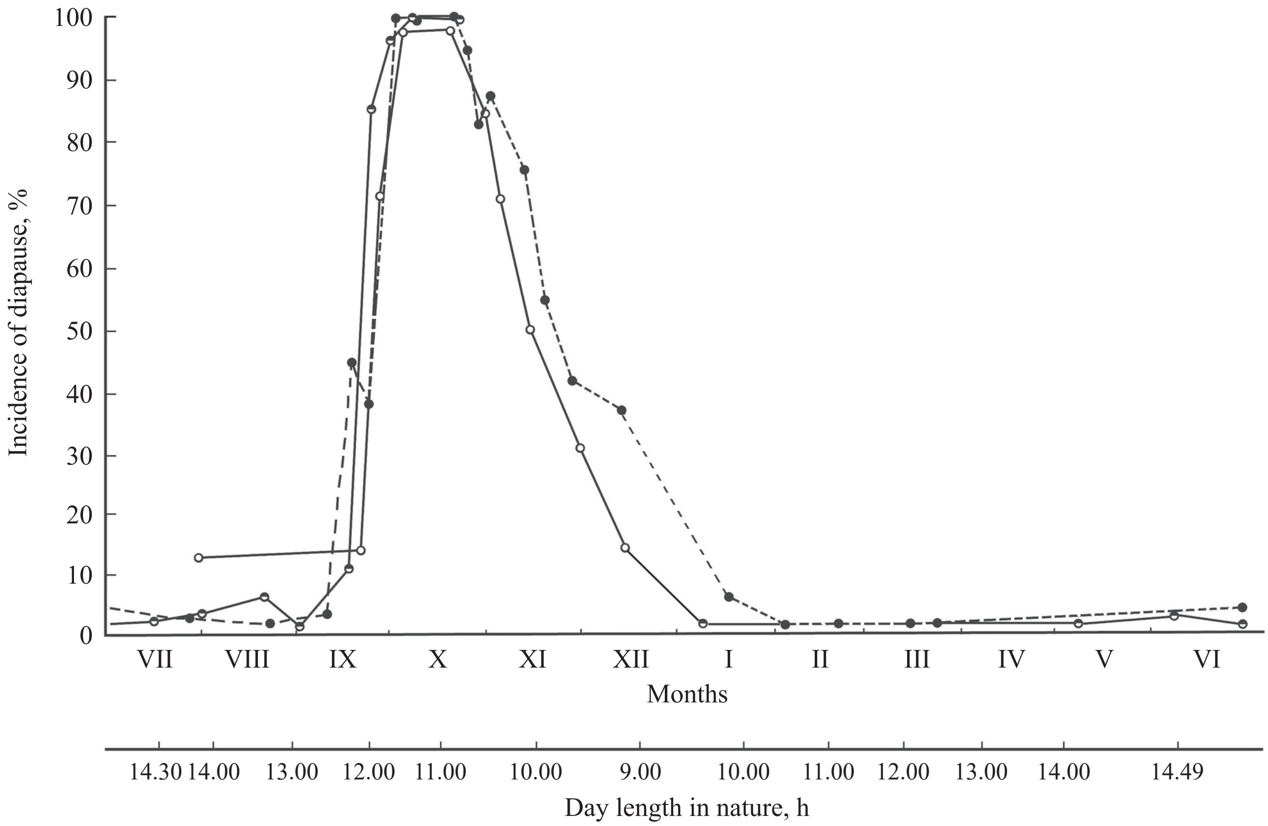

Fig. 8. The fraction of diapausing females of *Lygus hesperus* (Knight) in samples collected in different periods from the natural population in Davis (California, USA; 38.6°N, 121.7°W) (after Beards and Strong, 1966). The physiological state was determined by the presence of eggs in the oviducts of dissected females. Data for three consecutive years of study are shown.

second half of September, when the day length decreases to 12.5 h. In early October all the females remain in diapause (Fig. 8).

However, the percentage of diapausing individuals in the natural *L. hesperus* populations decreases drastically already in November, so that in January all the bugs are physiologically ready to resume activity and reproduce. Females lay eggs in December–February. Hatching of nymphs is probably delayed by the relatively low temperatures, since the first nymphs appear not earlier than the beginning of April. Although early diapause termination in the overwintering bugs appears unusual, it is consistent with the results of observations in the same region (Shafter, California, USA; 35.5°N, 119.3°W), performed by another author (Leigh, 1966; see Fig. 9). In the latter case, the earliest diapausing females were recorded as early as in September; the incidence of diapause increased very rapidly in October, reaching the peak in the middle of that month, and by January nearly all the females were already reproductively active.

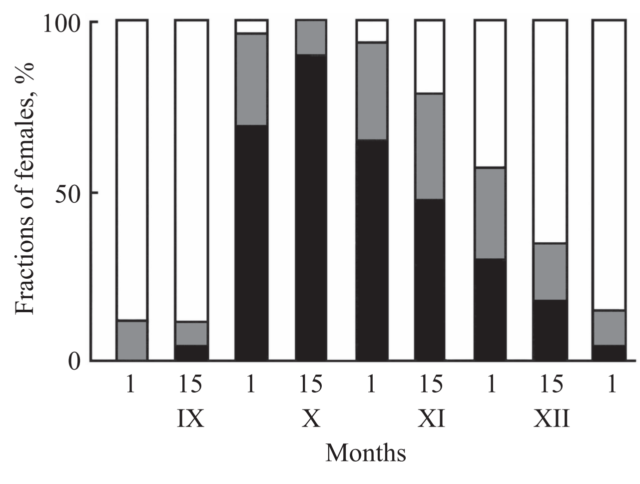

Fig. 9. The fractions of diapausing and active females of *Lygus hesperus* (Knight) in the natural populations in Shafter (California, USA; 35.5°N, 119.3°W) during the autumn and winter months (after Leigh, 1966). Black, diapausing females; white, active females; gray, females at early stages of oogenesis. The physiological state was determined during dissection.

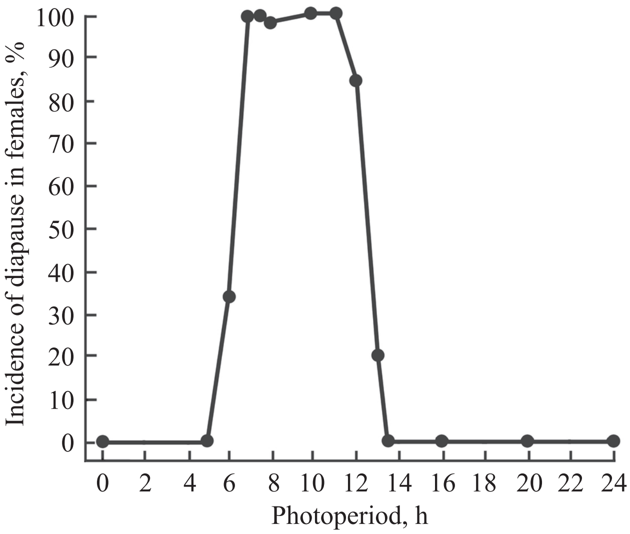

Fig. 10. Photoperiodic response of winter adult diapause induction in *Lygus hesperus* (Knight) at 27°C; population from Davis (California, USA; 38.6°N, 121.7°W) (after Beards and Strong, 1966).

The conditions of adult diapause induction were experimentally studied in *L. hesperus* population from Davis. At 27°C the bugs formed diapause under short-day conditions at day lengths from 6 to 13 h. The right ecologically significant PhPR threshold was close to 12.5 h (Beards and Strong, 1966; Fig. 10). In special experiments, physiologically active bugs were transferred from long-day conditions (16 h of light a day) to short-day ones (10 h), and diapausing bugs were transferred from short-day to long-day conditions. These experiments showed that photoperiodic cues were perceived by both nymphs and adults (Beards and Strong, 1966). A later study demonstrated that diapause induction most strongly depended on the day length during development of the IV instar nymphs. The critical day length inducing adult diapause was reached in nature on September 1. However, laboratory experiments showed that the short day was required not only for induction of diapause in *L. hesperus* but also for its maintenance, because as few as 10 long-day cues during the adult life span terminated diapause, i.e., completely eliminated the effect of the short-day conditions (Spurgeon, 2017).

Later, extensive studies of the responses controlling the seasonal development of *L. hesperus* were carried out on two populations from the south of North America: Shafter (California, USA; 35.5°N, 119.3°W) and Maricopa (Arizona, USA; 33.5°N, 112.5°W). Research was focused on the temperature parameters of development of all the ontogenetic stages at constant (Cooper and Spurgeon, 2012, 2013, 2015) and variable temperatures (Spurgeon and Brent, 2019), the physiology and control of reproduction (Brent, 2010a, 2010b; Brent and Spurgeon, 2011), the specific morphological traits of diapausing bugs (Spurgeon and Brent, 2010), the sex-related difference in diapause induction (Spurgeon and Brent, 2015), and the thermal stability of PhPR (Spurgeon, 2020). In particular, the possibility of endogenous changes in the propensity for diapause was observed in laboratory cultures of *L. hesperus* maintained for a long time under constant conditions (Spurgeon, 2012). On the whole, the new results not only confirmed the previous data but also considerably expanded our understanding of the ecological mechanisms underlying the synchronization of seasonal development of *L. hesperus* with the local climate conditions.

Lygus elisus Van Duzee, 1914 (pale legume bug)

This species is distributed in the west of North America, from Alaska to New Mexico (USA), extending as far eastwards as Iowa. Although *L. elisus* is not as abundant in North America as *L. hesperus*, it is still one of the most widespread members of the genus *Lygus* and one of the few plant bugs that strongly damage rape seeds (Schwartz and Foottit, 1992). The complex of the most significant *Lygus* pests in Texas comprised 87% of *Lygus hesperus*, 12% of *L. lineolaris*, and 1% of *L. elisus* (Bommireddy et al., 2004).

The temperature parameters of pre-adult development were experimentally studied, and the LTT of nymphal development was determined in *L. elisus* population from Lubbock (Texas, USA; 33.6°N, 101.9°W; Bommireddy et al., 2004; Fig. 11).

Another studied population of *L. elisus* was that from Lethbridge (Alberta, Canada; 49.7°N, 112.8°W), where the species had been earlier believed to produce two generations per vegetation season (Salt, 1945); however, according to the later data (Butts and Lamb, 1991), *L. elisus* has only one complete annual generation in this region. The species overwinters at the adult stage.

Genus ***Lygocoris*** Reuter, 1875

Lygocoris pabulinus (Linnaeus, 1761) (common green capsid)

This is a Holarctic species, widely distributed in Eurasia and across the whole of North America, including Alaska and Canada (Kelton, 1971; Yasunaga, 1991;

Wheeler and Henry, 1992; Schaefer and Panizzi, 2000; Vinokurov et al., 2010).

This bug produces 2 annual generations in Central Europe and only 1 generation in the north (Sweden); the partial III generation was observed in the Netherlands in particularly warm years. The species uses two groups of hosts: woody plants (apple, pear, prune, cherry, hawthorn, etc.), on which its eggs overwinter and its early-instar nymphs feed for a short time, and herbaceous plants (nettle, Russian dock, potato, sugar beet, and many others), on which the greatest part of the life cycle is realized in summer (Southwood and Leston, 1959; Blommers et al., 1997).

The temperature parameters of development were studied in *L. pabulinus* population from Schuilenburg (Belgium; 52.4°N, 6.5°E) (Mols, 1990; Table 4).

The seasonal cycle of *L. pabulinus* was also studied in detail in Wageningen (the Netherlands; 52.0°N, 5.7°E) (Blommers et al., 1997). At the end of summer, as the day length during nymphal development decreases to 16.5 h and less, the females leave the herbaceous plants on which they developed in summer and start laying diapausing eggs on young shoots of various shrubs and trees, not only deciduous but also coniferous ones. The I generation nymphs hatch from the overwintered eggs in April–May and feed for a short time on woody plants, consuming phloem sap from thin apical portions of the shoots, buds, and young fruits. Then the nymphs migrate onto herbaceous plants, which provide better nutrition (Blommers et al., 1997); development cannot be completed successfully on woody hosts. The long-day conditions (17 h and more) during development stimulate the females to lay summer (non-diapausing) eggs in the stems of herbaceous plants.

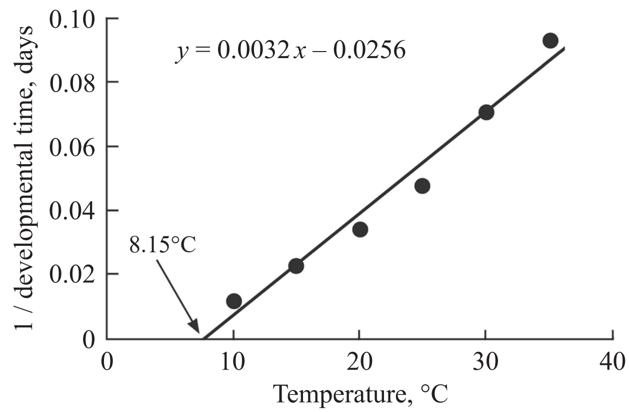

Fig. 11. The influence of temperature on the nymphal development rate of *Lygus elisus* Van Duzee; population from Lubbock (Texas, USA; 33.6°N, 101.9°W) (after Bommireddy et al., 2004). Arrow marks the lower temperature threshold of nymphal development.

The II generation nymphs of *L. pabulinus* stay on herbaceous plants during their entire life. The short day (16.5 h and less) during the second half of summer induces migration of the females onto woody plants where they lay hibernating eggs; exposure to even several short days constitutes a sufficient cue. In experiments, the V instar nymphs were found to be more sensitive to short-day cues as compared to the II instar nymphs (Blommers et al., 1997).

The embryonic diapause in *L. pabulinus* was terminated by cooling the eggs to −4...+3°C for 6 weeks and subsequent incubation at +17°C for at least 2 weeks. The eggs which had overwintered on woody plants started hatching regardless of the SET above the LTT value for overwintering eggs (4°C). During 15 years of observations in Bristol (England), the SET varied from 201 to 325 degree-days (Wightman, 1968). For some

Table 4. The developmental time of immature stages of *Lygocoris pabulinus* (Linnaeus) at constant temperatures; population from Schuilenburg (Belgium; 52.4°N, 6.5°E) (after Mols, 1990)

Stage	Mean developmental time (± SE, days) at different temperatures, °C				
	11.3	14.5	19.0	20.0	25.0
Egg	32.2 ± 2.0	23.4 ± 1.3	17.6 ± 1.0	13.5 ± 0.6	11.0 ± 0.7
I instar nymph	7.1 ± 1.7	6.6 ± 1.6	4.0 ± 0.4	3.3 ± 1.0	2.8 ± 0.7
II instar nymph	7.0 ± 1.6	6.4 ± 1.6	3.6 ± 0.5	3.4 ± 0.5	2.8 ± 0.7
III instar nymph	7.5 ± 1.8	6.9 ± 1.6	3.9 ± 0.8	3.4 ± 0.9	3.1 ± 1.1
IV instar nymph	8.4 ± 1.7	7.7 ± 1.6	4.6 ± 0.5	3.7 ± 0.8	2.9 ± 0.8
V instar nymph	11.8 ± 0.5	10.8 ± 1.0	6.4 ± 0.8	5.8 ± 0.5	5.5 ± 0.8

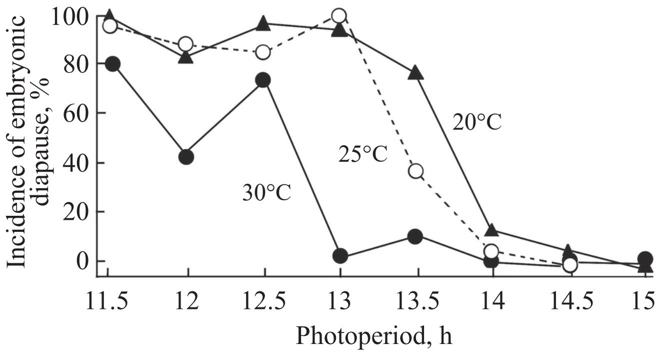

Fig. 12. Induction of winter embryonic diapause in *Stenotus rubrovittatus* (Matsumura); population from Azuchu (Japan; 35.0°N, 135.9°E) (after Shigehisa, 2008). Bugs of the maternal generation were reared from egg to adult at different photoperiods and at constant temperatures of 20, 25, and 30°C.

insect species including *L. pabulinus*, resumption of development in spring was found to require a certain level of substrate humidity (Blommers et al., 1997; Kerzhner and Josifov, 1999; Wheeler, 2001). The onset of vegetation in spring is directly related to sap flow and, correspondingly, to the humidity level of the plant tissues surrounding the bug eggs.

The seasonal development of *L. pabulinus* is accompanied by a cardinal change of the host plants, from woody to herbaceous ones. This phenomenon is rarely observed in multivoltine true bugs although it is rather typical of aphids (Homoptera).

Genus ***Stenotus*** Jakovlev, 1877

Stenotus rubrovittatus (Matsumura, 1913)
(sorghum plant bug)

This bug is distributed in the south of the Russian Far East, in China, Korea, and Japan (Kerzhner, 1972; Kerzhner and Josifov, 1999; Vinokurov et al., 2010).

In Hiroshima (Japan; 34.4°N, 132.4°E) *S. rubrovittatus* produces four annual generations. Its nymphs hatch from the overwintered eggs in mid-April. The light trap capture data revealed four distinct peaks of the adult flight: the first half of June (I), the second half of July (II), the first half of August (III), and the second half of September (IV). Adult bugs of all the generations migrate from wild herbaceous vegetation onto rice fields (Hayashi and Nakazawa, 1988).

The dynamics of embryonic diapause induction was monitored in the natural population of this species from Azuchu (Japan, Hiroshima Prefecture; 35.0°N, 135.9°E). For this purpose, females were sampled every 5 days starting from August, and the number of diapausing eggs laid by the females from different samples was recorded. The fraction of diapausing eggs was found to increase rapidly since the beginning third of September and to reach 100% in early October (Shigehisa, 2008).

The roles of the temperature and day length in induction of winter embryonic diapause in *S. rubrovittatus* from the same Azuchu population were studied in the laboratory (Shigehisa, 2008; see Fig. 12). Bugs of the maternal generation were reared under different conditions, and the physiological state of the eggs produced by them was determined. The critical day length at 20 and 25°C was found to be close to 13.5 h. A higher temperature (30°C) considerably reduced the propensity for diapause, but up to 80% of the eggs still diapaused even at a short photoperiod with 11.5 h of light a day.

Stenotus binotatus (Fabricius, 1794)
(timothy plant bug)

This is a Euro-Siberian species which has been introduced to North America, Hawaii, Australia, and New Zealand. Its populations known from Sakhalin Island, the South Kuril Islands, and Japan may also have resulted from introduction (Kerzhner and Josifov, 1999; Namyatova et al., 2013). This bug damages perennial herbaceous plants (Puchkov, 1972) and overwinters at the egg stage.

In Great Britain nymphs of *S. binotatus* hatch in early June; adults emerge in July but practically disappear already in August (Southwood and Leston, 1959). According to other authors (Butler, 1923), adult bugs can be found in nature from June to October. Thus, *S. binotatus* produces one annual generation in Great Britain.

In Obihiro (Japan; 42.9°N, 143.2°E) the I instar nymphs of *S. binotatus* appear on the spikelets of the cock's-foot *Dactylis glomerata* in mid-June; adults emerge in July and usually disappear in nature as early as the beginning of August. Feeding on the seeds is essential for nymphal development, and the nymphs occurring on other parts of the plant do not survive past the III instar (Hori et al., 1985). In Obihiro the species also has one generation a year.

CONCLUSIONS

This review contains the available data on seasonal development of plant bugs of the tribe Mirini (subfamily Mirinae), providing an overview of the seasonal patterns of these bugs and also evaluation of the current level of knowledge of their seasonal adaptations.

Based on the literature data, we have compared the ecological responses involved in control of seasonal development in 14 species from 5 genera of Mirini: *Adelphocoris*, *Apolygus*, *Lygus*, *Lygocoris*, and *Stenotus*. All the studied species are broadly polyphagous and produce different numbers of generations in different climate zones. The members of four genera hibernate at the embryonic stage while bugs of the genus *Lygus* do so at the adult stage. All these plant bugs attract the researchers' attention due to high economic significance, since they are regarded as principal pests of various leguminous crops within their vast ranges. *Adelphocoris triannulatus*, found in sweet potato fields in Japan, stands out because of specific features that are unknown in other *Adelphocoris* species, namely cannibalism in nymphs and phytozoophagy in adults (Tajima et al., 2018). Among other plant bugs of the tribe Mirini, such trophic specialization combining plant and animal diets has been found only in *Lygus pratensis* (Wheeler, 2001).

Comparison of three polyphagous *Adelphocoris* species, co-occurring in cotton fields in China, demonstrated a clear correlation between the host range and the distribution area. *Adelphocoris lineolatus* and *A. suturalis* can feed on over 100 plant species and have wide geographic distribution; by contrast, the narrow host range of *A. fasciaticollis*, comprising no more than 30 plant species, restricts its distribution to the territories of China (central, northern, and southeastern regions) and Korea (Kerzhner and Josifov, 1999).

A pronounced ability for long flights, related to the search for flowering vegetation, was found in members of the genus *Adelphocoris* (Craig, 1963; Puchkov, 1966; Ewen, 1966) and some species of the genus *Lygus*, in particular *L. pratensis*. Adults of the latter species have been recorded at altitudes up to 915 m above sea level (Johnson and Southwood, 1949).

Unlike most insects, which migrate in the state of reproductive diapause (Johnson, 1969; Saulich, 1999), the migrating females of the genus *Adelphocoris* contain mature eggs in their oviducts. This feature allows them to successfully colonize new areas even in the absence of males, since females do not need to mate after migration (Lu et al., 2009a).

The temperature parameters of development were determined for most of the experimentally studied Mirini species. In particular, the developmental time of individual stages and the duration of the whole pre-adult period at different temperatures were determined; the development thresholds and the SET needed to complete a generation were calculated using linear regression equations. These data were combined with the results of field observations to determine the exact number of annual generations.

The role of day length in the control of seasonal development was analyzed in detail in three species of the genus *Adelphocoris*: *A. triannulatus*, *A. suturalis*, and *A. lineolatus*, which have a photoperiodically controlled winter embryonic diapause, although their photosensitive stages are different. In *A. suturalis* the highest day-length sensitivity is observed in the I instar nymphs of the maternal generation (Feng et al., 2012), whereas in *A. triannulatus* and *A. lineolatus* the day-length cues are perceived by adults of the maternal generation (Ewen, 1966; Tajima et al., 2018). If the photoperiod changes during the life span of *A. triannulatus* females, i.e., if long-day conditions change to short-day ones in autumn, the physiological status of the eggs produced by the females may also change (Tajima et al., 2018). While the natural day length exceeds the PhPR threshold, the females produce actively developing (non-diapausing) eggs; when the day length decreases below the threshold value, they switch to laying hibernating eggs. So far, such examples are known only in a few insect species; in particular, the same feature was reported for the rice leaf bug *Trigonotylus caelestialium* Kirkaldy from the tribe Stenodemini of the subfamily Mirinae (Kudô and Kurihara, 1989).

The conditions inducing and terminating adult diapause were studied in greatest detail in the North American bug *Lygus hesperus*. In the southern United States, the main factor of diapause induction is the day length during development of the IV instar nymphs. In early October all the females in the natural populations are in hibernation, but the percentage of hibernating individuals decreases rapidly already in November, and in January all the bugs are physiologically ready to resume activity and to reproduce. Although early termination of winter adult diapause in *L. hesperus* appears unusual, it was confirmed by special observations performed by another author in the same region (Leigh, 1966), and also experimentally demonstrated (Spurgeon, 2017). The short day was found to be necessary not only for induction of diapause in *L. hesperus* but also for its maintenance, because as few as 10 long-day cues during the adult lifespan completely eliminated the effect of the short-day conditions (Spurgeon, 2017). Extensive studies of the seasonal adaptations in *L. hesperus*, carried out in two populations from the south of North America (California and Arizona: Spurgeon and Brent, 2015), considerably expanded our understanding of the ecological mechanisms controlling the seasonal development in plant bugs.

The seasonal development of *Lygocoris pabulinus* is an unusual but clear example of an obligate change of the host plant during the year. Eggs of this species hibernate in the tissues of woody plants, the nymphs hatching from them migrate onto herbaceous plants, and the summer generations also develop on herbaceous plants. Such a seasonal cycle is more characteristic of aphids (Homoptera) than of true bugs.

In conclusion, our analysis of the available literature indicates that the seasonal development in the tribe Mirini is still poorly understood in spite of high economic importance of these bugs. Most publications are limited to the data on temperature parameters of development and deal with only a few experimentally studied species. The essential role of photoperiodic adaptations in the control of seasonal development has been analyzed only in certain populations of some species (e.g., *Adelphocoris triannulatus*), even though such data are crucial for predicting the seasonal development and spread of harmful and beneficial insects, since the seasonal cycle of each geographic population of a given species is strictly synchronized with the local conditions.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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