

# Diapause in the Seasonal Cycle of Stink Bugs (Heteroptera, Pentatomidae) from the Temperate Zone

A. Kh. Saulich and D. L. Musolin

*St. Petersburg State University, St. Petersburg, 199034 Russia*

*St. Petersburg State Forest Technical University, St. Petersburg, 194021 Russia*

Received June 15, 2011

**Abstract**—The paper reviews the data on diapause and related phenomena in stink bugs (Heteroptera: Pentatomidae). Using stink bugs as examples, the consecutive stages of the complex dynamic process of diapause (such as diapause preparation, induction, initiation, maintenance, termination, post-diapause quiescence, and resumption of direct development) are described and discussed. Out of 43 pentatomid species studied in relation to diapause in the Temperate Zone up to date, the majority (38 species) overwinter as adults, two species—as eggs, and another two species—as nymphs. *Pentatoma rufipes* is believed to be able to overwinter at different stages of its life cycle. Less than 5 % of pentatomid species are probably able to overwinter twice. Only five species have obligate diapause, others have the facultative one. Day-length and temperature are the main diapause inducing factors in the majority of species. The role of food in the control of seasonal development is essential in the pentatomid species feeding on plant seeds. In different species, different stages are sensitive to day-length. Some pentatomids retain sensitivity to photoperiod even after diapause, others lose it and become photo-refractory (temporarily or permanently). In Pentatomidae, such seasonal adaptations as photoperiodic control of nymphal growth rates, seasonal body colour change, migrations, and summer diapause (aestivation) are widely represented, whereas wing and/or wing muscle polymorphism has not been reported yet. In the subfamily Podopinae, induction of facultative reproductive winter diapause is under the control of photoperiod and temperature. All species feed on seeds and their seasonal development to a great extent reflects availability of food. However, the same food preferences and pattern of seasonal development are also characteristic to many species from the subfamily Pentatominae. All species of the subfamily Asopinae are predators. Among them, *Picromerus bidens* and *Apateticus cynicus* have obligate embryonic winter diapause, which is rare among true bugs. At the same time, *A. cynicus* and *Podisus maculiventris* belong to the same tribe but have different types of diapause: obligate embryonic diapause in *A. cynicus* and facultative adult diapause in *P. maculiventris*. Other Asopinae species studied up to date have facultative adult diapause controlled by photoperiod and temperature with probably only one exception: in *Andrallus spinidens*, adult diapause is controlled by temperature, and photoperiod plays only a secondary role. Thus, in spite of the similar habits and feeding types among Asopinae, the species of this subfamily have different types of diapause and the latter is controlled by different factors. In the subfamily Pentatominae, most species overwinter as adults and induction of their diapause is controlled by the long-day type photoperiodic response, in spite of the differences in their feeding preferences (within phytophagy). However, there are some exceptions in this subfamily, too: *Palomena prasina*, *P. angulosa* and *Menida scotti* have obligate diapause, which conditions univoltinism in these pentatomids. In *M. scotti*, only females have obligate adult diapause, whereas males remain physiologically active through the whole winter, this pattern being unusual for Heteroptera. The univoltine seasonal cycle of this species with summer diapause (aestivation) and apparent migrations is similar to that of shield bugs (Scutelleridae). According to the analysis of seasonal development, the evolution of seasonal adaptations in Pentatomidae does not directly reflect their phylogeny. However, individual genera, small tribes or even subfamilies have similar complexes of seasonal adaptations. At the same time, Pentatominae is a large and apparently collected taxon, but most of species in this subfamily have the same facultative adult diapause.

**DOI:** 10.1134/S0013873812010010

According to the recent views, diapause is a hormonally determined state of an organism characterized by a complex of morphological, physiological, and behavioral traits known as the diapause syndrome (Tauber et al., 1986). Phenomena analogous to diapause have been observed in various groups of plants

and animals. Although varying considerably in a number of characters, they are aimed at solving the same ecological problem, namely the problem of adaptation to the climatic rhythm. This eco-physiological adaptation has been presently better studied in insects than in other organisms, which is reflected in the vast litera-

ture devoted to the problem itself and the specific traits of diapause in different groups of arthropods. However, the level of knowledge varies strongly between different insect taxa. In particular, true bugs (Heteroptera) yield noticeably to such orders as Lepidoptera or Diptera in the number of species studied in this respect and the depth of research, despite the fact that Heteroptera is one of the largest insect orders characterized by extreme diversity of seasonal adaptations and a great economic significance (Schuh and Slater, 1995; Musolin and Saulich, 1996; Panizzi et al., 2000; Saulich and Musolin, 2007a). This paper is the first one in the world literature to review the specific traits of diapause and associated phenomena in representatives of the stink bug family (Pentatomidae).

Stink bugs form the third largest family of Heteroptera, which comprises about 4700 species (over 10% of the entire order) grouped in 900 genera and 8–11 subfamilies (Gapon, 2008; Henry, 2009; Vinokurov et al., 2010). Despite the relatively large size of stink bugs and the availability of material, only few species from 3 subfamilies: Asopinae (= Stiretrinae), Podopinae, and Pentatominae, have been studied more or less thoroughly. The first two subfamilies are comparatively small and morphologically uniform groups comprising no more than 300 species each, whereas Pentatominae, including over 3000 species, appears to be a composite group (Gapon, 2008).

The aim of this communication is to summarize the published and original experimental data on the specific features of diapause and its regulation in representatives of the three above subfamilies of stink bugs and to estimate the similarity and variation in the seasonal schemes formed in species of different taxa within the same family. The greatest attention is paid to the inhabitants of Temperate Zone, whose diapause is largely associated with overwintering and is better studied than that of the tropical forms.

Among the 43 species of stink bugs in which diapause has been studied (Table 1), the great majority (38 species) overwinter as adults; 2 species, namely *Picromerus bidens* (Larivière and Laroche, 1989) and *Apateticus cynicus* (Jones and Coppel, 1963), overwinter as eggs, and 2 species, namely *Carbula humerigera* (Kiritani, 1985a, 1985b) and *Pentatoma rufipes*, as nymphs. The ability to enter diapause at different stages was recorded only in *P. rufipes* (Southwood and Leston, 1959; Puchkov, 1961). In a number of species, for example in *Perillus biocula-*

*tus* (Jasič, 1975) and *Graphosoma lineatum* (Puchkov, 1961; Nakamura et al., 1996), some individuals may overwinter twice. The painted bug *Bagrada crucifera-rum* may be physiologically active (i.e., form no diapause) throughout the year, at least in India (Singh and Malik, 1993). Such distribution of the overwintering stages approximately corresponds to the situation observed in the entire order, where species diapausing as adults clearly prevail (Ruberson et al., 1998; Saulich and Musolin, 2007a).

Diapause in insects may be *obligate*, in which case it is hereditary determined and present in each generation regardless of the external conditions, or *facultative*, in which case it is controlled by external factors and does not necessarily occur in each generation. Among the experimentally studied species of stink bugs, only 6 species (about 14%) were shown to have an obligate diapause (Table 1).

Diapause is undoubtedly a complex and dynamic process which may be subdivided into the following phases (Fig. 1): induction, preparation for diapause, onset, development, and termination of diapause, post-diapause quiescence and, finally, resumption of active development (Hodek, 1996; Saulich and Volkovich, 2004; Košťál, 2006; Volkovich, 2007; Saulich and Musolin, 2007a; Belozarov, 2009, etc.). Below, we shall consider these sequential phases of diapause by the example of stink bugs.

## INDUCTION OF DIAPAUSE

There are various abiotic and biotic factors that may act as external signals inducing the onset of diapause. In most stink bug species with a winter diapause, the principal role in diapause induction belongs to the day length (Table 1).

### *Photoperiod*

The short day and low temperature are signs of the approaching autumn. The onset of facultative winter diapause is controlled in this case by the photoperiodic response (PhPR) of a long-day type.

The first phase of induction involves the day-length sensitive stage and accumulation of photoperiodic information. Perception of the photoperiodic cues is known to occur at a certain stage of development, which is strictly species-specific and usually is the one directly preceding the diapausing stage (Saunders, 1976; Saulich and Volkovich, 2004). It has been shown that sensitivity to day length in different species may appear at different stages of development,

**Table 1.** The diapause and associated adaptations facilitating synchronization of the seasonal cycle with external conditions in species of the family Pentatomidae

Species	Type of diapause	Factors inducing diapause	Diapausing stage	References
<b>Subfamily PODOPINAE</b>				
<b>Tribe Graphosomatini</b>				
<i>Graphosoma lineatum</i> L.	F	PP, T, PP-regulation of adult color	Adult	Musolin and Saulich, 1995; Nakamura et al., 1996; Musolin, Saulich, 2001; Tullberg et al., 2008; Gamberale-Stille et al., 2010; Johansen et al., 2010
<i>G. rubrolineatum</i> (Westwood)	F	North: PP, T; South: PP, Tr	Adult	Nakamura and Numata, 1999
<i>Dybowskyia reticulata</i> (Dallas)	F	PP, T	Adult	Nakamura and Numata, 1997a, 1998; Numata, 2004
<b>Tribe Scotinopharini</b>				
<i>Scotinophara lurida</i> (Burmeister)	F	PP, T	Adult	Fernando, 1960; Cho et al., 2007, 2008; Lee et al., 2001;
<b>Subfamily ASOPINAE</b>				
<b>Tribe Amyoteini</b>				
<i>Apateticus cynicus</i> (Say)	O	–	Egg	Whitmarsh, 1916; Jones and Coppel, 1963; Javahery, 1994
<i>Arma custos</i> (F.)	F	PP, T, PP-regulation of nymph color	Adult	Volkovich and Saulich, 1994
<i>Podisus maculiventris</i> (Say)	F	PP, T	Adult	Goryshin et al., 1988; Volkovich et al., 1991
<b>Tribe Jallini</b>				
<i>Perillus bioculatus</i> F.	F	PP, T, Tr	Adult	Jasič, 1967, 1975; Shagov, 1977; Izhevskii and Ziskind, 1981; Volkovich et al., 1990; Horton et al., 1998
<i>Zicrona coerulea</i> L.	F	PP, T	Adult	Saulich, unpublished data; McPherson, 1982
<b>Tribe Platinopini</b>				
<i>Andrallus spinidens</i> (F.)	F	T	Adult	Shintani et al., 2010
<i>Picromerus bidens</i> L.	O	– (F aestivation in adults)	Egg	Leston, 1955; Larivière and Larochelle, 1989; Musolin, 1996; Musolin and Saulich, 2000
<b>Subfamily PENTATOMINAE</b>				
<b>Tribe Aeliini</b>				
<i>Aelia acuminata</i> (L.)	F	PP, T	Adult	Honěk, 1969; Hodek, 1971a, 1977
<i>Ae. fieberi</i> Scott	F	PP, T	Adult	Nakamura and Numata, 1995, 1997b
<i>Ae. rostrata</i> Boheman	F	– (O aestivation in adults)	Adult	Dikyar, 1981; Cakmak et al., 2008
<i>Ae. sibirica</i> Reuter	F	PP, T	Adult	Burov, 1962
<b>Tribe Antestiini</b>				
<i>Plautia stali</i> Scott	F	PP, PP-regulation of nymph and adult color	Adult	Kotaki and Yagi, 1987; Kotaki, 1998a, 1998b; Numata and Kobayashi, 1994

**Table 1** (Contd.)

Species	Type of diapause	Factors inducing diapause	Diapausing stage	References
<b>Tribe Carpororini</b>				
<i>Dichelops melacanthus</i> (Dallas)	F	PP, PP-regulation of nymph growth and adult color	Adult	Chocorosqui and Panizzi, 2003
<i>Dolycoris baccarum</i> L.	F	PP, PP-regulation of nymph growth	Adult	Perepelitsa, 1971; Conradi-Larsen and Sømme, 1973; Hodková et al., 1989; Hodek and Hodková, 1993; Nakamura, 2003;
<i>Palomena angulosa</i> Motschulsky	O	PP-regulation of nymph growth	Adult	Hori, 1986; Hori and Kimura, 1993
<i>P. prasina</i> L.	O	PP-regulation of nymph growth, seasonal changes in adult color	Adult	Southwood and Leston, 1959; Saulich and Musolin, 1996, 2007a
<b>Tribe Eysarcorini</b>				
<i>Carbula humerigera</i> Uhler	F	PP, PP-regulation of nymph growth (F aestivation in adults)	Nymph	Kiritani, 1985a, 1985b
<i>Eysarcoris aeneus</i> (Scopoli)	F	PP	Adult	Yao, 2002
<i>Ey. lewisi</i> Distant	F	PP, PP-regulation of nymph growth	Adult	Hori and Inamura, 1991; Hori and Kimura, 1993
<i>Ey. ventralis</i> (Westwood)	F	PP	Adult	Noda and Ishii, 1981; Nakazawa and Hayashi, 1983
<b>Tribe Menidini</b>				
<i>Menida scotti</i> Puton	O	–	Adult	Koshiyama et al., 1993, 1994, 1997
<b>Tribe Pentatomini</b>				
<i>Acrosternum hilare</i> (Say)	F	PP, T	Adult	Wilde, 1969; Javahery, 1990; McPherson and Tecic, 1997
<i>Euschistus conspersus</i> Uhler	F	PP, PP-regulation of adult color	Adult	Cullen and Zalom, 2000, 2006; Toscano and Stern, 1980
<i>Eu. heros</i> F.	F	PP, PP-regulation of adult color	Adult	Panizzi and Niva, 1994; Mourao and Panizzi, 2000, 2002
<i>Eu. ictericus</i> L.	F	PP, PP-regulation of adult color	Adult	McPherson, 1984
<i>Eu. servus</i> (Say)	F	PP, PP-regulation of adult color	Adult	Borges et al., 2001
<i>Eu. tristigmus tristigmus</i> (Say)	F	PP, PP-regulation of adult color	Adult	McPherson, 1975, 1979, 1982
<i>Nezara antennata</i> Scott	F	PP (F aestivation in adults)	Adult	Noda, 1984
<i>N. viridula</i> (L.)	F	PP, PP-regulation of nymph growth and adult color	Adult	Musolin and Numata, 2003a, 2003b; Musolin et al., 2007
<i>Oebalus poecilus</i> (Dallas)	F	PP, PP-regulation of adult color	Adult	Santos et al., 2003; Greve et al., 2003; Albuquerque, 1993

**Table 1** (Contd.)

Species	Type of diapause	Factors inducing diapause	Diapausing stage	References
<i>Oe. ypsilon</i> (De Geer)	F	PP, PP-regulation of adult color	Adult	Vecchio et al., 1994
<i>Pentatoma rufipes</i> L.	O	–	Nymph	Southwood and Leston, 1959; Puchkov, 1961; Saulich, unpublished data
<i>Thyanta calceata</i> (Say)	F	PP, PP-regulation of adult color	Adult	Oetting and Yonke, 1971; McPherson, 1977, 1982
<b>Tribe Piezodorini</b>				
<i>Piezodorus hybneri</i> (Gmelin)	F	PP	Adult	Higuchi, 1994; Endo et al., 2007
<b>Tribe Strachiini</b>				
<i>Bagrada hilaris</i> (Burmeister) (= <i>B. cruciferarum</i> Kirkaldy)		Homodynamic development		Singh and Malik, 1993
<i>Eurydema oleracea</i> L.	F	PP	Adult	Fasulati, 1979
<i>Eu. rugosum</i> Motschulsky	F	PP, Tr	Adult	Numata and Yamamoto, 1990; Ikeda-Kikue and Numata, 1994, 2001
<b>Tribe Rhynchorini</b>				
<i>Rhynchoris humeralis</i> (Thunberg) (= <i>Biprorulus bibax</i> Breddin)	F	PP	Adult	James, 1990a, 1990b, 1991, 1993
<b>Tribe Cappaeini</b>				
<i>Halyomorpha halys</i> Stål	F	PP	Adult	Watanabe, 1980; Hoebeke and Carter, 2003; Niva and Takeda, 2003; Toyama et al., 2006

Notes: Types of diapause: facultative (F) or obligate (O); cues inducing diapause: photoperiod (PP), temperature (T), and trophic factor (Tr).

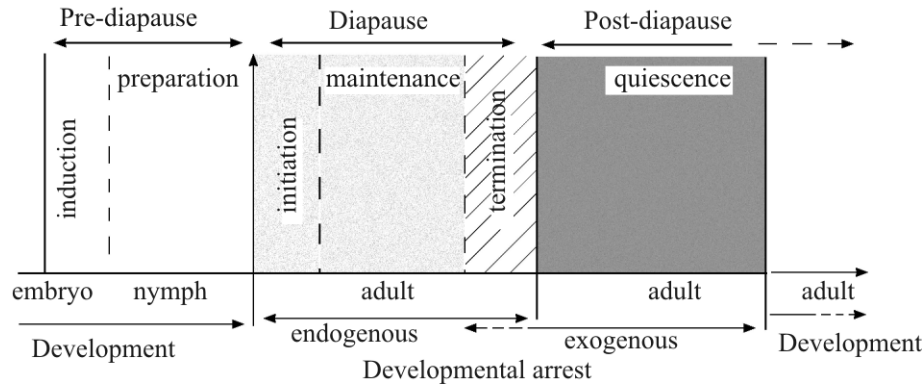
from the egg to the adult, or extend over several stages. The imaginal diapause, typical of most stink bugs, is characterized by the greatest variation in the position of the sensitive stage. Even in the same type of diapause, the day-length sensitive period may correspond to different development stages and have a different duration (Table 2; Musolin and Saulich, 1999).

The duration and position of the sensitive stage largely determine the entire pattern of seasonal development and the adaptive capacities of the species (Saulich, 1994).

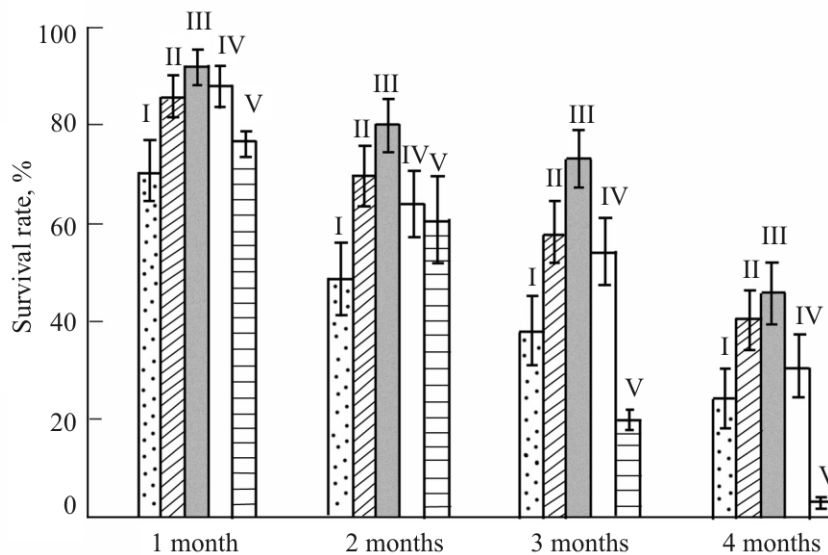
The sensitive stage is a necessary component of the PhPR. During this stage, the daily photoperiodic signals accumulate, forming the so-called *batch of photoperiodic information*. The number of photoperiodic cycles triggering diapause or active development in 50% of individuals was referred to as the *critical packet of photoperiodic information* (Goryshin and Tyschenko, 1972) or as the *required day number* (Saunders, 1976). This parameter shows how many

days with the alternative day length are required for photoperiodic induction of diapause or an active state in 50% of individuals; together with the photoperiodic threshold, the required day number is an important component of the insect PhPR.

The process of accumulation of photoperiodic signals was studied in few species of stink bugs. However, in all the cases, a particular state (diapause or active development) was induced only by complete packets of short-day (SD) or long-day (LD) photoperiodic information. In particular, the experimentally determined packet of SD information for *Podisus maculiventris* was 10 or 11 days. At a higher temperature, the same number of days under short-day conditions proved to be insufficient for diapause induction; diapause in 30% of females could be induced only by 16 days of exposure to short-day conditions. An increase in the number of diapausing individuals of *P. maculiventris* at high temperatures is related to the large packet of SD information. At +24°C the duration



**Fig. 1.** Schematic depiction of sequential phases of diapause, by the example of hemimetabolous species with imaginal diapause (modified after Košťál, 2006).



**Fig. 2.** The effect of age on survival of *Podisus maculiventris* females at low temperatures (+8°C; humidity 90–95%) (after Goryshin et al., 1989). Age of females (days after imaginal molt): 11–13 (I), 14–16 (II), 17–19 (III), 20–22 (IV), 22–25 (V). Abscissa: experiment variants, duration of the cold period.

of the nymphal development is reduced to 21 days, and at +28°C, to 16 days. Since the nymphs become sensitive to day length starting from the III instar, only a small fraction of individuals have the time to accumulate the needed sum of SD signals at high temperatures (Volkovich et al., 1991).

The end of the onset of diapause cannot always be determined. A reliable indicator of the completely formed diapause is the survival rate of diapausing individuals at low temperatures. For example, the higher survival rate of *P. maculiventris* at the favorable overwintering temperature of +8°C was observed in the individuals that were transferred into the cold 17–19 days after the imaginal molt (Fig. 2). It may be concluded that pre-diapause feeding of the bugs stopped and the diapause was completely established

by that particular moment. The bugs transferred into the cold before or after this moment showed a lower resistance to adverse overwintering conditions.

### Temperature

Although temperature usually acts as a mere modifier of the photoperiodic effect, in some insects it is known to be the main cue of diapause induction. The leading role of temperature in diapause induction was the most clearly demonstrated in tropical flies (Denlinger, 1986). Among the stink bugs studied in this respect, the winter imaginal diapause was found to be regulated by temperature only in *Andrallus spinidens*: some individuals always entered diapause at temperatures below +25°C, regardless of the day length (Fig. 3; Shintani et al., 2010).

**Table 2.** Stages sensitive to day length in species of the family Pentatomidae with photoperiodically induced winter diapause

Stage	Species
<b>Nymphal diapause</b>	
Nymphs	<i>Carbula humerigera</i> (Pentatominae; Kiritani, 1985a, 1985b)
<b>Imaginal diapause</b>	
Nymphs of II instar	<i>Oebalus poecilus</i> (Pentatominae; Albuquerque, 1993)
Nymphs starting from III instar	<i>Podisus maculiventris</i> (Pentatominae; Volkovich et al., 1991)
Nymphs of last (IV and V) instars, or nymphs of last (V) instar and adults	<i>Dolycoris baccarum</i> (Pentatominae; Perepelitsa, 1971) <i>Eysarcoris lewisi</i> (Pentatominae; Hori and Kimura, 1993)
Mostly adults	<i>Graphosoma lineatum</i> (Podopinae; Musolin and Maisov, 1998) <i>Arma custos</i> (Asopinae; Saulich and Volkovich, 1996) <i>Perillus bioculatus</i> (Asopinae; Jasič, 1967, 1975) <i>Aelia acuminata</i> (Pentatominae; Hodek, 1971a) <i>Acrosternum hilare</i> (Pentatominae; Wilde, 1969) <i>Nezara viridula</i> (Pentatominae; Ali and Ewies, 1977) <i>Plautia stali</i> (Pentatominae; Kotaki and Yagi, 1987)

However, such examples are rare; more frequently, temperature only modifies the photoperiodic effect during diapause induction. The main function of temperature is the optimal timing of diapause during the season. In warm years the winter diapause shifts onto later dates due to the PhPR threshold decreasing under the action of high temperatures, whereas in cold years an earlier induction of diapause takes place. In general, an increase in temperature suppresses the tendency to diapause whereas a drop in temperature facilitates diapause. However, the signal function of temperature cannot be always distinguished from direct suppression of activity by low temperatures. In many cases, especially in southern species that overwinter as adults, the absence of oviposition is caused by direct suppression of maturation and/or oviposition by the low ambient temperature, rather than by induction of reproductive diapause (Saulich and Musolin, 2009).

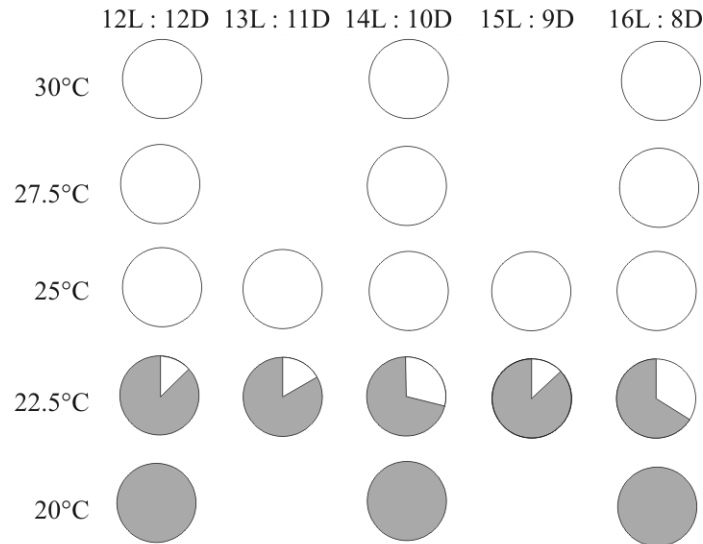
Of great significance for the manifestation of PhPR is its thermal optimum which determines the PhPR efficiency under natural conditions. The wider the optimum, the more important is the day length for regulation of seasonal development. The range of temperatures allowing an adequate response to day length varies strongly between the species. It appears to be closely related to other critical external factors. For example, due to the narrow and high thermal optimum of PhPR in the predatory bug *Arma custos* (Fig. 4),

active development of this species is possible only at temperatures above +27°C even under long-day conditions (Volkovich and Saulich, 1994).

#### *Food*

The interaction of photoperiod and temperature creates a reliable ecological mechanism regulating the timely onset of diapause in a particular season. However, there are cases when another factor, namely the trophic one, is added to this tandem.

The signal significance of the trophic factor in regulation of the seasonal development was studied in great detail in the cabbage bug *Eurydema rugosum* that has an imaginal diapause. In Japan (34°N) the nymphs of this species feed on leaves and seeds of various crucifers. Individuals of the first generation feed on wild crucifers (brown mustard) that die out already in early summer. The imaginal molt takes place in mid-June, and most of the adults enter diapause. Since the cultivated crucifers (such as radish and cabbage) remain green much longer, most of the first-generation adults living on them reproduce actively and give rise to the second generation, which undergoes imaginal molt at the end of summer and forms the overwintering population (Ikeda-Kikue and Numata, 2001). In order to determine the role of individual factors in regulation of seasonal development of this species, the nymphs were reared on rape leaves



**Fig. 3.** The roles of photoperiod and temperature (°C) in diapause induction in *Andrallus spinidens* (after Shintani et al., 2010). Light sectors: active females; gray sectors: diapausing females.

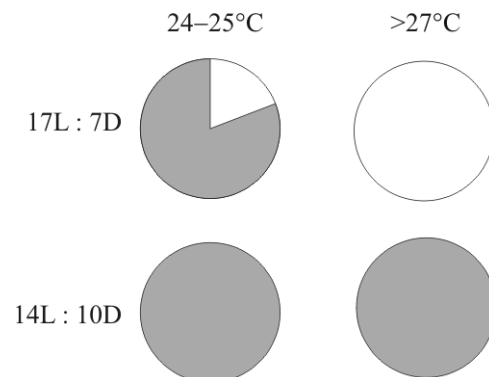
and seeds under the experimental conditions resembling the natural ones (Fig. 5).

The nymphs of *Eu. rugosum* developed in June under long-day conditions, synchronously on different diets. Most adults of both sexes that molted in July and were reared on rape leaves remained active; the females laid eggs and gave rise to the second generation. By contrast, nearly all the adults that molted at the same time but were reared on rape seeds entered diapause. The nymphs of the second generation were also reared on rape leaves; however, most of the adults that molted in September entered diapause (Fig. 5). These experiments clearly showed that although photoperiod played the principal role in induction of winter diapause, the response was significantly modified by the diet in mid-summer, which thus affected the voltinism of the population. In laboratory experiments (Fig. 6) it was shown that food acted as a signal in this species only under long-day conditions, whereas under short-day ones all the females entered diapause regardless of the diet (Numata and Yamamoto, 1990; Numata, 2004).

The role of the food plant in diapause induction is known for many species of phytophagous insects. The shortage of food or a decrease in its quality usually increases the tendency to diapause. However, in *Eu. rugosum* the trophic conditions facilitating the onset of diapause were no less favorable: both the survival rate and the body weight of nymphs feeding on rape seeds were even higher than the same para-

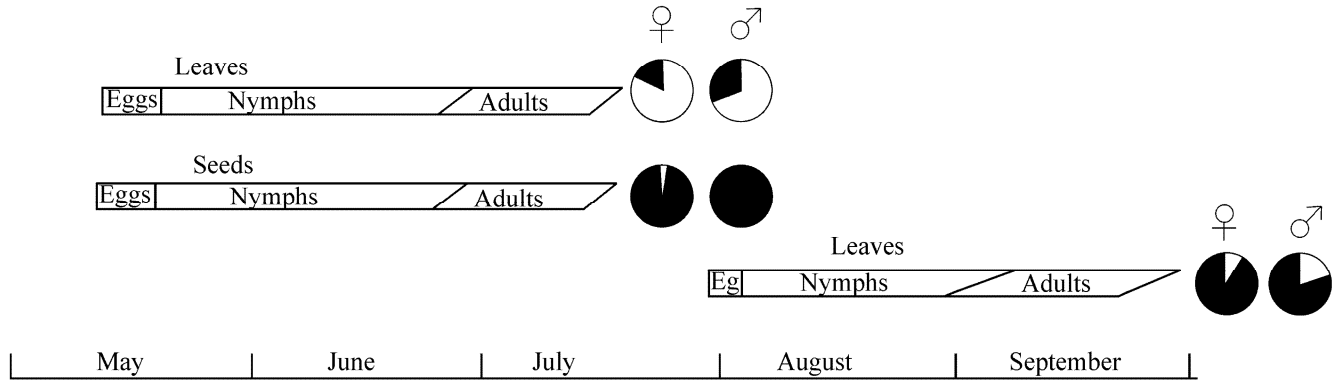
eters of nymphs feeding on leaves (Numata and Yamamoto, 1990). Therefore, the cue for diapause induction in this species was the phenophase of the food plant rather than its trophic value. The availability of seeds and the absence of leaves act as ecological signals of the approaching end of the vegetation season and the need for a winter diapause.

It was experimentally demonstrated that the diapause induced by the short day in insects feeding on leaves or seeds (the short-day diapause) differed in its properties from the diapause induced under long-day conditions in insects feeding on rape seeds (the “trophic” diapause). The short-day diapause was terminated under the action of low temperatures, which is typical of most species with winter diapause, after which the bugs became completely insensitive to day



**Fig. 4.** The roles of photoperiod and temperature in diapause induction in *Arma custos* from Belgorod Province (after Volkovich and Saulich, 1994; Saulich and Musolin, 2007a). Light sectors: active females; gray sectors: diapausing females.





**Fig. 5.** The effect of food on diapause induction in *Eurydema rugosum* in Japan (Osaka) under quasi-natural conditions (after Ikeda-Kikue and Numata, 2001). Light sectors: active development; black sectors: diapause.

length. The “trophic” diapause was not terminated by low temperatures, and the bugs retained photoperiodic sensitivity even after exposure to cold (Ikeda-Kikue and Numata, 1994).

The effect of diet on PhPR has some specific traits in predatory bugs as well. For example, in the two-spotted stink bug *Perillus bioculatus* (a laboratory culture originating from Canada, ~46°N) kept in the same photoperiodic regime (16 h of light), all the individuals feeding on eggs and larvae of the Colorado potato beetle *Leptinotarsa decemlineata* remained active whereas those feeding on the diapausing adults of this beetle entered diapause (Shagov, 1977). Similar results were later obtained in experiments with a population originating from the USA (46.5°N): under the same photoperiods (16, 15, and 14 h), the fraction of diapausing *P. bioculatus* adults was greater on the diet of old instar nymphs of the Colorado potato beetle

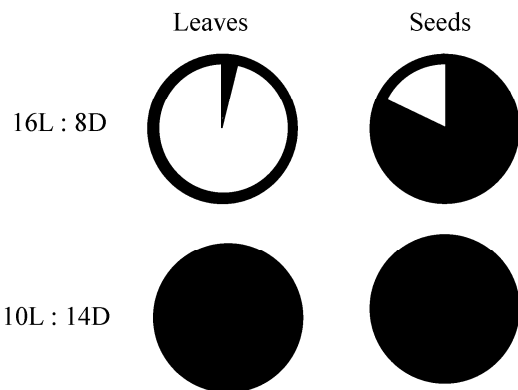
than on the diet of eggs and young instar nymphs of the beetle (Fig. 7). Thus, the age structure of the prey population acted as a cue for diapause induction in the predator (Horton et al., 1998). However, similar to the phytophagous bugs, the signal role of food manifested itself only under long-day conditions.

Unlike the oligophagous *P. bioculatus*, the polyphagous species *Podisus maculiventris* has a trophic range including no less than 75 species of insects from 8 orders (McPherson, 1982). As could be expected, this species revealed a much weaker influence of food on PhPR. The fraction of diapausing individuals among those reared in the laboratory on an unfavorable diet (larvae of the housefly *Musca domestica*) increased only in the threshold zone.

DIAPAUSE

As noted above (see Table 1), the great majority of stink bugs overwinter as adults. Diapause at this stage was mostly studied in the females, where it manifests itself in arrested ovary development, suppressed oogenesis, and the absence of oviposition. In the males the onset of diapause is usually (but not always!) marked with suppression of sexual activity and pheromone production, and also with arrested development of the testes and/or accessory glands. In both sexes, diapause is accompanied by active growth of the fat body, changes in the biochemical composition of tissues, and reduced oxygen consumption.

In many species of true bugs both males and females overwinter; in case of facultative diapause, the parameters of its photoperiodic induction show no significant difference between the sexes. This was demonstrated in *Dybowskyia reticulata* (Nakamura,



**Fig. 6.** The roles of photoperiod and food in diapause induction in *Eurydema rugosum* females in Japan (Osaka) at +25°C (after Numata and Yamamoto, 1990; Numata, 2004). Light sectors: active females; black sectors: diapausing females.

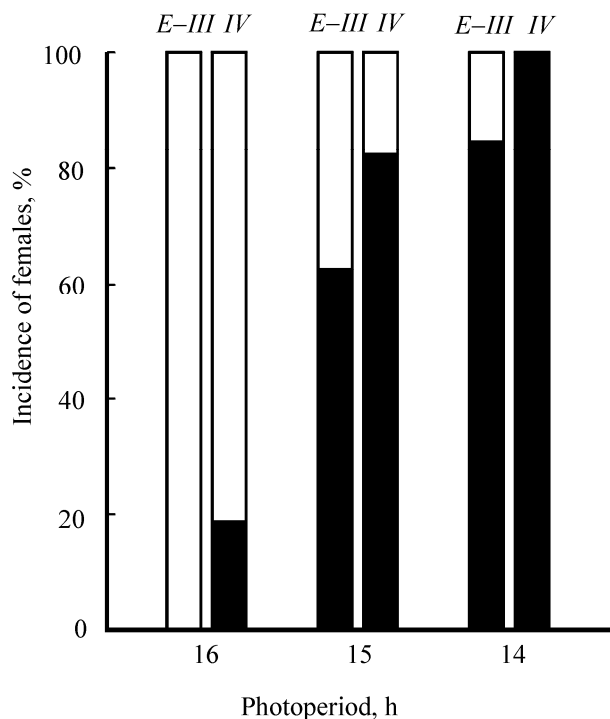
Numata, 1998), *Nezara viridula* (Fig. 8; Musolin and Numata, 2003a; Takeda et al., 2010), and many other species. The gonads of both sexes remain inactive until the end of the diapause and the overwintering period (Takeda et al., 2010).

In some species, the males and females overwinter in different physiological states. For example, in *Menida scotti* the diapause is obligate but the males have mature sperm already in autumn; in the process of mating, which may occur even during overwintering, they supply the females with nutrients, probably increasing their chances of a successful overwintering (Koshiyama et al., 1993, 1994).

It is known that diapause provides general nonspecific tolerance of insects to adverse environmental conditions, including cold. The survival of insects at low temperatures has recently attracted considerable attention of researchers (Leather et al., 1993; Bale, 1993, 1996; Hodková and Hodek, 2004, etc.) but the data on Heteroptera are still scarce. Three strategies of surviving below-zero temperatures are known in insects: freeze avoidance, freeze tolerance, and cryoprotective dehydration (Zachariassen, 1985; Bale, 2002; Sinclair et al., 2003). Most species of insects, including heteropterans, follow the first strategy: they can undergo cooling without formation of ice in their cells. At the same time, some insects survive complete freezing of their body fluids. No species using the second and third strategies have been presently found among Heteroptera.

The cold tolerance of insects under experimental conditions can be estimated by the *supercooling point* (SCP) measured by the thermoelectric method. It has been shown in several species that the SCP value is not constant throughout the year. For example, the SCP value of *Graphosoma lineatum* in Czech Republic was about  $-7^{\circ}\text{C}$  in May–June, decreased to  $-14\text{...}-12^{\circ}\text{C}$  in August–October, dropped to  $-18^{\circ}\text{C}$  in December–January, and then increased again by spring (Šlachta et al., 2002). A similar pattern of SCP dynamics was observed in *Scotinophara lurida* in Korea (Cho et al., 2007).

The seasonal trends are not always so distinct. For example, in a laboratory culture of *Podisus maculiventris* originating from the USA ( $38^{\circ}\text{N}$ ), the SCP values of non-diapausing eggs and I instar nymphs were  $-34.1 \pm 0.28^{\circ}\text{C}$  and  $-29.0 \pm 0.40^{\circ}\text{C}$ , respectively, despite the fact that these bugs overwinter as adults. At the same time, the SCP values of diapausing and ac-



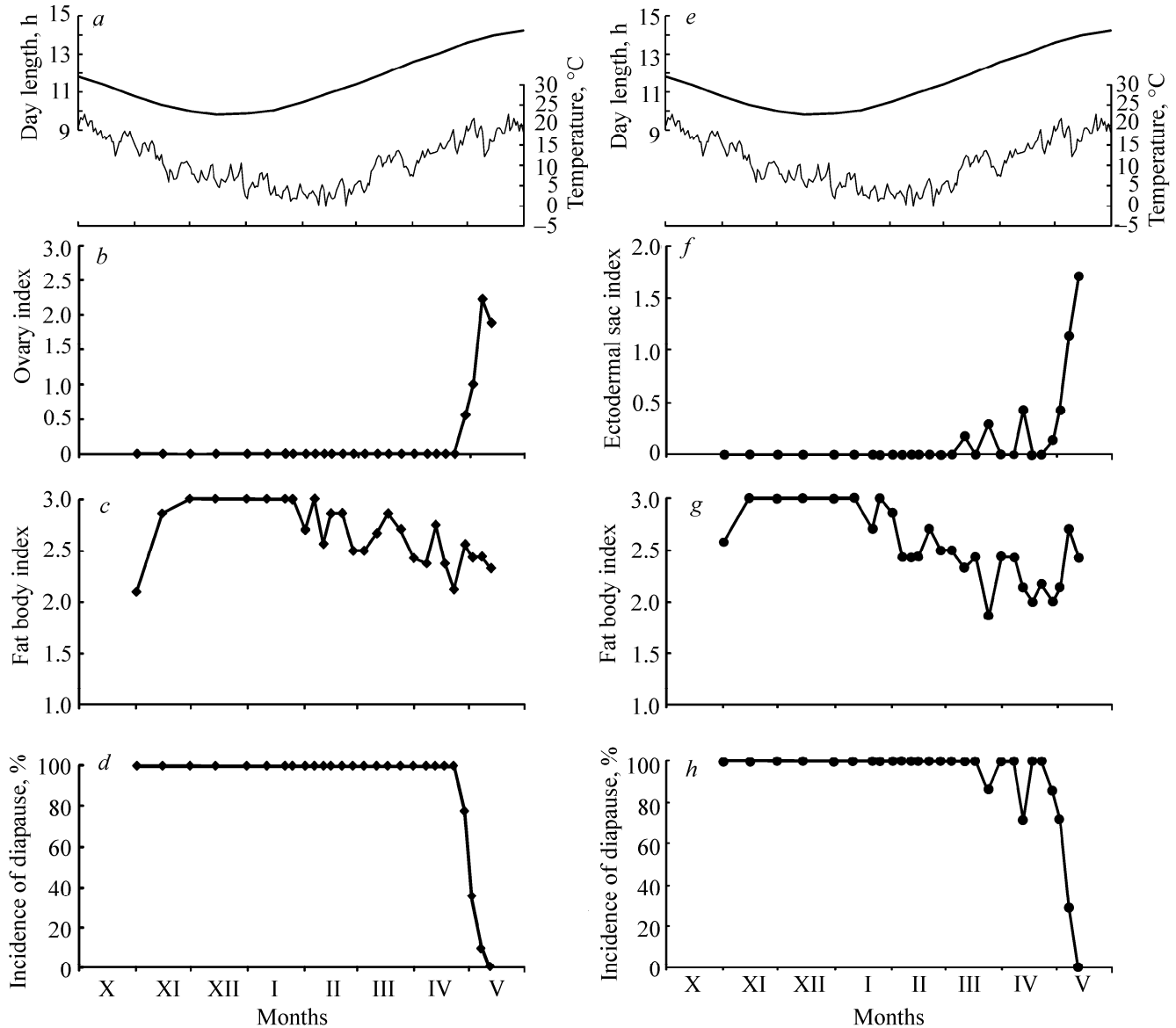
**Fig. 7.** The effect of photoperiod and food (eggs and larvae of different instars of the Colorado potato beetle) on diapause induction in *Perillus bioculatus* females from the USA at  $+23^{\circ}\text{C}$  (after Horton et al., 1998a). (E-III) eggs and young instar nymphs; (IV) old instar nymphs. Light sections of bars: active females; black sections of bars: diapausing females.

tive females were very similar:  $-17.8 \pm 0.46^{\circ}\text{C}$  and  $-15.0 \pm 0.60^{\circ}\text{C}$ , respectively (Borisenko, 1987). The diapausing ( $-11.7 \pm 0.7^{\circ}\text{C}$ ) and active ( $-10.4 \pm 0.8^{\circ}\text{C}$ ) adults of *Nezara viridula* from South Carolina (USA) also showed almost no difference in this parameter (Elsy, 1993). These data testify to a weak relation or no relation at all between cold tolerance and diapause in the above species.

The relation between diapause and cold tolerance was considered in some special publications (Denlinger, 1991; Danks, 2000; Bale, 2002, etc.). In general, diapause is considered to be necessary for increasing cold tolerance and successful overwintering of insects living in the Temperate Zone and having a facultative winter diapause, but there are quite a few exceptions to this rule (Denlinger, 1991; Šlachta et al., 2002).

#### DEVELOPMENT AND TERMINATION OF DIAPAUSE

The gradual changes that occur during diapause and finally result in its ending are usually referred to as “diapause development” or reactivation. Both terms reflect the fact that diapause is not only a specific physiological state but also a dynamic process whose



**Fig. 8.** Dynamics of physiological indices during overwintering under quasi-natural conditions in females and males of *Nezara viridula* in Japan (Kyoto) (modified after Takeda et al., 2010); (a, e) day length and temperature; (b) ovary index in females: from 0 (diapause: transparent ovarioles, no oocytes in germarium) to 3 (reproduction: semi-transparent ovarioles with mature eggs); (c, g) fat body index: from 1 (reproduction: fat body small, loose, weakly developed) to 3 (diapause: fat body expanded, dense, well developed); (d) diapause incidence in females; (f) ectodermal sac index: from 0 (diapause: sacs transparent, empty, compact) to 3 (reproduction: sacs enlarged, filled with semi-transparent white-yellow secretion); (h) incidence of diapausing in males.

ending is followed by resumption of activity. Termination of diapause is achieved by deblocking of neurosecretory centers as a result of spontaneous or induced reactivation.

The specific features of the state of diapause and the processes taking place during diapause are still insufficiently studied. Based on the studies of the gradual changes that occur during imaginal diapause, Hodek (1983) distinguished horotelic (slow, spontaneous) and tachytelic (fast, induced) processes in the diapause development. In the latter case, diapause can

be terminated by action of low temperatures (cold reactivation) or changes in the day length (photoperiodic reactivation).

#### Cold Reactivation

*Cold reactivation* was experimentally shown to be of primary significance for most insect species in the Temperate Zone. Their activity is usually resumed after exposure to temperatures from 0 to +10°C, some species having narrower ranges of temperature favorable for diapause termination. Negative temperatures

**Table 3.** Parameters of development and fecundity of *Podisus maculiventris* females after a 3-month exposure to different temperatures in the state of diapause (mean  $\pm$  SE; after Goryshin et al., 1989)

Diet	Temperature, °C	Preoviposition period, days	Lifespan of ovipositing females, days	Number of eggs laid
Larvae of <i>Calliphora vicina</i>	+8.2	6.3 $\pm$ 0.4	31.9 $\pm$ 2.3	238.4 $\pm$ 28.5
	+6.8	7.0 $\pm$ 0.1	35.5 $\pm$ 5.5	275.7 $\pm$ 67.2
	+10.9	7.4 $\pm$ 1.2	32.1 $\pm$ 5.0	185.7 $\pm$ 36.9
Larvae of <i>Galleria mellonella</i>	+8.2	6.2 $\pm$ 0.5	42.2 $\pm$ 6.5	379.7 $\pm$ 74.0
	+6.8	6.4 $\pm$ 0.3	44.1 $\pm$ 5.3	390.0 $\pm$ 51.4
Larvae of <i>Tribolium castaneum</i>	+8.2	6.6 $\pm$ 0.3	36.7 $\pm$ 3.1	328.4 $\pm$ 45.0

usually hinder the reactivation process, as do temperatures exceeding +15°C. The thermal requirements of diapausing stages are mostly determined by the living conditions and geographic origin of the species but are almost independent of the exact stage at which overwintering occurs (Saulich and Volkovich, 2004).

The conditions of overwintering and reactivation affect the physiological state of the subsequent stages. Even slight deviations from the reactivation optimum may have considerable negative aftereffects. For example, diapause in *Podisus maculiventris* was most efficiently terminated at +6...+8°C; such conditions also facilitated the maximum survival rate of the adults and high fecundity of the females (Table 3).

The duration of cold exposure required for diapause termination varies from 1 to 6 months depending on the species. The neuroendocrine centers are gradually deblocked by cooling and become capable of providing immediate stimulation when the temperature rises.

#### *Spontaneous Termination of Diapause*

This type of reactivation is based on endogenous processes and may proceed under the same conditions under which diapause was induced. Spontaneous reactivation is the most successful in species with a weak diapause, which is generally typical of insects of tropical and subtropical origin. Since the conditions never remain constant in the nature, true spontaneous reactivation can be observed only under stable experimental conditions. The possibility of reactivation under constant conditions was shown for many heteropterans, including the stink bugs *Carbula humerigera* (Kiritani, 1985b), *Plautia stali* (Kotaki, 1998a, 1998b), *Nezara viridula* (Musolin et al., 2007), and others.

Spontaneous reactivation usually follows a prolonged period of diapause development, the timing of diapause termination varying between the individuals.

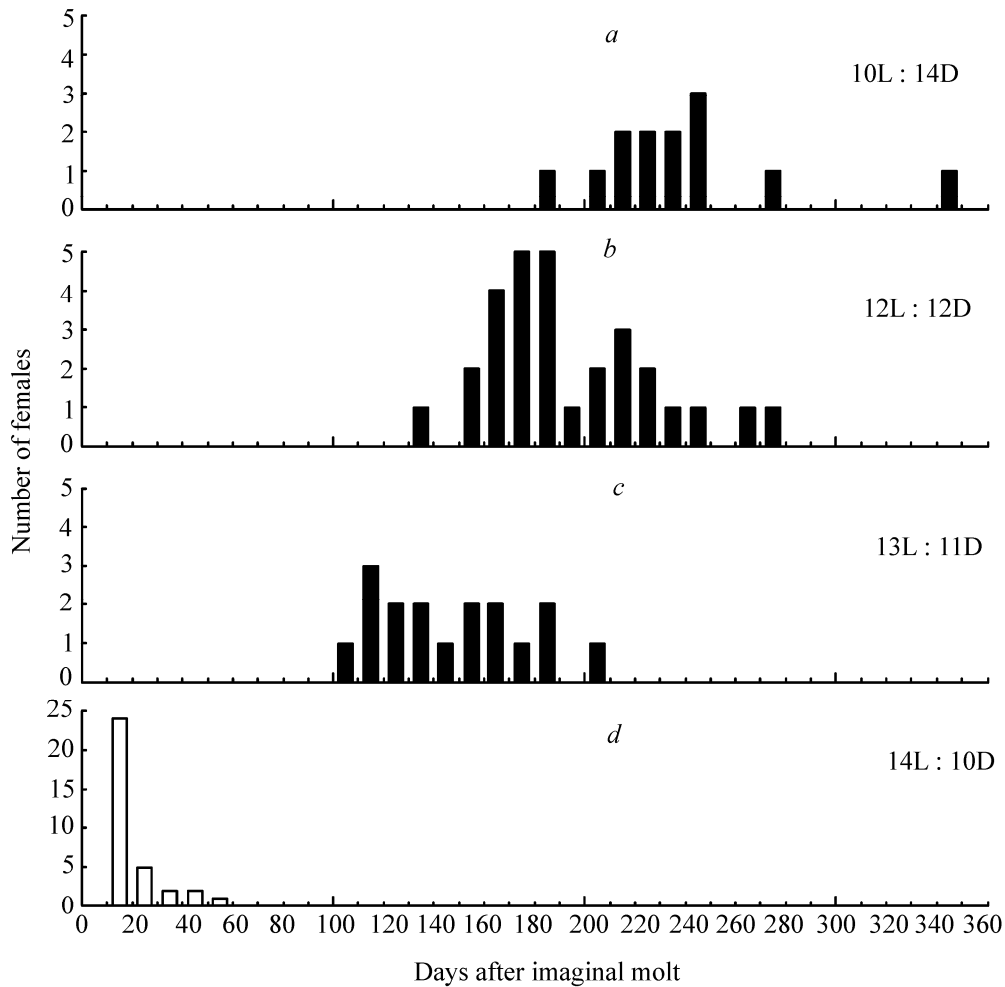
For example, the difference in the timing of oviposition between the earliest and the latest females of *N. viridula* in different short-day regimes at +25°C varied from 106 (13 h; Fig. 9c) to 158 days (10 h; Fig. 9a), whereas in the non-diapausing females the range of variation was only 43 days at the same temperature (Fig. 9d). In case of overwintering under natural conditions, the difference in the timing of oviposition between the earliest and the latest females was only 23 days (Musolin et al., 2007).

The rate of spontaneous reactivation in *N. viridula* depended on the photoperiodic conditions of diapause induction and the subsequent regime. In other words, the diapause induced and maintained under different photoperiodic conditions varied in strength: a shorter photophase corresponded to a stronger diapause and a later onset of oviposition (Figs. 9a–9c).

#### *Photoperiodic Reactivation*

Termination of diapause under the influence of photoperiodic conditions alternative to those which have induced diapause can be observed in all the insects that remain sensitive to day length during diapause. This way of reactivation is typical of species with larval and imaginal diapause.

*Photoperiodic reactivation* is also based on interaction of spontaneous and induced processes. This is indicated by the variable duration of the long-day activation period at different stages of the diapause. During the initial period the diapause is not deep but the reactivation capacity is blocked the most strongly. Therefore, insects transferred in autumn from short-day to long-day conditions do not undergo fast activation (which may manifest itself, e.g., by oviposition in case of imaginal diapause). Later, due to development of the horotelic process, the morphogenetic block becomes weaker and the time required for photoperiodic activation gradually shortens.



**Fig. 9.** The pre-oviposition period in *Nezara viridula* females in different photoperiodic regimes at +25°C (after Musolin et al., 2007); (a–d) different photoperiods (d after Musolin and Numata, 2003a).

The photoperiodic responses terminating diapause sometimes show amazing similarity with those inducing diapause, and the threshold values may be nearly the same. The coinciding PhPR curves may indicate that the reactivating effect results from the same physiological mechanism which controls the onset of diapause. In other cases, for example in *Nezara viridula*, the PhPR curves may be of somewhat different shapes (Musolin et al., 2007).

The interaction of spontaneous and induced processes during diapause termination was demonstrated in the spined soldier bug *Podisus maculiventris*. The bugs in which diapause was induced by a 12-h photoperiod at +20°C were then transferred into a 16-h photoperiod at +20 or +24°C (Table 4). At +20°C oviposition started on average 23–26 days after transfer, its timing being almost independent of the age of diapaus-

ing insects. A higher temperature resulted in an earlier onset of oviposition (Table 4).

In other experiments with the same population of *P. maculiventris*, diapause was induced under short-day conditions: 8 h of light (Fig. 10; Chloridis et al., 1997). As a result of spontaneous reactivation at +23°C (Fig. 10, curve C) the females started laying eggs on the 47th day, which also indicated that the diapause formed at 8 h of light was weaker. Exposure to cold under short-day conditions (+4 °C for 10 days: Fig. 10, curve E) hastened the onset of oviposition and increased the fraction of ovipositing females as compared to those in the experiment in which the females kept under constant short-day conditions at +23°C (Fig. 10, curve C). However, even on the 130th day the fraction of ovipositing females was only slightly over 40%. A greater stimulating effect was observed after

**Table 4.** Photoperiodic reactivation of diapausing adults of *Podisus maculiventris* (after Goryshin et al., 1989)

Temperature, °C	Age of adults at the moment of transfer to 16 h, days	Number		Time of onset of oviposition, days (mean ± SE)
		of pairs	of reactivated ind., %	
+20	18	25	100	23.0 ± 1.65
	25	23	100	26.1 ± 1.37
	27–29	11	100	25.2 ± 2.42
+24	25–30	26	100	17.8 ± 0.93

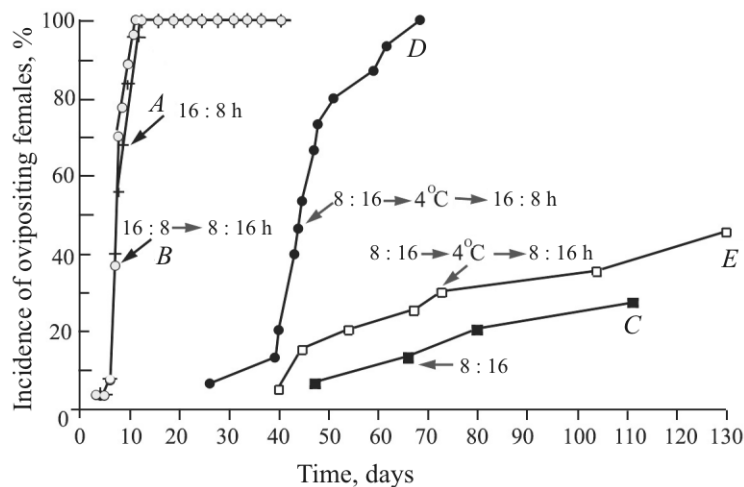
consecutive action of cold and the long day (Fig. 10, curve *D*): oviposition started already on the 25th day, and all the females were reactivated by the 70th day.

These results show that spined soldier bugs remain sensitive to day length during diapause, which is a prerequisite for its photoperiodic termination. Moreover, day-length sensitivity is preserved even after exposure to cold. Photoperiodic sensitivity during diapause appears to be typical of many species overwintering as adults. In particular, this phenomenon was observed in *Graphosoma lineatum* (Nakamura et al., 1996) and *Eysarcoris lewisi* (Hori and Kimura, 1993). It is interesting that diapause induction requires exposure to short-day conditions starting from the III nymphal instar in the spined soldier bug (see above) and from the V instar in *E. lewisi*, whereas photoperiodic termination of diapause in both species requires exposure to long-day conditions only at the adult stage. Thus, the sensitive periods of induction and termination of diapause differ in length: the processes

of diapause induction require a much longer action of the cue and involve more profound changes in the endocrine system than the processes leading to reactivation.

#### POST-DIAPAUSE PERIOD

Studies of various insect species from the temperate climate have shown that in most of them diapause ends already in December and the most severe period of winter is spent in the state of post-diapause quiescence (Danilevsky, 1961; Hodek, 1971b, 1996; Hodková, 1982; Ushatinskaya, 1990; Saulich and Volkovich, 2004; Košťál, 2006; Saulich and Musolin, 2007a, etc.). According to a very precise definition suggested by Košťál (2006: p. 121), post-diapause quiescence is “exogenously imposed inhibition of development and metabolism, which follows the termination of diapause when conditions are not favorable for resumption of direct development.” Post-diapause quiescence performs both functions of diapause: survival and syn-



**Fig. 10.** Oviposition dynamics in *Podisus maculiventris* females in different photoperiodic regimes at +23°C (after Chloridis et al., 1997); (A) development of females from egg to adult at long day (16L : 8D); (B) on the 13th day after final molt, females were transferred from long-day conditions to short-day ones (8 L : 16D); (C) constant short-day conditions (8L : 16D); (D) development first at short day (8L : 16D), then at +4°C in darkness for 10 days, then at long day (16L : 8D); (E) development first at short day (8L : 16D), then at +4°C in darkness for 10 days, then at short day (8L : 16D).

chronization of development; it complements diapause rather than replaces it, ensuring more precise seasonal synchronization (Veerman, 1985; Belozarov, 2009). Among the external factors controlling the resumption of development in spring, the most important ones for insects in the temperate latitudes are the photoperiod, temperature, and presence of food, i.e., the same factors which regulate the onset of diapause in autumn.

#### *Photoperiod*

Although under experimental conditions the long day often hastens the resumption of development, few species appear to be capable of photoperiodic reactivation in the nature. Prolonged exposure to cold usually results in temporary or permanent photoperiodic refractoriness, i.e., insensitivity to photoperiod: the insects acquire the ability to develop at any day length. Therefore in spring, with the onset of warm weather, most species of bugs resume activity regardless of the day length and reproduce until the end of their lives. Such a neutral response to photoperiod after diapause was first described in the firebug and referred to as *Pyrrhocoris*-like response (Hodek, 1971b, 1977).

By contrast with the species that lose photoperiodic sensitivity irreversibly, in some species this property is lost in autumn or winter but restored at the beginning of summer after a short refractory period. This type of response was first discovered in the bishop's mitre *Aelia acuminata* and referred to as *Aelia*-like, or recurrent response (Hodek, 1971a). This phenomenon was later observed in other stink bugs, such as *Dolycoris baccarum* (Hodek, 1977), *Eurydema rugosum* (Ikeda-Kikue, Numata, 1992), and *Graphosoma lineatum* (Nakamura et al., 1996). The resumed photoperiodic sensitivity may allow the insects to enter diapause more than once during their lifespan, and therefore to switch to a multiyear life cycle. This type of response may occur in *Perillus bioculatus* as well (Jasič, 1967).

#### *Temperature*

It is well known that resumption of development in spring is controlled by increasing temperatures. However, since the temperature regime in spring is highly unstable, some species overwintering as nymphs or adults and forming close associations with particular food plants (mono- or oligophages) or phenophases, would benefit from using more precise external cues, in particular the day length, as triggers of spring reactivation. Nevertheless, according to the data available,

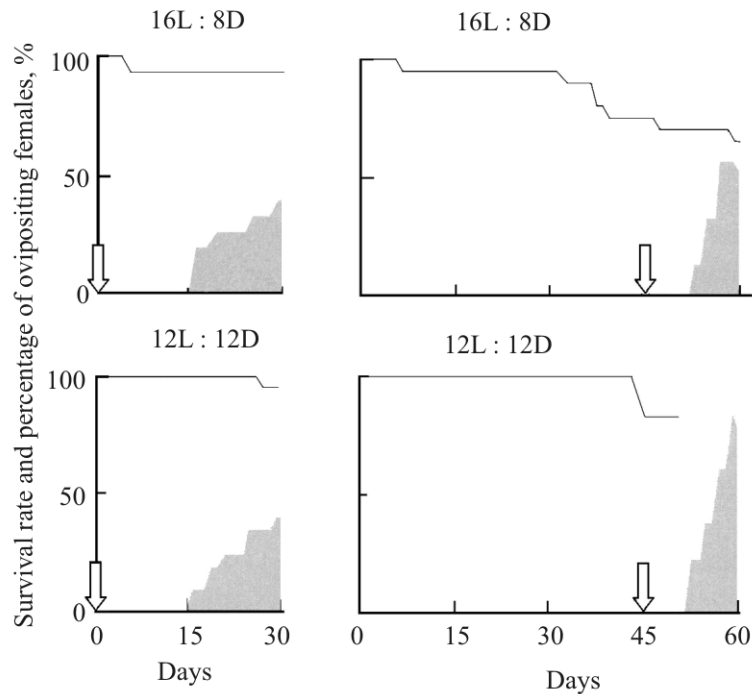
most species capable of photoperiodic diapause termination under laboratory conditions irreversibly lose their day-length sensitivity during overwintering in the field. Therefore in spring, with the onset of warm weather, the bugs resume activity and start to reproduce regardless of the day length.

Diapause in overwintered females of *Eurydema rugosum* in central Japan was shown to be completely terminated by the beginning of April. The bugs at that period were in the state of post-diapause quiescence and did not start to reproduce due to the suppressing effect of low temperatures. This suppression could be eliminated by neither the presence of food nor the long day. Oviposition started only after the temperature exceeded the lower threshold of post-diapause morphogenesis (Ikeda-Kikue and Numata, 1992). In a similar manner, the females of *Aelia fieberi* transferred into the laboratory (+25°C) in late March or early April and supplied with favorable food started to lay eggs much earlier than in the outdoors, where their oviposition was suppressed with low temperature (Nakamura and Numata, 1997b). Once started, oviposition continued till the end of the female lifespan.

#### *Food*

One of the important components of the environment, essential for reactivation of insects in spring, is the presence of adequate food resources. Their role is particularly distinct in regulation of post-diapause development of the species feeding on fruits and seeds. The role of food as a trigger of spring reproduction was demonstrated in experiments with *Dybowskyia reticulata* (Nakamura and Numata, 1997a). The females collected in the field and transferred into the laboratory in March started to lay eggs under both long-day and short-day conditions, but only in the presence of food (Fig. 11).

In the absence of food oviposition was delayed by a considerable period in both regimes. The availability of food stimulated reproduction (the moment of the appearance of food is marked with an arrow in Fig. 11). Thus, the onset of reproduction in this species in spring is not controlled by either temperature or photoperiod but is solely determined by the availability of food. In summer, the presence of food and its quality usually act as secondary cues, whereas in spring the absence of food becomes the main factor hindering gonad maturation.



**Fig. 11.** Survival and oviposition in *Dybowskyia reticulata* females from Japan (Osaka), transferred from the field to the laboratory conditions in late March (after Nakamura and Numata, 1997a; Numata, 2004). Light areas: non-ovipositing females; shaded areas: females that started laying eggs. Arrows mark the moment when food became available. The temperature was +25°C.

#### OTHER ADAPTATIONS FACILITATING SYNCHRONOUS INDUCTION AND TERMINATION OF WINTER DIAPAUSE IN A PARTICULAR SEASON

Most heteropterans of the Temperate Zone spend summer in the active state that includes growth, development, reproduction, dispersal, and preparation for overwintering. In a few species the reproduction period is shifted towards the beginning or the end of the summer, a part of the summer season being spent in the dormant state. The bugs reveal various seasonal adaptations allowing them to synchronize the summer phases of the life cycle with the most favorable periods within a particular season.

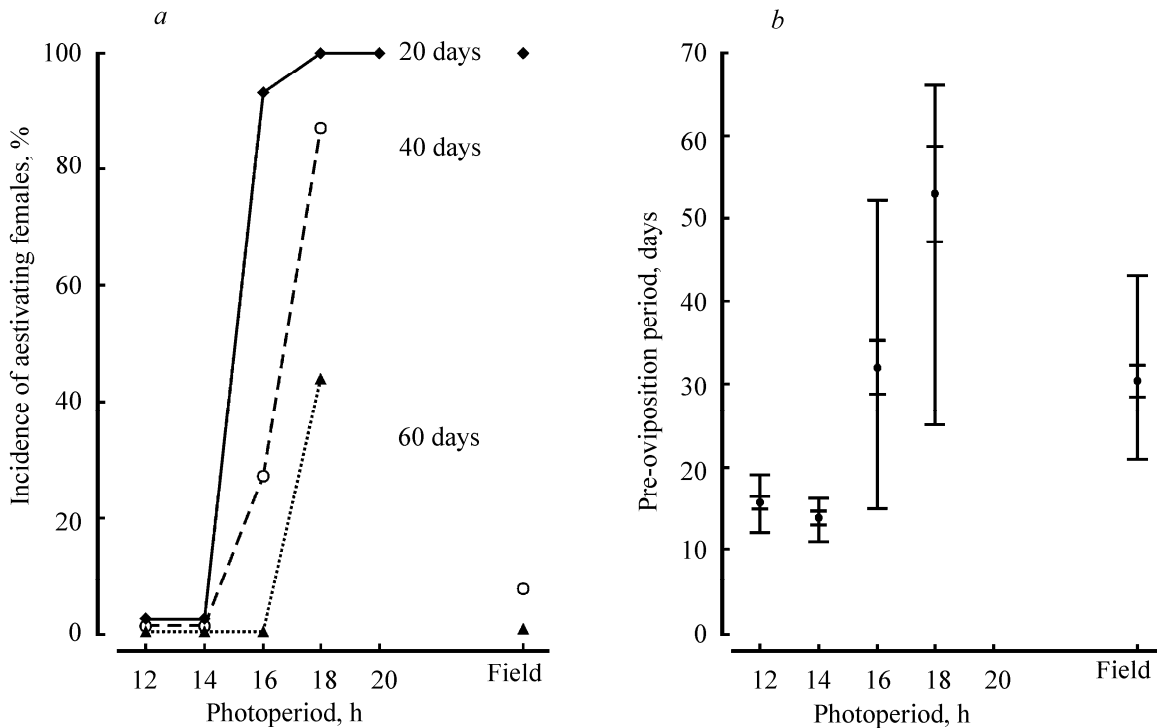
##### *Regulation of the Nymphal Growth Rate*

The growth rate of the nymphs and, correspondingly, the duration of the nymphal period are largely affected by the ambient temperature: an increase in temperature within the thermal optimum range hastens development, and a decrease hinders it. However, the development rate depends on other factors as well. In particular, one of the important seasonal adaptations in insects is photoperiodic regulation of the nymphal

growth rate: the nymphs may develop faster under certain photoperiodic conditions and slower under others. In a greater fraction of species development is accelerated by the short-day conditions: as the day length decreases in autumn, the nymphal growth rate increases so as to reach the overwintering stage before the environmental conditions get worse. Such an adaptation was first described in the firebug *Pyrrhocoris apterus* (Saunders, 1983; Numata et al., 1993; Saulich et al., 1993) and later found in the stink bugs *Arma custos* (Volkovich and Saulich, 1994) and *Palomena prasina* (Saulich and Musolin, 1996; Musolin and Saulich, 1999) as well as in many other bug species (Musolin and Saulich, 1997).

However, despite its clear adaptive significance, photoperiodic regulation of the growth rate is not a universal phenomenon. The nymphs of some species grow faster under long-day conditions; moreover, responses to day length may be directly opposite in different populations of the same species. Such differences were found, in particular, between the populations of *Dolycoris baccarum* from Norway and Japan (Conradi-Larsen and Sømme, 1973; Nakamura, 2003) and between the populations of *Nezara viridula* from





**Fig. 12.** Photoperiodic induction of summer diapause in *Picromerus bidens* (after Musolin and Saulich, 2000); (a) PhPR of induction of summer diapause under laboratory (+24.5°C) and natural conditions in Belgorod Province (The pre-oviposition period was between July 6 and August 23; the PhPR was determined on the 20th, 40th, and 60th day after final molt); (b) duration of the pre-oviposition period under the same conditions (mean  $\pm$  SE; min–max).

Egypt and Japan (Ali and Ewiess, 1977; Musolin and Numata, 2003a). These examples show that this feature can manifest itself at the population level, ensuring a high level of adaptation of the local population to specific living conditions. At the same time, in some species the nymphal growth rate does not depend on photoperiodic conditions. For example, no distinct relations between the duration of nymphal development and the photoperiodic conditions were observed in *Podisus maculiventris* (Goryshin et al., 1988b), *Picromerus bidens* (Musolin and Saulich, 1997), and some other species.

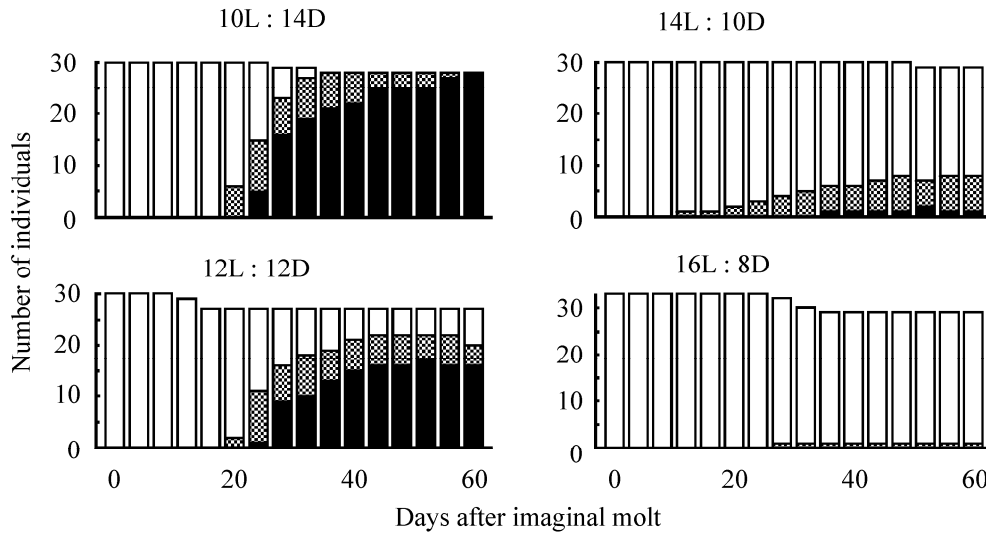
The physiological mechanism underlying this adaptation is still insufficiently studied. Further research will be necessary to understand the exact nature of the effect of photoperiod (acceleration of development under certain conditions or retardation under other conditions) and the relations between these phenomena and summer diapause.

#### Summer Diapause

Diapause not only ensures survival of insects during winter but may also perform protective and synchronizing functions in summer. In the latter case diapause

is formed under the conditions of long day and high temperatures. It may be obligate, occurring every year and in every generation, or facultative, controlled by external factors, such as the short-day PhPR (Saulich and Volkovich, 1996). Although summer diapause, or aestivation, is more frequently observed in insects from tropical or subtropical climate (Masaki, 1980), species with such a diapause can also be found in the temperate regions; among stink bugs such examples are *Nezara antennata* (Noda, 1984) and *Carbula humerigera* (Kiritani, 1985a, 1985b). Adults of some species migrate into the mountains before aestivation (*Aelia rostrata* in Turkey ascends to about 1500 m above sea level: see Şişli, 1965).

Aestivation was recently discovered in *Picromerus bidens*; experiments showed that it was induced by the short-day PhPR (Musolin, 1996; Musolin and Saulich, 1996, 2000). Under short-day conditions (12 and 14 h) all the females started laying eggs synchronously, on average on the 15th day after imaginal molt, whereas no reproduction took place in July in other laboratory regimes and outdoors (Figs. 12a, 12b). The females kept under constant long-day conditions, and also those outdoors (where the day length at the moment of



**Fig. 13.** The effect of day length on coloration of *Nezara viridula* females in Japan (Osaka) at +20°C (after Musolin and Numata, 2003a). Light sections of bars: green; black sections of bars: brown; shaded sections of bars: intermediate coloration.

imaginal molt was approximately 16.5 h) gradually reactivated, and almost all the individuals started laying eggs within two months' time.

#### Seasonal Changes in Coloration

Changes in the body coloration during the season are typical of many true bugs and are often controlled by the photoperiod (Musolin and Saulich, 1996, 1999; Saulich and Musolin, 2007a). In some cases they are observed at the diapausing stage, in others they occur at one of the preceding stages and do not seem to be connected to diapause at all.

The existence of two color morphs was described in *Thyanta calceata* (McPherson, 1977). The seasonal forms of *Euschistus tristigmus tristigmus* (McPherson, 1979) and *Oebalus ypsilongriseus* (Vecchio et al., 1994) are so different in coloration and structural characters that they used to be regarded as separate species.

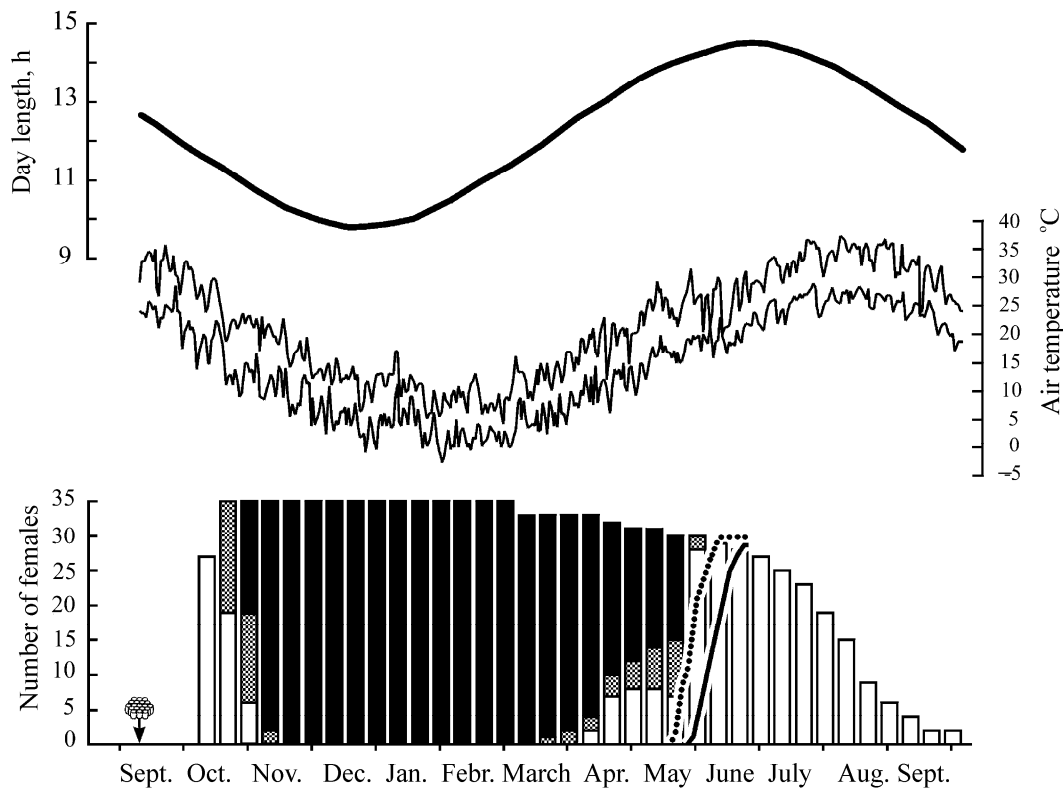
Changes in coloration at the adult stage can be often observed in true bugs and are usually related to diapause (Musolin and Saulich, 1996). For example, the freshly molted adults of *Nezara viridula* may be either green or yellow, depending on the genetic morph. The same coloration is preserved during reproduction. However, individuals of the diapausing generation turn brown soon after the imaginal molt (Fig. 13; Musolin and Numata, 2003a) and retain this coloration until the complete termination of diapause in spring. The color changes are regulated by the day length and

correlated with the physiological state of the individual (Harris et al., 1984; Musolin and Numata, 2003a; Musolin et al., 2007).

Similar diapause-related color changes in the adults under short-day conditions were described in the stink bugs *Plautia stali* (Kotaki and Yagi, 1987) and *Euschistus servus* (Borges et al., 2001). Adults of *Graphosoma lineatum* have a paler and duller coloration before overwintering than in spring (Tullberg et al., 2008). The degree of melanization in *Podisus maculiventris* also changes during the season, the bugs being paler in summer than in spring or autumn; these changes, however, mostly depend on the temperature rather than on the day length (Aldrich, 1986).

Analysis of the above examples of seasonal coloration changes in insects easily reveals the main trend: the prevalence of brown coloration or dull texture of the integuments in overwintering insects. This makes them less conspicuous, providing passive protection from predators (the seasonal camouflage). Dark coloration may also give a certain adaptive advantage in thermoregulation, even during winter. The significance of seasonal coloration changes is especially high in the species forming large aggregates in places of hibernation and/or aestivation, which is common among stink bugs.

The seasonal color polyphenism is irreversible in some species. In other species coloration changes gradually in the process of induction of imaginal diapause. Such seasonal changes may be reversible. The



**Fig. 14.** Seasonal coloration changes in females of *Nezara viridula* under natural conditions in Japan (Osaka) (modified after Musolin and Numata, 2003b). Arrow marks the moment when the egg batches were transferred into outdoor conditions. The nymphs and males are not shown. The histogram shows the number and color of females; dotted line: the total number of mating females; solid line: that of ovipositing females. Light sections of bars: green adults; black sections of bars: brown adults; shaded sections of bars: adults with intermediate coloration. The temperature is shown as the minimum and maximum daily values.

reversal of coloration in spring was studied, for example, in the southern green stink bug *Nezara viridula* maintained under natural conditions in central Japan (Musolin and Numata, 2003b; Musolin et al., 2010; Takeda et al., 2010). At the beginning of overwintering, the non-reproducing adults changed their color from green to brown and remained brown during the entire winter. In spring the initial green coloration was restored, after which the females started to reproduce (Fig. 14).

#### CONCLUSION

The above review of data concerning diapause in the experimentally studied stink bugs (43 species) of the Temperate Zone has revealed no distinct trends in the position (embryonic, nymphal, or imaginal) and type of diapause (obligate or facultative) in particular taxa within the family Pentatomidae. At the same time, our analysis has allowed us to estimate the similarity of seasonal adaptations in species belonging to different taxa of stink bugs.

Species of the subfamily Podopinae overwinter as adults (Table 1), the onset of their diapause being controlled by the day length and temperature. Since all these species feed on seeds, their seasonal development is largely determined by the availability of food. However, the same type of food and pattern of seasonal development are typical of many species of the subfamily Pentatominae (in particular, most representatives of the tribe Aeliini).

All species of the subfamily Asopinae are predators. The subfamily includes 2 species from different tribes: *Picromerus bidens* (tribe Platinopini) and *Apateticus cynicus* (tribe Amyoteini) having an obligate embryonic diapause, which is a rare phenomenon among Heteroptera. At the same time, *A. cynicus* and *Podisus maculiventris* belong to the same tribe but have different types of diapause: the former species has an obligate embryonic diapause and the latter, a facultative imaginal diapause. Other studied species of this subfamily have a facultative imaginal diapause controlled

by the day length and temperature. *Andrallus spinidens* represents an exception, since its imaginal diapause is controlled by temperature while the day length appears to be of little significance. Thus, even though species of the subfamily Asopinae have a similar biology and mode of feeding (all of them are predators), they diapause at different stages of development under the influence of different factors.

On the contrary, most representatives of the subfamily Pentatominae overwinter as adults and have a diapause controlled by the long-day PhPR, despite the diversity in their modes of feeding. However, this subfamily also includes some species with an obligate diapause determining the univoltine seasonal cycle: *Palomena prasina*, *P. angulosa*, and *Menida scotti*. The latter species is unusual in that only the females have an obligate reproductive diapause whereas the males remain physiologically active during winter (Koshiyama et al., 1994, 1997). Quite unexpectedly, the bugs *Pentatoma rufipes* with an obligate nymphal diapause and *Nezara viridula* with a facultative imaginal diapause belong to the same tribe Pentatomini. Among the studied species of the tribe Aeliini, an obligate imaginal diapause was observed only in *Aelia rostrata*; the species has a univoltine seasonal cycle including aestivation and distinct seasonal migrations, which is almost identical to that of shield bugs of the family Scutelleridae.

Thus, analysis of seasonal development of stink bugs has shown that evolution of their seasonal adaptations does not correspond precisely to their phylogeny. However, similar complexes of seasonal adaptations are formed within individual genera (for example, *Palomena* with an obligate diapause and photoperiodic regulation of nymphal growth rates, or *Euschistus* with photoperiodic regulation of color polymorphism), small tribes (for example, Aeliini), or even subfamilies (Podopinae). At the same time, the large family Pentatominae, despite being a composite taxon, is quite uniform in that most of the species have a facultative imaginal diapause.

The knowledge of ecology and the pattern of seasonal development of a species may help to clarify its taxonomic position. For example, *Dybowskyia reticulata* is considered within the tribe Tarisini by some authors (Vinokurov et al., 2010), and within Graphosomatini by others (Gapon, 2008). In its ecological characteristics *D. reticulata* resembles the species included in the tribe Graphosomatini.

The seasonal changes in coloration are more widespread in stink bugs (mostly those having an imaginal diapause) than in other taxa of true bugs. However, such common seasonal adaptations as polymorphism of wings and/or wing musculature (Saulich and Musolin, 2007b) have not yet been found in Pentatomidae.

In general, despite intensive studies of seasonal adaptations in Pentatomidae and other families of Heteroptera carried out in the recent decades, the diapause and ecological mechanisms of its regulation have been studied in less than 1% of the known species of stink bugs.

#### ACKNOWLEDGMENTS

This work was financially supported by the Federal Program in Support of Leading Academic Schools (grant NSh-3332.2010.4), the Inessa Charitable Foundation, and ISEFOR (no. 245268; FP7-KBBE-2009-1-2-08).

#### REFERENCES

1. Aldrich, J.R., "Seasonal Variation of Black Pigmentation under the Wings in a True Bug (Hemiptera: Pentatomidae): a Laboratory and Field Study," Proc. Entomol. Soc. Wash. **88** (3), 409–421 (1986).
2. Albuquerque, G.S., "Planting Time as a Tactic to Manage the Small Rice Stink Bug, *Oebalus poecilus* (Hemiptera, Pentatomidae), in Rio Grande do Sul, Brazil," Crop Protection **12** (8), 627–630 (1993).
3. Ali, M. and Ewiess, M.A., "Photoperiodic and Temperature Effects on Rate of Development and Diapause in the Green Stink Bug, *Nezara viridula* L. (Heteroptera: Pentatomidae)," Zeit. Angew. Entomol. **84**, 256–264 (1977).
4. Bale, J.S., "Classes of Insect Cold Hardiness," Functional Ecol. **7**, 751–753 (1993).
5. Bale, J.S., "Insect Cold Hardiness: A Matter of Life and Death," Eur. J. Entomol. **93**, 369–382 (1996).
6. Bale, J.S., "Insect and Low Temperatures: from Molecular Biology to Distributions and Abundance," Phil. Trans. R. Soc. London B **357**, 849–862 (2002).
7. Belozero, V.N., "New Aspects in Investigations of Diapause and Non-Diapause Dormancy Types in Insects and Other Arthropods," Entomol. Obozr. **88** (1), 3–15 (2009) [Entomol. Rev. **89** (2), 127–136 (2009)].
8. Borges, M., Zhang, A.J., Camp, M.J., and Aldrich, J.R., "Adult Diapause Morph of the Brown Stink Bug, *Euschistus servus* (Say) (Heteroptera: Pentatomidae)," Neotrop. Entomol. **30** (1), 179–182 (2001).

9. Borisenko, I.A., "Dynamics of Cold Tolerance during Development of the Spined Soldier Bug *Podisus maculiventris* Say," Byul. Vses. NII Zashch. Rast. **69**, 12–16 (1987).
10. Burov, V.N., "Factors Affecting Population Dynamics and Harmfulness of Wheat Stink Bugs of the Genus *Aelia* (Heteroptera, Pentatomidae)," Entomol. Obozr. **41** (2), 262–273 (1962).
11. Cakmak, O., Bashan, M., and Kocak, E., "The Influence of Life-Cycle on Phospholipid and Triacylglycerol Fatty Acid Profiles of *Aelia rostrata* Boheman (Heteroptera: Pentatomidae)," J. Kans. Entomol. Soc. **81** (3), 261–275 (2008).
12. Chloridis, A.S., Koveos, D.S., and Stamopoulos, D.C., "Effect of Photoperiod on the Induction and Maintenance of Diapause and the Development of the Predatory Bug *Podisus maculiventris* (Hem.: Pentatomidae)," Entomophaga **42** (3), 427–434 (1997).
13. Cho, J.R., Lee, M., Kim, H.S., and Boo, K.S., "Effect of Photoperiod and Temperature on Reproductive Diapause of *Scotinophara lurida* (Burmeister) (Heteroptera: Pentatomidae)," J. Asia-Pacific Entomol. **11**, 53–57 (2008).
14. Cho, J.R., Lee, M., Kim, H.S., et al., "Cold Hardiness in the Black Rice Bug, *Scotinophara lurida*," Physiol. Entomol. **32**, 167–174 (2007).
15. Chocorosqui, V.R. and Panizzi, A.R., "Photoperiod Influence on the Biology and Phenological Characteristics of *Dichelops melacanthus* (Dallas, 1851) (Heteroptera: Pentatomidae)," Braz. J. Biol. **63** (4), 655–664 (2003).
16. Conradi-Larsen, E.M. and Sømme, L., "Notes on the Biology of *Dolycoris baccarum* L. (Het., Pentatomidae)," Nor. Entomol. Tidssk. **20**, 245–247 (1973).
17. Cullen, E.M. and Zalom, F.G., "Phenology-Based Field Monitoring for Conspense Stink Bug (Hemiptera: Pentatomidae) in Processing Tomatoes," Env. Entomol. **29** (3), 560–567 (2000).
18. Cullen, E.M. and Zalom, F.G., "*Euschistus conspersus* Female Morphology and Attraction to Methyl (2E,4Z)-decadienoate Pheromone-Baited Traps in Processing Tomatoes," Entomol. Exp. Appl. **119** (2), 163–173 (2006).
19. Danilevsky, A.S., *Photoperiodism and Seasonal Development of Insects* (Len. Gos. Univ., Leningrad, 1961) [in Russian].
20. Danks, H.V., "Dehydration in Dormant Insects," J. Insect Physiol. **46**, 837–852 (2000).
21. Denlinger, D.L., "Dormancy in Tropical Insects," Annu. Rev. Entomol. **31**, 239–264 (1986).
22. Denlinger, D.L., "Relationship between Cold Hardiness and Diapause," in *Insects at Low Temperatures*, Ed. by R.E. Lee, Jr. and D.L. Denlinger (Chapman & Hall, New York, 1991), pp. 174–198.
23. Dikyar, R., "Biology and Control of *Aelia rostrata* in Central Anatolia," Bull. Org. Eur. Mediterr. Protect. Plant **11** (2), 39–41 (1981).
24. Elsey, K.D., "Cold Tolerance of the Southern Green Stink Bug (Heteroptera: Pentatomidae)," Env. Entomol. **22**, 567–570 (1993).
25. Endo, N., Yasuda, T., Matsukura, K., et al., "Possible Function of *Piezodorus hybneri* (Heteroptera: Pentatomidae) Male Pheromone: Effects of Adult Age and Diapause on Sexual Maturity and Pheromone Production," Appl. Entomol. Zool. **42** (4), 637–641 (2007).
26. Fasulati, S.R., "Photoperiodic Response and Coloration of the Brassica Bug *Eurydema oleracea* L. (Heteroptera, Pentatomidae)," Entomol. Obozr. **57** (1), 15–23 (1979).
27. Fernando, H.E., "A Biological and Ecological Study of the Pentatomid Bug, *Scotinophara lurida* (Burm.) in Ceylon," Bull. Entomol. Res. **51**, 559–576 (1960).
28. Gamberale-Stille, G., Johansen, A.I., and Tullberg, B.S., "Change in Protective Coloration in the Striated Shieldbug *Graphosoma lineatum* (Heteroptera: Pentatomidae): Predator Avoidance and Generalization among Different Life Stages," Evol. Ecol. **24** (2), 423–432 (2010).
29. Gapon, D.A., *A Taxonomic Review of the World Fauna of Stink Bugs (Heteroptera: Pentatomidae) of the Subfamilies Asopinae and Podopinae*, Candidate's Dissertation in Biology (St. Petersburg, 2008) [in Russian].
30. Goryshin, N.I., Volkovich, T.A., Saulich, A.Kh., et al., "The Role of Temperature and Photoperiod in the Control of Development and Diapause in the Spined Soldier Bug *Podisus maculiventris* (Hemiptera, Pentatomidae)," Zool. Zh. **67** (8), 1149–1161 (1988a).
31. Goryshin, N.I., Saulich, A.Kh., Volkovich, T.A., et al., "The Effect of the Trophic Factor on Development and Photoperiodic Reaction in the Spined Soldier Bug *Podisus maculiventris* (Hemiptera, Pentatomidae)," Zool. Zh. **67** (9), 1324–1332 (1988b).
32. Goryshin, N.I., Volkovich T.A., Saulich, A.Kh., et al., *Ecology of the Spined Soldier Bug Podisus maculiventris*, Available from VINITI, No. 115-B-90 (Moscow, 1989) [in Russian].
33. Goryshin, N.I. and Tyshchenko, G.F., "Experimental Analysis of Photoperiodic Induction in Insects," Trudy Biol. NII Len. Gos. Univ. **21**, 68–89 (1972).
34. Greve, C., Fortes, N.D.F., and Grazia, J., "Immature Stages of *Oebalus poecilus* (Heteroptera, Pentatomidae)," Iheringia Ser. Zool. **3** (1), 89–96 (2003).
35. Harris, V.E., Todd, J.W., and Mullinix, B.G., "Color Change as an Indicator of Adult Diapause in the Southern Green Stink Bug, *Nezara viridula*," J. Agric. Entomol. **1** (1), 82–91 (1984).
36. Henry, T.J., "Biodiversity of Heteroptera," in *Insect Biodiversity: Science and Society*, Ed. by R.G. Footitt and P.H. Adler (Blackwell Publ., Oxford, 2009), pp. 223–263.

37. Higuchi, H., "Photoperiodic Induction of Diapause, Hibernation and Voltinism in *Piezodorus hybneri* (Heteroptera: Pentatomidae)," *Entomol. Sci.* **29** (4), 585–592 (1994).
38. Hodek, I., "Sensitivity to Photoperiod in *Aelia acuminata* (L.) after Adult Diapause," *Oecologia* (Berlin) **6**, 152–155 (1971a).
39. Hodek, I., "Termination of Adult Diapause in *Pyrrhocris apterus* (Heteroptera: Pyrrhocoridae) in the Field," *Entomol. Exp. Appl.* **14** (2), 212–222 (1971b).
40. Hodek, I., "Photoperiodic Response in Spring in Three Pentatomidae (Heteroptera)," *Acta Entomol. Bohemoslov.* **74**, 209–218 (1977).
41. Hodek, I., "Role of Environmental Factors and Endogenous Mechanisms in the Seasonality of Reproduction in Insects Diapausing as Adults," in *Diapause and Life Cycle Strategies in Insects*, Ed. by V.K. Brown and I. Hodek (Dr. W. Junk Publ., The Hague, 1983), pp. 9–33.
42. Hodek, I., "Diapause Development, Diapause Termination and the End of Diapause," *Eur. J. Entomol.* **93**, 475–487 (1996).
43. Hodek, I. and Hodková, M., "Role of Temperature and Photoperiod in Diapause Regulation in Czech Populations of *Dolycoris baccarum* (Heteroptera, Pentatomidae)," *Eur. J. Entomol.* **90**, 95–98 (1993).
44. Hodková, M., "Interaction of Feeding and Photoperiod in Regulation of the Corpus Allatum Activity in Females of *Pyrrhocris apterus* L. (Hemiptera)," *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* **86**, 477–488 (1982).
45. Hodková, M. and Hodek, I., "Photoperiod, Diapause and Cold-Hardiness," *Eur. J. Entomol.* **101**, 445–458 (2004).
46. Hodková, M., Hodek, I., and Sømme, L., "Cold is Not a Prerequisite for the Completion of Photoperiodically Induced Diapause in *Dolycoris baccarum* from Norway," *Entomol. Exp. Appl.* **52**, 185–188 (1989).
47. Hoebeke, E.R. and Carter, M.E., "*Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): a Polyphagous Plant Pest from Asia Newly Detected in North America," *Proc. Entomol. Soc. Wash.* **105** (1), 225–237 (2003).
48. Honěk, A., "Induction of Diapause in *Aelia acuminata* (L.) (Heteroptera, Pentatomidae)," *Acta Entomol. Bohemoslov.* **66**, 345–351 (1969).
49. Hori, K., "Effect of Photoperiod on Nymphal Growth of *Palomena angulosa* Motschulsky (Hemiptera: Pentatomidae)," *Appl. Entomol. Zool.* **21** (4), 597–605 (1986).
50. Hori, K. and Inamura, R., "Effects of Stationary Photoperiod on Reproductive Diapause, Nymphal Growth, Feeding and Digestive Physiology of *Eysarcoris lewisi* Distant (Heteroptera: Pentatomidae)," *Appl. Entomol. Zool.* **26** (4), 493–499 (1991).
51. Hori, K. and Kimura, A., "Effect of Stationary Photoperiod on Diapause Induction of *Eysarcoris lewisi* Distant (Heteroptera: Pentatomidae) and the Developmental Stage Sensitive to Stimulus for Reproductive Diapause," *Appl. Entomol. Zool.* **28**, 53–58 (1993).
52. Horton, D.R., Hinojosa, T., and Olson, S.R., "Effect of Photoperiod and Prey Type on Diapause Tendency and Preoviposition Period in *Perillus bioculatus* (Hemiptera: Pentatomidae)," *Can. Entomol.* **130**, 315–320 (1998).
53. Ikeda-Kikue, K. and Numata, H., "Effects of Diet, Photoperiod and Temperature on the Postdiapause Reproduction in the Cabbage Bug, *Eurydema rugosa*," *Entomol. Exp. Appl.* **64** (1), 31–36 (1992).
54. Ikeda-Kikue, K. and Numata, H., "Effect of Low Temperature on the Termination of Photoperiodic and Food-Mediated Diapause in the Cabbage Bug, *Eurydema rugosa* Motschulsky (Heteroptera: Pentatomidae)," *Appl. Entomol. Zool.* **29** (2), 229–236 (1994).
55. Ikeda-Kikue, K. and Numata, H., "Timing of Diapause Induction in the Cabbage Bug *Eurydema rugosum* (Heteroptera: Pentatomidae) on Different Host Plants," *Acta Soc. Zool. Bohemoslov.* **65**, 197–205 (2001).
56. Izhevskii, S.S. and Ziskind, L.A., "The Prospects of Using Introduced Stink Bugs *Perillus bioculatus* (Fabr.), *Podisus maculiventris* (Say), and *Oplomus nigripennis* var. *pulcher* Dull. (Pentatomidae: Hemiptera) against *Leptinotarsa decemlineata* Say (Chrysomelidae: Coleoptera)," in *Biological Suppression of Quarantine Pests and Weeds* (Moscow, 1981), pp. 20–37 [in Russian].
57. James, D.G., "Energy Reserves, Reproductive Status and Population Biology of Overwintering *Biprorulus bibax* (Hemiptera: Pentatomidae) in Southern New South Wales Citrus Groves," *Austral. J. Zool.* **38** (4), 415–422 (1990a).
58. James, D.G., "Seasonality and Population Development of *Biprorulus bibax* Breddin (Hemiptera: Pentatomidae) in Southwestern New South Wales," *Gen. Appl. Entomol.* **22**, 61–66 (1990b).
59. James, D.G., "Maintenance and Termination of Reproductive Dormancy in an Australian Stink Bug, *Biprorulus bibax*," *Entomol. Exp. Appl.* **60** (1), 1–5 (1991).
60. James, D.G., "Apparent Overwintering of *Biprorulus bibax* Breddin (Hemiptera: Pentatomidae) on *Eremocitrus glauca* (Rutaceae)," *Austral. Entomol.* **20** (40), 129–132 (1993).
61. Jasič, I., "A Contribution to the Knowledge of the Diapause in *Perillus bioculatus* (Fabr.) (Heteroptera, Pentatomidae)," *Acta Entomol. Bohemoslov.* **64**, 333–334 (1967).
62. Jasič, I., "On the Life Cycle of *Perillus bioculatus*," *Acta Entomol. Bohemoslov.* **72** (6), 383–390 (1975).
63. Javahery, M., "Biology and Ecological Adaptation of the Green Stink Bug (Hemiptera: Pentatomidae) in Quebec and Ontario," *Ann. Entomol. Soc. Amer.* **83** (2), 201–206 (1990).
64. Javahery, M., "Development of Eggs in Some True Bugs (Hemiptera-Heteroptera). Part I. Pentatomidae," *Can. Entomol.* **126**, 401–433 (1994).

65. Johansen, A.I., Exnerová, A., and Svádová, K.H., et al., "Adaptive Change in Protective Coloration in Adult Striated Shieldbugs *Graphosoma lineatum* (Heteroptera: Pentatomidae): Test of Detectability of Two Color Forms by Avian Predators," *Ecol. Entomol.* **35** (5), 602–610 (2010).
66. Jones, P.A. and Coppel, H.C., "Immature Stages of *Apateticus cynicus* (Say) (Hemiptera: Pentatomidae)," *Can. Entomol.* **95**, 770–779 (1963).
67. Kiritani, Y., "Timing of Oviposition and Nymphal Diapause under the Natural Daylengths in *Carbula humerigera* (Heteroptera: Pentatomidae)," *Appl. Entomol. Zool.* **20**, 252–256 (1985a).
68. Kiritani, Y., "Effect of Stationary and Changing Photoperiods on Nymphal Development in *Carbula humerigera* (Heteroptera: Pentatomidae)," *Appl. Entomol. Zool.* **20**, 257–263 (1985b).
69. Koshiyama, Y., Fujisaki, K., and Nakasuji, F., "Mating and Diapause in Hibernating Adults of *Menida scotti* Puton (Heteroptera: Pentatomidae)," *Res. Pop. Ecol. Kyoto* **36**, 87–92 (1994).
70. Koshiyama, Y., Fujisaki, K., and Nakasuji, F., "Effect of Mating during Hibernation on Life History Traits of Female Adults of *Menida scotti* (Heteroptera: Pentatomidae)," *Chugoku Kontyu* **11**, 11–18 (1997).
71. Koshiyama, Y., Tsumuki, H., Muraji, M., et al., "Transfer of Male Secretions to Females through Copulation in *Menida scotti* (Heteroptera: Pentatomidae)," *Appl. Entomol. Zool.* **28**, 325–332 (1993).
72. Košťál, V., "Eco-Physiological Phases of Insect Diapause," *J. Insect Physiol.* **52**, 113–127 (2006).
73. Kotaki, T., "Age-Dependent Change in Effects of Chilling on Diapause Termination in the Brown-Winged Green Bug, *Plautia crossota stali* Scott (Heteroptera: Pentatomidae)," *Entomol. Sci.* **1** (4), 485–489 (1998a).
74. Kotaki, T., "Effects of Low Temperature on Diapause Termination and Body Color Change in Adults of a Stink Bug, *Plautia stali*," *Physiol. Entomol.* **23** (1), 53–61 (1998b).
75. Kotaki, T. and Yagi, S., "Relationship between Diapause Development and Coloration Change in Brown-Winged Green Bug, *Plautia stali* Scott (Heteroptera: Pentatomidae)," *Jpn. J. Appl. Entomol. Zool.* **31** (4), 285–290 (1987).
76. Larivière, M.-C. and Larochelle, A., "*Picromerus bidens* (Heteroptera: Pentatomidae) in North America, with a World Review of Distribution and Bionomics," *Entomol. News* **100** (4), 133–146 (1989).
77. Leather, S.R., Walker, K.F.A., and Bale, J.S., *The Ecology of Insect Overwintering* (Cambridge Univ. Press, Cambridge, 1993).
78. Lee, K.-Y., Ahn, K.-S., Kang, H.-J., et al., "Host Plants and Life Cycle of Rice Black Bug, *Scotinophara lurida* (Burmeister) (Heteroptera: Pentatomidae)," *Korean J. Appl. Entomol.* **40** (4), 309–313 (2001).
79. Leston, D., "The Life-Cycle of *Picromerus bidens* (L.) (Hem., Pentatomidae) in Britain," *Entomol. Month. Mag.* **91**, 109 (1955).
80. Masaki, S., "Summer Diapause," *Annu. Rev. Entomol.* **25**, 1–25 (1980).
81. McPherson, J.E., "Life History of *Euschistus tristigmus tristigmus* (Hemiptera: Pentatomidae) with Information on Adult Seasonal Dimorphism," *Ann. Entomol. Soc. Amer.* **68** (2), 333–334 (1975).
82. McPherson, J.E., "Effect of Developmental Photoperiod on Adult Color and Pubescence in *Thyanta calceata* (Hemiptera: Pentatomidae) with Information on Ability of Adults to Change Color," *Ann. Entomol. Soc. Amer.* **70**, 373–376 (1977).
83. McPherson, J.E., "Effects of Various Photoperiods on Morphology in *Euschistus tristigmus tristigmus* (Hemiptera: Pentatomidae)," *Great Lakes Entomol.* **12** (1), 23–26 (1979).
84. McPherson, J.E., *Pentatomoidea (Hemiptera) of Northeastern North America. Carbondale and Edwardsville* (South Illinois Univ. Press, Illinois, 1982).
85. McPherson, J.E., "Life History and Laboratory Rearing of *Euschistus ictericus* (Hemiptera: Pentatomidae), with Descriptions of Immature Stages," *J. New York Entomol. Soc.* **92** (1), 53–60 (1984).
86. McPherson, J.E. and Tecic, D.L., "Notes on the Life Histories of *Acrosternum hilare* and *Cosmopepla bimaculata* (Heteroptera: Pentatomidae) in Southern Illinois," *Great Lakes Entomol.* **30**, 79–84 (1997).
87. Mourao, A.P.M. and Panizzi, A.R., "Diapause and Different Seasonal Morphs of *Euschistus heros* (Fabr.) (Hemiptera: Pentatomidae) in Northern Parana State," *Anais Soc. Entomol. Brasil* **29** (2), 205–218 (2000).
88. Mourao, A.P.M. and Panizzi, A.R., "Photophase Influence on the Reproductive Diapause, Seasonal Morphs, and Feeding Activity of *Euschistus heros* (Fabr., 1798) (Hemiptera: Pentatomidae)," *Revista Bras. Biol.* **62** (2), 231–238 (2002).
89. Musolin, D.L., "Photoperiodic Induction of Aestivation in the Stink Bug *Picromerus bidens* (Heteroptera, Pentatomidae). A Preliminary Report," *Zool. Zh.* **75** (12), 1901–1904 (1996) [*Entomol. Rev.* **76** (8), 1058–1060 (1996)].
90. Musolin, D.L., Fujisaki, K., and Numata, H., "Photoperiodic Control of Diapause Termination, Color Change and Postdiapause Reproduction in the Southern Green Stink Bug, *Nezara viridula*," *Physiol. Entomol.* **32**, 64–72 (2007).
91. Musolin, D.L. and Maisov, A.V., "Day-Length Sensitivity during Diapause Induction and Termination in the Shield Bug *Graphosoma lineatum* L. (Heteroptera, Pentatomidae)," in *Problems of Entomology in Russia. Proc. XI Congr. of the Russian Entomological Society, St. Petersburg, 23–29 September, 1997, Vol. 2*, Ed. by G.S. Medvedev et al. (St. Petersburg, 1998), p. 44 [in Russian].

92. Musolin, D.L. and Numata, H., "Photoperiodic and Temperature Control of Diapause Induction and Color Change in the Southern Green Stink Bug *Nezara viridula*," *Physiol. Entomol.* **28** (2), 65–74 (2003a).
93. Musolin, D.L. and Numata, H., "Timing of Diapause Induction and Its Life-History Consequences in *Nezara viridula*: Is It Costly to Expand the Distribution Range?" *Ecol. Entomol.* **28** (6), 694–703 (2003b).
94. Musolin, D.L. and Saulich, A.Kh., "Factorial Regulation of the Seasonal Cycle in the Stink Bug *Graphosoma lineatum* L. (Heteroptera, Pentatomidae). I. Temperature and Photoperiodic Responses," *Entomol. Obozr.* **74** (4), 736–743 (1995) [*Entomol. Rev.* **75** (9), 84–93 (1996)].
95. Musolin, D.L. and Saulich, A.Kh., "Photoperiodic Control of Seasonal Development in Bugs (Heteroptera)," *Entomol. Obozr.* **75** (3), 489–506 (1996) [*Entomol. Rev.* **76** (7), 849–864 (1996)].
96. Musolin, D.L. and Saulich, A.Kh., "Photoperiodic Control of Nymphal Growth in True Bugs (Heteroptera)," *Zool. Zh.* **76** (5), 530–540 (1997) [*Entomol. Rev.* **77** (6), 768–780 (1997)].
97. Musolin, D.L. and Saulich, A.H., "Diversity of Seasonal Adaptations in Terrestrial True Bugs (Heteroptera) from the Temperate Zone," *Entomol. Sci.* **2** (4), 623–639 (1999).
98. Musolin, D.L. and Saulich, A.H., "Summer Dormancy Ensures Univoltinism in the Predatory Bug *Picromerus bidens* (Heteroptera, Pentatomidae)," *Entomol. Exp. Appl.* **95**, 259–267 (2000).
99. Musolin, D.L. and Saulich, A.H., "Environmental Control of Voltinism of the Stinkbug *Graphosoma lineatum* in the Forest-Steppe Zone (Heteroptera: Pentatomidae)," *Entomol. Gen.* **25** (4), 255–264 (2001).
100. Musolin, D.L., Tougou, D., and Fujisaki, K., "Too Hot to Handle? Phenological and Life-History Responses to Simulated Climate Change of the Southern Green Stink Bug *Nezara viridula* (Heteroptera: Pentatomidae)," *Global Change Biol.* **16** (1), 73–87 (2010).
101. Nakamura, K., "Effect of Photoperiod on Development and Growth in a Pentatomid Bug, *Dolycoris baccarum*," *Entomol. Sci.* **6** (1), 11–16 (2003).
102. Nakamura, K., Hodek, I., and Hodková, M., "Recurrent Photoperiodic Response in *Graphosoma lineatum* (Heteroptera: Pentatomidae)," *Eur. J. Entomol.* **93**, 519–523 (1996).
103. Nakamura, K. and Numata, H., "Photoperiodic Sensitivity in Adults of *Aelia fieberi* (Heteroptera: Pentatomidae)," *Eur. J. Entomol.* **92**, 609–613 (1995).
104. Nakamura, K. and Numata, H., "Effects of Environmental Factors on Diapause Development and Postdiapause Oviposition in a Phytophagous Insect, *Dybowskyia reticulata*," *Zool. Sci.* **14**, 1021–1026 (1997a).
105. Nakamura, K. and Numata, H., "Seasonal Life Cycle of *Aelia fieberi* (Heteroptera: Pentatomidae)," *Ann. Entomol. Soc. Amer.* **90**, 625–630 (1997b).
106. Nakamura, K. and Numata, H., "Alternative Life Cycles Controlled by Temperature and Photoperiod in the Oligophagous Bug, *Dybowskyia reticulata*," *Physiol. Entomol.* **23**, 69–74 (1998).
107. Nakamura, K. and Numata, H., "Environmental Regulation of Adult Diapause of *Graphosoma rubrolineatum* (Westwood) (Heteroptera: Pentatomidae) in Southern and Northern Populations of Japan," *Appl. Entomol. Zool.* **34** (3), 323–326 (1999).
108. Nakazawa, K. and Hayashi, H., "Bionomics of the Stink Bugs and Allied Bugs Causing the Pecky Rice. 1. Development and Occurrence of Diapausing Females in *Eysarcoris ventralis* Westwood and *Cletus punctiger* (Dallas)," *Bull. Hiroshima Pref. Agr. Exp. Station.* **46**, 21–32 (1983) [in Japanese with English summary].
109. Niva, C.C. and Takeda, M., "Effects of Photoperiod, Temperature and Melatonin on Nymphal Development, Polyphenism and Reproduction in *Halyomorpha halys* (Heteroptera: Pentatomidae)," *Zool. Sci.* **20** (8), 963–970 (2003).
110. Noda, T., "Short Day Photoperiod Accelerates the Oviposition in the Oriental Green Stink Bug, *Nezara antennata* Scott (Heteroptera: Pentatomidae)," *Appl. Entomol. Zool.* **19** (1), 119–120 (1984).
111. Noda, H. and Ishii, T., "Effect of Photoperiod and Temperature on the Ovarian Development of the White-Spotted Stink Bug, *Eysarcoris ventralis* (Heteroptera: Pentatomidae)," *Jpn. J. Appl. Entomol. Zool.* **25** (1), 33–38 (1981).
112. Numata, H., "Environmental Factors that Determine the Seasonal Onset and Termination of Reproduction in Seed-Sucking Bugs (Heteroptera) in Japan," *Appl. Entomol. Zool.* **39** (4), 565–573 (2004).
113. Numata, H. and Kobayashi, S., "Threshold and Quantitative Photoperiodic Responses Exist in an Insect," *Experientia* **50**, 969–971 (1994).
114. Numata, H., Saulich, A.H., and Volkovich, T.A., "Photoperiodic Responses of the Linden Bug, *Pyrrhocoris apterus*, under Conditions of Constant Temperature and under Thermoperiodic Conditions," *Zool. Sci.* **10**, 521–527 (1993).
115. Numata, H. and Yamamoto, K., "Feeding on Seeds Induces Diapause in the Cabbage Bug, *Eurydema rugosa*," *Entomol. Exp. Appl.* **57**, 281–284 (1990).
116. Oetting, R.D. and Yonke, T.R., "Biology of Some Missouri Stink Bugs," *J. Kansas Entomol. Soc.* **44**, 446–459 (1971).
117. Panizzi, A.R., McPherson, J.E., James, D.G., et al., "Stink Bugs (Pentatomidae)," in *Heteroptera of Economic Importance*, Ed. by C.W. Schaefer and A.R. Panizzi (CRC Press, Boca Raton, 2000), pp. 421–474.
118. Panizzi, A.R. and Niva, C.C., "Overwintering Strategy of the Brown Stink Bug in Northern Parana," *Pesquisa Agr. Brasil.* **29** (3), 509–511 (1994).



119. Perepelitsa, L.V., "The Role of Photoperiod in the Development of *Dolycoris baccarum*," Byul. Vses. NII Zashch. Rast. **21**, 11–13 (1971).
120. Puchkov, P.V., *Fauna of Ukraine. Vol. 21, Issue 1: Shield Bugs* (Akad. Nauk UkrSSR, Kiev, 1961) [in Russian].
121. Ruberson, J.R., Kring, T.J., and Elkassabany, N., "Overwintering and the Diapause Syndrome of Predatory Heteroptera," in *Predatory Heteroptera: Their Ecology and Use in Biological Control*, Ed. by M. Coll and J.R. Ruberson (Thomas Say Publ. in Entomology, Entomol. Soc. of America, Lanham, 1998), pp. 49–69.
122. Santos, R.S.S., Redaelli, L.R., Diefenbach, L.M.G., et al., "Characterization of the Imaginal Reproductive Diapause of *Oebalus poecilus* (Dallas) (Hemiptera: Pentatomidae)," *Revista Brasil. Biol.* **63** (4), 695–703 (2003).
123. Saulich, A.Kh., "The Significance of Abiotic Factors for Shaping of Secondary Ranges in Adventive Insect Species," *Entomol. Obozr.* **73** (3), 591–605 (1994).
124. Saulich, A.Kh. and Musolin, D.L., "Univoltinism and Its Regulation in Some Temperate True Bugs (Heteroptera)," *Eur. J. Entomol.* **93** (3), 507–518 (1996).
125. Saulich, A.Kh. and Musolin, D.L., "Times of the Year: the Diversity of Seasonal Adaptations and Ecological Mechanisms Controlling Seasonal Development of True Bugs (Heteroptera) in the Temperate Climate," *Trudy Biol. NII SPbGU* **53**, 25–106 (2007a).
126. Saulich, A.Kh. and Musolin, D.L., *Seasonal Development of Aquatic and Semi-Aquatic Bugs* (Heteroptera) (St. Petersburg, 2007b) [in Russian].
127. Saulich, A.Kh. and Musolin, D.L., "Seasonal Development and Ecology of Anthocorids (Heteroptera, Anthocoridae)," *Entomol. Obozr.* **88** (2), 257–201 (2009) [*Entomol. Rev.* **89** (5), 501–528 (2009)].
128. Saulich, A.Kh. and Volkovich, T.A., "Univoltinism and Its Regulation in Insects," *Entomol. Obozr.* **75** (2), 244–258 (1996).
129. Saulich, A.Kh. and Volkovich, T.A., *Ecology of Photoperiodism in Insects* (St. Petersburg, 2004) [in Russian].
130. Saulich, A.Kh., Volkovich, T.A., and Numata, H., "Thermal and Photoperiodic Control of Development in the Linden Bug *Pyrrhocoris apterus* (Hemiptera, Pyrrhocoridae) under Natural Conditions," *Vestnik SPbGU Ser. 3 Biol.*, No. 4, 31–39 (1993).
131. Saunders, D.S., *Insect Clocks* (Pergamon Press, Oxford, 1976).
132. Saunders, D.S., "A Diapause Induction-Termination Asymmetry in the Photoperiodic Responses of the Linden Bug *Pyrrhocoris apterus* and the Effect of Near Critical Photoperiods on Development," *J. Insect Physiol.* **29** (5), 399–405 (1983).
133. Schuh, R.T. and Slater, J.A., *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History* (Cornell Univ. Press, Ithaca, 1995).
134. Shagov, E.M., "Photoperiodic Response and Its Variation in *Perillus*," *Ekologiya* **4**, 751–753 (1977).
135. Shintani, Y., Masuzawa, Y., Hirose, Y., et al., "Seasonal Occurrence and Diapause Induction of a Predatory Bug *Andrallus spinidens* (F.) (Heteroptera: Pentatomidae)," *Entomol. Sci.* **13**, 273–279 (2010).
136. Sinclair, B.J., Vernon, P., Klok, C.J., and Chown, S.L., "Insects at Low Temperatures: an Ecological Perspective," *Trends Ecol. Evol.* **18** (5), 257–262 (2003).
137. Singh, Z., *Southern Green Stink Bug and Its Relationship to Soybeans: Bionomics of the Southern Green Stink Bug *Nezara viridula* (Hemiptera: Pentatomidae) in Central India* (Metropolitan Book Co. Ltd, Delhi, 1973).
138. Singh, Z. and Malik, V.S., "Biology of Painted Bug (*Bagrada cruciferarum*)," *Indian J. Agric. Sci.* **63** (10), 672–674 (1993).
139. Şişli, M.N., "The Effect of the Photoperiod on the Induction and Termination of the Adult Diapause of *Aelia rostrata* Boh. (Hemiptera: Pentatomidae)," *Comm. Fac. Sci. Univ. Ankara* **10**, 62–69 (1965).
140. Šlachta, M., Vambera, J., Zahradníčková, H., and Košťál, V., "Entering Diapause is a Prerequisite for Successful Cold-Acclimation in Adult *Graphosoma lineatum* (Heteroptera: Pentatomidae)," *J. Insect Physiol.* **48** (11), 1031–1039 (2002).
141. Southwood, T.R.E. and Leston, D., *Land and Water Bugs of the British Isles* (Frederick Warne and Co., London, 1959).
142. Takeda, K., Musolin, D.L., and Fujisaki, K., "Dissecting Insect Responses to Climate Warming: Overwintering and Post-Diapause Performance in the Southern Green Stink Bug, *Nezara viridula*, under Simulated Climate-Change Conditions," *Physiol. Entomol.* **35** (4), 343–353 (2010).
143. Tauber, M.J., Tauber, C.A., and Masaki, S., *Seasonal Adaptations of Insects* (Oxford Univ. Press, New York, 1986).
144. Toscano, N.C. and Stern, V.M., "Seasonal Reproductive Condition of *Euschistus conspersus*," *Ann. Entomol. Soc. Amer.* **73** (1), 85–88 (1980).
145. Toyama, M., Ihara, F., and Yaginuma, K., "Formation of Aggregations in Adults of the Brown Marmorated Stink Bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): The Role of Antennae in Short-Range Locations," *Appl. Entomol. Zool.* **41** (2), 309–315 (2006).
146. Tullberg, B., Gamberale-Stille, G., Bohlin, T., and Merilaita, S., "Seasonal Ontogenetic Color Plasticity in the Adult Striated Shieldbug *Graphosoma lineatum* (Heteroptera) and Its Effect on Detectability," *Behav. Ecol. Sociobiol.* **62**, 1389–1396 (2008).

147. Ushatinskaya, R.S., *Cryptic Life and Anabiosis* (Nauka, Moscow, 1990) [in Russian].
148. Vecchio, M.C., Grazia, J., and Albuquerque, G.S., "Seasonal Dimorphism in *Oebalus ypsilon* (De Geer, 1773) (Hemiptera, Pentatomidae) and a New Synonym," *Revista Bras. Entomol.* **38** (1), 101–108 (1994).
149. Veerman, A., "Diapause," in *Spider Mites. Their Biology, Natural Enemies and Control. Vol. 1A*, Ed. by W. Helle and M.W. Sabelis (Elsevier Sci. Publ., Amsterdam, 1985), pp. 279–316.
150. Vinokurov, N.N., Kanyukova, E.V., and Golub, V.B., *Catalogue of the Heteroptera of Asian Part of Russia* (Nauka, Novosibirsk, 2010) [in Russian].
151. Volkovich, T.A., "Diapause in the Life Cycles of Lacewings (Neuroptera, Chrysopidae)," *Trudy Biol. NII SPbGU* **53**, 234–304 (2007).
152. Volkovich, T.A., Kolesnichenko, L.I., and Saulich, A.Kh., "The Role of Thermorhythms in the Development of the Two-Spotted Stink Bug *Perillus bioculatus* (Hemiptera, Pentatomidae)," *Zool. Zh.* **69** (6), 70–81 (1990).
153. Volkovich, T.A. and Saulich, A.Kh., "Photoperiodic and Thermal Control of Diapause and Coloration in the Stink Bug *Arma custos*," *Zool. Zh.* **73** (10), 26–37 (1994).
154. Volkovich, T.A., Saulich, A.Kh., and Goryshin, N.I., "The Day-Length Sensitive Stage and Accumulation of Photoperiodic Information in the Spined Soldier Bug *Podisus maculiventris* Say (Heteroptera: Pentatomidae)," *Entomol. Obozr.* **70** (1), 14–22 (1991).
155. Watanabe, M., "Study of the Life Cycle of the Brown Marmorated Stink Bug, *Halyomorpha mista*," *Insectarium* **17**, 168–173 (1980).
156. Whitmarsh, R.D., "Life-History Notes on *Apateticus cynicus* and *maculiventris*," *J. Econ. Entomol.* **9**, 51–53 (1916).
157. Wilde, G.E., "Photoperiodism in Relation to Development and Reproduction in the Green Stink Bug," *J. Econom. Entomol.* **62** (3), 629–630 (1969).
158. Zachariassen, K.E., "Physiology of Cold Tolerance in Insects," *Physiol. Rev.* **65**, 799–832 (1985).
159. Yao, M., "Development, Number of Annual Generations, and the Relationship of Effective Heat Unit and to Abundance of Overwintered Adults in the Following Year of the White-Spotted Spined Bug, *Eysarcoris aeneus* (Scopoli) (Heteroptera: Pentatomidae)," *Jpn. J. Appl. Entomol. Zool.* **46** (1), 15–21 (2002).