

## Diversity of Seasonal Adaptations in Terrestrial True Bugs (Heteroptera) from the Temperate Zone\*

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**Abstract.** Heteropterans occupy a wide range of habitats characterized by pronounced seasonality of environmental conditions. In the temperate zone, they use different seasonal adaptations to survive and successfully utilize resources under these sometimes severe circumstances. To review the known adaptations, we use two approaches. First (as suggested by Tauber *et al.*, 1986), all seasonal adaptations are divided into three categories (dormancy, seasonal migration and seasonal polyphenism) with further subdivision of each category into diapause-mediated and non-diapause responses. We suggest here an alternative approach based on the four seasons of the yearly cycle when these adaptations either used by insects or at survival of which these adaptations are aimed to. In the group of winter adaptations, we discuss basic traits of winter diapause (metabolic parameters, facultative and obligatory nature, photoperiodic induction, sensitive stages, temperature dependence, geographical variation of photoperiodic response, use of host plant status and temperature as alternative cues for diapause induction, cold-hardiness etc.). The spring complex of adaptations has been less studied and includes different types of post-diapause photoperiodic sensitivity that are evidently adaptive under different circumstances. As summer and autumn adaptations, we discuss summer diapause, photoperiodic control of nymphal development and coloration of nymphs and adults, behavioral adaptations and migration. Some general considerations and directions for further research are also given.

**Key words:** Heteroptera, seasonal cycles, seasonality, diapause, dormancy, life cycle strategy, photoperiodism.

### Introduction

Heteroptera is the largest group of insects (in rank of order or suborder of Hemiptera) with incomplete metamorphosis. This group includes at least 38,000 known species of 75 families and the majority of these families occur throughout the world with the exception of Antarctica (Schuh & Slater, 1995). The great age of the group and their adaptability have resulted in significant morphological and ecological diversity.

True bugs successfully utilize a wide range of very different habitats. In the terrestrial ecosystems, many species live in soil on plant roots or on the soil surface (e.g. Cydnidae and Pyrrhocoridae), in various layers

of vegetation (e.g. Tingidae, Pentatomidae, Miridae or Aradidae), in association with ants or termites in their nests (e.g. Enicocephalidae, Anthocoridae or Termitaphidae) or in the webs of spiders (e.g. Nabidae or Reduviidae). Representatives of some other families live in the aquatic ecosystems: in water (e.g. Nepidae and Belostomatidae), on the water surface (Gerromorpha) or in the intertidal zone (e.g. Leptopodomorpha) (Southwood & Leston, 1959; Kerzhner & Jaczewski, 1964; Schuh & Slater, 1995). Many species of true bugs feed on fungi or different parts of plants (from roots to fruits, pollen or mature seeds). Others are known to be predators upon insects or other arthropods. Some heteropterans are hematophagous. A large group of species in different families are characterized by mixed feeding and these species feed on both animal and plant materials (Southwood & Leston, 1959; Schaefer, 1981, 1997; Puchkov, 1987; Dolling, 1991; Schuh & Slater, 1995).

\* Dedicated to our teachers Prof. O. A. Kataev and Dr. N. I. Goryshin on the occasions of their 75th birthdays.

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Most of the regions and habitats occupied by heteropterans are characterized by a pronounced seasonality of environmental conditions and very often such conditions as temperature, food or humidity are favorable during only a restricted period of the annual cycle and are rather unfavorable over the rest of the year. It is apparent that to survive and successfully utilize resources under such conditions, heteropterans had to develop a set of special *seasonal* adaptations.

In this paper, current knowledge regarding seasonal adaptations and peculiarities of seasonal development in terrestrial Heteroptera from the temperate zone will be reviewed. This zone is a very wide geographical region that stretches between the tropics and the frigid zone. Environmental conditions differ significantly in different parts of the temperate zone, but at least two features are common to all its parts: (1) environmental conditions are characterized by more or less pronounced seasonality with (2) typically cold (or cool) winter and warm (or hot) summer seasons.

In many parts of the zone, winter temperature drops much below the range optimal for active development of insects. This means that any adaptations that allow insects to increase chances of successful overwintering are of great value. On the other hand, not only low winter temperatures are dangerous for insects. Among others, we should mention unpredictable weather fluctuations such as occasional warm spells in late autumn and early winter, slight frosts in late spring or extremely high summer temperatures that may cause temporal deterioration of environmental conditions (mostly, food resources). Moreover, fluctuations in the state of biotic components of ecosystems (such as condition of host plants or prey-predator relationships) might also have a seasonal basis.

Sometimes, the adaptations evolved by heteropterans are common for many insect species, while in other cases they are species-specific, rare or unique as far as can be concluded taking into consideration the available data.

#### *Two approaches to classification of seasonal adaptations*

The term *seasonal adaptation* is widely used and seems to be easily understandable, although in some not-trivial cases it might not be so clear whether a particular response may be treated as a seasonal adaptation or not. Neither Tauber *et al.* (1986) nor specialized dictionaries give a clear definition of seasonal adaptations. In this paper, we understand *seasonal adaptation as the ability of organisms (in the form of physiological, biochemical or behavioral re-*

*sponses) to survive or take advantages in utilization of resources under seasonally changing environmental conditions.*

The diversity of these adaptations together with differences in the stages at which different species are able to survive unfavorable seasons results in the marked diversity of seasonal patterns shown by heteropterans.

Tauber *et al.* (1986) suggested all seasonal adaptations in insects be divided into three categories (dormancy, seasonal migration and seasonal polyphenism) with further subdivision of each category into diapause-mediated and non-diapause responses (p. 11). Dormancy and migration are two principal strategies aimed at avoidance of unfavorable consequences of environmental seasonality. As a profound case of dormancy (Danks, 1987, p. 9), diapause allows insects to escape in *time*, migration allows this in *space*. Seasonal polyphenism (or polymorphism) is characterized by the existence of several seasonal forms (morphs) within a given species, and these forms might differ in coloration, body size or proportions, degree of development of wings etc. In many cases, both the seasonal polyphenism and migration are closely related to diapause.

Another approach to classification of seasonal adaptations is based on the four seasons of the yearly cycle when these adaptations either used by insects or at survival of which these adaptations are aimed to (it might be different as, for instance, in the case of prospective dormancy when insects enter winter diapause at the end of summer, well in advance of actual deterioration of environmental conditions). This approach seems to be less physiological, but more ecological, as it reflects both the seasonality of unfavorable environmental conditions and the diversity of adaptations by which insects cope with them. The application of this approach is presented below. There are no doubts that any attempt to classify complex biological phenomena is conventional and has own restrictions, advantages and disadvantages. Nevertheless, we hope that our review will make understanding of seasonal development in Heteroptera easier.

## **Winter Adaptations**

### *Facultative and obligatory nature of winter diapause*

It is apparent that winter diapause is a typical form of dormancy characterized by a reduced metabolic rate as well as other physiological and behavioral changes.

Respiratory activity as an index of metabolic rate

was measured in diapause and non-diapause individuals of several heteropterans: in the mirid with egg diapause, *Leptopterna dolobrata* (Braune, 1976, 1980), and in species with adult diapause, the pyrrhocorid *Pyrrhocoris apterus* (Sláma, 1964; Hodek & Hodková, 1981), the pentatomids *Perillus bioculatus* (Shagov, 1969), *Dolycoris baccarum* (Conradi-Larsen & Sømme, 1978), *Arma custos* (Volkovich & Saulich, 1994) and the coreid *Anasa tristis* (Fielding, 1988). It was shown that during at least some stages of diapause development, respiratory rate is as little as 20–50% compared with non-diapause individuals.

Table 1 lists some examples of winter diapause associated with different stages of metamorphosis in temperate heteropterans from different families.

Both types of diapause (facultative and obligatory) are found in different species of Heteroptera. In most of those rare cases when two or more populations of the same species were studied, winter diapause was shown to have the same (obligatory or facultative)

nature. However, in two species the situation was different. Thus, Parker (1975) studied two populations of the anthocorid *Anthocoris nemorum* in northern and southern Britain and found that the northern population was univoltine with *obligatory* adult diapause, while the southern population was bivoltine and diapause in this population was *facultative* and induced by short day length. It was shown that the differences between these populations were genetically determined and were not simply physiological responses to the different length of the growing season. When samples of the northern population were brought to the south and reared along with those from the southern population, they entered obligatory diapause under the regime with a very long photophase while those from the southern population produced a second generation without entering diapause.

Another very unusual case is the mirid *Adelphocoris lineolatus*. Ewen (1966) reported that in a northern (Canadian) population, the day length experienced by

Table 1. Some examples of species from different families of Heteroptera with obligatory and facultative (photoperiodically induced) winter diapause.

Diapause stage	Obligatory diapause (univoltine seasonal cycle)	Facultative diapause (uni- or polyvoltine seasonal cycles)
Egg	<i>Leptopterna dolobrata</i> and <i>Calocoris roseomaculatus</i> (Miridae: Braune, 1971, 1980) <i>Picromerus bidens</i> (Pentatomidae: Larivière & Laroche, 1989)	<i>Cavelerius saccharivorus</i> (Lygaeidae: Hokyo <i>et al.</i> , 1983) <i>Pseudatomoscelis seriatus</i> (Miridae: Gaylor & Sterling, 1977) <i>Trigonotylus coelestialium</i> (Miridae: Okuyama, 1982; Kudó & Kurihara, 1988, 1989) <i>Alydus calcaratus</i> (Alydidae: Musolin <i>et al.</i> , 1999) <i>Carbula humerigera</i> (Pentatomidae: Kiritani, 1985a, b) <i>Poecilocoris lewisi</i> (Scutelleridae: Tanaka <i>et al.</i> , 1995)
Nymph	<i>Coptosoma scutellatum</i> (Plataspidae: Saulich & Musolin, 1996 and unpubl.)	<i>Lygus hesperus</i> (Miridae: Beards & Strong, 1966) <i>Lygus lineolaris</i> and <i>L. borealis</i> (Miridae: Gerber & Wise, 1995) <i>Aelia acuminata</i> (Pentatomidae: Hodek, 1979) <i>Arma custos</i> (Pentatomidae: Volkovich & Saulich, 1994) <i>Podisus maculiventris</i> (Pentatomidae: Goryshin <i>et al.</i> , 1988) <i>Jalysus spinosus</i> * (Berytidae: Elsey, 1974) <i>Orius</i> spp. (Anthocoridae: van den Meiracker, 1994; Ito & Nakata, 1998a, 1998b) <i>Anasa tristis</i> (Coreidae: Nechols, 1988) <i>Pyrrhocoris apterus</i> (Pyrrhocoridae: Hodek, 1968) <i>Corythucha cydoniae</i> (Tingidae: Neal <i>et al.</i> , 1992; Braman & Pendley, 1993) <i>Riptortus clavatus</i> (Alydidae: Numata & Hidaka, 1982) <i>Neocoryphus bicrucis</i> (Lygaeidae: Solbreck, 1979) <i>Lygaeus equestris</i> (Lygaeidae: Solbreck & Sillén-Tullberg, 1981) <i>Nabis americanoferus</i> and <i>N. roseipennis</i> (Nabidae: Yeargan & Barney, 1996)
Adult	<i>Eurygaster integriceps</i> (Scutelleridae: Viktorov, 1967) <i>Coreus marginatus</i> (Coreidae) and <i>Palomena prasina</i> (Pentatomidae) (Saulich & Musolin, 1996)	

\* referred as *Jalysus wickhami* by Ruberson *et al.* (1998).

the parental generation determined whether eggs of the next generation entered diapause or not. It seems paradoxical that this response was not found in the southern population of this species, which was reported in the same paper to produce two generations per year.

In some respects, diapause, or more generally dormancy, is a more *physiological* than *seasonal* adaptation. However, in cases when induction of this physiological state is controlled by environmental seasonal cues, i.e. when insects use environmental signals to enter this resistant state, this inductive mechanism should be considered as a kind of seasonal adaptation.

#### Photoperiodic induction of diapause

It is obvious that photoperiodic induction of diapause is the most important seasonal adaptation in heteropterans (as well as other insects) of the temperate zone (all examples shown in Table 1 as species with facultative diapause have photoperiodically controlled induction of diapause). In the majority of species with facultative adult diapause, photoperiodic signals are perceived by nymphs of one or two last instars and by adults and the adult stage is the ultimate sensitive stage. However, in some species, photoperiodic sensitivity is restricted by a specific period of nymphal or adult stages (Fig. 1; Table 2). While most heteropteran species tested in this respect were shown to be sensitive to constant photoperiod, adults of the migratory lygaeid *Neacoryphus bicrucis* entered diapause only in response to a decrease in day length (Solbreck, 1979). It is remarkable that a decrease in day length from 16 h to 10 h induced diapause in all individuals, while a change from 18 h to 14 h was not effective. This finding emphasized the importance of photoperiodic threshold in the response of diapause induction.

Temperature dependence is an important feature of the photoperiodic response of diapause induction. In many species of heteropterans, the absolute level of temperature modifies the photoperiodic response: in the species with a long-day type of response, a decrease in temperature causes an increase in a critical day length. For instance, this kind of temperature dependence was demonstrated in the Belgorod populations of *Pyrrhocoris apterus* (Numata *et al.*, 1993) and the pentatomid *Graphosoma lineatum* (Musolin & Saulich, 1995). It is likely that under natural conditions the threshold day length is important as a signal for entering diapause only over a *particular* ("ecologically significant") range of temperature. The combination of day length and temperature necessary

#### A. *Eysarcoris lewisi*

Nymphal instars					Adult	Incidence of diapause, %
1*	2	3	4	5		
	■					5.6
	■	■				0.0
	■	■	■			0.0
	■	■	■	■		5.9
		■	■	■		10.0
			■	■		10.5
				■		11.1
					■	<b>100.0</b>

#### B. *Arma custos*

Nymphal instars					Adult	Incidence of diapause, %
1	2	3	4	5		
■	■	■	■	■		0.0
■	■	■	■			0.0
■	■	■				0.0
■	■					0.0
						0.0
					■	<b>84.0</b>
				■	■	<b>100.0</b>
			■	■	■	<b>100.0</b>
		■	■	■	■	<b>100.0</b>
■	■	■	■	■	■	<b>100.0</b>

Fig. 1. Stages sensitive to photoperiodic conditions in two species of pentatomid bugs. A. *Eysarcoris lewisi* (after Hori & Kimura, 1993). Black areas—short day (12L–12D), white areas—long day (16L–8D), 25°C. 1\*—room conditions (about 12L–12D, 25°C). B. *Arma custos* (after Saulich & Volkovich, 1996). Black areas—short day (14L–10D), white areas—long day (18L–6D), 28°C.

for diapause induction was shown in *P. apterus* (Fig. 2). This temperature dependence of photoperiodic response may also be a kind of seasonal adaptation.

On the other hand, the photoperiodic response is more thermostable in some other heteropteran species such as the alydid *Riptortus clavatus* (Numata, 1985; Kobayashi & Numata, 1995) and the pentatomid *Arma custos* (Volkovich & Saulich, 1994). These responses seem to be less flexible under conditions in which ambient temperature might differ from year to year and might significantly influence successfulness of pre-diapause feeding and survival.

Geographical variation of critical day length is a seasonal adaptation of a *species* (not *population*) level.

Table 2. Stage(s) sensitive to photoperiodic conditions in heteropterans with photoperiodically induced winter diapause.

Diapause stage and sensitive stage	Species
<b>Egg diapause</b>	
Early instar (female) nymphs of parental generation	<i>Pseudatomoscelis seriatus</i> (Miridae: Gaylor & Sterling, 1977)
Adults of parental generation	<i>Trigonotylus coelestialium</i> (Miridae: Kudô & Kurihara, 1989) <i>Nysius groenlandicus</i> (Lygaeidae: Bocher, 1975)
<b>Nymphal diapause</b>	
Nymphs	<i>Carbula humerigera</i> (Pentatomidae: Kiritani, 1985b)
<b>Adult diapause</b>	
Nymphs of last instar (V) or instars (IV and V) and adults	<i>Dolycoris baccarum</i> (Pentatomidae: Perepelitza, 1971) <i>Eysarcoris lewisi</i> (Pentatomidae: Hori & Kimura, 1993) <i>Pyrrhocoris apterus</i> (Pyrrhocoridae: Hodek, 1974; 1983; Volkovich & Goryshin, 1978) <i>Anasa tristis</i> (Coreidae: Fielding, 1988) <i>Riptortus clavatus</i> (Alydidae: Kobayashi & Numata, 1993) <i>Jalysus spinosus</i> * (Berytidae: Elsey, 1974) <i>Lygaeus equestris</i> (Lygaeidae: Solbreck & Sillén-Tullberg, 1981) <i>Arma custos</i> (Pentatomidae: Saulich & Volkovich, 1996) <i>Podisus maculiventris</i> (Pentatomidae: Volkovich <i>et al.</i> , 1991) <i>Oncopeltus fasciatus</i> (Lygaeidae: Dingle, 1974) <i>Orius sauteri</i> and <i>O. minutus</i> (Anthocoridae: Ito & Nakata, 1998a)
Mainly adults	
Nymphs beginning with III instar	
Last instar nymphs or very young adults	
Only nymphs are sensitive to short-day signals	

\* referred as *Jalysus wickhami* by Ruberson *et al.* (1998).

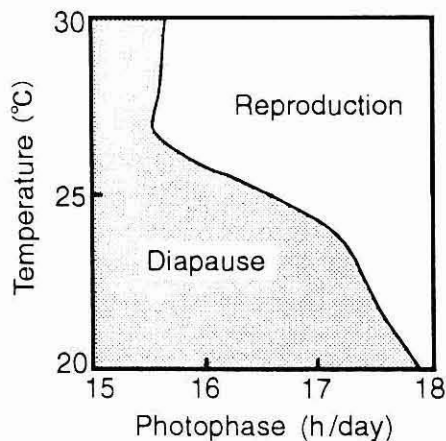


Fig. 2. Effect of photoperiod and temperature on the induction of adult diapause in *Pyrrhocoris apterus* (Pyrrhocoridae: after Numata *et al.*, 1993).

Among the Heteroptera, such a difference in value of critical day length was demonstrated experimentally between three populations of *Pyrrhocoris apterus* (Volkovich & Goryshin, 1978) and between four populations of the lygaeid *Lygaeus equestris* (Solbreck & Sillén-Tullberg, 1981). These data confirmed a general trend (the populations from the higher latitudes have longer critical day length) and this seems to be very important from the viewpoint of geographical variation of environmental conditions and seasonal patterns of environmental cues.

#### Other cues in diapause induction

It is well known that not only day length but also other environmental cues (such as temperature, moisture or humidity, quality of food etc.) might be used by insects in timing of their seasonal development (Tauber *et al.*, 1986; Danks, 1987). Some examples (although very rare to date in Heteroptera) will be given here and in the following sections.

As just mentioned, temperature might be an independent cue for induction of dormancy, while usually it is very difficult to distinguish whether temperature acts as a direct regulator of development or is taken as an environmental signal. Among heteropterans, it was shown that the predatory anthocorid *Orius albidipennis* is not sensitive to day length and reproductive diapause in this species is dependent only on temperature (Chyzik *et al.*, 1995).

Food is another vitally important environmental factor. There is no sense in discussing how quality and quantity of food are important for both mono- and polyphagous species of insects. In many cases, the principal significance of seasonal adaptations is synchronization of the next stage(s) or next generations with the season when high quality food is readily available.

A special type of seasonal adaptation is when insects use a status of host plant or prey as a cue for timing of their seasonal development. A good example of this

kind of adaptation used by a heteropteran species is known in the pentatomid *Eurydema rugosum* (= *rugosa*). This species enters adult diapause under short-day conditions if the food is leaves or seeds of *Brassica* sp. Under long-day conditions, bugs raised on leaves become reproductive, while those raised on seeds enter diapause even despite a long day (Numata & Yamamoto, 1990). This was surprising because *nutritionally* seeds of *Brassica* sp. are better food than leaves for both nymphs and adults of this species. Two interesting phenomena were observed in this heteropteran: first, this species can use current status of the host plant as a cue for diapause induction, and second, food-mediated diapause differs from that induced by photoperiodic conditions in terms of both factors that induce and terminate dormancy (Ikeda-Kikue & Numata, 1994).

#### Overwintering strategies

It is believed that in most heteropteran species both males and females have the same overwintering strategy and in the case of facultative diapause, the dormancy is induced in response to the same environmental signal(s). It was experimentally proved to be true in some species: for instance, the photoperiodic response curves of males and females almost completely coincided in *Riptortus clavatus* (Kobayashi & Numata, 1993) and in the pentatomid *Dybowskyia reticulata* (Nakamura & Numata, 1998).

However, a sexual difference in overwintering was also shown in some other heteropteran species. Thus, an unusual case of such difference between the sexes is known in the pentatomid *Menida scotti*. Observations and experiments conducted by Koshiyama *et al.* (1994) suggested that diapause in this species is induced obligatorily in females, but not in males. Adults hibernate in aggregations, and copulate there in two seasons, in November and April. Males have enlarged bulbus ejaculatorius and reservoir of the ectadene throughout almost entire hibernation, while volume of testis decreases from the start of hibernation till January and then increases till March. In females, ovarian development is suppressed completely until spring. Moreover, males donate the secretions stored in their bulbus ejaculatorius and reservoir of the ectadene to females during copulation and it was supposed that females digest them (Koshiyama *et al.*, 1993). This means that mating during hibernation might be advantageous for females. It is also supposed that parasitization by a fly *Phasia sinensis* (that is significantly higher in males than in females) also makes mating during hibernation highly advantageous (Koshiyama

*et al.*, 1994, 1997).

Another unusual overwintering strategy was recently found in the anthocorids *Orius sauteri* and *O. minutus* by Ito & Nakata (1998a, b). It was demonstrated that females of both species have a normal long-day type photoperiodic response, while they are sensitive to short day length at the nymphal stage only. Males of both of these species do not enter diapause. They are physiologically active and copulate with females even under short-day conditions. When insects were exposed to low temperatures, males died significantly earlier than females. Also, it was shown that all males of both species die by early winter when exposed to natural conditions, while from 40 to 65% of females successfully survived the winter. These results are in agreement with the findings of Kingsley & Harrington (1982) and Ruberson *et al.* (1998) on another anthocorid *Orius insidiosus*: females of this species overwinter being apparently inseminated and fully prepared for reproduction in spring, while males, perhaps, do not survive winter.

Some heteropterans are also known to have survival rates that differ between the sexes. For example, winter survival of the pentatomid *Nezara viridula* in Central Japan is as little as 40 to 50% and survival of females is 11% higher than that of males (Kiritani *et al.*, 1962).

Furthermore, Horton *et al.* (1998) discussed similar cases in Anthocoridae and Dolling (1991) mentioned some instances in Miridae where sexual maturation and pairing occurred in the autumn and only the mated females survived the winter. It is still not clear why the heteropteran species described above use this strategy to overwinter.

#### Cold-hardiness

The next group of complex adaptations may be termed cold-hardiness. There have been a large number of studies into the strategies that enable insects to survive in the harshest of winter conditions and an impressive amount of detailed information has been accumulated in recent years (see: Leather *et al.*, 1993; Bale, 1996; Danks, 1996). At the same time, Heteroptera still remains a poorly studied group of insects with respect to cold-hardiness adaptations. Nevertheless, some investigations have been performed in *Pyrhcoris apterus* (Hodková & Hodek, 1994, 1997) from Central Europe. It was shown that a decrease in supercooling point (SCP), and thus the increase in cold-hardiness is controlled by day length and influenced by temperature.

In the population of *Nezara viridula* from South

Carolina, Elsey (1993) showed that SCP did not differ significantly between diapause and non-diapause bugs (ranged between  $-11.7 \pm 0.7^\circ\text{C}$  and  $-10.4 \pm 0.8^\circ\text{C}$ ) and proposed that cold tolerance and diapause are independent phenomena in this species. Elsey (1993) also reported SCPs for two other pentatomids ( $-14.7^\circ\text{C}$  for *Murgantia histrionica* and  $-15.0^\circ\text{C}$  for *Euschistus servus*), while their physiological state was not indicated. Eguagie (1974) reported that the lowest SCP in overwintering adults of the lace bug *Tingis ampliata* in England was around  $-27.0^\circ\text{C}$  and while a variation was high, there was no significant difference in this parameter between the sexes. MacPhee (1964) found much lower SCPs (ranging between  $-37.2$  and  $-31.7^\circ\text{C}$ ) in overwintering eggs of five mirids from Nova Scotia (Canada) that during winter are exposed to the surrounding air temperatures. Very low SCPs were also found in the eggs ( $-34.1 \pm 0.28^\circ\text{C}$ ) and first instar larvae ( $-29.0 \pm 0.40^\circ\text{C}$ ) of the pentatomid *Podisus maculiventris* (a laboratory population originated from North America,  $38^\circ\text{N}$ ; Borisenko, 1987), although this species overwinters at the adult stage. At the same time the SCPs of non-diapause and diapause females were very similar ( $-15.0 \pm 0.60^\circ\text{C}$  and  $-17.8 \pm 0.46^\circ\text{C}$  respectively). These species may be the only true bugs which have been studied in respect to cold-hardiness adaptations and it is clear that further research is needed to better understand overwintering in Heteroptera.

### Spring Adaptations

In contrast to the winter adaptations, which have been studied in a considerable number of heteropterans, a spring complex of seasonal adaptations (namely, those which are essential in the end of unfavorable and the beginning of favorable seasons) has been significantly less well studied and is thus less well understood. However, the timing of resumption of active development, feeding and reproduction in spring is of great importance for both overwintered and new generations. Many early-season events (such as mortality, finding host plant(s) and mates) can significantly influence the subsequent life of population (Fielding, 1990).

#### *Resumption of active development*

In spring, temperature is perhaps the most important of all the environmental cues and factors, although its role and the mechanism of its influence in termination of winter diapause and resumption of active development are not clear and seem to be

different in different species (Hodek, 1977; Leather *et al.*, 1993). On the other hand, it was shown that at least some species use photoperiod as a cue for resumption of active development. For example, two coreids *Anasa tristis* and *Cletus punctiger* remain photoperiodically sensitive throughout autumn, winter and spring (Fielding, 1988; Ito, 1988).

#### *Recurrent photoperiodic sensitivity*

Many insect species lose their sensitivity to day length irreversibly after completion of diapause, and in the case of adult diapause, individuals reproduce until death that inevitably occurs in the same season. Hodek & Hodková (1982) found this response in *Pyrrhocoris apterus* and called the phenomenon a "Pyrrhocoris-like" photoperiodic response. Later, the same type of response was found in the pentatomid *Aelia fieberi* (Nakamura & Numata, 1995). However, some species can respond to diapause-promoting day length again after starting post-diapause oviposition. This was first discovered by Hodek (1971, 1977, 1979) in *Aelia acuminata* and termed *the recurrent photoperiodic response*. Among terrestrial heteropterans, this type of response has since been found in several other species: *Dolycoris baccarum* (Hodek, 1977), *Riptortus clavatus* (Numata, 1987), *Eurydema rugosum* (Ikeda-Kikue & Numata, 1992), *Graphosoma lineatum* (Nakamura *et al.*, 1996; Musolin & Maysov, 1998), *Dybowskyia reticulata* (Nakamura & Numata, 1997).

Recurrent photoperiodic response has been suggested to enable insects to enter diapause more than once within their life cycle. This adaptation may be favorable for long-living insects in the temperate zone and especially in cooler seasons when these species cannot fully realize their reproductive potential. Recurrent photoperiodic responses enable these species to enter diapause twice and reproduce during two seasons (Hodek & Hodková, 1982).

Different types of post-diapause photoperiodic sensitivity are evidently adaptive under different circumstances. However, as was correctly noted by Nakamura & Numata (1995), there is no sharply defined dividing line between the two types of response. Even in *Pyrrhocoris apterus*, a small proportion of individuals may resume photoperiodic sensitivity (Hodek, 1974).

#### *Role of food in post-diapause development*

One of the environmental stresses that insects meet in the spring or in the beginning of summer (especially, in the southern part of the temperate zone) is a scarcity of nutritious food resources. Thus, an ability

of post-diapause coreid *Cletus punctiger* to survive for a fairly long time without food has an apparent adaptive value (Ito, 1984). An effect of starvation on reproduction was also studied in *Pyrrhocoris apterus* (Hodková, 1982) and *Riptortus clavatus* (Numata & Hidaka, 1984; Numata, 1985) and it was demonstrated that the post-diapause ovarian development as well as commencement of oviposition were delayed under long-day but starved conditions. It is concluded that food is a major factor in timing of the post-diapause reproduction. Moreover, it was supposed that in *Anasa tristis*, food plants also served as a token stimulus to terminate winter adult diapause (Fielding, 1990).

### Summer and Autumn Adaptations

For most (if not all) species of Heteroptera from the temperate zone, summer is a season for active development, although a few species are known to spend at least a part of this season in a dormant state and to shift reproduction to the beginning or end of summer.

True bugs evolved many different kinds of adaptations aimed at optimization of reproduction, use of resources, timing of their active development and preparation for dormancy, and in some non-trivial cases it is difficult to say whether a particular adaptation has a value in terms of optimization of seasonal development or not.

#### Environmental control of nymphal growth

It was shown experimentally that nymphs of several species of heteropterans grow more slowly or more

rapidly under different photoperiodic conditions, i.e. nymphal development in these species can be controlled by day length. This is a type of seasonal adaptation, which seems to be widely used by heteropterans (for a detailed review see: Musolin & Saulich, 1997). Similar to the photoperiodic response of diapause induction, there are two groups of species in which duration of nymphal development is controlled by photoperiodic conditions.

In the pentatomids *Dolycoris baccarum* (Conradi-Larsen & Sømme, 1973), *Nezara viridula* (Ali & Ewies, 1977) and *Carbula humerigera* (Kiritani, 1985 b) nymphal growth was accelerated by long-day conditions and retarded by short-day conditions. This response was particularly strong in *N. viridula* and was observed in this species over a wide range of temperatures (from 20 to 30°C). In *Carbula humerigera*, photoperiodic control of nymphal development was also marked and a 30–40-day retardation of growth at the nymphal stage under short-day conditions was considered a facultative winter diapause (Kiritani, 1985b).

However, in a considerably greater number of heteropterans this acceleration of nymphal growth appeared to be related not to long days, but to short days (Musolin & Saulich, 1997). Such response was rather strong in the pentatomid *Palomena prasina*: at 20°C, the acceleration of growth amounted to 25% of the total duration of the nymphal period (Saulich & Musolin, 1996; Musolin & Saulich, 1997). The nymphs of a closely related pentatomid species, *Palomena angulosa*, grew 1.56-fold faster under short-day than under long-day conditions (Hori, 1988).

The most comprehensive data on duration of nymph-

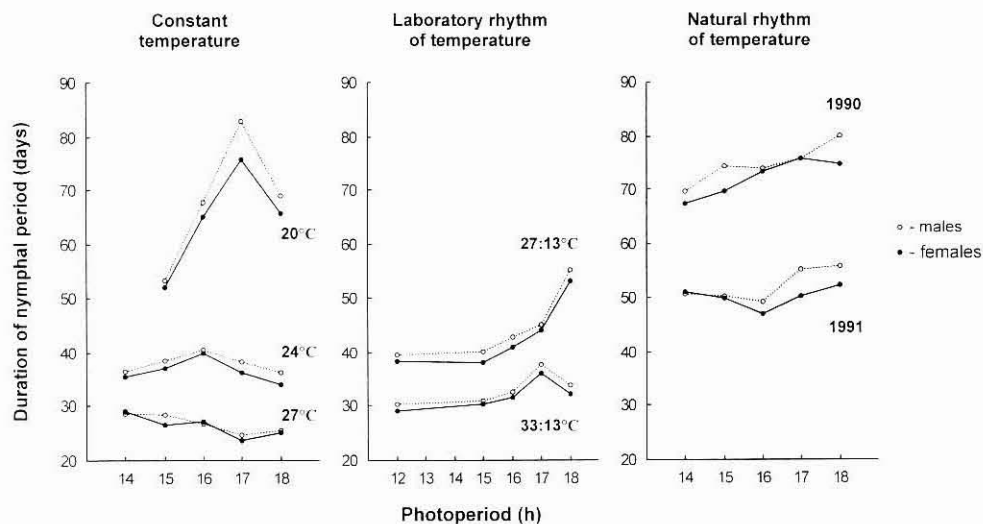


Fig. 3. Effect of photoperiodic conditions on the duration of nymphal period in *Pyrrhocoris apterus* (Pyrrhocoridae) under different temperatures (after Musolin & Saulich, 1997).



phal development under different photoperiodic conditions are available in *Pyrrhocoris apterus* (Numata *et al.*, 1993; Musolin & Saulich, 1997). This species was studied both at constant temperatures and under conditions of natural and laboratory thermorhythms. For instance, at a constant temperature of 20°C as duration of photophase increased from 15 to 17 h, so did the duration of nymphal development and the difference amounted to 50% of the total duration of the nymphal period. The tendency was also observed under many other temperature conditions (Fig. 3).

In general, photoperiodic control of nymphal development was more pronounced at lower temperatures. The most significant part of retardation of nymphal growth occurred in the fifth (last) instar, which was the longest stage of nymphal development. In the species with facultative diapause, this response allows acceleration of development at beginning and end of the summer season when days are short and thus promotes bi- or polyvoltine developmental schemes and full use of resources. In univoltine species, the value of this adaptation is likely to be limited by synchronization of adult emergence (Musolin & Saulich, 1997).

#### *Environmental control of coloration and polymorphism*

Another example of a response to environmental conditions that might have adaptive significance is photoperiodic control of insect coloration. This phenomenon has been revealed experimentally in several heteropteran species. Thus, photoperiod and temperature experienced during the nymphal stage were shown to determine degree of metathorax pigmentation in adults of *Riptortus clavatus*: adults emerged under long-day conditions had more in number and

larger in size white spots than those reared as nymphs under short-day conditions and this response was gradual (Kobayashi & Numata, 1993, 1995). Current day length determines coloration of adults of *Nezara viridula* and reversible changes of coloration from green to brown or reddish seem to be more or less correlated with physiological state (diapause or reproductive activity) of individuals (Harris *et al.*, 1984; Seymour & Bowman, 1994; Takizawa, 1994; Musolin & Numata, unpubl.). Dolling (1973) reported that day length controlled the appearance of two color forms in the mirid *Notostira elongata*: long-day (summer) individuals were green and short-day (autumn) individuals were brown. A very similar response was also found in the pentatomid *Thyanta calceata* by McPherson (1977). It is likely that brown (as in *N. elongata* and *T. calceata*) or reddish (as in *N. viridula*) coloration of overwintering individuals is more cryptic and has an adaptive value before or just after hibernation.

Also, two seasonal forms differing morphologically and in coloration are known in two pentatomids *Euschistus tristigmus tristigmus* (McPherson, 1974, 1979) and in *Oebalus ypsilon* (Vecchio *et al.*, 1994). This seasonal dimorphism even resulted in incorrect treatment of these forms as independent species.

In two other stink bugs *Plautia crossota stali* (Numata & Kobayashi, 1994) and *Arma custos* (Volkovich & Saulich, 1994) photoperiodic conditions determined body coloration of nymphs. In both species, short day induced the appearance of darker form, while long day promoted the predominance of light-colored nymphs (Fig. 4). It is supposed that this response may participate in thermoregulation and consequently have adaptive value.

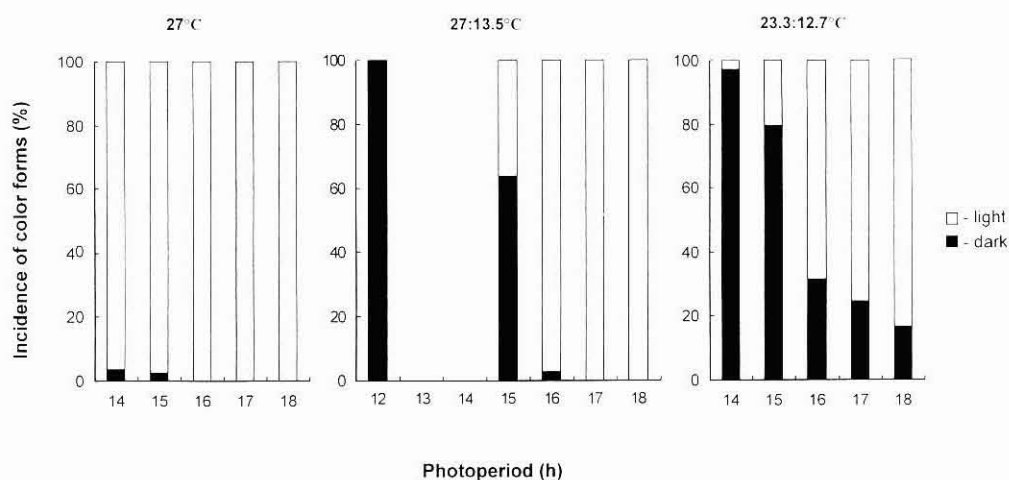


Fig. 4. Effect of photoperiodic and temperature conditions on incidence of dark and light color forms of nymphs in *Arma custos* (Pentatomidae: data from Volkovich & Saulich, 1994).

### *Host-plant related adaptations*

A set of rather complicated relationships was found in the phytophagous tingid *Stephanitis pyrioides*, its specialist predator mirid *Stethoconus japonicus* and their host plant (Neal & Haldemann, 1992). Both predator and prey overwinter as eggs within the tissues of azalea plant. The predator alters its oviposition site on azalea as the summer progresses and this results in a delay in hatching of overwintered eggs in the next season. The timing of the annual shift in oviposition site was shown to coincide with a decline in leaf moisture. Nymphs of the predator begin to hatch in the field when early instars of the second generation of its prey (which is more abundant than the first generation) are present. Thus, the late hatching of overwintered eggs of this specialist predator results in synchrony with the prey resource.

### *Behavioral adaptations*

The next group of adaptations may be called behavioral adaptations. Not so many examples have been reported in Heteroptera, although they probably are very important, especially in reproduction. Thus, the presence of very sexually active males of the lygaeid *Oncopeltus sandarachatus* induced premature termination of diapause in females of *Oncopeltus fasciatus*, a species with low sexual activity (Hayes & Dingle, 1983). This response is supposed to represent a well-coordinated *diapause-migration strategy*. In *Lygaeus equestris*, the presence of active males also had some influence on copulation and oviposition in females (Sillén-Tullberg, 1984). However, Hodková *et al.* (1991) showed that in *Pyrrhocoris apterus*, the presence of reproductively active females had a much less important effect than photoperiod on reproductive activity and diapause of males.

A quite different type of behavioral adaptations was reported in *Pyrrhocoris apterus* by Honěk & Šrámková (1976), who showed that during the warm season the nymphs of this species actively selected microhabitats with particular, not highest, temperatures. It is proposed that this selection regulates the speed of development and maintains the univoltine cycle of the species in a particular region.

A complex pattern of parental care has evolved in a gregarious cydnid *Parastrachia japonensis* in response to severe pressure from both biotic and abiotic environmental factors (Tachikawa & Schaefer, 1985; Tsukamoto & Tojo, 1992; Filippi-Tsukamoto *et al.*, 1995). All reproduction in this species must coincide with a short period during which fallen drupes of olacaceous plant *Schoepfia jasminodora* in a proper

condition are available. Progressive provisioning was demonstrated to be essential for nymphal survival under environmental conditions where the sole food resource is scarce and ephemeral in time and space. In general, Tallamy & Schaefer (1997) discuss principal features and adaptive value of maternal care in Hemiptera and stress that "it is only when host-plant seasonality or other unidentified phenomena prevent the distribution of eggs over space and time that relict maternal behaviour persists" (p. 94).

### *Summer dormancy*

As mentioned above, some heteropterans are dormant at least during part of the summer. For instance, in *Carbula humerigera*, an adult summer diapause (aestivation) in a form of extended preoviposition period is induced by increasing day length at the beginning of summer (Kiritani, 1985a, 1987). Oviposition commences after the summer solstice when day length decreases. Moreover, both females that emerged earlier and later in the season begin oviposition synchronously. This mechanism of oviposition triggering is considered to be an adaptation which allows nymphs to avoid the long-day part of the season and ensures entering winter diapause for the offspring (Kiritani, 1985a). The pentatomid *Picromerus bidens* is another heteropteran, the life cycle of which includes summer diapause that results in the shift of oviposition towards September and successful overwintering of eggs and maintains a univoltine seasonal cycle (Musolin, 1996; Musolin & Saulich, 1998 and unpubl.).

As discussed above, *Eurydema rugosum* enters diapause in response not only to short-day conditions but also to the feeding on seeds of its host plant and there is a certain physiological difference between photoperiodically induced and food-mediated diapause in this species (Numata & Yamamoto, 1990; Ikeda-Kikue & Numata, 1994). These two kinds of dormancy differ also in the terms of seasonal timing and the food-mediated diapause should be considered an aestivation that is followed by the winter diapause (Ikeda-Kikue, 1991).

### *Dispersal and migrations*

High natural mobility of insects is a prerequisite for dispersal aimed at searching for more comfortable environmental conditions, sites for oviposition, food sources etc. Most heteropterans can fly for only short distances. Thus, *Cletus punctiger* flies from one host plant to another within a confined area (Ito, 1980) and this may be considered aseasonal migrations in the

terms suggested by Tauber *et al.* (1986). Apparently, more complicated forms of migratory behavior have evolved on the basis of these primitive micromigrations.

Seasonal migrations have a regular character and are an integral part of the species life history. Like diapause, they are strongly associated with both particular stages of metamorphosis and seasons (Dingle, 1972, 1996). Migrants are characterized by a high flight activity and inhibition of many physiological processes, especially those related with reproduction. For example, the scutellerid *Eurygaster integriceps* has a univoltine seasonal cycle with obligatory adult diapause (Viktorov, 1967). Adult bugs migrate to forests in the northern parts of the species' range and to mountains in its southern part to overwinter in very large groups (up to 900 individuals per plant: Brown, 1962). The dormancy in this species consists of two stages. The first is an aestivation that lasts for about two months while the weather is relatively warm, and this stage is followed by a short period of activity. Then, bugs fly to their hibernation place. In the mountains, aestivation takes place at a higher elevation from which bugs migrate down for hibernation. When the temperature falls to about +9–10°C, bugs cease movements and enter winter diapause. In the spring after diapause termination bugs return to the fields.

In many species of heteropterans, the migratory syndrome is linked with an alary polymorphism. In this case, there is an interaction between the three related syndromes: diapause, seasonal polyphenism (polymorphism) and migration. This phenomenon is most pronounced in semiaquatic species (Vepsäläinen, 1978; Spence & Andersen, 1994). In this paper, we focused on seasonal adaptations of terrestrial bugs among which *Oncopeltus fasciatus* can be treated as a representative species. This species is remarkable because of its long distance annual migrations in which individuals of different generations are involved. In the temperate zones of North America, migrants appear for the first time in late spring to mid-summer and produce one to three generations depending on the latitude and local climate. The bugs are not able to survive northern winters, but can overwinter in diapause in regions with milder climates. A short-day diapause in *O. fasciatus* leads to a delay in reproduction and extensive migratory flight, which is enhanced by diapause (Dingle, 1978). In contrast to the temperate populations, those from the tropics are active throughout the year and display little dispersal flights aimed at searching for optimal food sources only

(Dingle & Baldwin, 1983). Extensive examination of different populations of *O. fasciatus* revealed significant differences in morphological and life-history traits: body size and wing length were larger and females started oviposition at later ages in the migrants. They also showed longer tethered flights (Dingle, 1978, 1991).

## Conclusions and Future Directions

This is the first attempt to review seasonal adaptations evolved by terrestrial Heteroptera from the temperate zone. The research carried out and presented here can offer a clearer view of the problem as well as raise some questions and indicate directions for further investigations.

It is apparent that in the temperate zone where environmental conditions show pronounced seasonality, diapause (and especially, photoperiodic programming of diapause induction) plays a pivotal role in seasonal development of Heteroptera as well as of insects from other orders. However, if photoperiodic control of diapause induction has been revealed and studied in a relatively large number of heteropterans, this cannot be pertained equally to other seasonal adaptations evolved by true bugs. The ecological significance of these "other" seasonal adaptations (such as diapause termination whenever it takes place, cold-hardiness and behavioral adaptations) has been underestimated. Analysis of one type of non-diapause seasonal adaptations (photoperiodic control of nymphal growth: Musolin & Saulich, 1997) revealed that several heteropterans tested adequately in this respect show similar trends. In many species, the adaptive significance of this response has become clear.

The title of this paper, i.e. seasonal adaptations of *terrestrial Heteroptera from the temperate zone*, implies three questions that might be important from both ecological and evolutionary points of view: are these adaptations specific only for this group or how dramatically do they differ from those of (1) aquatic and semiaquatic bugs, (2) heteropterans from the tropics and subtropical regions, and (3) insects from other groups?

Only a few of the 38,000 known species from some of the 75 heteropteran families have been studied in respect to environmental control of seasonal development to a greater or lesser extent. This means that our discussions are limited and we are very far from a level that will allow acceptable analysis (as was done, for example, with life cycles of the ground crickets: Masaki *et al.*, 1987; Masaki & Walker, 1987 etc.).

Preliminary analysis based mostly on the literature showed, for example, that the characteristic diapause stage differs significantly among families of Heteroptera in the temperate zone (Musolin, 1997). Thus, many representatives of Miridae, Nabidae, Rhopalidae, Tingidae and some species of Coreidae and Pentatomidae have winter diapause at the egg stage. Nymphal diapause is comparatively rare, but is more common in Aradidae, Pentatomidae, Scutelleridae, Tingidae and Coreidae than in other families. In contrast, adult diapause seems to be most common type of winter diapause and is apparently dominant in temperate Pentatomoidea (93% of the species from this superfamily known in Central Europe: Hertzfel, 1982) and in terrestrial predatory heteropterans from the temperate zone (76.7% of 57 species studied to date and reviewed by Ruberson *et al.*, 1998). Further analysis became more complicated when it was shown that some species can overwinter at different ontogenetic stages and others have more than one period of dormancy in their life cycle. A special research that combines laboratory and field approaches is necessary to ultimately clarify seasonal patterns of any species.

Not enough information is available for such comparative analysis of the seasonal adaptations evolved by the temperate and tropical/subtropical species as was done in some other groups of insects (e.g. in the *Dianemobius* ground crickets by Masaki *et al.* [1987] or *Drosophila melanogaster* species group by Kimura [1988]). We hope that this review will in some way lend impetus to successful research into seasonal adaptations of Heteroptera on the whole and in tropical/subtropical species in particular.

Furthermore, it should be emphasized that seasonal adaptations do not exist alone, but are incorporated into more programmed or more flexible *seasonal cycles*. As mentioned above, diapause (in the temperate zone, mostly hibernation) is a pivotal element in any seasonal cycle. However, other seasonal adaptations such as the existence of a second dormant period, environmental control of nymphal growth, relationships with host plant(s), predators and parasites, timing of reproduction and migration etc., might substantially modify seasonal cycles. All this means that diversity of seasonal cycles in Heteroptera should be even more impressive than diversity of seasonal adaptations shown here, but this is the subject for other investigations.

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## References

- Ali, M. & Ewiess, M. A. 1977. Photoperiodic and temperature effects on rate of development and diapause in the green stink bug, *Nezara viridula* L. (Heteroptera: Pentatomidae). *Zeitschrift für Angewandte Entomologie*, **84**: 256–264.
- Bale, J. S. 1996. Insect cold hardiness: A matter of life and death. *European Journal of Entomology*, **93**: 369–382.
- Beards, G. W. & Strong, F. E. 1966. Photoperiod in relation to diapause in *Lygus hesperus* Knight. *Hilgardia (Journal of Agricultural Science Published by The California Agricultural Experimental Station)*, **37**: 345–362.
- Böcher, J. 1975. Notes on the reproductive biology and egg-diapause in *Nysius groenlandicus* (Zett.) (Heteroptera: Lygaeidae). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, **138**: 21–38.
- Borisenko, I. A. 1987. Dynamics of cold-hardiness in ontogeny of a predatory bug *Podisus maculiventris* Say. *Bulleten' Vsesojuznogo Nauchno-issledovatel'skogo Instituta Zashiti Rastenii*, **69**: 12–16 (In Russian.)
- Braman, S. K. & Pendley, A. F. 1993. Temperature, photoperiod, and aggregation effects on development, diapause, reproduction, and survival of *Corythucha cydoniae* (Heteroptera: Tingidae). *Journal of Entomological Science*, **28**: 417–426.
- Braune, H.-J. 1971. Der Einfluss der Temperatur auf Eidiapause und Entwicklung von Weichwanzen (Heteroptera, Miridae). *Oecologia*, **8**: 223–266.
- Braune, H.-J. 1976. Effects of temperature on the rates of oxygen consumption during morphogenesis and diapause in egg stage of *Leptopterna dolobrata* (Heteroptera, Miridae). *Oecologia*, **25**: 77–87.
- Braune, H.-J. 1980. Ökophysiologische Untersuchungen über die Steuerung der embryonalen Diapause bei Insekten am Beispiel von *Leptopterna dolobrata* (Heteroptera, Miridae). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*, **107**: 32–112.

- Brown, E. S. 1962. Researches on the ecology and biology of *Eurygaster integriceps* Put. (Hemiptera, Scutelleridae) in Middle East countries, with special reference to the overwintering period. *Bulletin of Entomological Research*, **53**: 445–514.
- Chyzik, R., Klein, M. & Ben-Dov, Y. 1995. Overwintering biology of the predatory bug *Orius albidipennis* (Hemiptera: Anthocoridae) in Israel. *Biocontrol Science and Technology*, **5**: 287–296.
- Conradi-Larsen, E. M. & Sømme, L. 1973. Notes on the biology of *Dolycoris baccarum* L. (Het., Pentatomidae). *Norsk Entomologisk Tidsskrift*, **20**: 245–247.
- Conradi-Larsen, E. M. & Sømme, L. 1978. The effects of photoperiod and temperature on imaginal diapause in *Dolycoris baccarum* from Southern Norway. *Journal of Insect Physiology*, **24**: 243–249.
- Danks, H. V. 1987. Insect Dormancy: An Ecological Perspective. Biological Survey of Canada, Ottawa.
- Danks, H. V. 1996. The wider integration of studies on insect cold-hardiness. *European Journal of Entomology*, **93**: 383–403.
- Dingle, H. 1972. Migration strategies of insects. *Science*, **175**: 1327–1335.
- Dingle, H. 1974. Diapause in a migrant insect, the milkweed bug *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae). *Oecologia*, **17**: 1–10.
- Dingle, H. 1978. Migration and diapause in tropical, temperate, and island milkweed bugs. In Dingle, H. (ed.), *Evolution of Insect Migration and Diapause*: 254–276. Springer-Verlag, New York.
- Dingle, H. 1991. Evolutionary genetics of animal migration. *American Zoologist*, **31**: 253–264.
- Dingle, H. 1996. *Migration: The Biology of Life on the Move*. Oxford University Press, New York.
- Dingle, H. & Baldwin, J. D. 1983. Geographic variation in life histories: A comparison of tropical and temperate milkweed bugs (*Oncopeltus*). In Brown, V. K. & Hodek, I. (eds.), *Diapause and Life Cycle Strategies in Insects*, Series Entomologica, **23**: 143–165. Junk, The Hague.
- Dolling, W. R. 1973. Photoperiodically determined phase production and diapause termination in *Notostira elongata* (Geoffroy) (Hemiptera: Miridae). *Entomological Gazette*, **24**: 75–79.
- Dolling, W. R. 1991. *The Hemiptera*. Natural History Museum Publication, Oxford University Press, Oxford.
- Else, K. D. 1974. *Jalysus spinosus*: Reproductive diapause. *Environmental Entomology*, **3**: 156–158.
- Else, K. D. 1993. Cold tolerance of the southern green stink bug (Hemiptera: Pentatomidae). *Environmental Entomology*, **22**: 567–570.
- Eguagie, W. E. 1974. Cold hardiness of *Tingis ampliata* (Hemiptera: Tingidae). *Entomologia Experimentalis et Applicata*, **17**: 204–214.
- Ewen, A. B. 1966. A possible endocrine mechanism for inducing diapause in the eggs of *Adelphocoris lineolatus* (Goeze) (Hemiptera: Miridae). *Experientia*, **22**: 470.
- Fielding, D. J. 1988. Photoperiodic induction of diapause in the squash bug, *Anasa tristis*. *Entomologia Experimentalis et Applicata*, **48**: 187–193.
- Fielding, D. J. 1990. Photoperiod and food regulate termination of diapause in the squash bug, *Anasa tristis*. *Entomologia Experimentalis et Applicata*, **55**: 119–124.
- Filippi-Tsakamoto, L., Nomakuchi, S., Kuki, K. & Tojo, S. 1995. Adaptiveness of parental care in *Parastrachia japonensis* (Hemiptera: Cydnidae). *Annals of the Entomological Society of America*, **88**: 374–383.
- Gaylor, M. J. & Sterling, W. L. 1977. Photoperiodic induction and seasonal incidence of embryonic diapause in the cotton fleahopper, *Pseudatomoscelis seriatus*. *Annals of the Entomological Society of America*, **70**: 893–897.
- Gerber, G. H. & Wise, I. L. 1995. Seasonal occurrence and number of generations of *Lygus lineolaris* and *L. borealis* (Hemiptera: Miridae) in Southern Manitoba. *The Canadian Entomologist*, **127**: 543–559.
- Goryshin, N. I., Volkovich, T. A., Saulich, A. H., Vagner, M. & Borisenko, I. A. 1988. The role of temperature and photoperiod in the control of development and diapause in a predatory bug, *Podisus maculiventris* (Hemiptera, Pentatomidae). *Zoologicheskii Zhurnal*, **67**: 1149–1161. (In Russian, English summary.)
- Harris, V. E., Todd, J. W. & Mullinix, B. G. 1984. Color change as an indicator of adult diapause in the southern green stink bug, *Nezara viridula*. *Journal of Agricultural Entomology*, **1**: 82–91.
- Hayes, J. L. & Dingle, H. 1983. Male influence on the duration of reproductive diapause in the large milkweed bug, *Oncopeltus fasciatus*. *Physiological Entomology*, **8**: 251–256.
- Hertzel, G. 1982. Zur Phänologie und Fortpflanzungsbiologie einheimischer Pentatomiden-Arten (Hemiptera). *Entomologische Nachrichten und Berichte*, **26**: 69–72.
- Hodek, I. 1968. Diapause in females of *Pyrrhocoris apterus* L. (Hemiptera). *Acta Entomologica Bohemoslovaca*, **65**: 422–435.
- Hodek, I. 1971. Sensitivity to photoperiod in *Aelia acuminata* (L.) after adult diapause. *Oecologia*, **6**: 152–155.
- Hodek, I. 1974. Development of diapause in *Pyrrhocoris apterus* females in the middle period of winter dormancy (Hemiptera). *Věstník Československé Společnosti Zoologické*, **38**: 161–169.
- Hodek, I. 1977. Photoperiodic response in spring in three Pentatomoidea (Hemiptera). *Acta Entomologica Bohemoslovaca*, **74**: 209–218.
- Hodek, I. 1979. Intermittent character of adult diapause in *Aelia acuminata* (Hemiptera). *Journal of Insect Physiology*, **25**: 867–871.
- Hodek, I. & Hodková, M. 1981. Relationship between respiratory rate and diapause intensity in adults of two heteropteran species. *Věstník Československé Společnosti Zoologické*, **45**: 27–34.
- Hodek, I. & Hodková, M. 1982. Regulation of postdiapause reproduction by recurrent photoperiodic response. In Bennettová, B. et al. (eds.), *Advances in Regulation of Insect Reproduction*: 119–124. Institute of Entomology, Czech Academy of Sciences, České Budějovice.
- Hodková, M. 1982. Interaction of feeding and photoperiod in regulation of the corpus allatum activity in females of *Pyrrhocoris apterus* L. (Hemiptera). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*, **86**: 477–488.
- Hodková, M. & Hodek, I. 1994. Control of diapause and

- supercooling by the retrocerebral complex in *Pyrrhocoris apterus*. *Entomologia Experimentalis et Applicata*, **70**: 237–245.
- Hodková, M. & Hodek, I. 1997. Temperature regulation of supercooling and gut nucleation in relation to diapause of *Pyrrhocoris apterus* (L.) (Heteroptera). *Cryobiology*, **34**: 70–79.
- Hodková, M., Zieglerová, J. & Hodek, I. 1991. Diapause in males of *Pyrrhocoris apterus* (L.) (Heteroptera) and its dependence on photoperiod and the activity of females. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*, **118**: 279–285.
- Hokyo, N., Suzuki H. & Murai, M. 1983. Egg diapause in the oriental chinch bug, *Cavelerius saccharivorus* Okajima (Heteroptera: Lygaeidae). 1. Incidence and intensity. *Applied Entomology and Zoology*, **18**: 382–391.
- Honěk, A. & Šrámková, K. 1976. Behavioral regulation of developmental cycle in *Pyrrhocoris apterus* L. (Heteroptera: Pyrrhocoridae). *Oecologia*, **24**: 277–281.
- Hori, K. 1988. Effects of stationary photoperiod on nymphal growth, feeding and digestive physiology of *Palomena angulosa* Motschulsky (Hemiptera: Pentatomidae). *Applied Entomology and Zoology*, **23**: 401–406.
- Hori, K. & Kimura, A. 1993. Effect of stationary photoperiod on diapause induction of *Eysarcoris lewisi* Distant (Heteroptera: Pentatomidae) and the developmental stage sensitive to stimulus for reproductive diapause. *Applied Entomology and Zoology*, **28**: 53–58.
- Horton, D. R., Lewis, T. M., Hinojosa, T. & Broers, D. A. 1998. Photoperiod and reproductive diapause in the predatory bugs *Anthocoris tomentosus*, *A. antevolens*, and *Deraeocoris brevis* (Heteroptera: Anthocoridae, Miridae) with information on overwintering sex ratios. *Annals of the Entomological Society of America*, **91**: 81–86.
- Ikeda-Kikue, K. 1991. Experimental Analysis of the Environmental Factors That Control the Life Cycle of the Cabbage Bug, *Eurydema rugosa* Motschulsky. Ph.D. Dissertation. Osaka City University, Osaka.
- Ikeda-Kikue, K. & Numata, H. 1992. Effect of diet, photoperiod and temperature on the post-diapause reproduction in the cabbage bug, *Eurydema rugosa*. *Entomologia Experimentalis et Applicata*, **64**: 31–36.
- Ikeda-Kikue, K. & Numata, H. 1994. Effect of low temperature on the termination of photoperiodic and food-mediated diapause in the cabbage bug, *Eurydema rugosa* Motschulsky (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, **29**: 229–236.
- Ito, K. 1980. Seasonal changes in flight ability of *Cletus punctiger* (Heteroptera: Coreidae). *Applied Entomology and Zoology*, **15**: 36–44.
- Ito, K. 1984. The effect of feeding on the subsequent starvation longevity in post-hibernating *Cletus punctiger* (Heteroptera: Coreidae). *Applied Entomology and Zoology*, **19**: 461–467.
- Ito, K. 1988. Diapause termination in *Cletus punctiger* Dallas (Heteroptera: Coreidae) in the field. *Japanese Journal of Applied Entomology and Zoology*, **32**: 63–67. (In Japanese, English abstract.)
- Ito, K. & Nakata, T. 1998a. Effect of photoperiod on reproductive diapause in the predatory bugs, *Orius sauteri* (Poppius) and *O. minutus* (Linnaeus) (Heteroptera: Anthocoridae). *Applied Entomology and Zoology*, **33**: 115–120.
- Ito, K. & Nakata, T. 1998b. Diapause and survival in winter in two species of predatory bugs, *Orius sauteri* and *O. minutus*. *Entomologia Experimentalis et Applicata*, **89**: 271–276.
- Kerzhner, I. M. & Jaczewski, T. L. 1964. 19. Order Hemiptera (Heteroptera)—True Bugs. In Bei-Bienko, G. Ya. (ed.), *Keys to the Insects of the European USSR: in 5 vols. 1. Apteriygota, Paleoptera, Hemimetabola*: 655–845. Nauka (Academy of Sciences of the USSR, Zoological Institute), Moscow-Leningrad. (In Russian.)
- Kimura, M. T. 1988. Adaptations to the temperate climates and evolution of overwintering strategies in the *Drosophila melanogaster* species group. *Evolution*, **42**: 1288–1297.
- Kingsley, P. C. & Harrington, B. J. 1982. Factors influencing termination of reproductive diapause in *Orius insidiosus* (Hemiptera: Anthocoridae). *Environmental Entomology*, **11**: 461–462.
- Kiritani, K., Hōkyo, N. & Kimura, K. 1962. Differential winter mortality relative to sex in the population of southern green stink bug, *Nezara viridula* (Pentatomidae, Hemiptera). *Japanese Journal of Applied Entomology and Zoology*, **6**: 242–245.
- Kiritani, Y. 1985a. Timing of oviposition and nymphal diapause under the natural daylength in *Carbula humerigera* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, **20**: 252–256.
- Kiritani, Y. 1985b. Effect of stationary and changing photoperiods on nymphal development in *Carbula humerigera* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, **20**: 257–263.
- Kiritani, Y. 1987. Effect of stationary and changing photoperiods on oviposition in *Carbula humerigera* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, **22**: 29–34.
- Kobayashi, S. & Numata, H. 1993. Photoperiodic responses controlling the induction of adult diapause and the determination of seasonal form in the bean bug, *Riptortus clavatus*. *Zoological Science*, **10**: 983–990.
- Kobayashi, S. & Numata, H. 1995. Effects of temperature and photoperiod on the induction of diapause and the determination of body coloration in the bean bug, *Riptortus clavatus*. *Zoological Science*, **12**: 343–348.
- Koshiyama, Y., Fujisaki, K. & Nakasuji, F. 1994. Mating and diapause in hibernating adults of *Menida scotti* Puton (Heteroptera: Pentatomidae). *Researches on Population Ecology*, **36**: 87–92.
- Koshiyama, Y., Fujisaki, K. & Nakasuji, F. 1997. Benefit of mating during hibernation for male adults of *Menida scotti* (Heteroptera: Pentatomidae). *Chugoku Kontyu*, **11**: 1–9.
- Koshiyama, Y., Tsumuki, H., Muraji, M., Fujisaki, K. & Nakasuji, F. 1993. Transfer of male secretions to females through copulation in *Menida scotti* (Heteroptera: Pentatomidae). *Applied Entomology and Zoology*, **28**: 325–332.
- Kudō, S. & Kurihara, M. 1988. Seasonal occurrence of egg diapause in the rice leaf bug, *Trigonotylus coelestialium* Kirkaldy (Hemiptera: Miridae). *Applied Entomology and Zoology*, **23**: 365–366.
- Kudō, S. & Kurihara, M. 1989. Effect of maternal age on

- induction of egg diapause in the rice leaf bug, *Trigonotylus coelestialium* Kirkaldy (Heteroptera, Miridae). *Japanese Journal of Entomology*, **57**: 440–447.
- Larivière, M.-C. & Laroche, A. 1989. *Picromerus bidens* (Heteroptera: Pentatomidae) in North America, with a world review of distribution and bionomics. *Entomological News*, **100**: 133–146.
- Leather, S. R., Walker, K. F. A. & Bale, J. S. 1993. *The Ecology of Insect Overwintering*. Cambridge University Press, Cambridge.
- MacPhee, A. W. 1964. Cold-hardiness, habitat and winter survival of some orchard arthropods in Nova Scotia. *The Canadian Entomologist*, **96**: 617–625.
- Masaki, S., Shirado, I. & Nagase, A. 1987. Tropical, subtropical and temperate life cycles in ground crickets. *Insect Science and Its Application*, **8**: 475–481.
- Masaki, S. & Walker, T. J. 1987. Cricket life cycles. In Hetch, M. K. *et al.* (eds.), *Evolutionary Biology*, **21**: 349–423. Plenum Press, New York.
- McPherson, J. E. 1974. Photoperiod effects in a southern Illinois population of the *Euschistus tristigmus* complex (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America*, **67**: 943–952.
- McPherson, J. E. 1977. Effect of developmental photoperiod on adult color and pubescence in *Thyanta calceata* (Hemiptera: Pentatomidae) with information on ability of adults to change color. *Annals of the Entomological Society of America*, **70**: 373–376.
- McPherson, J. E. 1979. Effects of various photoperiods on morphology in *Euschistus tristigmus tristigmus* (Hemiptera: Pentatomidae). *The Great Lakes Entomologist*, **12**: 23–26.
- Musolin, D. L. 1996. Photoperiodic induction of aestivation in the stink bug *Picromerus bidens* (Heteroptera, Pentatomidae). A preliminary report. *Zoologicheskii Zhurnal*, **75**: 1901–1904. (In Russian, English summary.) [Translation in *Entomological Review*, **76**: 1058–1060, 1996].
- Musolin, D. L. 1997. *Seasonal Cycles of Heteroptera: Diversity and Environmental Control*. Ph.D. Dissertation. Saint-Petersburg State University, Saint-Petersburg (In Russian.)
- Musolin, D. L. & Maysov, A. V. 1998. Perception of photoperiodic information during the induction and termination of diapause in the stink bug *Graphosoma lineatum* L. (Heteroptera, Pentatomidae). In Medvedev, G. S. *et al.* (eds.), *The Problems of Entomology in Russia* [Proceedings of XI Congress of Russian Entomological Society, St. Petersburg, 23–29 September, 1997], **2**: 44. St. Petersburg. (In Russian.)
- Musolin, D. L., Maysov, A. V. & Saulich, A. H. 1999. Egg diapause in *Alydus calcaratus* (L.) (Heteroptera: Alydidae): photoperiodic induction under natural temperature conditions. *Applied Entomology and Zoology*, **34**: 469–473.
- Musolin, D. L. & Saulich, A. H. 1995. Factorial regulation of the seasonal cycle of the stink bug *Graphosoma lineatum* L. (Heteroptera, Pentatomidae). 1. Temperature and photoperiodic responses. *Entomologicheskoe Obozrenie*, **74**: 736–743. (In Russian, English summary.) [Translation in *Entomological Review*, **75**: 84–93, 1996.]
- Musolin, D. L. & Saulich, A. H. 1997. Photoperiodic control of nymphal growth in bugs (Heteroptera). *Zoologicheskii Zhurnal*, **76**: 530–542. (In Russian, English summary.) [Translation in *Entomological Review*, **77**: 768–780, 1997.]
- Musolin, D. L. & Saulich, A. H. 1998. Two periods of dormancy in the seasonal cycle of *Picromerus bidens* (Heteroptera, Pentatomidae): The results of laboratory and field experiments. In Bunnhofer, V. & Soldán, T. (eds.), *Book of Abstracts, VIth European Congress of Entomology* [České Budějovice, August 23–29, 1998], **1**: 281–282.
- Nakamura, K., Hodek, I. & Hodková, M., 1996. Recurrent photoperiodic response in *Graphosoma lineatum* (Heteroptera: Pentatomidae). *European Journal of Entomology*, **93**: 519–523.
- Nakamura, K. & Numata, H. 1995. Photoperiodic sensitivity in adults of *Aelia fieberi* (Heteroptera: Pentatomidae). *European Journal of Entomology*, **92**: 609–613.
- Nakamura, K. & Numata, H. 1997. Effects of environmental factors on diapause development and postdiapause oviposition in a phytophagous insect, *Dybowskyia reticulata*. *Zoological Science*, **14**: 1021–1026.
- Nakamura, K. & Numata, H. 1998. Alternative life cycles controlled by temperature and photoperiod in the oligophagous bug, *Dybowskyia reticulata*. *Physiological Entomology*, **23**: 69–74.
- Neal, J. W., Jr. & Haldemann, R. L. 1992. Regulation of seasonal egg hatch by plant phenology in *Stethoconus japonicus* (Heteroptera: Miridae), a specialist predator of *Stephanitis pyrioides* (Heteroptera: Tingidae). *Environmental Entomology*, **21**: 793–798.
- Neal, J. W., Jr., Tauber, M. J. & Tauber, C. A. 1992. Photoperiodic induction of reproductive diapause in *Corythucha cydoniae* (Heteroptera: Tingidae). *Environmental Entomology*, **21**: 1414–1418.
- Nichols, J. R. 1988. Photoperiodic responses of the squash bug (Heteroptera: Coreidae): diapause induction and maintenance. *Environmental Entomology*, **17**: 427–431.
- Numata, H. 1985. Photoperiodic control of adult diapause in the bean bug, *Riptortus clavatus*. *Memoirs of the Faculty of Science, Kyoto University, Series of Biology*, **10**: 29–48.
- Numata, H. 1987. Photoperiodic sensitivity after diapause termination in the bean bug, *Riptortus clavatus* Thunberg (Heteroptera: Coreidae). *Applied Entomology and Zoology*, **22**: 352–357.
- Numata, H. & Hidaka, T. 1982. Photoperiodic control of adult diapause in the bean bug, *Riptortus clavatus* Thunberg (Heteroptera: Coreidae). I. Reversible induction and termination of diapause. *Applied Entomology and Zoology*, **17**: 530–538.
- Numata, H. & Hidaka, T. 1984. Photoperiodic control of adult diapause in the bean bug, *Riptortus clavatus* Thunberg (Heteroptera: Coreidae). IV. Food and post-diapause development. *Applied Entomology and Zoology*, **19**: 443–447.
- Numata, H. & Kobayashi, S. 1994. Threshold and quantitative photoperiodic responses exist in an insect. *Experientia*, **50**: 969–971.
- Numata, H., Saulich, A. H. & Volkovich, T. A. 1993. Photoperiodic responses of the linden bug, *Pyrrhocoris apterus*, under conditions of constant temperature and under thermoperiodic conditions. *Zoological Science*, **10**: 521–527.

- Numata, H. & Yamamoto, K. 1990. Feeding on seeds induces diapause in the cabbage bug, *Eurydema rugosa*. *Entomologia Experimentalis et Applicata*, **57**: 281–284.
- Okuyama, S. 1982. Role of day-length in the oviposition of dormant eggs by the rice leaf bug, *Trigonotylus coelestialium* Kirkaldy, and conditions for release from the dormancy. *The Annual Report of the Society of Plant Protection of North Japan*, **33**: 89–92. (In Japanese.)
- Parker, N. J. B. 1975. An investigation of reproductive diapause in two British populations of *Anthocoris nemorum* (Hemiptera: Anthocoridae). *Journal of Entomology. Series A, General Entomology*, **49**: 173–178.
- Perepelitza, L. V. 1971. A role of photoperiod in development of *Dolycoris baccarum*. *Bulleten' Vsesojuznogo Nauchno-issledovatel'skogo Instituta Zashiti Rastenii*, **21**: 11–13. (In Russian.)
- Puchkov, V. G. 1987. Order True Bugs–Hemiptera. In Vasiliev, V. P. (ed.), *Pests of Agricultural Plants and Forests: in 3 vols. 1. Pest Nematodes, Molluscs, Arthropods*: 279–305. Urozhay, Kiev. (In Russian.)
- Ruberson, J. R., Kring, T. J. & Elkassabany, N. 1998. Overwintering and the diapause syndrome of predatory Hemiptera. In Coll, M. & Ruberson, J. R. (eds.), *Predatory Hemiptera: Their Ecology and Use in Biological Control*: 49–69. Thomas Say Publications in Entomology, Entomological Society of America, Lanham, MD.
- Saulich, A. Kh. & Musolin, D. L. 1996. Univoltinism and its regulation in some temperate true bugs (Hemiptera). *European Journal of Entomology*, **93**: 507–518.
- Saulich, A. H. & Volkovich, T. A. 1996. Monovoltinism in insects and its regulation. *Entomologicheskoe Obozrenie*, **75**: 244–258. (In Russian, English summary.) [Translation in *Entomological Review*, **76**: 205–217, 1996]
- Schaefer, C. W. 1981. The land bugs (Hemiptera: Heteroptera) and their adaptive zones. *Rostria*, **33** (Supplement): 67–83.
- Schaefer, C. W. 1997. The origin of secondary carnivory from herbivory in Hemiptera (Hemiptera). In Raman, A. (ed.), *Ecology and Evolution of Plant-Feeding Insects in Natural and Man-Made Environments*: 229–239. International Scientific Publications, New Delhi.
- Schuh, R. T. & Slater, J. A. 1995. True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History. Cornell University Press, Ithaca.
- Seymour, J. E. & Bowman, G. J. 1994. Russet coloration in *Nezara viridula* (Hemiptera: Pentatomidae): an unreliable indicator of diapause. *Environmental Entomology*, **23**: 860–863.
- Shagov, E. M. 1969. Some peculiarities of physiology of *Perillus bioculatus* (Hemiptera, Pentatomidae) during winter dormancy. *Zoologicheskii Zhurnal*, **48**: 827–836. (In Russian, English summary.)
- Sillén-Tullberg, B. 1984. Copulation as a determinant of non-diapause development in female *Lygaeus equestris*. *Entomologia Experimentalis et Applicata*, **36**: 261–264.
- Sláma, K. 1964. Hormonal control of respiratory metabolism during growth, reproduction, and diapause in female adults of *Pyrrhocoris apterus* L. (Hemiptera). *Journal of Insect Physiology*, **10**: 283–303.
- Solbreck, C. 1979. Induction of diapause in a migratory seed bug, *Neacoryphus bicrucis* (Say) (Heteroptera: Lygaeidae). *Oecologia*, **43**: 41–49.
- Solbreck, C. & Sillén-Tullberg, B. 1981. Control of diapause in a "monovoltine" insect, *Lygaeus equestris* (Heteroptera). *Oikos*, **36**: 68–74.
- Southwood, T. R. E. & Leston, D. 1959. Land and Water Bugs of the British Isles. Frederick Warne and Co., London.
- Spence, J. R. & Andersen, N. M. 1994. Biology of water striders: Interaction between systematics and ecology. *Annual Review of Entomology*, **39**: 101–128.
- Tachikawa, S. & Schaefer, C. W. 1985. Biology of *Parastrachia japonensis* (Hemiptera: Pentatomoidea: ?-idae). *Annals of the Entomological Society of America*, **78**: 387–397.
- Takizawa, H. 1994. Effect of temperature and photoperiod on the induction of brown color type (forma *aurantica* Costa) adult of the southern green stink bug, *Nezara viridula* L. (Heteroptera: Pentatomidae). *Bulletin of the National Institute of Sericultural and Entomological Science*, **11**: 27–35. (In Japanese, English summary.)
- Tallamy, D. W. & Schaefer, C. 1997. Maternal care in the Hemiptera: Ancestry, alternatives, and current adaptive value. In Choe, J. C. & Crespi, B. J. (eds.), *The Evolution of Social Behavior in Insects and Arachnids*: 94–115. Cambridge University Press, New York.
- Tanaka, S. I., Natuhara, Y. & Imai, C. 1995. Photoperiods inducing nymphal diapause accelerate oviposition in *Poeciloricis lewisi* Distant (Heteroptera: Scutelleridae). *Proceedings of 55th Meeting of Entomological Society of Japan and 39th Meeting of Japanese Society of Applied Entomology and Zoology* [Obihiro, August 25–28, 1995]: 134. (In Japanese.)
- Tauber, M. J., Tauber, C. A. & Masaki, S. 1986. Seasonal Adaptations of Insects. Oxford University Press, New York.
- Tsukamoto, L. & Tojo, S. 1992. A report of progressive provisioning in a stink bug, *Parastrachia japonensis* (Hemiptera: Cydnidae). *Journal of Ethology*, **10**: 21–29.
- van den Meiracker, R. A. F. 1994. Induction and termination of diapause in *Orius* predatory bugs. *Entomologia Experimentalis et Applicata*, **73**: 127–137.
- Vecchio, M. C. D., Grazia, J. & Albuquerque, G. S. 1994. Dimorfismo sazonal em *Oeobalus ypsilon* (De Geer, 1773) (Hemiptera, Pentatomidae) e uma nova sinonímia. *Revista Brasileira de Entomologia*, **38**: 101–108.
- Vepsäläinen, K. 1978. Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In Dingle, H. (ed.), *Evolution of Insect Migration and Diapause*: 218–253. Springer-Verlag, New York.
- Viktorov, G. A. 1967. The Problem of Population Density Dynamics in Insects with an Example of the Soun Bug, *Eurygaster integriceps*. Nauka, Moscow. (In Russian.)
- Volkovich, T. A. & Goryshin, N. I. 1978. Evaluation and accumulation of photoperiodic information in *Pyrrhocoris apterus* L. (Hemiptera, Pyrrhocoridae) during the induction of oviposition. *Zoologicheskii Zhurnal*, **57**: 46–55. (In Russian, English summary.)
- Volkovich, T. A. & Saulich, A. H. 1994. The predatory bug *Arma custos*: photoperiodic and temperature control of diapause and coloration. *Zoologicheskii Zhurnal*, **73**: 26–37. (In Russian, English summary.) [Translation in *Entomological Review*, **74**: 151–162, 1995]



- Volkovich, T. A., Saulich, A. H. & Goryshin, N. I. 1991. Day-length sensitive stage and accumulation of photoperiodic information in the predatory bug *Podisus maculiventris* (Heteroptera, Pentatomidae). *Entomologicheskoe Obozrenie*, **70**: 14–22. (In Russian, English summary.) [Translation in *Entomological Review*, **70**: 159–165, 1991]
- Yeargan, K. V. & Barney, W. E. 1996. Photoperiodic induction of reproductive diapause in the predators *Nabis americanus* and *Nabis roseipennis* (Heteroptera: Nabidae). *Annals of the Entomological Society of America*, **89**: 70–74.

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