Invasive Stink Bugs and Related Species (Pentatomoidea)

Biology, Higher Systematics, Semiochemistry, and Management

Edited by
J. E. McPherson

Front Cover photographs, clockwise from the top left:

Adult of *Piezodorus guildinii* (Westwood), Photograph by Ted C. MacRae; Adult of *Murgantia histrionica* (Hahn), Photograph by C. Scott Bundy; Adult of *Halyomorpha halys* (Stål), Photograph by George C. Hamilton; Adult of *Bagrada hilaris* (Burmeister), Photograph by C. Scott Bundy; Adult of *Megacopta cribraria* (F.), Photograph by J. E. Eger; Mating pair of *Nezara viridula* (L.), Photograph by Jesus F. Esquivel. Used with permission. All rights reserved.

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Diapause in Pentatomoidea[1]

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[1] This chapter was modified, expanded, and updated from "Diapause in the seasonal cycle of stink bugs (Heteroptera, Pentatomidae) from the Temperate Zone" by A. Kh. Saulich and D. L. Musolin (2012) (Copyright 2012 authors and Pleiades Publishing, Ltd.). Full Latin and common names along with authorities of pentatomoids mentioned in the text are given in **Table 11.2**. All specific eco-physiological terms that are **boldfaced** when mentioned the first time in the text are explained in the Glossary at the end of this chapter.

11.1 Introduction

In most habitats over the globe, both terrestrial and aquatic, environmental conditions constantly change. The nature and magnitude of these changes are different – they are rhythmic or unique, long-term or short, severe or mild, and involve only the physical environment or also include the biota. Accordingly, the effects of these environmental changes on individuals, populations, and species vary greatly (Danilevsky 1961, Tauber et al. 1986, Danks 1987).

To survive under conditions of the annual rhythm of climate and to cope with seasonal changes of the environment, insects, as with other living organisms, need special **seasonal adaptations**. Some of these adaptations are behavioral such as migration or burrowing. However, others often are represented by sequential changes of seasonal physiological states and involve periods of dormancy.

Dormancy is defined as *a state of suppressed development (developmental arrest), which is adaptive (that is ecologically or evolutionarily meaningful and not just artificially induced) and usually accompanied with metabolic suppression* (Koštál 2006). Insects have different forms of dormancy, which vary in their intensity (sometimes called deepness), but all of them are associated with increased nonspecific resistance to unfavorable conditions. Any form of dormancy in insects is a complex phenomenon that is aimed first at solving different seasonal ecological problems such as survival of cold winters, hot and dry periods of summers, rainy seasons, or times of years when food is scarce or of low quality. Another extremely important ecological function of insect dormancy is synchronization of intra- and interspecific relationships with other organisms of the ecosystem (Danilevsky 1961, Saunders 1976, Tauber et al. 1986, Saulich and Volkovich 2004). A widespread example of dormancy is diapause, which can be subdivided into winter diapause and summer diapause (see **Section 11.2.4**).

According to current views, **diapause** is *a profound, endogenously and centrally mediated interruption that routes the developmental program away from direct morphogenesis into an alternative diapause program of succession of physiological events; the start of diapause usually precedes the advent of adverse conditions and the end of diapause need not coincide with the end of adversity* (Koštál 2006). This state of an organism is characterized by a complex of morphological, physiological, and behavioral traits known as the **diapause syndrome** (Tauber et al. 1986). As a rule, insects in diapause have a lowered water content, decreased oxygen consumption, and an increased ability to survive suboptimal low and/or high temperatures as well as other environmental and antropogenic stresses (e.g., radiation or pesticides).

Another related term that needs to be defined is **quiescence**, which is *an immediate response (without central regulation) to a decline of any limiting environmental factor(s) below the physiological thresholds with immediate resumption of the processes if the factor(s) rise above them* (Koštál 2006). Quiescence is in many ways related to diapause but is definitely less ecologically important.

Different species of insects can survive adverse season (e.g., cold winters, hot peaks of summers, dry or rainy seasons) in different physiological states. Thus, some species can **overwinter** (i.e., simply survive winter) in a physiological state of deep and profound winter diapause or in quiescence. Similar diversity of patterns can be observed in summer; although some species are active throughout the summer, others have profound summer diapause or short quiescence.

Phenomena analogous to insect diapause have been observed in various groups of animals, plants, and fungi. All of these phenomena are aimed at solving the same ecological problem, namely adaptation to the rhythmicity of climatic conditions. This eco-physiological adaptation has been more thoroughly studied in insects than in other organisms, as evidenced by the vast literature devoted to the problem itself, and to the specific traits of diapause in different groups of insects and other arthropods. However, the level of knowledge varies strongly between different insect taxa. The true bugs (Heteroptera) have

received much attention in studies of diapause, although the number of species studied and the depth of the research have been noticeably less than in the Lepidoptera and Diptera.

The Pentatomoidea is one of the largest superfamilies of Heteroptera (see **Chapter 2**). Species in this superfamily have a wide range of seasonal adaptations, and many are economically important (Schuh and Slater 1995; Musolin and Saulich 1996a; McPherson and McPherson 2000; Panizzi et al. 2000; Saulich and Musolin 2007a,b, 2012, 2014; Henry 2009; Musolin 2012; Panizzi and Grazia 2015). Despite the relatively large size of pentatomoid bugs and the availability of specimens, only a few species that are economically important have been studied in detail in terms of seasonal cycles and seasonal development. The Pentatomidae is the third largest family of the Heteroptera. It comprises about 4,840–4,950 species (over 10% of the entire order) that are grouped into 900–940 genera and 8–11 subfamilies (Gapon 2008, Henry 2009; Vinokurov et al. 2010, see **Chapter 2**). Within this family, representatives of only three subfamilies (i.e., Asopinae [= Stiretrinae], Podopinae, Pentatominae) have been studied in terms of diapause, seasonal cycles, and seasonal development.

In this chapter, we review and discuss specific traits of diapause and associated phenomena in pentatomids and include rare examples from other (less well studied in this respect) families of Pentatomoidea.

11.2 Diapause as a Form of Dormancy in Pentatomoidea

Diapause is one of the most widely spread forms of insect dormancy. Vast literature is devoted to insect diapause, including its physiology, ecological functions, and, recently, genetics (Danilevsky 1961, Tauber et al. 1986, Danks 1987, Saulich and Volkovich 2004, Denlinger 2008, Denlinger and Lee 2010). In this section, we provide a brief overview of what is known about diapause in Pentatomoidea.

Diapause now is understood as a complex and dynamic process. In the less common cases, diapause is **obligate** (or **obligatory**), and the initiation of such diapause needs no external (i.e., **exogenous**) signals or cues because it represents a fixed and genetically strongly controlled component of the ontogenetic program, which is realized regardless of the environmental conditions in each **generation**. In more widespread cases, however, diapause is **facultative** and external (i.e., **exogenous**) token stimuli are necessary to induce the diapause state and, thus, individuals can switch between two ontogenetic alternatives, i.e., **direct** (or **active**) **development** or diapause (Koštál 2006; see **Section 11.2.3** for more details).

11.2.1 Phases of Diapause

Many different views on the stages or phases of diapause have been presented in the literature (see Danilevsky 1961; Saunders 1976; Tauber et al. 1986, Hodek 1996, 2002; Saulich and Volkovich 2004 for reviews). Recently Koštál (2006) suggested a simplified model of diapause which consisted of three major phases: prediapause, diapause, and postdiapause (**Figure 11.1**).

During the **prediapause phase**, direct ontogenetic development (morphogenesis) continues. This phase has two subphases in the species with facultative diapause and most likely only one in the species with obligate diapause. In the first group (i.e., the species with facultative diapause), diapause needs to be induced by an environmental cue and, thus, this cue needs to be perceived, transmitted, and interpreted by the neurohormonal system of the individual. This cue switches the ontogenetic pathway from direct development to diapause, and this period is called the **induction subphase**. At the same time, in the species with obligate diapause, there is no induction subphase because diapause is not induced. In other words, in the species with obligate diapause, this diapause is a necessary step (i.e., arrest) of development in each generation. Another part of the prediapause phase is a **preparation subphase**, during which individuals undergo behavioral and/or physiological change (e.g., acquire energy resources such as lipids or in some cases – starch, etc.), void the digestive system (gut), migrate and/or simply look for protective microhabitats (often called **hibernaculum** or **hibernacula**), sometimes change body color and so on.

During the next and more prolonged **diapause phase**, direct active development is **endogenously** (i.e., internally) arrested, and an alternative program of still mostly unknown physiological events proceeds. The diapause phase can be divided into three subphases. During the **initiation subphase**, direct development ceases, deep physiological preparations take place, and intensity (or deepness) of diapause may
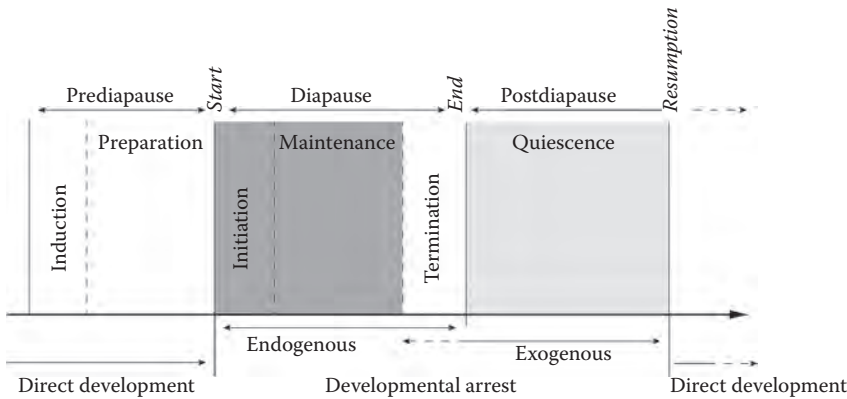
FIGURE 11.1   Schematic depiction of sequential phases of insect diapause. Thick line with arrowhead in the lower part of the figure indicates the passage of life of a hypothetical insect individual. Three major phases, namely prediapause, diapause, and postdiapause are named (on the top). Prediapause can be divided into the induction and preparation subphases and diapause into the initiation, maintenance, and termination subphases; postdiapause can be represented by quiescence. Developmental arrest may be endogenously (i.e., internally) or exogenously (i.e., externally) controlled (see at the bottom of the figure). More details are given in **Section 11.2.1**. Note that not all the (sub)phases must necessarily be found in all species and situations and this depiction might be applied to any type of diapause (i.e., embryonic, nymphal or adult; see **Section 11.2.2** for details). (Modified from V. Koštál, Journal of Insect Physiology 52: 113–127, 2006, with permission.)

increase. In some cases, individuals may continue accepting food or water, building energy reserves, and seeking suitable microhabitat during this subphase. These physiological processes are followed by the **maintenance subphase**, during which the endogenous developmental arrest persists regardless of environmental conditions. Specific token stimuli may help maintain diapause (or, in other words, prevent its termination). During this subphase, metabolic rate is relatively low and constant. Largely unknown physiological process(es) lead to more or less gradual decrease of diapause intensity and increase of sensitivity to diapause-terminating environmental conditions. With time, changes in environmental conditions can stimulate the decrease of diapause intensity to its minimum level and, thus, lead to the **termination subphase**. During this subphase, the intensity of diapause further decreases. By the end of the termination subphase, a usual active physiological state is mostly reached. Then, if conditions (primarily temperature) permit, direct development may overtly resume and the insects can begin moving, feeding, molting (in the case of nymphal/larval diapause) or copulating (in the case of adult diapause). However, if conditions are not yet permissive (usually, temperature is still too low and/or food is not available), the covert potentiality for direct development is restored but not realized and, as a result, the insects do not leave the diapause microhabitat and do not become fully active.

The diapause phase is followed by the **postdiapause phase**. Under field conditions, the diapause phase often ends as early as mid- or late winter or early spring, but temperature or other environmental conditions do not allow active development. In this case, insects experience **postdiapause quiescence**, an exogenously (i.e., externally) imposed inhibition of development and metabolism. When environmental conditions permit, the quiescence is followed by the full resumption of active development.

Our understanding of the nature and sequence of phases of insect diapause is still incomplete. The scheme outlined above and graphically represented in **Figure 11.1** was suggested by V. Koštál (2006), but a few other views and models have been suggested in the literature (Danilevsky 1961; Tauber et al. 1986; Danks 1987; Zaslavski 1988; Hodek 1996, 2002; Saulich and Volkovich 2004; Belozerov 2009). Below, we shall consider these sequential phases of diapause, using pentatomoids as examples.

11.2.2 Three Types of Diapause in Pentatomoidea: Embryonic (Egg), Nymphal, and Adult Diapause

Diapause in different insect species can be confined to any developmental stadium from embryo to adult. In the Heteroptera, three types of diapause are recognized including **embryonic** (or **egg**), **nymphal**, and

TABLE 11.1

Different Forms and Types of Winter Diapause in Pentatomoidea

Family	Total Number of Species Studied	Associations between Two Forms (Obligate and Facultative) and Three Types of Winter Diapause[1]		
		Embryonic	Nymphal	Adult
Acanthosomatidae	5			O – 3; F – 2
Cydnidae	6			O – 4; F – 2
Parastrachiidae	1			O – 1
Pentatomidae[2]	48	O – 2; F – 1	O – 1; F – 1	O – 3; F – 38
Plataspidae	4		O – 2	F – 2
Scutelleridae[2]	11		O – 3; F – 1	O – 4; F – 2
Tessaratomidae	2		O – 1	O – 1
Thaumastocoridae	1			F – 1
Thyreocoridae	4			O – 4
Subtotal		O – 2; F – 1	O – 7; F – 2	O – 20; F – 47
Total[2]	**82**	**3**	**9**	**67**

[1] Forms of diapause: F – facultative, O – obligate.

[2] In the rows Pentatomidae, Scutelleridae, and Total, the total number of species studied differs from the total number of diapause cases because some species do not have winter diapause (they have homodynamic seasonal development; see **Section 11.2.3**).

adult (sometimes called **reproductive**, or **imaginal**) **diapause** (**Table 11.1**). However, each species of insects, as a rule, can form diapause only at one particular developmental stage. Often (if not always), even within one stadium, there is a strict association of diapause with a particular ontogenetic stage. Cobben (1968) gave 16 different species-specific examples of timing of diapause only within the embryonic diapause in Heteroptera.

In the literature, however, there are examples of overwintering of insects from the same species or population at different stages of their life cycle. For example, nymphs and adults have been reported to overwinter together in *Ischnodemus sabuleti* (Fallen) (Lygaeidae; Tischler 1960) and *Chiloxanthus pilosus* (Fallen) (Saldidae; Cobben 1968). Finally, some species of true bugs have life cycles that last two or even more years and, thus, these species form diapause more than once in their life cycle; it usually happens during different developmental stadia (e.g., in Aradidae, Aphelocheiridae, and Reduviidae).

11.2.3 Two Forms of Diapause: Obligate and Facultative Diapause

As briefly mentioned above, diapause in insects may be of two forms. In some species, diapause is **obligate** (or **obligatory**) in which case, it does not need to be induced; it is determined hereditarily and always present in each generation regardless of external conditions. Obligate diapause in a particular species strictly determines a **univoltine seasonal cycle** (i.e., a pattern with one generation per year) over the entire range of the species because, in this case, active development is interrupted by obligate diapause in each generation (see **Chapter 12**). In other cases, diapause is **facultative**, and, therefore, it is induced by external (i.e., **exogenous**) factors and does not occur necessarily in each generation (**Table 11.1**). The facultative nature of diapause makes it possible to produce two or more generations during a year, with individuals of the last generation in the season entering facultative winter diapause.

Due to the facultative nature of diapause, different geographic populations of some species can produce different numbers of annual generations. **Voltinism** may also differ between particularly cold and warm years even in the same location.

In Pentatomoidea, both forms of diapause (i.e., facultative and obligate) have been documented. Among 79 experimentally studied species of stink bugs and their allies that have winter diapause, 29 species (about 37%) had an obligate winter diapause, whereas others (about 63%) had a facultative winter diapause (**Table 11.1**).

At the same time, no pronounced relationship between the form of diapause (i.e., facultative or obligate) and its type (i.e., association with a particular developmental stage – embryonic, nymphal or adult)

or taxonomic position of a species has been detected. In other words, if sufficiently studied, any combination of type and form of diapause can be found in any taxon within the Pentatomoidea.

The form of diapause (i.e., obligate or facultative) usually is considered a species-specific character in Heteroptera. However, biological diversity virtually is unlimited and, in some cases, when different populations of a species were studied, examples of intraspecific variation of diapause form and mechanisms of voltinism control have been reported (Hodek 1977). Thus, within one species with a wide range in the Northern Hemisphere, a tendency to enter diapause was much stronger in the northern populations with all bugs of these populations sometimes demonstrating obligate diapause. Closer to the range core in the Temperate Zone, populations were heterogeneous with some individuals having obligate and others having facultative diapause. Further south, most populations have facultative diapause or show a strong tendency towards **homodynamic seasonal development** (nondiapause development in any season and nonstop sequence of generations without any pronounced period of seasonal dormancy). It is likely that **day length** is less important in winter diapause induction as well as winter diapause, itself, because it is less ecologically important in the (sub)tropic populations of true bugs than in populations in the more temperate or cold climates. These tendencies have been demonstrated in the pentatomids *Euthyrhynchus floridanus* (Mead 1976, Richman and Whitcomb 1978) and *Podisus maculiventris* (De Clercq and Degheele 1993) in Florida (USA).

11.2.4 Two Seasonal Classes of Diapause: Winter and Summer Diapause

Insect diapause often is associated with winter and, in these cases, is called **winter diapause**, or **hibernation**. Such examples have been documented in thousands of species from all major insect orders (Danilevsky 1961, Saunders 1976, Tauber et al. 1986, Danks 1987). However, diapause as a special physiological state can take place during other times of the year too. Frequently, insects can enter facultative or obligate diapause in summer; in this case, such diapause is called **summer diapause**, or **estivation**. It is important to understand that in some species, even one individual can have two different diapauses at two different ontogenetic stages. This is the case, for example, in the pentatomid *Picromerus bidens*: this predatory species passes winter in the state of obligate winter embryonic diapause and then adults may enter facultative summer adult diapause (Musolin and Saulich 2000; see **Chapter 12**).

The ecological importance of dormancy during summer might be related to survival of extremely high temperatures and dry conditions. In some other cases, summer diapause also is important for survival during a rainy season or a period when food is too scarce. Finally, similarly to winter diapause, summer diapause may be important for fine synchronization of the species' seasonal cycle with local environmental conditions (see **Chapter 12**). Summer diapause in Heteroptera has been studied much less than winter diapause (Saulich and Musolin 2007b), and some interesting cases will be discussed in **Section 11.8**. However, in this chapter, we will concentrate mostly on winter diapause.

11.2.5 Diversity of Winter Diapause Patterns in Pentatomoidea

Among 82 species of Pentatomoidea in which seasonal development and/or winter dormancy have been studied at least to some extent, most species (67, or ≈82%) overwinter as adults (**Tables 11.1 and 11.2**). In five families (i.e., Acanthosomatidae, Cydnidae, Parastrachiidae, Thaumastocoridae, and Thyreocoridae) only adult diapause has been reported so far. Three species (i.e., *Picromerus bidens*, *Apoecilus* [= *Apateticus*] *cynicus*, and *Trochiscocoris hemipterus*) overwinter in the embryonic stage and all belong to Pentatomidae. In nine species, nymphs overwinter; among them, two species belong to Pentatomidae (*Carbula humerigera* and *Pentatoma rufipes*), two to Plataspidae (*Coptosoma mucronatum* and *Coptosoma scutellatum*), four to Scutelleridae (*Odontoscelis dorsalis*, *Odontoscelis fuliginosa*, *Odontoscelis lineola*, and *Poecilocoris lewisi*) and one to Tessaratomidae (*Musgraveia sulciventris*). Among all these species, only in *P. lewisi* and *M. sulciventris* does diapause appear to be strongly linked to a particular nymphal instar (fifth instar in *P. lewisi* [Tanaka et al. 2002] and second instar, before the commencement of feeding, in *M. sulciventris* [Cant et al. 1996]). In all other cases, nymphs of different instars can overwinter: second through third/fourth instars do this more often than fifth instars; there are no records so far of winter diapause in the first instar in Pentatomoidea (see **Table 11.2** for references).

TABLE 11.2

Diapause and Associated Seasonal Adaptations Facilitating Synchronization of the Seasonal Cycle with Environmental Conditions in Species of the Superfamily Pentatomoidea[1]

Species (Common Name)	Form of Diapause[2]	Factors (Cues) Inducing Diapause and Associated Seasonal Adaptations[3]	Type of Diapause	References
Family ACANTHOSOMATIDAE				
Subfamily Acanthosomatinae				
Acanthosoma denticaudum Jakovlev (= *A. denticauda japonica* Jensen-Haarup)	O	–	Adult	Hori et al. 1993
Acanthosoma haemorrhoidale angulatum Jakovlev (hawthorn shield bug)	O	–	Adult	Hori et al. 1993
Elasmostethus atricornis (Van Duzee)	O	–	Adult	Carter and Hoebeke 2003, Jones and McPherson 1980
Elasmucha grisea grisea (L.) (parent bug)	F	–	Adult	Melber et al. 1981, Ogorzałek and Trochimczuk 2009
Elasmucha lateralis (Say) (birch bug)	F	–	Adult	Jones and McPherson 1980
Family CYDNIDAE				
Subfamily Cydninae				
Cydnus aterrimus (Forster)	F	–	Adult	Putshkov 1961
Subfamily Sehirinae				
Adomerus biguttatus (L.)	O	–	Adult	Putshkov 1961
Sehirus cinctus cinctus (Palisot de Beauvois) (white-margined burrower bug)	O	–	Adult	Sites and McPherson 1982
Sehirus luctuosus Mulsant & Rey (forget-me-not shield bug)	O	–	Adult	Putshkov 1961, Southwood and Leston 1959
Tritomegas bicolor (L.) (pied shield bug)	F (?)	–	Adult	Putshkov 1961 (1 generation), Southwood and Leston 1959 (2 generations)
Subfamily Amnestinae				
Amnestus pusillus Uhler	O	–	Adult	Froeschner 1941
Family PARASTRACHIIDAE				
Parastrachia japonensis (Scott)	O	–	Adult	Filippi et al. 2000a,b; Tachikawa and Schaefer 1985; Tojo et al. 2005a,b
Family PENTATOMIDAE				
Subfamily Podopinae				
Tribe Graphosomatini				
Graphosoma lineatum (L.) (Italian striped bug)	F	PhP, T, PhP control of body color in adults	Adult	Gamberale-Stille et al. 2010; Johansen et al. 2010; Musolin and Saulich 1996a, 2001; Nakamura et al. 1996; Tullberg et al. 2008
Graphosoma rubrolineatum (Westwood)	F	North: PhP, T; South: PhP, Fd	Adult	Nakamura and Numata 1999

(*Continued*)

TABLE 11.2 (CONTINUED)

Diapause and Associated Seasonal Adaptations Facilitating Synchronization of the Seasonal Cycle with Environmental Conditions in Species of the Superfamily Pentatomoidea[1]

Species (Common Name)	Form of Diapause[2]	Factors (Cues) Inducing Diapause and Associated Seasonal Adaptations[3]	Type of Diapause	References
		Tribe Scotinopharini		
Scotinophara lurida (Burmeister) (black rice bug)	F	PhP, T	Adult	Cho et al. 2007, 2008; Fernando 1960; Lee et al. 2001
Dybowskyia reticulata (Dallas)	F	PhP, T	Adult	Nakamura and Numata 1997a, 1998; Numata 2004
		Subfamily Asopinae (= Stiretrinae)		
		Tribe Amyotini		
Apoecilus (= *Apateticus*) *cynicus* (Say)	O	–	Embryonic	Javahery 1994, Jones and Coppel 1963, Whitmarsh 1916
Arma custos (F.)	F	PhP, T, PhP control of body color in nymphs	Adult	Volkovich and Saulich 1995
Euthyrhynchus floridanus (L.)	F	–	Adult	Ables 1975, Mead 1976, Oetting and Yonke 1975
Podisus maculiventris (Say) (spined soldier bug)	F	PhP, T	Adult	Goryshin et al. 1988a, Volkovich et al. 1991b
		Tribe Jallini		
Perillus bioculatus F. (twospotted stink bug)	F	PhP, T, Fd	Adult	Horton et al. 1998; Izhevskii and Ziskind 1981; Jasič 1967, 1975; Shagov 1977; Volkovich et al. 1991a
Zicrona caerulea (L.) (blue shield bug)	F	PhP, T	Adult	McPherson 1982, Saulich (unpublished data)
		Tribe Platinopini		
Andrallus spinidens (F.)	F	T	Adult	Shintani et al. 2010
Picromerus bidens (L.) (spined stink bug)	O (winter) F (summer)	– PhP	Embryonic Adult	Larivière and Larochelle 1989, Leston 1955, Musolin 1996, Musolin and Saulich 2000
		Subfamily Pentatominae		
		Tribe Aeliini		
Aelia acuminata (L.) (bishop's mitre shield bug)	F	PhP, T	Adult	Hodek 1971a, 1977; Honěk 1969
Aelia fieberi Scott	F	PhP, T	Adult	Nakamura and Numata 1995, 1997b
Aelia rostrata Boheman (wheat stink bug)	F (winter) O (summer)	– –	Adult Adult	Dikyar 1981, Cakmak et al. 2008
Aelia sibirica Reuter	F	PhP, T	Adult	Burov 1962
		Tribe Antestiini		
Plautia stali Scott	F	PhP, PhP control of body color in nymphs and adults	Adult	Kotaki 1998a,b; Kotaki and Yagi 1987; Numata and Kobayashi 1994

(*Continued*)

TABLE 11.2 (CONTINUED)

Diapause and Associated Seasonal Adaptations Facilitating Synchronization of the Seasonal Cycle
with Environmental Conditions in Species of the Superfamily Pentatomoidea[1]

Species (Common Name)	Form of Diapause[2]	Factors (Cues) Inducing Diapause and Associated Seasonal Adaptations[3]	Type of Diapause	References
		Tribe Carpocorini		
Dichelops melacanthus (Dallas)	F	PhP, PhP control of growth rates in nymphs and body color in adults	Adult	Chocorosqui and Panizzi 2003
Dolycoris baccarum (L.) (sloe bug, berry bug, hairy shield bug)	F	PhP, PhP control of nymphal growth	Adult	Conradi-Larsen and Sømme 1973, Hodek and Hodková 1993, Hodková et al. 1989, Nakamura 2003, Perepelitsa 1971
Palomena angulosa (Motschulsky)	O	PhP control of growth rates in nymphs	Adult	Hori 1986, Hori and Kimura 1993
Palomena prasina (L.) (green shield bug)	O	PhP control of growth rates in nymphs, seasonal change of body color in adults	Adult	Saulich and Musolin 1996, 2007b; Southwood and Leston 1959
		Tribe Eysarcorini		
Carbula humerigera (Uhler)	F (winter)	PhP, PhP control of growth rates in nymphs	Nymphal (2nd–5th instars)	Kiritani 1985a,b
	F (summer)	PhP	Adult	
Eysarcoris aeneus (Scopoli)	F	PhP	Adult	Yao 2002
Eysarcoris lewisi (Distant)	F	PhP, PhP control of growth rates in nymphs	Adult	Hori and Inamura 1991, Hori and Kimura 1993
Eysarcoris ventralis (Westwood)	F	PhP	Adult (females)	Nakazawa and Hayashi 1983, Noda and Ishii 1981
		Tribe Menidini		
Menida disjecta (Uhler) (= *M. scotti* Puton)	O	–	Adult	Koshiyama et al. 1993, 1994, 1997
		Tribe Pentatomini		
Chinavia hilaris (Say) (green stink bug)	F	PhP, T	Adult	Javahery 1990 (as *Acrosternum hilare* [Say]), McPherson and Tecic 1997, Wilde 1969
Euschistus conspersus Uhler (consperse stink bug)	F	PhP, PhP control of body color in adults	Adult	Cullen and Zalom 2000, 2006, Toscano and Stern 1980
Euschistus heros F. (Neotropical brown stink bug)	F	PhP, PhP control of body color in adults	Adult	Mourao and Panizzi 2000, 2002; Panizzi and Niva 1994
Euschistus ictericus (L.)	F	PhP, PhP control of body color in adults	Adult	McPherson and Paskewitz 1984
Euschistus servus (Say) (brown stink bug)	F	PhP, PhP control of body color in adults	Adult	Borges et al. 2001, McPherson 1982
Euschistus tristigmus tristigmus (Say) (dusky stink bug)	F	PhP, PhP control of body color in adults	Adult	McPherson 1974, 1975a,b, 1979, 1982

(*Continued*)

TABLE 11.2 (CONTINUED)

Diapause and Associated Seasonal Adaptations Facilitating Synchronization of the Seasonal Cycle with Environmental Conditions in Species of the Superfamily Pentatomoidea[1]

Species (Common Name)	Form of Diapause[2]	Factors (Cues) Inducing Diapause and Associated Seasonal Adaptations[3]	Type of Diapause	References
Nezara antennata Scott (Oriental green stink bug)	F (winter)	PhP, PhP control of body color in adults (winter)	Adult	Musolin (unpublished data), Noda 1984
	F (summer)	PhP, no color change in adults (summer)	Adult	
Nezara viridula (L.) (southern green stink bug)	F	PhP, PhP control of growth rates in nymphs and body color in adults	Adult	Ali and Ewiess, 1977; Musolin 2012; Musolin and Numata 2003a,b; Musolin et al. 2007
Oebalus poecilus (Dallas) (small green stink bug)	F	PhP, PhP control of body color in adults	Adult	Albuquerque 1993, Greve et al. 2003, Santos et al. 2003
Oebalus pugnax pugnax (F.) (rice stink bug)	F	–	Adult	McPherson 1982, McPherson and Mohlenbrock 1976
Oebalus ypsilongriseus (De Geer) (rice stink bug)	F	PhP, PhP control of body color in adults	Adult	Vecchio et al. 1994
Pentatoma rufipes (L.) (forest bug)	O	–	Nymphal (2nd–3rd instars)	Putshkov 1961, Saulich (unpublished data), Southwood and Leston 1959
Thyanta calceata (Say)	F	PhP, PhP control of body color in adults	Adult	McPherson 1977, 1978, 1982; Oetting and Yonke 1971
Tribe Piezodorini				
Piezodorus guildinii (Westwood) (redbanded stink bug)	F	PhP	Adult	Zerbino et al. 2013, 2014, 2015
Piezodorus hybneri (Gmelin)	F	PhP	Adult	Endo et al. 2007, Higuchi 1994
Tribe Strachiini				
Bagrada hilaris (Burmeister) (= *B. cruciferarum* Kirkaldy) (bagrada bug, painted bug)	Homodynamic development (i.e., no dormancy period), at least in South			Panizzi 1997, Siddiqui 2000, Singh and Malik 1993, Taylor et al. 2015
Murgantia histrionica (Hahn) (harlequin bug)	Homodynamic development (i.e., no dormancy period), at least in South			McPherson and McPherson 2000, Siddiqui 2000
Trochiscocoris hemipterus (Jakovlev)	F	–	Embryonic	Akramowskaya 1959, Asanova and Kerzhner 1969
Tribe Eurydemini				
Eurydema oleracea (L.) (brassica bug, green cabbage bug)	F	PhP	Adult	Fasulati 1979
Eurydema rugosa (= *E. rugosum*) Motschulsky (cabbage bug)	F	PhP, Fd	Adult	Ikeda-Kikue and Numata 1994, 2001; Numata and Yamamoto 1990
Tribe Rhynchocorini				
Biprorulus bibax Breddin	F	PhP	Adult	James 1990a,b, 1991, 1993
Tribe Cappaeini				
Halyomorpha halys (Stål) (= *Dalpada brevis* Walker) (brown marmorated stink bug)	F	PhP, T, PhP control of growth rates in nymphs and body color in nymphs and adults	Adult	Hoebeke and Carter 2003; Lee et al. 2013; Niva and Takeda 2002, 2003; Toyama et al. 2006; Watanabe 1980

TABLE 11.2 (CONTINUED)

Diapause and Associated Seasonal Adaptations Facilitating Synchronization of the Seasonal Cycle with Environmental Conditions in Species of the Superfamily Pentatomoidea[1]

Species (Common Name)	Form of Diapause[2]	Factors (Cues) Inducing Diapause and Associated Seasonal Adaptations[3]	Type of Diapause	References
Family PLATASPIDAE				
Coptosoma mucronatum Seedenstücker	O	–	Nymphal (2nd–4th instars)	Davidová-Vilímová and Štys 1982
Coptosoma scutellatum (Geoffroy)	O	–	Nymphal (2nd–4th instars)	Davidová-Vilímová 2006, Davidová-Vilímová and Štys 1982, Putshkov 1961, Saulich and Musolin 1996, Werner 2005
Megacopta cribraria (F.) (kudzu bug)	F	–	Adult	Chen et al. 2009, Eger et al. 2010, Gardner et al. 2013, Hosokawa et al. 2014, Zhang and Yu 2005, Zhang et al. 2012
Megacopta punctatissima (Montandon)	F	–	Adult	Tayutivutikul and Kusigemati 1992, Tayutivutikul and Yano 1990
Family SCUTELLERIDAE				
Subfamily Eurygastrinae				
Eurygaster integriceps Puton (sunn pest)	O	–	Adult	Brown 1962, Javahery 1995, Shinyaeva 1980, Viktorov 1967
Subfamily Scutellerinae				
Chrysocoris purpureus (Westwood)	F (summer)	T, H (?)	Adult	Roychoudhury 1998, 1999
Poecilocoris lewisi (Distant) (clown stink bug)	F (winter)	PhP	Nymphal (5th instar)	Tanaka et al. 2002, Tomokuni et al. 1993
	F (summer)	PhP	Adult	
Subfamily Odontotarsinae				
Phimodera flori Fieber	O	–	Adult	Davidová-Vilímová and Král 2003
Phimodera humeralis (Dalman) (= *Podops nodicollis* Burmeister)	O	–	Adult	Putshkov 1961
Subfamily Pachycorinae				
Pachycoris klugii Burmeister	F	–	Adult	Peredo 2002
Pachycoris stallii Uhler	F	–	Adult	Williams et al. 2005
Tetyra bipunctata (Herrich-Schäffer)	O	–	Adult	Gilbert et al. 1967, McPherson 1982
Subfamily Odontoscelinae				
Odontoscelis dorsalis (F.)	O	–	Nymphal (3rd–4th instars)	Putshkov 1961
Odontoscelis fuliginosa (L.)	O	–	Nymphal (3rd–4th instars)	Putshkov 1961
Odontoscelis lineola Rambur (lesser streaked shield bug)	O	–	Nymphal (3rd–4th instars)	Hawkins 2003, Putshkov 1961

(*Continued*)

TABLE 11.2 (CONTINUED)

Diapause and Associated Seasonal Adaptations Facilitating Synchronization of the Seasonal Cycle
with Environmental Conditions in Species of the Superfamily Pentatomoidea[1]

Species (Common Name)	Form of Diapause[2]	Factors (Cues) Inducing Diapause and Associated Seasonal Adaptations[3]	Type of Diapause	References
Family TESSARATOMIDAE				
Subfamily Natalicolinae				
Encosternum delegorguei Spinola	O	–	Adult	Dzerefos et al. 2009
Subfamily Oncomerinae				
Musgraveia sulciventris (Stål) (bronze orange bug)	O (winter)	–	Nymphal (2nd instar)	Cant et al. 1996, Hely 1964, McDonald 1969
	F (summer)	Fd	Adult	
Family THAUMASTOCORIDAE				
Subfamily Xylastodorinae				
Discocoris drakei Slater & Ashlock	F	–	Adult	Couturier et al. 2002
Family THYREOCORIDAE (= Family CORIMELAENIDAE)				
Corimelaena lateralis lateralis (F.)	O	–	Adult	McPherson 1972
Corimelaena obscura McPherson & Sailer	O	–	Adult	Bundy and McPherson 1997
Galgupha ovalis Hussey	O	–	Adult	Biehler and McPherson 1982
Thyreocoris scarabaeoides (L.) (scarab shield bug)	O	–	Adult	Putshkov 1961

[1] Only a few examples, particularly experimental studies that have been more thorough, are given for each family. Only families with several examples are divided into subfamilies and tribes. Species are listed alphabetically within each family/tribe/subfamily.

[2] Forms of diapause: F – facultative, O – obligate. If not indicated otherwise, diapause is winter diapause.

[3] Factors (cues) inducing diapause: PhP – photoperiod, T – temperature, Fd – food, H – humidity or precipitation; symbol "–" means *not applicable* for obligate diapause and *unknown* for facultative diapause.

In each particular insect species, usually only one ontogenetic stage can enter winter diapause. Within one species, the ability to enter diapause at different stages has been assumed to occur among pentatomoid species only in *Pentatoma rufipes*: Southwood and Leston (1959) and then Putshkov (1961) suggested that not only nymphs but also adults of this species can overwinter, although such an unusual pattern has not been proven and rare records of adults of this species early in spring might be misleading and related to parasitism (see **Chapter 12** for more details).

In several pentatomid species (e.g., *Perillus bioculatus* [Jasič 1975]; *Graphosoma lineatum* [Putshkov 1961, Nakamura et al. 1996]), some individuals likely can live longer than 1 year and, thus, overwinter twice (i.e., enter winter diapause in 2 consecutive years). This possibility also cannot be excluded in *Sinopla perpunctatus* Signoret (Faúndez and Osorio 2010).

The pentatomids *Bagrada hilaris* and *Murgantia histrionica* can be physiologically active throughout the whole year (i.e., apparently develop without entering pronounced diapause at any season), at least in southern areas (e.g., India [Singh and Malik 1993, Siddiqui 2000] or the United States of America [McPherson and McPherson 2000, Taylor et al. 2015]).

Based on the data from **Table 11.2**, we can conclude that winter adult diapause is the most widespread diapause in Pentatomoidea. This conclusion supports the earlier but less representative estimations that

winter adult diapause is most characteristic of the whole Heteroptera (Hertzel 1982; Ruberson et al. 1998; Saulich and Musolin 2007b, 2012; Esenbekova et al. 2015), although exceptions occur. For example, most species of plant bugs (Miridae) overwinter in the egg stage (Wheeler 2001).

11.3 Environmental Factors Controlling Induction of Winter Diapause

Ecological factors often have a dual mode of action on living organisms. They determine environmental conditions under which these organisms live; thus, they have a **vital function**. At the same time, many ecological factors might be used as reliable predictors of environmental changes that the ecosystem is going to face in the future; thus, they have a **signal function** and act as cues (Tyshchenko 1980). For instance, a vital mode of action of temperature determines a range within which a particular species can live, whereas the daily rhythm of temperature (**thermorhythm**) has a signal function and predicts the coming seasonal environmental changes.

Several abiotic and biotic factors that have regular rhythmicity in nature can be used by insects as signals (or cues) for synchronization of their seasonal development with environmental conditions. In many cases, insects use more than one cue, and, thus, the mode of action of different factors can be complex.

11.3.1 Day Length

Day length has an astronomic preciseness and no environmental factor can affect it. Thus, natural day length is the most reliable environmental cue available. Many species of insects use day length as a reliable cue for structuring their seasonal cycle and synchronizing their seasonal development with local environmental conditions. Precise seasonal dynamics of day length (and **night length**) are of critical importance here, but not the changes in energy or intensity of optical radiation.

In eco-physiological laboratory experiments when day length is set artificially, it is called **photoperiod** and determined as a ratio between the duration of the light period (i.e., **photophase**) and the dark period (i.e., **scotophase**). Graphically, it can be shown in the following way: L:D 16:8, meaning 16 hours of light followed by 8 hours of darkness every day in the laboratory.

Many insect species respond in different ways to day length and such physiological responses are called **photoperiodic responses (PhPR)**. These responses have been found in many species, including those in the Pentatomoidea (**Table 11.2**). In the Northern Hemisphere, for species with winter diapause, short (or shortening) day length becomes a signal of the approaching autumnal decrease of temperature and serves as a trigger for a hormonal cascade leading to a pause in active metamorphosis (i.e., diapause).

11.3.1.1 Photoperiodic Response of Diapause Induction

In the Northern Hemisphere, formation of facultative winter diapause is controlled by the **PhPR of a long-day type** (i.e., one that allows active development under long-day conditions and induces diapause under short-day conditions). Under long-day conditions (i.e., simulating early summer), individuals develop directly (so called active development) and produce the next generation; under short-day conditions (i.e., simulating autum or winter), individuals enter winter diapause.

Critical photoperiod (i.e., **critical day length**, or **photoperiodic threshold**), is one of the most important ecological characteristics of the PhPR. This parameter corresponds to the day length at which 50% of individuals of a particular population enter diapause. Typical PhPR of a long-day type has been found in many pentatomoid species. **Figure 11.2** demonstrates the PhPRs of diapause induction in two pentatomids, *Aelia fieberi* and *Plautia stali*. These insects had been reared and then maintained under particular constant photoperiodic conditions at 25°C from the day when they hatched from eggs. All females that experienced long-day conditions (i.e., with photophases 15 or 16 hours) became reproductive, whereas most females reared and then maintained under **short-day** conditions (scotophase of 12 hours or more) entered adult diapause. Thus, at 25°C, the critical photoperiod was approximately 13.5 hours for *P. stali* and about 14.5 hours for *A. fieberi* (Numata and Nakamura 2002). These examples clearly
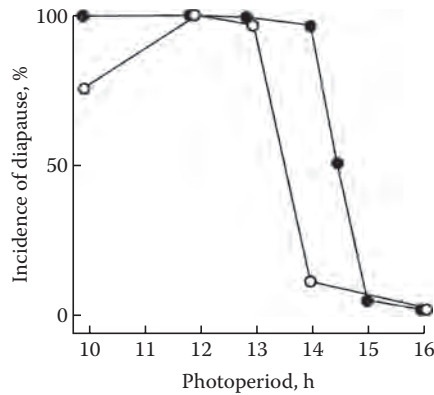
FIGURE 11.2   Photoperiodic responses of winter adult diapause induction in females of pentatomids *Plautia stali* (open circles) and *Aelia fieberi* (close circles) from Osaka area, Japan (34.7°N). Adults were reared from eggs and then maintained at 25°C under photoperiod indicated on the horizontal axis. (Modified from H. Numata and K. Nakamura, European Journal of Entomology 99: 155–161, 2002, with permission.)

demonstrate the **qualitative PhPR** of insects to day length: each individual responds in an "All or None" (i.e., "Yes or No") manner by choosing one of two alternative pathways: in the case of adult diapause – diapause or direct development (i.e., reproduction).

However, there are examples when the PhPR controls quantitative parameters such as duration of a particular stage, size, or degree of body pigmentation; in such cases, it is called the **quantitative PhPR** (Tyshchenko 1977, Zaslavski 1988, Numata and Kobayashi 1994, Musolin and Saulich 1997). **Figure 11.3** demonstrates a typical example of such a response. Females of the black rice bug, *Scotinophara lurida*, were reared from eggs to adults at 25°C under a long-day photoperiod L:D 16:8. Upon emergence, they were transferred to one of five short-day and long-day photoperiods and four temperatures (15, 20, 25, 30°C) to determine the PhPR, using the Days of first oviposition (DFO) as a criterion of the response (Cho et al. 2008). Under the three higher temperatures, there generally was a decreasing DFO in response to increasing day length, clearly demonstrating the quantitative nature of the PhPR; there was little or no response at 15°C.
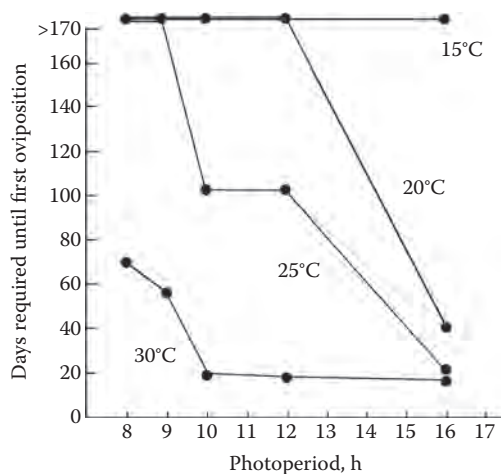
FIGURE 11.3   Effect of photoperiod and temperature on duration of the preoviposition period (i.e., days required until first oviposition) in females of the black rice bug, *Scotinophara lurida*, from Daesan, Korea (37°N). Females were reared from eggs to adults at 25°C under a photoperiod L:D 16:8 and upon emergence, adults were transferred to various experimental conditions (photoperiod is indicated on the horizontal axis, temperature is indicated next to the curves). (Data from J. R. Cho, M. Lee, H. S. Kim, and K. S. Boo, Journal of Asia-Pacific Entomology 11: 53–57, 2008, with permission.)

It also should be remembered that in the field, insects experience not constant but day-to-day **changing day-length conditions**: day length increases from winter until the day of summer solstice (June 20 to 22 in the Northern Hemisphere [i.e., **increasing day length**]) and then decreases until winter solstice (December 20 to 23 in the Northern Hemisphere [i.e., **decreasing day length**]). Many insect species can sense these small daily changes of day length and, thus, experiments with changing photoperiods often can give more information about mechanisms controlling species' seasonal development than experiments using constant photoperiods (Danilevsky 1961, Saunders 1976, Tauber et al. 1986, Saulich and Volkovich 2004).

11.3.1.2 Developmental Stage(s) Sensitive to Day Length

Diapause induction which happens during the prediapause phase (see **Section 11.2.1 and Figure 11.1**) involves the **day-length sensitive stage** and the process of accumulation of photoperiodic information. Perception of day-length signals/cues is known to occur at a certain stage of insect development, which is strictly species-specific and usually directly precedes the **diapausing stage** (Saunders 1976, Saulich and Volkovich 2004). **Sensitivity to day length** in different species may appear at different stages of development, from the egg to the adult, or extend over several stages but, again, is always strictly species-specific. The adult diapause, typical of most pentatomoids, is characterized by the greatest variation in which stage or stages are susceptible to day-length influence. Even in the same type of diapause, evaluation of the day-length information may take place at different development stages and have a different duration (**Table 11.3**; Musolin and Saulich 1999).

The duration and identity of the sensitive stage largely determine the entire pattern of seasonal development and the adaptive capabilities of the species (Saulich 1995). This is evident especially in cases of artificial displacement or transfer of insects into new geographic regions, which will be discussed in detail in **Chapter 12**.

11.3.1.3 Required Day Number

The sensitive stage is a necessary component of the PhPR. During this stadium, the daily photoperiodic signals are accumulated. Apparently, one short- or long-day signal is not enough to induce a response. The number of photoperiodic cycles triggering diapause or active development has been referred to as **a packet of photoperiodic information** (Goryshin and Tyshchenko 1972) or **the required day number** (Saunders 1976).

TABLE 11.3

Stages Sensitive to Day Length in Species of the Superfamily Pentatomoidea with Photoperiodically Induced Winter Diapause[1]

Sensitive Stages	Species (References)
Nymphal Diapause	
Nymphs	*Carbula humerigera* (Kiritani 1985a,b)
Adult Diapause	
Nymphs of 2nd instar	*Oebalus poecilus* (Albuquerque 1993)
Nymphs starting from 3rd instar and adults	*Podisus maculiventris* (Volkovich et al. 1991b)
Nymphs of last two (4th and 5th) instars, and adults or nymphs of last (5th) instar and adults	*Dolycoris baccarum* (Perepelitsa 1971) *Halyomorpha halys* (Niva and Takeda 2003) *Eysarcoris lewisi* (Hori and Kimura 1993)
Mostly adults	*Graphosoma lineatum* (Musolin and Maisov 1998) *Arma custos* (Saulich and Volkovich 1996) *Perillus bioculatus* (Jasič 1967, 1975) *Aelia acuminata* (Hodek 1971a) *Chinavia hilaris* (Wilde 1969) *Nezara viridula* (Ali and Ewiess 1977) *Plautia stali* (Kotaki and Yagi 1987)

[1] All species belong to Pentatomidae. Examples from other families are not available.

This parameter indicates how many short days are required for photoperiodic induction of winter diapause or how many long days are needed for induction of physiological activity (i.e., nondiapause state) in all individuals of a particular local population of the species. Together with the critical photoperiod (see **Section 11.3.1.1**), the required day number is an important component of the insect PhPR. These two parameters play different roles: critical photoperiod indicates when exactly in the season the diapause induction shall start, whereas the packet of photoperiodic information designates how many days after the arrival of critical photoperiod are needed for diapause induction in all members of the population.

The process of accumulation of photoperiodic signals has been studied only in few species of pentatomoids. However, in all cases, a particular state (diapause or active development) was induced only by complete packets of **short-day** or **long-day** photoperiodic information. For example, the experimentally determined packet of short-day information for female *Podisus maculiventris* was 10 or 11 days at 20°C. In other words, experience of 10 or 11 short days at 20°C was enough to induce diapause in 100% of females. At a higher temperature (24°C), the same number of days under short-day conditions proved to be insufficient for diapause induction: even larger packets of short-day signals (16 short days) induced diapause only in 30% of females. Thus, at higher temperatures, the packet of photoperiodic information (or the required day number) for diapause induction must be larger, and this might be related to the rates of nymphal growth. With increase of temperature from 20 to 24°C, nymphs grow faster and the duration of the nymphal period is reduced from 28 to 21 days, and to 16 days at 28°C. Because the nymphs become sensitive to day length starting from the third instar, only a small fraction of individuals have the time to accumulate the needed number of short-day signals at high temperatures and enter diapause; all other females fail to enter diapause under such conditions (Volkovich et al. 1991b).

The end of the diapause preparation and the start of the initiation subphases (see **Figure 11.1**) 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 adult *Podisus 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 emergence of adults (**Figure 11.4**). It is possible that prediapause feeding of the adults stopped, and the diapause was established completely at that particular moment. The adults transferred into the cold before or after this moment showed a lower resistance to adverse overwintering conditions and suffered higher mortality.
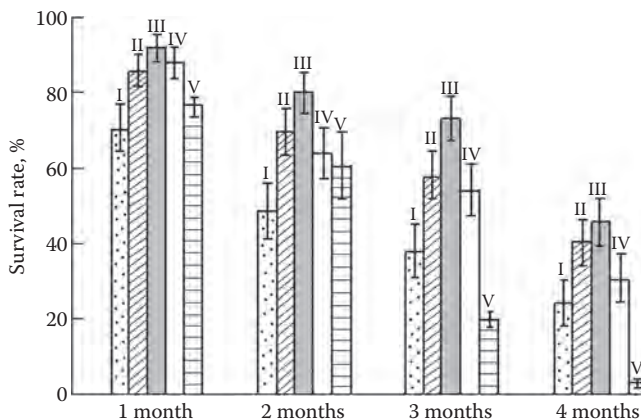
FIGURE 11.4   Effect of age on survival of low temperatures exposure of different duration (1 to 4 months at 8°C, photoperiod L:D 12:12, humidity 90–95%) in females of spined soldier bug, *Podisus maculiventris*. Nymphs were reared to adults and then maintained under constant experimental conditions: photoperiod L:D 12:12 at 20°C and then exposed to cold treatment of different durations. Age of females (days after emergence of adults): 11–13 (group I), 14–16 (group II), 17–19 (group III), 20–22 (group IV), 22–25 (group V). Horizontal line: experimental series (duration of the cold treatment). The laboratory culture originated from Missouri, the United States of America (about 38°N). (From N. I. Goryshin, T. A. Volkovich, A. Kh. Saulich and I. A. Borisenko, Manuscript deposited in the VINITI (Vsesojuzniy Institut Nauchno-tehnicheskoy Informacii [All-Union Institute of Scientific and Technical Information], Moscow, No. 115-B-90, 1989, with permission.)

11.3.2 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 has been most clearly demonstrated in tropical insects (Denlinger 1986).

Among the pentatomoids in which temperature has been studied from this standpoint, winter adult diapause has been found to be controlled primarily by temperature only in the pentatomid *Andrallus spinidens*. This predaceous, polyphagous species is distributed in the tropical and subtropical regions. In southern Japan (Takanabe; 32°N), it occurs on herbaceous plants in rice and other fields where it actively feeds on larvae of the noctuid moths *Spodoptera litura* F. and *Aedia leucomelas* (L.) (Shintani et al. 2010) and usually produces three or four generations a year. To control such a multivoltine seasonal cycle and form winter adult diapause in autumn, insects usually use day length as a cue (see **Section 11.3.1 and Chapter 12**), but this species utilizes a different cue. The long-term mean temperature in this region is 26.8°C at the beginning of September and 22.3°C at the end of September. Adults enter winter diapause primarily in response to this decrease of temperature, not the change of day length. Nymphs hatching at the end of October usually are not able to complete development to adults before winter and, apparently, cannot form diapause. Only adults can enter diapause and survive until spring. Therefore, it is important for the population to enter diapause before October.

In laboratory experiments, when nymphs and then adults of *Andrallus spinidens* were reared and then maintained under constant conditions, diapause could be induced in all photoperiodic regimes tested (with duration of the photophase of 12 to 16 h) but only at temperatures below 25°C. At higher temperatures, all individuals actively developed (i.e., were nondiapausing) irrespective of day length (**Figure 11.5**). Sensitivity to temperature is present at the nymphal and adult stages in this species. Diapause is terminated during winter under the influence of low temperatures, and the adult bugs resume their activity in spring (Shintani et al. 2010). Thus, the multivoltine seasonal cycle of *A. spinidens* is controlled primarily by the temperature, whereas photoperiod seems to perform only an additive function (Saulich and Musolin 2012).

Other examples of the control of winter diapause induction by temperature as in *Andrallus spinidens* are rare. For insects in the Temperate Zone, temperature's effect as a modifier of the PhPR during diapause induction seems to be more important and widespread. Even though many environmental factors likely influence the PhPR, in most species the modifying effect of temperature is the strongest.
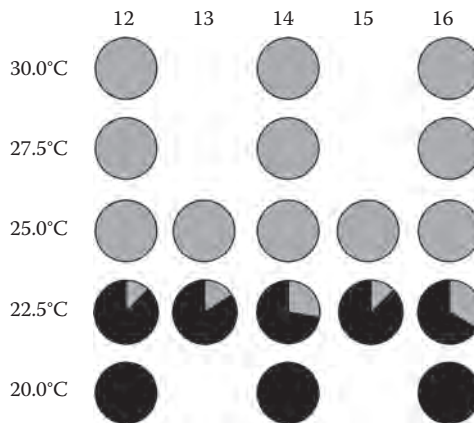
FIGURE 11.5 Effect of photoperiod and temperature on induction of winter adult diapause in the pentatomid *Andrallus spinidens* from Takanabe, Japan (32°N). Nymphs were reared to adults and then maintained under constant experimental conditions: temperature is indicated on the left; photoperiod on the top of the figure (as photophases, in hours). Light sectors: reproductive (i.e., nondiapause) females; black sectors: diapause females. (From Y. Shintani, Y. Masuzawa, Y. Hirose, R. Miyahara, F. Watanabe, and J. Tajima, Entomological Science 13: 273–279, 2010, with permission.)

11.3.2.1 Effect of Temperature on the Photoperiodic Response Curve during Induction of Winter Diapause

Low temperature usually promotes induction of winter diapause. In some species, this effect is most evident around the critical photoperiod, but, in others, it is most evident under short-day or long-day conditions. High temperatures (such as 30 to 32°C) can strongly suppress the effect of day length and even completely prevent induction of winter diapause in some species. On the other hand, low temperatures (usually 15°C or below) enhance the tendency towards winter diapause and all individuals enter diapause irrespective of the preceding day length.

Degree of sensitivity of the critical photoperiod to temperature varies in different species. It is even possible to organize different species on the basis of temperature sensitivity of their PhPRs of diapause induction from a strong dependence of the critical photoperiod on temperature to a temperature-stable PhPR with the critical photoperiod almost insensitive to temperature (Saulich and Volkovich 2004). Based on the data from many insect species, it has been shown that within a range of 20 to 27°C, a temperature shift of 5°C can cause a shift of critical photoperiod of approximately 1 hour (Danilevsky 1961). In other species, including *Podisus maculiventris*, a critical photoperiod of diapause induction basically remains stable within a temperature range of 17.5 to 25.5°C, even though a proportion of diapausing individuals generally decreases under short-day conditions and PhPR can be strongly suppressed under high temperatures (**Figure 11.6**; Goryshin et al. 1988a).

The results of experimental studies of winter adult diapause in the pentatomid *Scotinophara lurida* demonstrate that temperature can affect the quantitative PhPR in a similar way: the higher the temperature, the more diapause is suppressed even under typically diapause-inducing conditions (**Figure 11.3**; Cho et al. 2008).

The main ecological function of temperature in insect diapause onset is the optimal timing of diapause induction during the season. In warm years, winter diapause induction shifts to later dates due to the critical photoperiod decreasing under the action of high temperatures whereas in cold years, an earlier induction of winter diapause takes place. In general, an increase in temperature suppresses the tendency to enter winter diapause, whereas a drop in temperature facilitates induction of winter diapause. However, the signal function of temperature cannot always be distinguished (or separated) from the direct suppression of activity by low temperatures. In many cases, especially in southern species that overwinter as adults, the absence of oviposition in the field might often be caused by the direct suppression of maturation and/or oviposition by the low ambient temperature rather than by induction of winter adult diapause (Saulich and Musolin 2009).
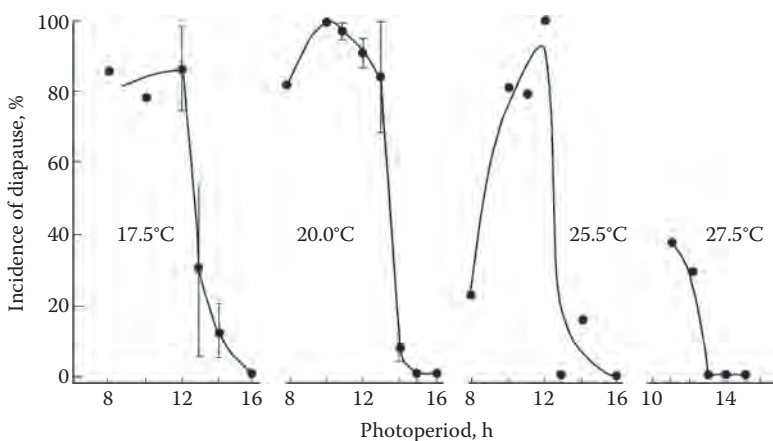
FIGURE 11.6 Effect of constant temperature on the photoperiodic response of winter adult diapause induction in females of the spined soldier bug, *Podisus maculiventris*. The laboratory culture originated from Missouri, the United States of America (about 38°N). Nymphs were reared to adults and then maintained under constant experimental conditions. Vertical lines are ranges of results in different replicates of the experiments. (From N. I. Goryshin, T. A. Volkovich, A. Kh. Saulich, M. Vagner, and I. A. Borisenko, Zoologicheskii Zhurnal [Zoological Journal] 67: 1149–1161, 1988, with permission.)
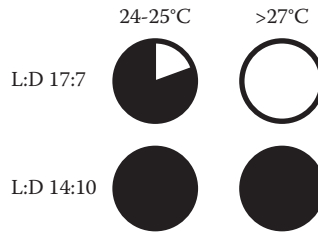
FIGURE 11.7   Effect of photoperiod and temperature in winter diapause induction in females of the predatory pentatomid *Arma custos* from Belgorod Province, Russia (50°N). Nymphs were reared to adults and then maintained under constant experimental conditions. Light sectors: reproductive (i.e., nondiapause) females; black sectors: diapause females. (Modified from T. A. Volkovich and A. Kh. Saulich, Entomological Review 74: 151–162, 1995, with permission.)

11.3.2.2 Temperature Optimum of Photoperiodic Response

As with other physiological responses, the PhPR has its own temperature optimum. Within this optimal range, the response is clear and ecologically meaningful (e.g., winter diapause is normally induced under short-day conditions), whereas outside the optimum, the PhPR does not work properly (e.g., too low or too high temperatures do not allow diapause to be properly formed and insects suffer high mortality). This temperature optimum is an ecologically important characteristic of PhPR because, to a high degree, it determines the effectiveness of the PhPR under natural conditions (Danilevsky 1961). The wider the range of the temperature optimum of the PhPR, the more important the role of day length in the control of the species' seasonal development.

The range of temperatures under which the PhPR fully manifests itself differs significantly between different species of insects. Temperature optimum likely evolved in intense relationships with other critically important characteristics of the PhPR. Thus, in the predatory pentatomid *Arma custos*, the temperature optimum of the PhPR is narrow (**Figure 11.7**) and associated with high temperatures, generally allowing nondiapause development in most females only when the temperature is higher than 27°C (Volkovich and Saulich 1995). This peculiarity of the PhPR of *A. custos* makes it virtually impossible for the seasonal cycle of this species to be bi- or multivoltine in the forest-steppe zone in Europe, in spite of the facultative (i.e., nonobligate) nature of its adult diapause: it is simply too cold in the region to allow nondiapause development and, thus, winter adult diapause is induced in each generation. Realized number of annual generations often is reduced because the time is limited when food is available, abundant, and of good quality (Saulich and Volkovich 1996).

Somewhat similar results were obtained in experiments with the pentatomid *Dybowskyia reticulata* in Japan (Nakamura and Numata 1998). The temperature optimum of the PhPR of this species also is shifted into the high temperature range; adequate response to day length occurs only at 27.5°C or higher, whereas even a slight decrease in temperature to 25°C induces diapause in all the individuals under both long- and short-day conditions. In Osaka (Japan; 34.7°N), *D. reticulata* completes one generation in cold years and two generations in warmer years. The relatively low summer temperature (25°C and lower) "switches off" the physiological mechanism of response to day length so that all the adults enter diapause regardless of the dates of their emergence. The need to limit the number of generations is related to the fact that *D. reticulata* is a narrow oligophage feeding on the seeds of umbellates, which are only available briefly in summer and shatter before the beginning of September (Nakamura and Numata 1998).

11.3.3 Food

The interaction of photoperiod and temperature creates a reliable ecological mechanism controlling the timely onset of diapause in a particular season. However, there are cases when another factor, namely trophic (food, or diet), is added to this usual tandem.

The primary value of the trophic factor in regulation of the seasonal development has been studied in great detail in the cabbage bug, *Eurydema rugosa* (= *E. rugosum*), which has a winter adult diapause. In Osaka (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 (e.g., brown mustard) that die out before early summer. The resulting adults emerge in mid-June and most enter diapause. Because the cultivated crucifers (such as radish and cabbage) remain green much longer, most of the first-generation adults feeding on them are reproductively active and give rise to individuals of the second generation, which become adults at the end of summer and form the overwintering population (Ikeda-Kikue and Numata 2001). To determine the role of individual factors in control of seasonal development of this species, the nymphs were reared to adults and then maintained on two different diets (i.e., leaves and seeds of rape, *Brassica napus* L.) under experimental conditions similar to those in the natural environment (**Figure 11.8**).

The nymphs of *Eurydema rugosa* developed in June under long-day conditions synchronously on the two diets. Most adults of both sexes that molted in July and were maintained on rape leaves remained physiologically active; the females copulated and laid eggs and gave rise to the second generation. By contrast, nearly all the adults that molted at the same time but were maintained on rape seeds entered diapause. The nymphs of the second generation also were reared on rape leaves; however, most of the adults that emerged in September entered diapause (**Figure 11.8**). These experiments clearly showed that although day length played the principal role in induction of winter adult diapause, the response was modified significantly by the food in mid-summer, which thus affected the voltinism of the population.

In laboratory experiments (**Figure 11.9**), it was shown further that food (again, leaves and seeds of rape) acted as a signal in this species only under long-day conditions. Under short-day conditions, all females of *Eurydema rugosa* 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 increase the tendency to enter diapause. However, in *Eurydema rugosa* the trophic conditions facilitating the onset of diapause were no less favorable than
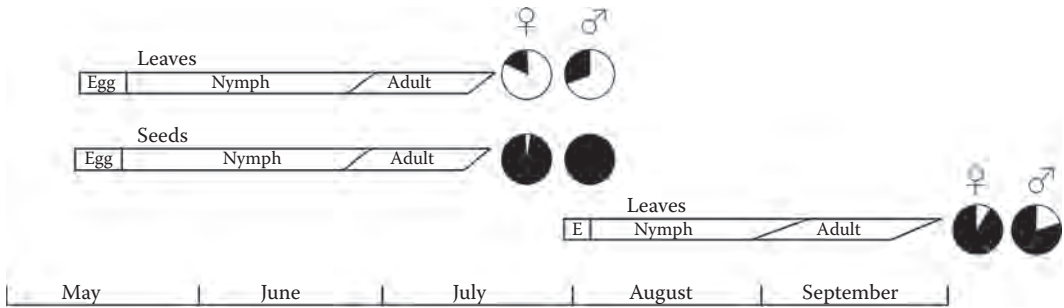
FIGURE 11.8 Effect of diet (leaves or seeds of rape) on winter adult diapause induction in the pentatomid *Eurydema rugosa* in Osaka, Japan (34.7°N) under quasi-natural conditions (nymphs and adults experienced natural day length and temperature). Light sectors: reproductive (i.e., nondiapause) adults; black sectors: diapause adults. (From K. Ikeda-Kikue and H. Numata, Acta Societatis Zoologicae Bohemoslovenicae 65: 197–205, 2001, with permission.)
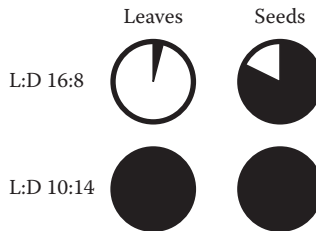
FIGURE 11.9 Effect of photoperiod and diet (leaves and seeds of rape) in winter adult diapause induction in females of the pentatomid *Eurydema rugosa* in Osaka, Japan (34.7°N). Nymphs were reared to adults and then maintained under constant experimental conditions (indicated on the left) at 25°C. Light sectors: reproductive (nondiapause) females; black sectors: diapause females. (From H. Numata, Applied Entomology and Zoology 39: 565–573, 2004, with permission.)

those promoting nondiapause development: both the survival rate and the body weight of nymphs fed on rape seeds were higher than for nymphs fed on leaves because the nutritional quality of seeds is higher than that of leaves (Numata and Yamamoto 1990). Therefore, the cue for diapause induction in this species, at least in part, was the phenological phase of development of the food plant (i.e., type of diet) rather than simply its nutritional value. The absence of leaves and the availability of seeds act as ecological signals of the approaching end of the **vegetative season** and the need for a winter diapause for *E. rugosa*.

It has been demonstrated experimentally that diapause induced by short-day conditions in insects feeding on leaves or seeds (i.e., the short-day diapause) differs in its properties from the diapause induced under long-day conditions in insects feeding on rape seeds (i.e., the **food-mediated, or trophic diapause**). The short-day diapause was terminated under the influence of low temperatures, which is typical of most species with winter diapause, after which the bugs became completely insensitive to day length. The food-mediated diapause was not terminated by low temperature, at least in the laboratory, and its properties remain to be studied (Ikeda-Kikue and Numata 1994).

The effect of diet on the PhPR of diapause induction has some specific traits in predatory bugs as well. For example, in the pentatomid *Perillus bioculatus* (a laboratory culture that originated from Canada; about 46.0°N) kept in the same photoperiodic regime (photophase 16 hours), all individuals feeding on eggs and larvae of the Colorado potato beetle *Leptinotarsa decemlineata* Say remained physiologically active, whereas those feeding on the diapausing adults of this beetle entered diapause (Shagov 1977). Similar results were obtained later in experiments with a population that originated from the United States of America (46.5°N): under the same photoperiods (photophases 14, 15, and 16 hours), the fraction of diapausing *P. bioculatus* adults was greater on the diet of older instar larvae of *L. decemlineata* than on eggs and younger instar larvae of the beetle (**Figure 11.10**). Thus, the age structure of the prey population acted as a cue for winter diapause induction in the predator: presence of mature prey (food) was interpreted by the predatory pentatomid as a signal of approaching autumn (Horton et al. 1998). However, similar to phytophagous bugs, the signal role of food manifested itself only under long-day conditions.

Unlike the oligophagous pentatomid *Perillus bioculatus*, the polyphagous predaceous stink bug *Podisus maculiventris* has a wide trophic range including no less than 75 species of insects from eight orders
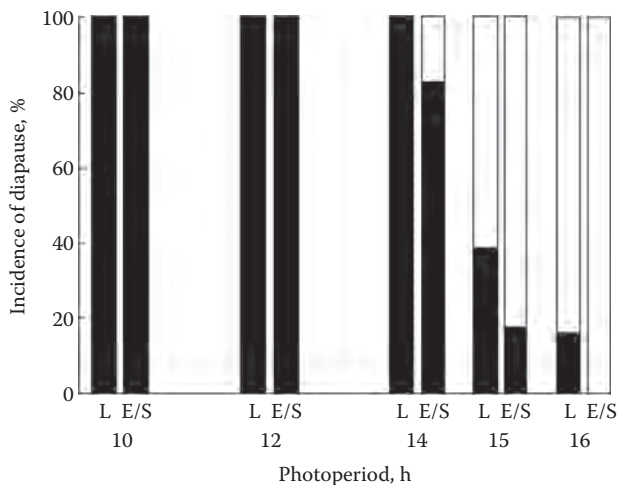
FIGURE 11.10 Effect of photoperiod and diet (eggs and larvae of different instars of the Colorado potato beetle, *Leptinotarsa decemlineata*) on diapause induction in the female pentatomid *Perillus bioculatus* from Wapato, Washington, the United States of America (46.5°N). Nymphs were reared to adults and then maintained under constant experimental conditions (photoperiod is indicated) at 23°C on two different diets. E/S – eggs and small larvae (younger instars) of the beetle; L – large larvae (older instars) of the beetle. Light sections of bars: reproductive (i.e., nondiapause) females; black sections of bars: diapause females. (Modified from D. R. Horton, T. Hinojosa, and S. R. Olson, The Canadian Entomologist 130: 315–320, 1998, with permission.)

(McPherson 1982). As could be expected, this predaceous stink bug revealed a much weaker influence of food on the PhPR of diapause induction. The fraction of diapausing individuals among those reared and then maintained in the laboratory on an unfavorable diet (larvae of the house fly, *Musca domestica* L.) increased only around the critical photoperiod (Goryshin et al. 1988b).

11.4 Winter Diapause *Per Se*

As noted above and evident from **Table 11.2**, the great majority of pentatomoids overwinter as adults. Winter diapause at this stage has been studied mostly in females, where it manifests itself most clearly in arrested ovarian development, suppressed oogenesis, the absence of oviposition, and presence of well-developed fat bodies. Thus, reproductively active females of *Nezara viridula* have mature (= chorionated) eggs or vitellogenic oocytes in their ovarioles, and weakly developed or loose fat bodies (**Figure 11.11C,E**).
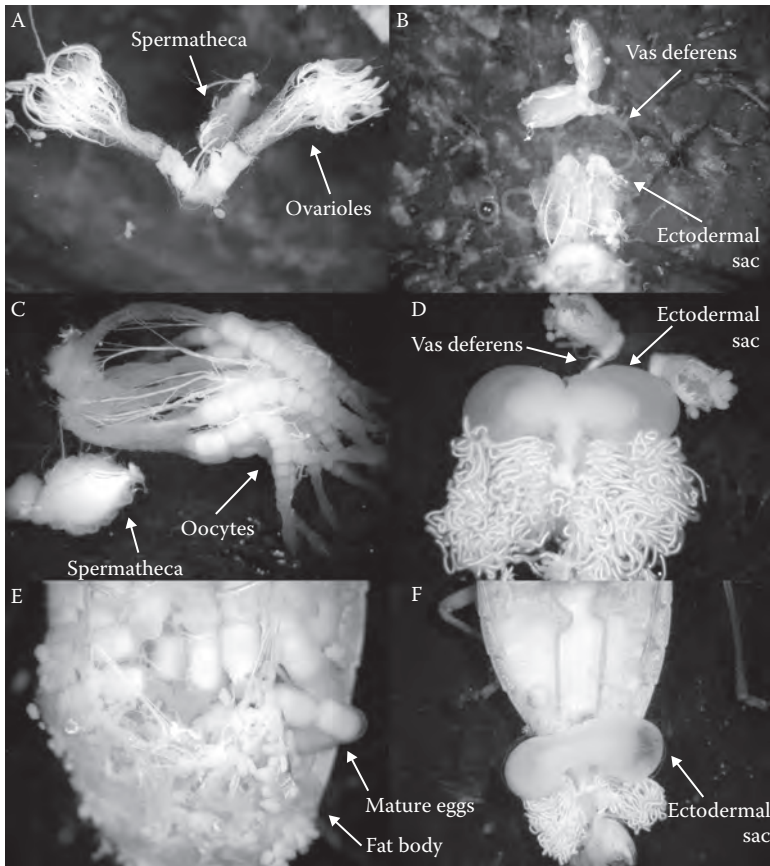
FIGURE 11.11   (See color insert.) State of gonadal development in diapause and nondiapause adults of the southern green stink bug, *Nezara viridula*. Nonreproductive female (virgin, prereproductive or in diapause): no oocytes in germaria, clear ovarioles, and empty spermatheca (A). Nonreproductive male (virgin, prereproductive or in diapause): clear vasa deferentia and collapsed ectodermal sac (B). Reproductive female (nondiapause): developing oocytes with yolk and expanded spermatheca (C); chorionated eggs in ovarioles and loose fat body (E). Reproductive male (nondiapause): yellow vasa deferentia and expanded ectodermal sac containing milky white secretion (D, F). For details on morphology and description of stages of gonadal development in *N. viridula* see Esquivel (2009). Note that in the original publication (Esquivel 2009) images (A) and (B) refer to the gonads without development in virgin adults. In diapause adults, the gonads remain basically in the same state until diapause termination. (A, B, C, and F are from J. F. Esquivel, Annals of the Entomological Society of America 102: 303–208, 2009, with permission; D and E are courtesy of Dr. Jesus F. Esquivel.)
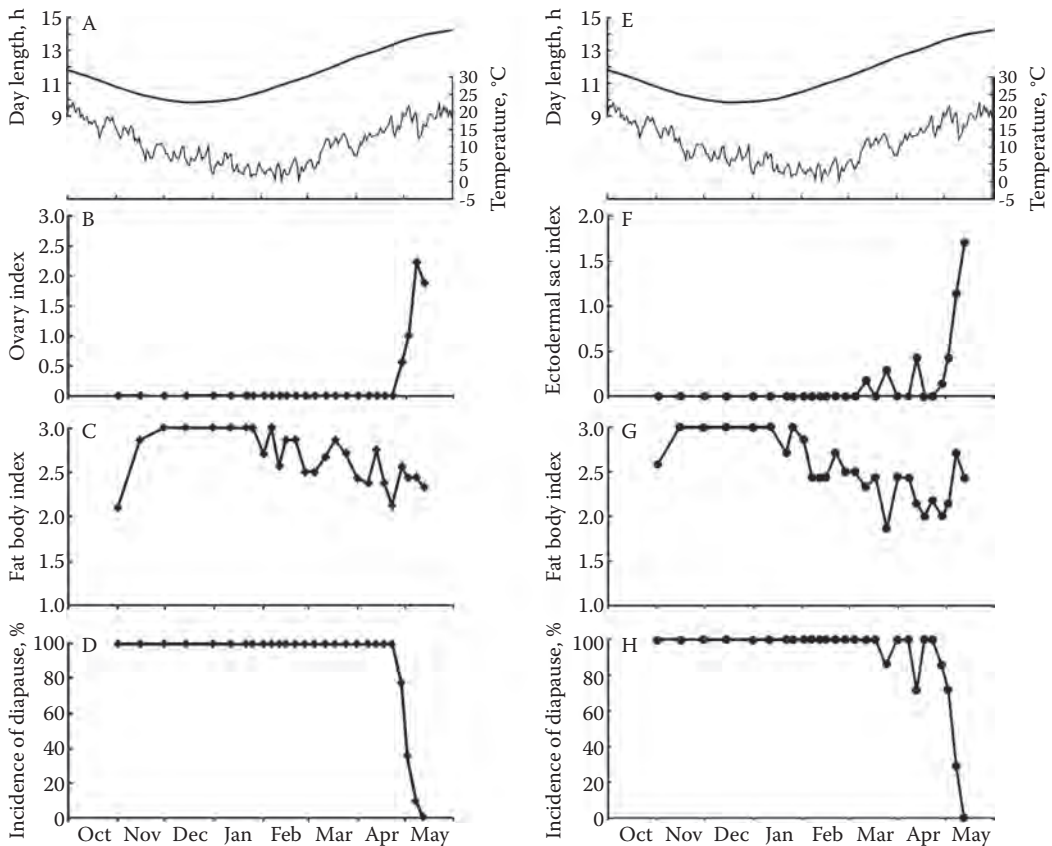
FIGURE 11.12 Dynamics of physiological indices during overwintering under quasi-natural conditions in females (left) and males (right) of the southern green stink bug, *Nezara viridula*, in Kyoto, Japan (35°N). A and E – natural day length and temperature; B – mean ovary index in females: from 0 (diapause: transparent ovarioles, no oocytes in germarium) to 3 (reproduction: semi-transparent ovarioles with mature eggs); C and G – mean fat body index: from 1 (reproduction: fat body small, loose, weakly developed) to 3 (diapause: fat body expanded, dense, well developed); D – incidence of diapause in females; F – mean ectodermal sac (accessory gland) index: from 0 (diapause: sacs transparent, empty, compact) to 3 (reproduction: sacs enlarged, filled with semi-transparent white-yellow secretion); H – incidence of diapause in males. (Modified from K. Takeda, D. L. Musolin, and K. Fujisaki, Physiological Entomology 35: 343–353, 2010, with permission.)

In contrast, in diapausing females of a similar age, differentiation and development of the oocytes is interrupted in the early stages. In these females, the ovarioles are clear, there are no oocytes in germaria, and the fat body is massive and dense (**Figure 11.11A**). In males the onset of diapause is usually (but not always!) marked with suppression of sexual activity and pheromone production, arrested or deeply suppressed development of the testes and/or accessory glands, and development of massive and dense fat bodies (compare **Figure 11.11B and Figure 11.11D,F**).

In both sexes, preparation for winter diapause is accompanied by active growth of the fat body (**Figure 11.12**), changes in the biochemical composition of tissues, in some cases – wax (or similar compounds) secretion (Dzerefos et al. 2009), migration (see **Section 11.7.1**), accumulation of specific nutrients (such as starch [Fedotov 1947]), and changes in behavior (**Figure 11.12**) and/or coloration (see **Section 11.7.4**). A period of diapause development is characterized by reduced oxygen consumption.

11.4.1 Peculiarities of Diapause in Females and Males

In many species of Pentatomoidea that exhibit winter adult diapause, those that are facultative diapausers show no significant difference between the sexes in the parameters of photoperiodic induction of

diapause. This has been demonstrated in the pentatomids *Aelia fieberi* (Nakamura and Numata 1997b), *Dybowskyia reticulata* (Nakamura and Numata 1998), *Nezara viridula* (**Figure 11.12**; Musolin and Numata 2003a, Takeda et al. 2010), and many other species. In many species, the gonads of both sexes remain inactive until the end of the diapause or even postdiapause quiescence (Takeda et al. 2010).

At the same time, there are species with pronounced difference in physiological state of females and males during winter diapause. Thus, the well studied sunn pest, *Eurygaster integriceps*, has a deep obligate winter adult diapause. In diapausing females of this species, all morphogenetic processes stop (or become deeply suppressed) whereas in diapausing males, spermatogenesis continues and by the end of diapause males have mature sperm (Shinyaeva 1980).

Some other species copulate in autumn and females store sperm until the next spring. In such case, males sometimes even do not survive until spring. This strategy is known in various heteropteran families such as Nabidae (Kott et al. 2000), Anthocoridae (Kobayashi and Osakabe 2009, Saulich and Musolin 2009), and Pyrrhocoridae (Socha 2010). Among the Pentatomoidea, this strategy has been recorded in *Menida disjecta* (= *M. scotti*). The winter adult diapause is obligate in this species, but the males already have mature sperm in autumn. In the process of mating, which may occur even during winter, the males supply the females with nutrients and, thus, likely increase the females' chances of successfully overwintering (Koshiyama et al. 1993, 1994).

Males of the white-spotted stink bug, *Eysarcoris ventralis*, also have mature testes in autumn, winter, and spring and are ready to copulate after transfer to high temperature in the laboratory, whereas long-day conditions are required for the start of ovarian development in females (Noda and Ishii 1981).

In the plataspid *Megacopta cribraria*, approximately 15% of overwintered females store live sperm from autumn until as late as mid-March. This trait not only allows them to oviposit without additional copulation in the spring but also likely increases the invasive potential of this species while it colonizes new areas because even one fertilized female can establish a new population of the pest (Golec and Hu 2015).

11.4.2 Cold Hardiness

Cold hardiness is an important issue in insect ecology and usually understood as the ability of an organism to survive at low temperatures (Leather et al. 1993). Diapause provides general nonspecific tolerance of insects to various adverse environmental conditions, including cold. The survival of insects at low temperatures recently has attracted considerable attention (e.g., Lee and Denlinger 1991; Bale 1993, 1996; Leather et al. 1993; Hodková and Hodek 2004; Danks 2005; Denlinger and Lee 2010), but the data for Heteroptera still are scarce.

In general, responses of insects to cold are complex and, as a rule, differ between diapausing and nondiapausing individuals, at different periods of the year, in different ontogenetic stages, and between populations. Nevertheless, based on their response to temperatures below the melting point of their body fluids, it has been suggested that insects can use three different strategies to cope with low temperatures:

(1) **freeze intolerance** (also called freeze avoidance, freeze susceptibility, or chill intolerance),
(2) **freeze tolerance** (also called freezing tolerance), and
(3) **cryoprotective dehydration**.

The freeze intolerant species cannot survive the formation of ice within their bodies and, thus, have evolved a set of biochemical, physiological, behavioral, and ecological measures/adaptations to prevent ice formation. In contrast, freeze tolerant insects can withstand ice formation, usually only in the extracellular fluids, and have a set of characteristics that enables them to survive such ice formation. Adoption of the strategy of cryoprotective dehydration allows the third group of insects to survive subzero temperatures by losing water to the surrounding environment, so resulting in an increase of the concentration of their body fluids and, thus, a decline in their melting point (to equilibration with the ambient temperature). As a result, they cannot freeze (Zachariassen 1985, Bale 2002, Sinclair et al. 2003, Chown and Nicolson 2004, Berman et al. 2013, Storey and Storey 2015).

As shown above, insects differ in their strategies to cope with cold, but most species, including all heteropterans studied thus far, follow the strategy of freeze intolerance. Even under harsh winter conditions (e.g., in Alaska), the freeze intolerant parent bug *Elasmostethus interstinctus* survives winter by **supercooling** (i.e., the physical phenomenon by which water and aqueous solutions remain unfrozen below their melting point if ice nucleating agents are absent; Barnes et al. 1996, Duman et al. 2004).

The relation between winter diapause and cold hardiness has been considered in numerous special publications (e.g., Denlinger 1991, Leather et al. 1993, Danks 2000, Bale 2002, Denlinger and Lee 2010). In general, winter diapause is thought to be necessary for increasing cold hardiness and successful overwintering of insects living in the Temperate Zone. However, there are several exceptions to this rule, where insects can survive winter without deep diapause, apparently using other specific ecophysiological strategies (Denlinger 1991, Šlachta et al. 2002).

The cold hardiness of insects under experimental conditions usually is estimated by **the supercooling point** (**SCP**) (i.e., the temperature at which spontaneous freezing occurs in a supercooled liquid, also referred to as the **crystallization temperature**). In several species, the SCP value is not constant throughout the year. For example, the SCP value of the Italian striped bug, *Graphosoma lineatum*, during 2000–2001 in the Czech Republic was about –7°C in May–June, decreased to –14 to –12°C in August–October, dropped to –18°C in December–January, and then increased again by spring (Šlachta et al. 2002). A similar pattern of SCP dynamics was observed in the stink bugs *Scotinophara lurida* in Korea (Cho et al. 2007) and *Halyomorpha halys* in the United States (Cira et al. 2016).

Seasonal trends are not always so distinct, however. For example, in a laboratory culture of the predaceous stink bug *Podisus maculiventris* originating from the United States of America (38°N), the SCP values of nondiapausing eggs and first instars were –34.1 ± 0.28°C and –29.0 ± 0.40°C, respectively, despite the fact that this species overwinters as adults. At the same time, the SCP values of diapausing and nondiapausing females were similar: –17.8 ± 0.46°C and – 15.0 ± 0.60°C, respectively (Borisenko 1987). The diapausing (–11.7 ± 0.7°C) and nondiapausing (–10.4 ± 0.8°C) adults of *Nezara viridula* from South Carolina (USA) also showed almost no difference in this parameter (Elsey 1993). These data testify to a weak relation or no relation at all between cold hardiness and diapause in the above species.

11.5 Diapause Development and Termination of Winter Diapause

The gradual changes that occur during the central diapause phase and finally result in its ending (i.e., termination) are usually referred to as **diapause development**. The term reflects the fact that diapause is not only a specific physiological state but also a dynamic process whose ending is followed by resumption of active development and often morphogenesis. Termination of diapause is achieved by resumption of activity of neurosecretory centers as a result of spontaneous or induced processes.

The specific features of the state of winter diapause and the processes taking place during diapause are still insufficiently studied. Based on the research of the gradual changes that occur during winter diapause development, Hodek (1983) distinguished two processes: **horotelic** (slow and spontaneous) and **tachytelic** (fast and induced; evolving at a rate faster than in the case of horotelic process).

Horotelic processes represent slow and internally regulated diapause development under more or less stable conditions (i.e., those under which diapause was induced). In this case, spontaneous diapause termination is free of external influence and does not require any stimuli. In contrast, the tachytelic processes take place when diapause development is influenced and accelerated by environmental conditions and diapause is externally and prematurely terminated by action of, for example, low temperatures (**cold termination of diapause**) or changes in the day length (**photoperiodic termination of diapause**). In other words, slow horotelic processes result in spontaneous diapause termination, whereas fast tachytelic processes accelerate diapause development and finally end up with externally induced diapause termination (Hodek 1983, 1996, 2002; Zaslavski 1988). These two processes are explained here separately and can be studied separately in the laboratory, but, in nature, stable conditions almost never exist and, thus, the tachytelic process (caused by, for example, cold in winter) is likely to override the slow horotelic process.

11.5.1 Spontaneous Termination of Winter Diapause

This type of termination of winter diapause is based on endogenous (horotelic) processes and may proceed under the same conditions under which diapause was induced. **Spontaneous diapause termination** is thought to be most important in species with a weak diapause, which generally is typical of insects of tropical and subtropical origin. Because the conditions never remain constant in most parts of the Earth, true spontaneous diapause termination can be observed only under stable laboratory conditions. The possibility of this type of winter diapause termination under constant conditions has been shown in laboratory experiments for many heteropterans, including the stink bugs *Carbula humerigera* (Kiritani 1985b), *Plautia stali* (Kotaki 1998a,b), *Nezara viridula* (Musolin et al. 2007), and others.

Spontaneous diapause termination usually follows a prolonged period of diapause development, with the timing of diapause termination varying between individuals. For example, Musolin et al. (2007) showed the timing of postdiapause oviposition between the earliest and the latest females of *Nezara viridula* in different short-day regimes at 25°C varied from 106 days (photophase 13 hours; **Figure 11.13C**) to 158 days (photophase 10 hours; **Figure 11.13A**), whereas in the nondiapausing females the range of variation was only 43 days at the same temperature (photophase 14 hours; **Figure 11.13D**). Under natural conditions, the difference in the timing of oviposition after overwintering between the earliest and the latest females was only 23 days (Musolin et al. 2007). These results demonstrate that rates of spontaneous diapause termination vary greatly between individuals.
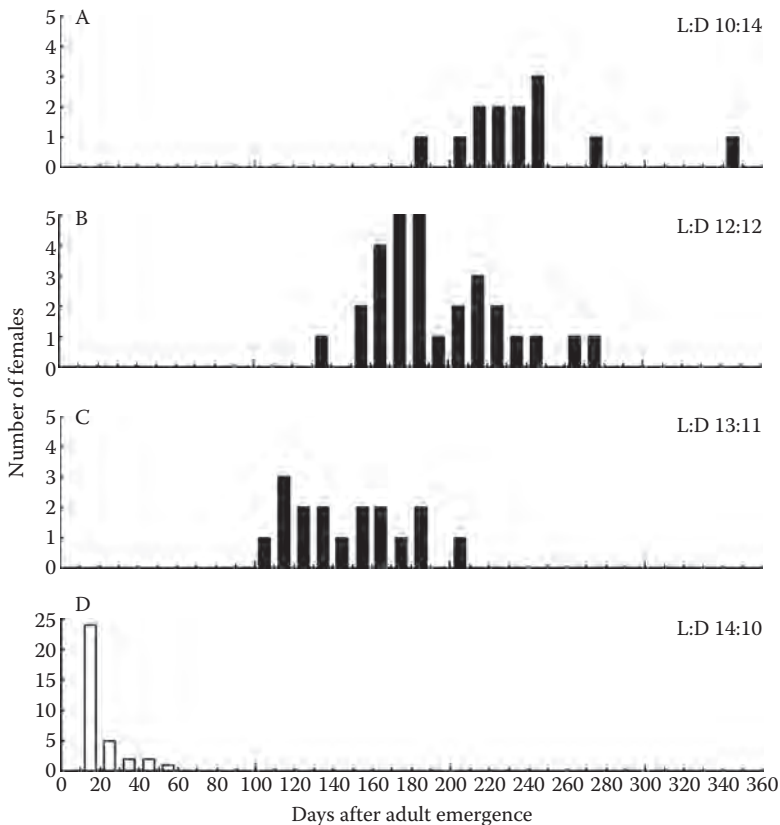

FIGURE 11.13 Effect of photoperiod on the preoviposition period in females of the southern green stink bug, *Nezara viridula,* from Osaka, Japan (34.7°N) at 25°C. Nymphs were reared to adults and then maintained under constant experimental conditions (From D. L. Musolin, K. Fujisaki, and H. Numata, Physiological Entomology 32: 64–72, 2007, with permission.)

The rate of spontaneous winter diapause termination in *Nezara viridula* depended on the photoperiodic conditions during the preceding diapause induction and the subsequent regime. In other words, the diapause that was induced and maintained under different photoperiodic conditions varied in its intensity: a shorter photophase corresponded to a stronger diapause and a later onset of the postdiapause oviposition (**Figure 11.13A–D**).

11.5.2 Cold Termination of Winter Diapause

Cold termination of diapause has been shown experimentally to be of primary significance for most insect species in the Temperate Zone although under field conditions, its effect often is difficult to separate from the spontaneous diapause termination processes (Hodek 1983, 1996, 2002).

Insect activity usually resumes after exposure of diapausing individuals to temperatures ranging from 0 to 10°C; some species have narrower ranges of temperature favorable for diapause termination. Negative temperatures usually hinder the diapause termination process, as do temperatures exceeding 15°C. The temperature requirements of diapausing stages are determined mostly by the living conditions and geographic origin of the species but are almost independent of the stage at which overwintering occurs (Saulich and Volkovich 2004).

Environmental conditions during overwintering and the diapause termination subphase (see **Figure 11.1**) affect the physiological state of the subsequent stages. For example, diapause in female *Podisus maculiventris* was most efficiently terminated by temperature from 6 to 8°C; such conditions generally facilitated the highest survival rate of the adults during diapause and highest reproductive indices after diapause (e.g., fecundity). Even slight deviations from the optimal conditions during diapause may have considerable negative consequences after diapause (e.g., low fecundity and/or survival rate; Goryshin et al. 1989).

The duration of cold exposure required for winter diapause termination varies from 1 to 6 months depending on the species. The neuroendocrine centers gradually resume activity in response to cold exposure and become capable of providing immediate stimulation when the temperature rises in spring (Tauber et al. 1986).

11.5.3 Photoperiodic Termination of Winter Diapause

After photoperiodic induction of diapause, many diapausing insect species remain sensitive to day length and diapause in such species can be terminated by changes of photoperiodic conditions. For example, if diapause was induced by short-day conditions, it can later be terminated by exposure to long-day conditions. This type of winter diapause termination is typical of species with larval (nymphal) and adult diapause.

Photoperiodic termination of winter diapause also is based on the interaction of spontaneous (i.e., horotelic) and induced (i.e., tachytelic) processes. This is indicated by the variable duration of the period required for long-day diapause termination at different stages of diapause. During the initiation subphase (see **Figure 11.1**), diapause is not intense/deep and not completely formed, but, nonetheless, the diapause termination capacity is blocked most strongly. Therefore, insects transferred in autumn from short-day to laboratory long-day conditions usually do not undergo fast photoperiodic termination of diapause (as evidenced, for example, by oviposition in adult diapause). Later, due to the progress of the horotelic process of diapause development, the blocking of morphogenesis becomes weaker, and the time required for photoperiodic termination of diapause (i.e., induced, tachytelic process) gradually shortens (Hodek 1983, 2002; Koštál 2006).

The photoperiodic responses of diapause termination sometimes show amazing similarity with those of diapause induction, and the critical photoperiod values may be nearly the same. The coinciding PhPR curves of diapause induction and termination may indicate that the terminating effect results from the same physiological mechanism that controls the onset of diapause. In other cases, for example in *Nezara viridula*, the PhPR curves may differ somewhat in shape, suggesting that more complicated mechanisms are involved (Musolin et al. 2007).

The interaction of spontaneous and induced processes during diapause termination were demonstrated in two studies using *Podisus maculiventris* that originated from Missouri, the United States of America (about 38°N). In the first experiment, diapause induction, termination, and postdiapause oviposition were studied after exposure of the bugs to different photoperiodic and temperature conditions (**Figure 11.14**; Chloridis et al. 1997). When females were reared from egg to adult and then maintained at long-day conditions (L:D 16:8) and 23°C and remained under the same conditions further, all of them were non-diapause and soon started oviposition (curve A). Basically, the same was recorded when females were reared from egg to adult and then maintained under the same long-day conditions (L:D 16:8) and 23°C but were transferred to short-day conditions (L:D 8:16) on day 13 after the final molt: these females were reproductive and did not stop oviposition at least during 27 days following the transfer from long-day to short-day conditions (curve B). On the contrary, all females reared from egg to adult and then maintained under short-day conditions (L:D 8:16) at 23°C entered diapause (curves C, D, and E). As a result of spontaneous diapause termination under constant short-day conditions (L:D 8:16) at 23°C (curve C), the females started laying eggs on day 47, which indicated that the diapause formed at the photoperiod L:D 8:16 and 23°C was not very deep and stable. Exposure to cold under the same short-day conditions (4°C for 10 days; curve E) hastened the onset of the postdiapause oviposition and increased the fraction of ovipositing females as compared to those in the trial in which the females were kept under constant short-day conditions at 23°C without any cold treatment (curve C). However, even on day 130, the fraction of ovipositing females was only slightly over 40% (curve E). A much greater diapause terminating effect was observed after consecutive action of cold (10 days at 4°C and darkness) and long-day conditions (L:D 16:8) and 23°C (curve D): oviposition started on day 25 (i.e., 10 days of low-temperature treatment plus 15 days of reproduction stimulating conditions), and all the females terminated diapause by day 70. These results show that adults of *P. maculiventris* remain sensitive to day length during winter diapause, which is a prerequisite for its photoperiodic termination. Moreover, day-length sensitivity is preserved even after exposure to cold.
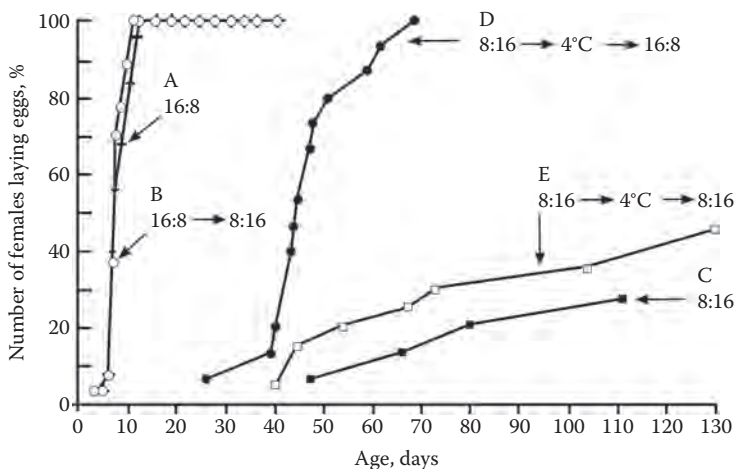
FIGURE 11.14 Oviposition dynamics in females of the spined soldier bug, *Podisus maculiventris*, under different photoperiodic conditions at 23°C (if otherwise not indicated). A – females reared from eggs to adults and then maintained at long-day conditions (L:D 16:8); B – females reared from eggs to adults and then maintained at long-day conditions (L:D 16:8); on day 13, after the final molt, females were transferred to short-day conditions (L:D 8:16); C – females reared from eggs to adults and then maintained at constant short-day conditions (L:D 8:16); D – females reared from eggs to adults and then maintained at short-day conditions (L:D 8:16); then on day 13, after the final molt, females were transferred to 4°C and darkness for 10 days, then to long-day conditions (L:D 16:8); E – females reared from eggs to adults and then maintained at short-day conditions (L:D 8:16); then on day 13, after the final molt, females were transferred to 4°C and darkness for 10 days, then to short-day conditions (L:D 8:16). The laboratory culture originated from Missouri, the United States of America (about 38°N). (From A. S. Chloridis, D. S. Koveos, and D. C. Stamopoulos, Entomophaga 42: 427–434, 1997, with permission.)

TABLE 11.4

Photoperiodic Termination of Diapause in Adult *Podisus maculiventris* (From N. I. Goryshin, T. A. Volkovich, A. Kh. Saulich, and I. A. Borisenko, Manuscript deposited in the VINITI (Vsesojuzniy Institut Nauchno-tehnicheskoy Informacii [All-Union Institute of Scientific and Technical Information]), Moscow, No. 115-B-90, 1989, with permission)[1]

Temperature, °C	Age of Adults at the Moment of Transfer to L:D 16:8	Number of Pairs	Proportion of Individuals That Terminated Diapause, %	Preoviposition Period, Days after Transfer (Mean ± S.E.)
20.0	25	23	100	26.1 ± 1.37
	27–29	11	100	25.2 ± 2.42
24.0	25–30	26	100	17.8 ± 0.93

[1] Diapause was induced under short-day conditions of L:D 12:12 at 20°C and then adults were transferred to the long-day conditions of L:D 16:8 at 20 and 24°C at different ages. The culture originated from Missouri, the United States of America (about 38°N).

The possibility of photoperiodic termination of winter adult diapause in *Podisus maculiventris* also was shown in another experiment with bugs that originated from the same Missouri population (**Table 11.4**). In that experiment, winter adult diapause was induced by short days (L:D 12:12) at 20°C, and adults on days 25 to 30 after emergence were transferred into long-day conditions (L:D 16:8) at 20 or 24°C. Under both temperatures, diapause soon terminated and females started oviposition. The higher temperature (24°C) had a stronger diapause terminating effect than the lower temperature (20°C), because preoviposition period was shorter at 24°C than at 20°C (**Table 11.4**). However, we cannot exclude that the difference in duration of the preoviposition period was caused by the effect of temperature on the postdiapause maturation rates rather than diapause termination process.

The photoperiodic sensitivity during winter diapause appears to be typical of many species overwintering as adults. In particular, this phenomenon was observed in the pentatomids *Halyomorpha halys* (Yanagi and Hagihara 1980), *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 third instar in *Podisus maculiventris* (see **Section 11.3.1.3 and Table 11.3**) and from the fifth instar in *E. lewisi* (Hori and Kimura 1993), whereas photoperiodic termination of winter diapause in both species requires exposure to long-day conditions only in the adult stage (Hori and Kimura 1993, Chloridis et al. 1997). Thus, the sensitive periods for induction and termination of winter adult diapause differ in length: the processes of diapause induction require a much longer action of the cue and likely involve more profound changes in the endocrine system than the processes leading to diapause termination. This conclusion was later supported by the results of experiments on winter diapause termination in *Scotinophara lurida* (Cho et al. 2008).

11.6 Environmental Factors Controlling Postdiapause Development in Spring

Studies of various insect species from the Temperate Zone in the Northern Hemisphere have shown that for most species, winter diapause ends before December, and the most severe part of winter is spent in a state of postdiapause quiescence (**Figure 11.1**; e.g., Danilevsky 1961; Hodek 1971b, 1996; Hodková 1982; Ushatinskaya 1990; Saulich and Volkovich 2004; Koštál 2006; Saulich and Musolin 2007b). According to a very precise definition suggested by Koštál (2006; p. 121), **postdiapause quiescence** is *an exogenously imposed inhibition of development and metabolism, which follows the termination of diapause when conditions are not favorable for resumption of direct development.* Postdiapause quiescence performs both functions of diapause: survival and synchronization of development; it complements winter diapause rather than replaces it, ensuring more precise seasonal synchronization (Veerman 1985, Belozerov 2009). Among the external factors controlling the resumption of active development in spring, the most important for pentatomoids in the temperate latitudes are day length, temperature, and

presence of food (i.e., the same factors and cues that control the onset of winter diapause in autumn; see **Section 11.3**).

Resumption of active development of pentatomoids after winter dormancy (see **Figure 11.1**) might manifest itself in different ways and involve different life processes depending on the type of winter diapause. In embryonic (egg) diapause, embryogenesis comes to an end; in larval (nymphal) diapause, metamorphosis continues; and, finally, in adult diapause, the blocking of oogenesis is removed and activity of reproductive glands resumes. Eco-physiological mechanisms controlling resumption of active development in spring have been studied mostly in species with winter adult diapause.

11.6.1 Day Length

Prolonged exposure to cold usually results in temporary or permanent **photoperiodic refractoriness** (i.e., insensitivity to photoperiod, when the insects lose the ability to measure or respond to day length and, thus, they develop without entering diapause under any day-length conditions). Therefore, in spring, with the onset of warm weather, most species of pentatomoids resume activity regardless of the day length and reproduce until the end of their lives. Such a neutral response to day length after diapause first was described in the fire bug, *Pyrrhocoris apterus* L., and referred to as ***Pyrrhocoris*-like response** (Hodek 1971b, 1977).

In contrast with species that lose photoperiodic sensitivity irreversibly, in some other species this sensitivity is lost in autumn or winter but restored at the beginning of summer after a short refractory period. Such a type of response first was discovered in the bishop's mitre shield bug, *Aelia acuminata*, and referred to as ***Aelia*-like**, or **recurrent response** (Hodek 1971a). This phenomenon later was observed in other pentatomoids, such as *Dolycoris baccarum* (Hodek 1977), *Eurydema rugosa* (Ikeda-Kikue and 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, switch to a prolonged perennial, or semivoltine, life cycle (see **Chapter 12**). This type of response was suggested as a possible option in the predaceous stink bug *Perillus bioculatus* as well (Jasič 1967).

11.6.2 Temperature

It is well known that resumption of active development in spring is controlled by increasing temperatures. However, because the temperature regime in spring is highly unstable, some species overwintering as nymphs or adults, and forming close associations with particular food plants (i.e., mono- or oligophages) or their phenological phases, would benefit from using more precise external cues, in particular day length, as triggers of spring activation. Nevertheless, according to the data available, most species capable of photoperiodic diapause termination under laboratory conditions irreversibly lose their daylength 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.

Winter adult diapause in overwintered females of *Eurydema rugosa* in central Japan was shown to be terminated completely by the beginning of April. The bugs at that time were in a state of postdiapause quiescence and did not start to reproduce due to the suppressing effect of low temperatures. This suppression could not be eliminated by either the presence of food or long-day conditions. Oviposition started only after the temperature exceeded the lower threshold of postdiapause morphogenesis (Ikeda-Kikue and Numata 1992). In a similar manner, the females of the pentatomid *Aelia fieberi* transferred into the laboratory (25°C) in late March or early April and supplied with favorable food started to oviposit much earlier than in the field, where their oviposition was suppressed by low temperature (Nakamura and Numata 1997b). Once started, oviposition continued until the end of the females' lives.

11.6.3 Food

One of the important components of the environment, essential for insect winter diapause termination and resumption of activity in spring, is the presence of adequate food resources. The role of food is particularly apparent in regulation of postdiapause development of species feeding on fruits and seeds. Food
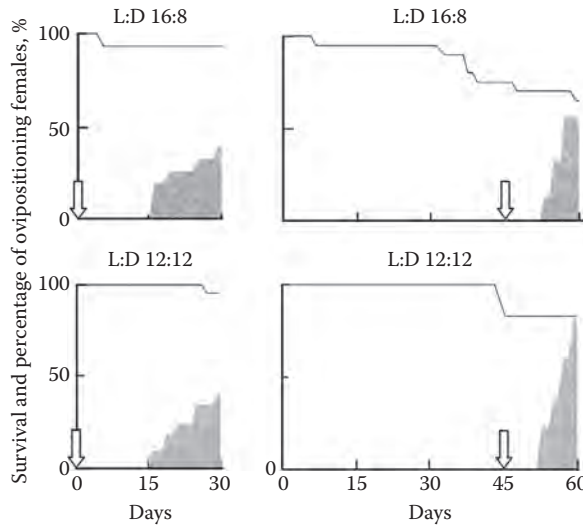
FIGURE 11.15 Survival and oviposition of females of the pentatomid *Dybowskyia reticulata* from Osaka, Japan (34.7°N) transferred in late March from the field to the laboratory short-day (L:D 12:12) and long-day (L:D 16:8) conditions at 25°C. Light areas: nonovipositing females; shaded areas: females that started laying eggs. Arrows mark the moment when food became available. (From H. Numata, Applied Entomology and Zoology 39: 565–573, 2004, with permission.)

as a trigger for spring reproduction was demonstrated in experiments with the pentatomid *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 (**Figure 11.15**).

In the absence of food, oviposition was delayed by a considerable period under both long- and short-day conditions. Availability of food stimulated reproduction (the moment of the appearance of food is marked with an arrow in **Figure 11.15**). Thus, the onset of reproduction in this species in spring is not controlled by either temperature or day length but is determined solely 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.

11.7 Seasonal Adaptations Associated with Winter Diapause

In addition to winter diapause, pentatomoids have a diverse set of seasonal adaptations that allow them to synchronize their growth and reproduction with the seasons optimal for such activities and dormancy periods with the harsh periods of the year.

11.7.1 Migrations to and from Overwintering Sites

Migration is a complex phenomenon widely spread throughout the Heteroptera, including the Pentatomoidea. It is difficult to define insect migration but Dingle (1996, p. 38) listed five characteristics that distinguish migration from other forms of movements. These are: (1) it is persistent; (2) it is straightened out; (3) it is undistracted by resources that would ordinarily halt it; (4) there are distinct departing and arriving behaviors; and (5) energy is reallocated to sustain it. Dingle (1996) also stressed that not all migrants display all of these characteristics all of the time, but most will display most of them at least part of the time during which they are migrating. Migrations often happen seasonally and differ from sporadic and short-distance dispersal and other forms of movements in space aimed at search for habitats for feeding, oviposition, etc. Distances covered by migrating true bugs might differ manyfold, from hundreds of meters to hundreds of kilometers (Saulich and Musolin 2007a,b).

Migration behavior in insects now is understood as a special behavioral and physiological syndrome (Johnson 1969, Dingle 1996). Migrating individuals are characterized by enhanced motion activity and suppression of other functions, particularly reproduction and feeding. Usually, migrating individuals are in adult diapause, and migration is triggered by temperature conditions and/or movements of air.

Seasonal migrations might be linked to both winter and summer diapauses, and microhabitats chosen by diapausing individuals in winter and summer might be the same or different in different species. Seasonal migrations also are strongly linked to particular species-specific stages of ontogenesis, take place in particular periods of the year, and lead to adaptive changes of habitats.

Within the Pentatomoidea, some species are considered to be strongly migratory (e.g., *Eurygaster integriceps, Eurygaster maura, Aelia rostrata, Aelia melanota*) whereas others are semi-migratory (e.g., *Aelia furcula, Dolycoris penicillatus*) or nonmigratory (*Aelia acuminata*) (Brown 1962, Javahery 1995).

Migrations towards overwintering microhabitats (called also **hibernation quarters**) and sites occupied during summer diapause (called also **estivation quarters**) have been studied in Scutelleridae, particularly in the sunn pest, *Eurygaster integriceps*, in Eastern Europe. Even though *Eurygaster* species do not fly as well as some lepidopterans or orthopterans do (Arnoldi 1947), distance, duration, and regularity of their migrations deserve special attention (Critchley 1998).

Three regular migration events can be distinguished in the life cycle of *Eurygaster integriceps*:

 (1) in spring from the hibernation quarters to the fields,
 (2) in summer from the fields to the estivation quarters in mountains, and
 (3) in autumn from the estivation quarters to the hibernation quarters.

Distances covered by these bugs seem to depend on geographic locations. Distant migrations (150–200 km) are typical for southern populations of *Eurygaster integriceps* that live in hot regions and migrate to overwinter at higher altitudes (e.g., Central Asia). Individuals from the more northern (and, thus, colder) regions and from lowland populations normally do not need to fly far to find cooler **overwintering quarters** and, thus, have shorter migrations (i.e., 20–50 km). Thus, in the center of the European part of Russia, *E. integriceps* overwinters in valley forest and forest belts and does not need to fly long distances. In such regions, seasonal migrations usually cover not more than 10–15 km. In special experiments with bugs labeled with radioactive isotopes in Stavropol Province (Russia), young overwintering adults were recorded up to 10 km from their feeding sites (Andrejev et al. 1958, 1964).

Eurygaster integriceps has three clear physiological/behavioral states (previously called *instincts*, Arnoldi 1947): nomadic, aggregative, and migratory. The nomadic state can be seen not only in adults but also in nymphs that often move around. The aggregative state may be observed both during periods of activity and dormancy. Often, adults are nonuniformly distributed at the hibernation and estivation sites; they are numerous at some microhabitats, whereas other similar and close microhabitats are almost unpopulated. And, finally, the migratory state clearly is aimed at active search of favorable habitats first for estivation and then for hibernation (Arnoldi 1947, Brown 1962, Critchley 1998).

11.7.2 Formation of Aggregations

Formation of large aggregations at different times of the year is characteristic of many species from various families of Pentatomoidea. Among these species, the phenomenon is more visible in the sunn pest, *Eurygaster integriceps* (Brown 1962), the parent bug *Elasmostethus humeralis* (Kobayashi and Kimura 1969), pentatomids *Menida disjecta* (Inaoka et al. 1993) and *Halyomorpha halys* (Hoebeke and Carter 2003, Nielsen and Hamilton 2009, Nielsen et al. 2011), and plataspids *Coptosoma scutellatum*, *C. mucronatum* (Davidová-Vilimová and Štys 1982), *Caternaultiella rugosa* Schouteden (Gibernau and Dejean 2001), and *Megacopta cribraria* (Eger et al. 2010, Suiter et al. 2010).

Aggregations can differ in size ranging from comparatively small groups of up to a few dozen bugs (e.g., in pentatomids *Biprorulus bibax* [James 1990a,b], *Euschistus heros* [Panizzi and Niva 1994], *Halys fabricii* [as *Halys dentatus*], and *Erthesina fullo* [Dhiman et al. 2004]) to groups of thousands (e.g., the parastrachiid *Parastrachia japonensis* can have as many as 4,000 adults that form an overwintering aggregation of up to 2 meters in size [Tachikawa and Schaefer 1985]).

In most species, aggregations are formed by adults, but cases are known where nymphs aggregate (e.g., overwintering aggregations of plataspid *Coptosoma scutellatum*; Davidová-Vilimová and Štys 1982) or both adults and nymphs do so (*Caternaultiella rugosa* Schouteden; Gibernau and Dejean 2001).

In large aggregations, individuals of different categories (hibernating, estivating, or nondiapausing) can have advantages over nonaggregated individuals including enhanced mating opportunities (Hibino 1985); shelter from adverse environmental conditions (Kiritani 2006) or parasitoids (*Caternaultiella rugosa* Schouteden; Gibernau and Dejean 2001); reduced desiccation (Lockwood and Storey 1986, Vulinec 1990); and combined chemical defense against predators (Cocroft 2001). However, there are possible negative effects too, because large aggregations are likely to attract predators and parasitoids or stimulate development of pathogens. This has been shown in the case of *Nezara viridula* and its parasitoid *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae) in Hawaii (Nishida 1966, Jones and Westcot 2002).

Ecological importance of seasonal aggregations during diapause has been studied in the subsocial shield bug *Parastrachia japonensis* in East Asia. This subsocial species is monophagous and feeds only on seeds of *Schoepfia jasminodora* Siebold et Zuccarini (Olacaceae). The fruits and seeds of the shrub are available only for a couple of weeks per year and to synchronize its seasonal cycle with that of the shrub, *P. japonensis* spends about 10 months annually in adult diapause and forms large aggregations (Tachikawa and Schaefer 1985; Tsukamoto and Tojo 1992; Nomakuchi et al. 1998; Filippi et al. 2000b; Tojo et al. 2005a,b). Formation of these aggregations decreases the metabolic rate in diapausing bugs which, in turn, increases their survival rate during long dormancy over hot summer or cold winter periods when food is not available. Elegant laboratory experiments demonstrated that oxygen consumption was twice as low in bugs in aggregations compared to isolated individuals. Interestingly, group size was not important if compared to the physical contacts with other individuals of the same species. It was suggested that such contacts stimulate excretion of a chemical compound functioning as an aggregation pheromone and promoting formation of aggregations (Tojo et al. 2005b). A few other eco-physiological adaptations allow the species to survive for an extended period when food resources are unreliable (Tojo et al. 2005a,b).

Pentatomoids also produce aggregation pheromones for either food or mate location or to identify overwintering habitats. Thus, males of the stink bug *Halyomorpha halys* produce a recently identified two-component aggregation pheromone (Khrimian 2005; Khrimian et al. 2008, 2014). The species also responds to a kairomone, which is an aggregation pheromone of a sympatric Asian pentatomid *Plautia stali*, although this stimulus is only attractive beginning in early August (Aldrich et al. 2009, Nielsen et al. 2011, Weber et al. 2014).

In autumn, during a period of preparation for winter diapause, many pentatomoids (e.g., *Halyomorpha halys*, *Menida disjecta*, *Urochela quadrinotata*) search for hibernation quarters and, in so doing, can enter houses and other buildings in large numbers, often becoming a serious nuisance (Kobayashi and Kimura 1969, Inaoka et al. 1993, Watanabe et al. 1995, Hoebeke and Carter 2003, Inkley 2012, Lee et al. 2014).

11.7.3 Photoperiodic Control of Nymphal Growth Rate

The growth rate of nymphs and, correspondingly, the duration of the nymphal stadia in Pentatomoidea are affected largely by ambient temperatures; an increase in temperature within the temperature optimum range hastens development, and a decrease hinders it. However, the developmental rate depends on other factors and cues as well. In particular, one of the important seasonal adaptations in insects is **photoperiodic control** (i.e., **regulation**) **of the nymphal growth rate**; nymphs may develop faster under certain photoperiodic conditions and slower under others. Such adaptation is a quantitative PhPR (see **Section 11.3.1.1**). In several species, under low to moderate temperatures, development is accelerated by short-day conditions. As day length decreases in autumn, the nymphal growth rate increases so as to reach the overwintering stage before environmental conditions get worse. Such an adaptation first was described in fire bug, *Pyrrhocoris apterus* (Pyrrhocoridae; Saunders 1983, Numata et al. 1993, Saulich et al. 1993), and later found in the predatory stink bug *Arma custos* (Volkovich and Saulich 1995), green shield bug, *Palomena prasina* (Saulich and Musolin 1996, Musolin and Saulich 1999), and many

other heteropteran species (Musolin and Saulich 1997). Recently, Niva and Takeda (2003) noted that in *Halyomorpha halys*, short day accelerated nymphal development, whereas long day accelerated reproductive maturation. The two types of photoperiodic responses at different stages may help maintain the univoltinism of *H. halys* in the field, assuring the right timing for diapause and reproduction.

As with diapause induction, there must be some (preceding) stages that are sensitive to the cue inducing this response (i.e., day length). For some species, these stages already are known. Thus, in the stink bug *Eysarcoris lewisi*, acceleration or retardation of further nymphal growth is controlled by the photoperiodic conditions experienced by the nymphs during the third instar, whereas the physiological state (reproduction versus diapause) is controlled by conditions experienced only by nymphs during the fifth instar or adult stage (Hori and Kimura 1993).

However, despite its clear adaptive significance, photoperiodic control of growth rate is not a universal phenomenon in pentatomoids. Nymphs of some bugs 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 populations of the sloe bug, *Dolycoris baccarum*, from Norway and Japan (Conradi-Larsen and Sømme 1973, Nakamura 2003) and between populations of *Nezara viridula* from Egypt and Japan (Ali and Ewiess 1977, Musolin and Numata 2003a). These examples show that this trait can manifest itself at the population level, ensuring a high level of adaptation of the local population to specific living conditions, and that seasonal adaptations can differ between populations.

At the same time, in some species, the nymphal growth rate does not depend on photoperiodic conditions. For example, no distinct relations between the durations of nymphal stadia and photoperiodic conditions were observed in *Podisus maculiventris* (Goryshin et al. 1988b). In *Picromerus bidens* (Musolin and Saulich 1997, 2000), the effect of day length was small.

The physiological mechanism underlying this adaptation still has not been studied sufficiently. Further research will be necessary to understand the exact nature of the effect of day length (acceleration of development under certain conditions or retardation under other conditions) and the relationships between these phenomena and winter or summer diapauses.

11.7.4 Seasonal Polyphenism

The external appearance of individuals of the same species and developmental stage can change seasonally in some insect species. These changes can happen during the ontogenetic development of the same individuals or occur in representatives of different generations of the same species. Such cases often are difficult to notice and classify, and genetic and physiological mechanisms behind these changes are poorly understood. However, diversity of such forms often are described in terms of polymorphism or polyphenism.

Polymorphism usually is understood as the presence in a population of two or more distinct phenotypes (morphs, forms) at the same ontogenetic stage (discontinuous variation; Kennedy 1961; Walker 1986; Nijhout 2003; Saulich and Musolin 2007a,b; Simpson et al. 2011; Rogers 2015). Polymorphism can be divided into:

– **genetic polymorphism** (different phenotypes are produced by different genotypes), and

– **environmental**, or **ecological polymorphism**, or **polyphenism**, or **conditional polyphenism** (different phenotypes are produced by one genotype under different environmental conditions).

Several distinct genetically controlled color morphs of *Nezara viridula* (Hokkanen 1986, Ohno and Alam 1992, Musolin 2012; see **Chapter 7**), wing size polymorphism in many aquatic and semi-aquatic Heteroptera (Saulich and Musolin 2007a), and all cases of sexual dimorphism, can be considered examples of genetic polymorphism.

Wing polymorphism recently was reported in the Neotropical genus *Braunus* Distant (Pentatomidae). However, degree of manifestation, nature (i.e., genetic or environmental polymorphism), and control mechanism are not known, as yet, because most species of *Braunus* are known from only few specimens (Barão et al. 2016).

Polyphenism covers cases when environmental conditions determine which phenotype will be realized. Phenotypic plasticity can result from variation in developmental, physiological, biochemical, and behavioral processes that are sensitive to environmental variables (Nijhout and Davidowitz 2009, Simpson et al. 2011). If changes in frequencies of phenotypes are regular (annual) and controlled by environmental conditions, then such cases of polymorphism can be called **seasonal polyphenism**.

In Heteroptera, cases of **seasonal changes of wing size and degree of development of wing muscles or other organs** are good examples of seasonal polyphenism. They allow many true bug species to survive unfavorable seasons, migrate or disperse, and effectively use available resources. However, whereas wing size/wing muscle seasonal polyphenism is widely represented in some ecological and taxonomic groups of Heteroptera (e.g., aquatic and semi-aquatic bugs [Gerromorpha and Nepomorpha]; Saulich and Musolin 2007a), it remains basically unknown in Pentatomoidea. The only known exception is possibly a burrower bug, *Scaptocoris carvalhoi* Becker, distributed in Brazil (Nardi et al. 2008) and represented by two distinct wing forms. **Long-winged** (i.e., **macropterous**) individuals demonstrate a greater locomotion capacity than **short-winged** (i.e., **brachypterous**) individuals, and only long-winged adults can fly. The exact mechanism of control of this wing polyphenism is not known, but a significant increase in the frequency of long-winged adults has been noticed during the swarming season suggesting that the wing polyphenism is seasonal and highly functional. Furthermore, this seasonality may be related to the scarceness of rain during the developmental period of the nymphs. In this case, the lack of rain can result in a decrease in the moisture content of the soil and act as an inducing factor for wing development mechanisms (Nardi et al. 2008).

Another category of seasonal polyphenism is **seasonal body color polyphenism** or **seasonal body color change**, widely represented in the Pentatomoidea. There are numerous examples of this phenomenon where seasonal body color polyphenism often is linked to changes in the physiological state of individuals, namely formation of winter diapause, and often is under photoperiodic control (Musolin and Saulich 1996b, 1999; Saulich and Musolin 2007b).

There are two forms of adults of the dusky stink bug, *Euschistus tristigmus tristigmus*, which differ in morphology and body color. For many years, the two forms were considered different species or subspecies, but it was discovered they were seasonal forms of the same species (McPherson 1975a). The two forms could be produced under experimental conditions by manipulation of the rearing photoperiods (long-day versus short-day; McPherson 1974, 1975a,b, 1979). Subsequently, similar patterns of photoperiodic control of adult body coloration were reported in a few other pentatomids: *Thyanta calceata* (McPherson 1977, 1978), *Plautia stali* (Kotaki and Yagi 1987), *Oebalus ypsilongriseus* (Vecchio et al. 1994, Panizzi 2015), *Euschistus servus* (Borges et al. 2001), *Euschistus conspersus* (Cullen and Zalom 2006), *Nezara viridula* (Musolin and Numata 2003a, Musolin 2012), *Piezodorus guildinii* (Zerbino et al. 2014, 2015), and others. In even more pentatomoids, seasonal body color polyphenism has been reported, but its control mechanism remains unknown (e.g., *Halys fabricii* [as *Halys dentatus*] and *Erthesina fullo*; Dhiman et al. 2004).

In *Halyomorpha halys*, seasonal polyphenism of body color and other morphological characters manifests itself in both nymphal and adult stages (Niva and Takeda 2002). For example, the red color on the sternum of adults is more common in nondiapausing adults and may be related to reproductive maturity. The pronotum of fifth instars reared from hatching under short-day conditions (L:D 11:13) shows a darker, brown-marbled color pattern with less creamy-yellowish speckles, than that of the nymphs reared under long-day conditions (L:D 16:8). Temperature also influences body coloration of nymphs, and higher temperature enhances the long-day effect. The fifth instars reared under short-day conditions, which are destined to diapause when they become adults, have shorter white stripes on the pronotum, smaller body size, less frequent feeding, and more lipid accumulation than the long-day reared nymphs. In another experiment, cohorts of nymphs were transferred from long-day and high temperature conditions (L:D 16:8 at 25°C) to short-day and low temperature conditions (L:D 11:13 at 20°C) for the durations of the second–fifth and fourth–fifth stadia and for the fifth stadium. It was found that the longer the exposure to short-day and low temperature conditions during the nymphal stage, the greater the expression of short-day-associated characteristics observed in the fifth instars and adults (Niva and Takeda 2002, 2003).

The seasonal color polyphenism is irreversible in some species; in others, coloration changes gradually and may be reversible. For example, the freshly molted adults of *Nezara viridula* may be either green or yellow, depending on the genetic morph (a case of genetically controlled color polymorphism; see above in this **Section and in Chapter 7**). The same green or yellow body coloration is preserved during reproduction (**Figures 11.16 and 11.17A**). However, diapausing individuals of both sexes turn from green or yellow to reddish-brown soon after the adults emerge (**Figures 7.1D, and Figures 11.16 and 11.17B–F**; Musolin and Numata 2003a) and retain this coloration until the complete termination of diapause. These adult body color changes are controlled by day length and correlated with the physiological state (diapause versus nondiapause) of the individual (Harris et al. 1984, Musolin and Numata 2003a, Musolin et al. 2007, Musolin 2012).

The same pattern for *Nezara viridula* also was observed under field conditions in central Japan: reproductive adults of the summer generations were green (or yellow), although adults of the late-season generation normally did not reproduce but changed body color to reddish-brown and entered winter diapause (**Figure 7.1C,D**). After overwintering, the body color changed back to the initial green (yellow; **Figure 11.17G–H**), and the bugs began to reproduce (**Figure 11.18**; Musolin and Numata 2003b, Musolin et al. 2010, Takeda et al. 2010). A similar pattern was observed in the field in the redbanded stink bug *Piezodorus guildinii* (Zerbino et al. 2014, 2015).

Not so dramatic, but apparently an adaptive ontogenetic seasonal polyphenism was found in *Graphosoma lineatum*. In Sweden, the majority of newly eclosed adults of this species appearing in the late summer have no or very little red pigmentation. Instead, they exhibit a pale, light brownish (epidermis) and black (melanized cuticula) striation. These adults leave their host plants for overwintering in the ground. When they appear again on their flowering host plants in early summer after winter adult diapause, they show the typical red-and-black striation. Thus, the pale stripes turn red sometime before the postdiapause reproductive period. It is stressed that the two broad functions of protective coloration, camouflage and warning coloration, need not be mutually exclusive. It also is apparent that the five nymphal instars are all colored in various shades of brown and black and appear quite cryptic when feeding on seeds in the dried umbels of host plants (Tullberg et al. 2008).

In *Podisus maculiventris*, the degree of melanization also changes over the seasons, and adults are brighter in mid-summer than in spring or autumn. However, this response is mostly controlled by temperature, not day length (Aldrich 1986).

Analysis of the above examples of seasonal body color changes in pentatomoids easily reveals the dominant 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 also may give a certain adaptive advantage in **thermoregulation**, even during the winter. However, exceptions also are known (e.g., the pentatomid *Oebalus poecilus* is darker during the reproductive season than during overwintering; Albuquerque 1993).

The significance of seasonal body color changes is especially high in species forming large aggregations in winter and/or summer diapause sites; these color changes are common among pentatomoids.

It is important to note that day-length-controlled body color polyphenism has been found not only in adults where, in some cases it precedes diapause or is not directly linked to diapause, but also has been found in nymphs. In the nymphs of the pentatomid *Plautia stali* in Japan, six coloration forms (phenotypes) can be distinguished with cuticle color varying from green to dark brown (**Figure 11.19**). The incidence of these forms is controlled by photoperiod: under long-day conditions, incidence of brightly-colored nymphs is higher; under short-day conditions, more intense pigmentation is evident. Diapause in this species also is controlled by day length, but it is linked to the adult stage (**Figure 11.19**; Numata and Kobayashi 1994).

Somewhat similar was found in the predatory pentatomid *Arma custos* (Volkovich and Saulich 1995). In this species, short-day and low-temperature conditions stimulated appearance of dark-colored nymphs, whereas under long-day and high-temperature conditions incidence of nymphs with such coloration pattern was much lower and most or all nymphs were brightly colored (**Figure 11.20**). Similarly to the just described case of *Plautia stali*, induction of adult diapause and body color determination in nymphs in *A. custos* are two independently controlled processes because they are not only linked to different developmental stages (adults and nymphs) but also have different temperature optima. Thus, the
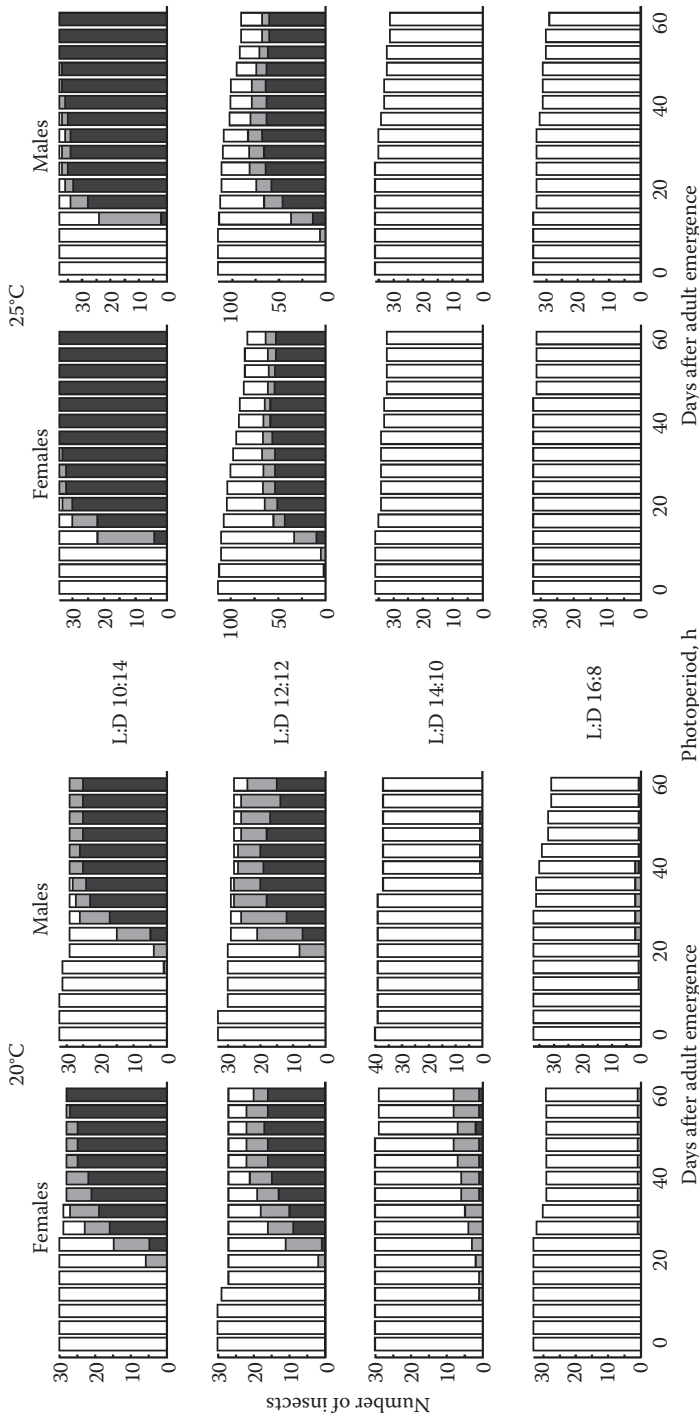
FIGURE 11.16 Effect of photoperiod and temperature on body coloration of adults of the southern green stink bug, *Nezara viridula*, from Osaka, Japan (34.7°N). Nymphs were reared to adults and then maintained under constant experimental conditions indicated in the figure: photoperiod is indicated in the center; temperature was 20°C (left) or 25°C (right). The body color of adults is shown as follows: light sections of bars: green; shaded sections of bars: intermediate coloration; black sections of bars: brown/russet. Note that normally brown/russet coloration of adults is associated with diapause (see text for details). (From D. L. Musolin and H. Numata, Physiological Entomology 28: 65–74, 2003, with permission.)
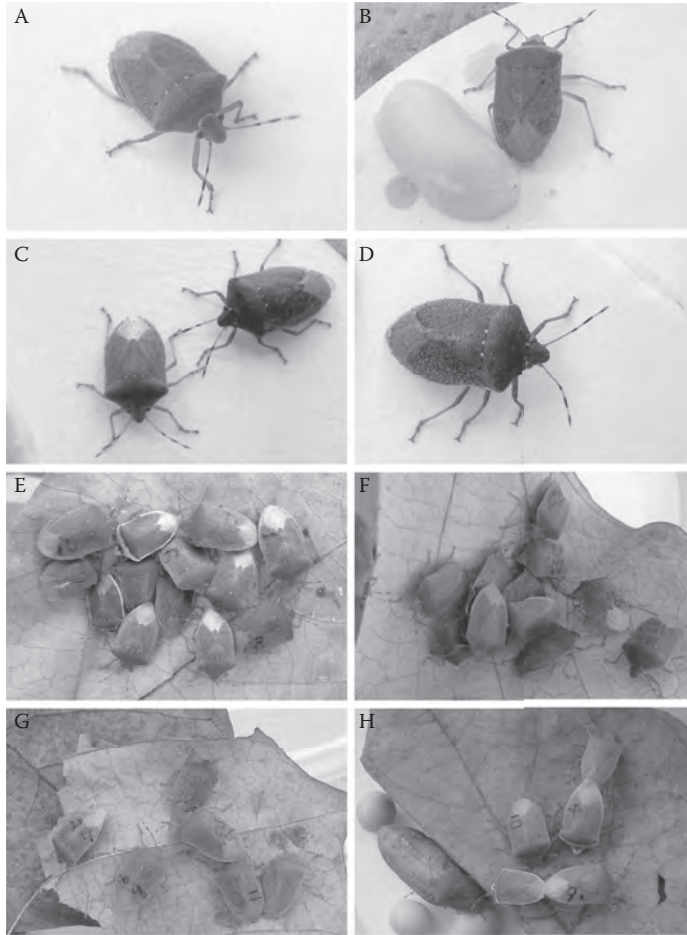
FIGURE 11.17   (See color insert.) Diapause-associated body color changes in the southern green stink bug, *Nezara viridula*, reared under laboratory or quasi-natural outdoor conditions. Laboratory rearing in Kyoto (Japan): reproductive (i.e., nondiapause) green adult (A). Adults of the intermediate body color grade (B, C left). Diapausing russet (brown) adults (C right, D). Outdoor rearing in Kyoto: mostly intermediate colored and russet overwintering adults at the early stages of diapause (November–December; E, F); adults of different body color grades at the later stage of diapause (March; G); diapause termination, body color change and beginning of postdiapause reproduction (April; H). (From D. L. Musolin, *Physiological Entomology* 37: 309–322, 2012, with permission.)

PhPR of adult diapause induction is most clear at high temperatures (27 to 30°C) and completely suppressed by low temperature, whereas photoperiodic control of body color in nymphs manifested itself under all tested conditions (Volkovich and Saulich 1995). Taking into consideration that incidence of dark-colored nymphs is much higher under short-day and low-temperature conditions (**Figure 11.20**), it might be speculated that appearance of pigmented nymphs is related to thermoregulation and takes place in colder periods of late spring (and early autumn in the regions where two generations can be produced per year; see **Chapter 12**). It is well documented that melanization of insect cuticle in the spring and autumn (when days are short) enhances absorption of solar insulation and, as a result, the body temperature can be up to 10 to 15°C higher than the air temperature (Hoffmann 1974, Tauber et al. 1986). Lighter color, due to low pigmentation, helps avoid overheating during the hottest days in mid-summer.

An interesting and complex case of seasonal body color change was reported in the parent bug, *Sinopla perpunctatus* (Faúndez and Osorio 2010). In southern Chile (53°S), this species has a univoltine seasonal cycle. Young adults of both sexes are dark green when they emerge in late summer as are the leaves on
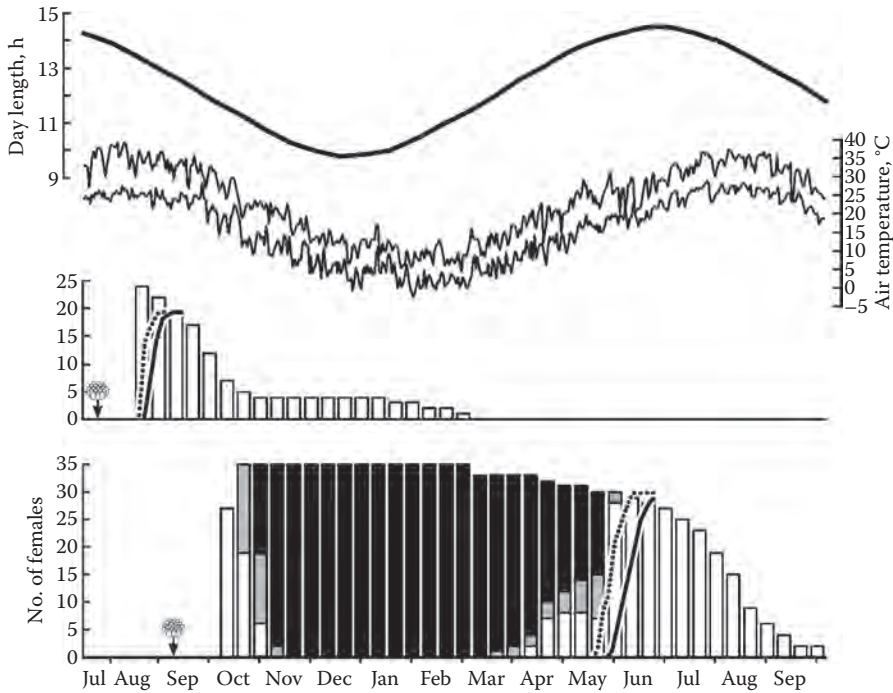
FIGURE 11.18 Seasonal body color changes in female of the southern green stink bug, *Nezara viridula*, under natural conditions in Osaka, Japan (34.7°N). The upper experimental series corresponds to the mid-summer reproductive (i.e., nondiapause and directly breeding) generation; the lower series, the late-season diapausing generation. Arrow marks the moment when the egg clusters were transferred into outdoor conditions to start each experimental series. The nymphs and males are not shown. The histogram shows the number and color of females as follows: Light sections of bars: green females; shaded sections of bars: females with intermediate body color; black sections of bars: brown/russet females. Dotted line: the total number of mating females; solid line: that of ovipositing females. The temperature is shown as the minimum and maximum daily values. (Modified from D. L. Musolin and H. Numata. Ecological Entomology 28: 694–703, 2003, with permission.)

their host plant. For overwintering, adults change body color to orange, which also is adaptive because leaves are reddish/brown in the autumn and the litter in which the adults overwinter is dark. In spring, both females and males change body color and starting at this moment the trajectories of body color begin to differ between the sexes. Males turn dark green and die after copulation. Females, on the other hand, turn light green, and their body color corresponds to the color of the lower surfaces of leaves where females guard their only egg cluster; they remain with the resulting brood until the nymphs reach the last instar. Only after this prolonged guarding, females turn dark green and then either die or probably overwinter again. It has been speculated that this seasonal polyphenism (or at least one of its phase, namely, light green to dark green transition) is not regulated by day length but, rather, linked to sexual maturation and copulation, as this transition is characteristic only of females. The control mechanism of body color change in this species still needs to be determined. Nevertheless, the whole pattern looks very adaptive and linked to parental care, a behavioral strategy well known in acanthosomatids and some other true bugs (Cobben 1968, Tallamy and Wood 1986, Kudo 2006).

In the case of **seasonal morphological polyphenism**, **seasonal forms** (sometimes called **seasonal morphs**) can differ morphologically. For example, the bugs can have different shapes of spines on the pronotum as in the pentatomids *Euschistus tristigmus tristigmus* (McPherson 1975a,b), *Oebalus ypsilongriseus* (Vecchio et al. 1994, Panizzi 2015), *Euschistus heros* (Mourâo and Panizzi 2002), and *Dichelops melacanthus* (Chocorosqui and Panizzi 2003). These are the examples of irreversible seasonal polyphenism.
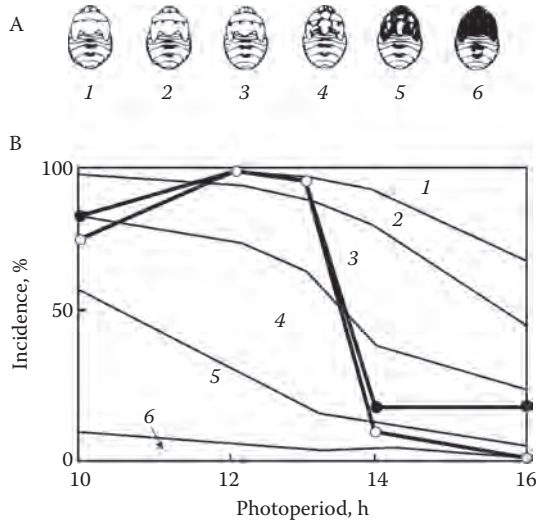
FIGURE 11.19 Effect of photoperiod on body color of the fifth instar nymphs, and photoperiodic response of adult diapause induction in the pentatomid *Plautia stali* from Tawaramoto, Japan (34.5°N). Grades of body color in fifth instars (A) are shown above the graph (B) with comparison of the photoperiodic response curves controlling the induction of adult diapause in females and males (thick lines) and the determination of body color of nymphs (thin lines). Close circles, males; open circles, females. Incidence on the vertical axis refers to the incidence of diapause (thick lines) and the incidence of color grades of nymphs (thin lines). Nymphs were reared and adults were then maintained under constant photoperiodic conditions (indicated under the horizontal axis) at temperature 25°C. Numerals on the graph indicate grades of body color in nymphs. (From H. Numata and S. Kobayashi, Experientia 50: 969–971, 1994, with permission.)
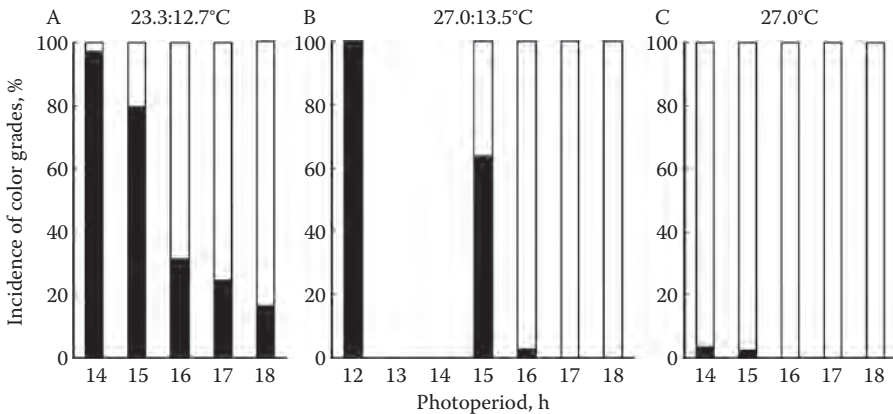
FIGURE 11.20 Effect of photoperiod and temperature on body color of nymphs of the predatory pentatomid *Arma custos* from Belgorod Province, Russia (50°N). Nymphs were reared to adults and then maintained under constant photoperiods (indicated under the horizontal axes) but different temperatures: A – outdoor rearing under constant photoperiods and mean day temperature 23.3°C and mean night temperature 12.7°C (i.e., a rhythm of mean temperatures 23.3:12.7°C); B – laboratory rearing under constant photoperiods and constant day temperature 27.0°C and constant night temperature 13.5°C (i.e., rhythm of temperature 27.0:13.5°C); C – laboratory rearing under constant photoperiods and constant temperature 27.0°C. Overall mean temperature in the treatment B was higher than in the treatment A, but lower than in the treatment C. Light sections of bars: brightly-colored nymphs; black sections of bars: dark-colored nymphs. (Modified from T. A. Volkovich and A. Kh. Saulich, Entomological Review 74: 151–162, 1995, with permission.)

Interestingly, if the definition of polyphenism, or environmental polymorphism, is analysed (different phenotypes are produced by one genotype under different environmental conditions), it becomes apparent that any case of photoperiodically controlled diapause induction can be considered as an example of such polyphenism: diapause and nondiapause phenotypes are produced by one genotype even though after overwintering (or the end of summer diapause), the diapause phenotype becomes undistinguishable from the nondiapause phenotype. This concept was introduced by Walker (1986), but in the literature facultative diapause and polyphenism are still usually treated separately.

11.8 Summer Diapause (Estivation)

As briefly discussed above (**Section 11.2.4**), diapause can take place not only in winter, but also in summer. In the latter case, diapause is formed under conditions of long day and high temperature and often associated with low humidity and low food availability. Such diapause not only ensures survival of insects during a season of unfavorable conditions but may also perform synchronizing functions in summer by postponing the subsequent ontogenetic stages to later periods (see **Chapter 12**). Similarly to winter diapause, summer diapause can be obligate (i.e., occurring every year and in each generation) or facultative (i.e., induced by external factors such as day length, temperature, or food; see **Section 11.2.3**; Masaki 1980; Saulich and Volkovich 1996, 2004). It also may be linked to any developmental stage from egg to adult, but this link is usually species-specific (i.e., a species can estivate only in a particular stage; see **Section 11.2.2**). In contrast to winter diapause, summer diapause does not last long and its duration is unlikely to be more than a few weeks.

Some true bug species may be able to form both winter and summer diapauses in their seasonal cycle (e.g., pentatomids *Scotinophara lurida* [Fernando 1960] and *Picromerus bidens* [Musolin and Saulich 1996b, 2000]). These diapauses can be linked to the same or (what happens more often) different ontogenetic stages and be of the same or different forms (obligate or facultative).

Even though environmental conditions (at least thermal and photoperiodic) differ greatly between summer and winter, in many respects summer diapause is similar to winter diapause. Both of them are formed well in advance of the actual deterioration of environmental conditions. Preparation for summer diapause is associated with pronounced physiological changes and increasing nonspecific resistance to unfavorable conditions similar to a set of adaptations well known for winter diapause. However, summer diapause is much less studied and likely to be less common among Pentatomoidea as well as other insects.

Although summer diapause is observed more frequently in insects from the tropical or subtropical zones (Masaki 1980), species that include summer diapause in their seasonal cycles also can be found in the Temperate Zone. Among pentatomoids, studied examples of summer adult diapause include the Oriental green stink bug, *Nezara antennata* (Noda 1984), *Carbula humerigera* (Kiritani 1985a,b), the predatory pentatomid *Picromerus bidens* (Musolin 1996; Musolin and Saulich 1996b, 2000), and a scutellerid *Poecilocoris lewisi* (Tanaka et al. 2002).

Adults of some species migrate into the mountains before summer diapause (the pentatomid *Aelia rostrata* in Turkey ascends to about 1,500 meters above sea level; Şişli 1965). Some species can migrate twice – first to the estivation quarters and later in the season – from the estivation quarters to the hibernation quarters (e.g., berry bug, *Dolycoris baccarum*; Krambias 1987).

Even these few example of summer diapause in pentatomoids demonstrate clearly the importance of this seasonal adaptation in insect life cycles and the ways in which this additional period of dormancy can optimize seasonal development of populations.

Finally, in some species or populations, diapause that is formed in summer does not end in autumn and instead lasts until the end of winter. Such a pattern might be called **summer–winter diapause**. This diapause pattern, for example, might explain what is occurring in the plataspid *Coptosoma scutellatum* (see **Chapter 12**). Every such case must be studied comprehensively because summer–winter diapause might, in fact, turn out to consist of two diapauses (i.e., summer and winter) with short and hardly detectable period between them.

11.9 Other Seasonal Adaptations

It is obvious that winter diapause is an important seasonal adaptation of pentatomoids as well as the great majority of other terrestrial and aquatic insects. It not only is crucial for surviving winters in many (if not most) regions of the globe but also important for synchronizing insects' life cycles with local conditions (Danilevsky 1961, Saunders 1976, Tauber et al. 1986, Danks 1987). However, winter diapause is actually only one (although very complex) seasonal adaptation out of many species- or population-specific physiological, biochemical, behavioral, ecological, or morphological adaptations utilized by true bugs and other insects in seasonally variable environments (Musolin and Saulich 1996b, 1997, 1999; Saulich and Musolin 1996, 2007a,b, 2009, 2012, 2014; Numata and Nakamura 2002; Numata 2004). Many of these adaptations are still more or less directly linked to overwintering (as with seasonal migrations or polyphenism; see **Section 11.7**), whereas others likely are not. A few examples of adaptations that are not directly related to overwintering, but still enhance the ability of pentatomoids to survive and take advantage in utilization of seasonally variable environmental conditions, are given below in this section.

Parental care (or **maternal care**, **care behavior**, **maternal instinct**) is an interesting peculiarity of Pentatomoidea. In most cases, this subsocial behavior is probably not linked directly to winter diapause but apparently is an important element of seasonal development and the reproductive cycle. Parental care is characteristic of many families of Pentatomoidea, such as Acanthosomatidae (Tallamy and Wood 1986, Tallamy and Schaefer 1997, Tallamy 2001, Faúndez and Osorio 2010), Cydnidae (Filippi et al. 2009), Scutelleridae (Nakahira 1994, Peredo 2002), Parastrachiidae (Filippi et al. 2000b, 2001; Gibernau and Dejean 2001), and Tessaratomidae (Gogala et al. 1998, Monteith 2006).

A comparative analysis of parental care in heteropteran taxa demonstrates that there are different levels of complexity of such behavior ranging from rather simple responses to complex patterns (Tallamy and Schaefer 1997, Hanelová and Vilímová 2013). In numerous primitive cases, females simply protect egg masses with their bodies from parasitoids and predators (including conspecific males) until nymphs hatch. In other cases (e.g., burrower bugs *Sehirus luctuosus* and *Tritomegas bicolor*), females not only guard egg clusters but also carry them from one microhabitat to another, trying to find the most favorable conditions for embryogenesis (Korinek 1940). In even more sophisticated cases of parental care, females not only guard their eggs and nymphs but also bring food for the progeny or even produce additional nonfertilized eggs as food for young nymphs after hatching (e.g., *Adomerus triguttulus* [Nakahira 1994], *Parastrachia japonensis* [Filippi et al. 2000b], *Canthophorus niveimarginatus* [Filippi et al. 2009]). The ecological importance of parental care as a seasonal adaptation is well documented in the Acanthosomatidae, Cydnidae, and Parastrachiidae but still needs to be further evaluated and properly understood.

Seasonal change in reproductive allocation varies during the reproductive period in the parent bug, *Elasmostethus interstinctus* (Mappes et al. 1996). At the beginning and middle of the reproductive period, females lay smaller eggs than at the end of the period. Cluster size and number of eggs per clutch decrease in laying sequence, earlier clusters being much larger than later clusters. Lifetime fecundity of females correlate positively with female size: large females produce more eggs and live longer than small ones. At the same time, egg size does not vary with female size. Offspring survival until adulthood increases with egg weight. In this species, individuals overwinter before reproduction, and, because the nymphs from later-laid eggs have the least time to gather resources before overwintering, it may be important for the later-laid eggs to be of higher quality. Reproductive allocation varies during the reproductive period; females allocate relatively more resources to offspring number at the beginning of the reproductive season and more to offspring quality at the end of their life (Mappes et al. 1996).

Seasonal food plant change allows insects to fully utilize the warm season even if the primary food plant is not available from early spring to late autumn. Thus, in Germany, during spring and early summer, nymphs of the parent bug *Elasmucha grisea* develop exclusively on birch (*Betula pendula* Roth) and cannot develop successfully on alder [*Alnus glutinosa* (L.) Gärtner] before early August. Only then do the adults shift to alder and utilize it until the end of the season. Alternative choice tests and oviposition experiments in the laboratory also showed a preference of adult *E. grisea* for birch in spring and alder in summer. This changing food plant preference guarantees an optimum efficiency of the reproductive

potential of this species as the two generations of *E. grisea* feed on the two food plants successively (Melber et al. 1981).

A somewhat similar situation has been found in a few polyphagous pentatomids such as *Halyomorpha halys* (= *H. mista*) (Kawada and Kitamura 1983), *Nezara viridula*, *Piezodorus guildinii*, and *Euschistus heros* (Panizzi 1997, 2007). Undoubtedly, polyphagy allows many pentatomoids to use several food plants, produce more generations, and fully utilize local thermal conditions by earlier commencement of active development in spring and later formation of winter diapause (or developing without any dormancy period in some tropical regions) compared to monophagous true bugs.

Seasonal variation of microhabitat selection is somewhat different than the just described seasonal food plant change. In tropical Brazil, *Phloea subquadrata* (Phloeidae) does not need the pronounced winter diapause; its adults and nymphs are active all year round, but the egg-laying season is restricted mainly to the warm, rainy season. To deal with the annual sequence of dry and wet seasons, this species has evolved a seasonal change in microhabitat selection: under dry weather conditions, phloeids are found closer to the base of the host tree [*Plinia cauliflora* (Mart.) Kausel; Myrtaceae] trunks; in the rainy season, the bugs climb and live higher on the same tree (Salomão and Vasconcellos-Neto 2010).

11.10 Conclusions

The above review of diapause in the experimentally studied pentatomoids (82 species), mostly from the Temperate Zone, has revealed no distinct trends in the type (embryonic, nymphal, or adult), form (obligate or facultative), or seasonal class (winter or summer) of diapause in particular taxa within the superfamily.

Earlier analysis of seasonal development of Pentatomidae resulted in a similar conclusion; evolution of their seasonal adaptations does not correspond precisely to the phylogeny of the family (Saulich and Musolin 2012). However, similar complexes of seasonal adaptations might be formed within individual genera (e.g., *Palomena* with an obligate diapause and photoperiodic control of nymphal growth rates, or *Euschistus* with photoperiodic control of body color polyphenism), small tribes (e.g., Aeliini), or even subfamilies (e.g., Podopinae). At the same time, the large subfamily Pentatominae, despite being a polyphyletic taxon, is quite uniform in that most of the species have facultative winter adult diapause.

The seasonal changes of body coloration are more widespread in Pentatomidae (mostly those having winter adult diapause) than in other taxa of true bugs. However, other seasonal adaptations that are common in some heteropteran taxa such as wing size/wing muscle seasonal polyphenism (Saulich and Musolin 2007a,b) have been found so far only in one pentatomoid species (burrower bug *Scaptocoris carvalhoi*; Nardi et al. 2008).

Knowledge of ecology and seasonal development of a species may in some cases help clarify its taxonomic position. For example, *Dybowskyia reticulata* is considered a member of the tribe Tarisini by some authors (Vinokurov et al. 2010) and a member of the Graphosomatini by others (Gapon 2008). In its ecological characteristics, *D. reticulata* resembles species of Graphosomatini and this ecological trait should be taken into consideration in its classification.

In general, despite intensive studies of seasonal adaptations in pentatomoids and other heteropteran taxa in recent decades, diapause and ecological mechanisms of its control have been studied in less than 1% of the known species of true bugs. Clearly, more research is needed.

The role that individual seasonal adaptations and their complexes play in the structure of the species' seasonal cycle will be discussed in detail in **Chapter 12**.

11.11 Acknowledgments

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11.13 Glossary

Definitions apply to usage in **Chapters 11 and 12** and do not necessarily cover all meanings of particular terms. Cross-referenced entries within a definition are **boldfaced**. In a few cases of specific terms, references are given (for full reference citations, see References Cited section of this chapter).

Active development: see **Active seasonal development** and **Active physiological state**

Active physiological state: (1) on the organism level, physiological state of an individual (i.e., growth and metamorphosis), opposite of **dormancy** (first of all **diapause**); **(2)** on the population level, corresponds to **active seasonal development**. Synonyms: **Active development**, **Nondiapause development**

Active seasonal development: development of nondiapause individuals or **generation(s)** (e.g., growth, metamorphosis, and reproduction). Synonyms: **Active development**, **Active physiological state**, **Nondiapause development**. Antonyms: **Diapause**, **Dormancy**

Adult diapause: diapause at the adult stage (both in females and males), typically manifests itself as arrested development of reproductive system (i.e., arrested maturation of gonads, activity of reproduction-related glands, blocked oogenesis, absence of oviposition, etc.) and absence of reproductive behavior. Synonyms: **Imaginal diapause**, **Reproductive diapause**

***Aelia*-like response:** restoration of sensitivity to **day length** after a short refractory period (during **winter diapause**; see Hodek 1971a). Synonym: **Recurrent response**

Aestivation: see **Summer diapause.** Alternative spelling: **Estivation**

Annual cycles: see **Seasonal cycle**

Apterous adults: see **Aptery**

Aptery: anatomical condition (i.e., morph or form) of an adult insect completely lacking any wings. Synonyms: **Apterous adults, Winglessness**

Bivoltinism: special case of **multivoltinism**, characterized by development of only two **generations** per year, one in spring (or early summer) and one in autumn (or late summer)

Body color polyphenism: see **Seasonal body color polyphenism**

Brachypterous adults: see **Short-winged adults**

Brachyptery: see **Short-winged adults**

Care behavior: see **Parental care**

Changing day length: (1) under field conditions: natural seasonal change of **day length**; day increases until the day of summer solstice (June 20 to 22 in the Northern Hemisphere [i.e., **increasing day length, or photoperiod**]) and then decreases until winter solstice (December 20 to 23 in the Northern Hemisphere [i.e., **decreasing day length, or photoperiod**]); **(2)** under laboratory conditions: a special experimental protocol mimicking natural seasonal change of **day length** set up as an artificial shortening or lengthening of **photophase** and **scotophase** from one day to another (or with another interval)

Changing photoperiod: see **Changing day length**

Chill intolerance: see **Freeze intolerance**

Civil twilights: the lightest parts of twilights; consist of the morning civil twilight (begins when the geometric center of the Sun is 6° below the horizon [i.e., civil dawn] and ends at sunrise or when the geometric center of the Sun is 0°50′ below the horizon) and evening civil twilight (begins

at sunset or when the geometric center of the sun is 0°50′ below the horizon and ends when the geometric center of the Sun reaches 6° below the horizon [civil dusk]); many insect species perceive civil twilights as a part of **photophase**

Cold hardiness: ability of an organism to survive at low temperature; it can be achieved by three strategies: **cryoprotective dehydration**, **freeze intolerance**, and **freeze tolerance**. Synonym: **Cold tolerance**

Cold termination of winter diapause: termination of **winter diapause** in response to exposure to low temperatures (usually above 0°C); often considered as a result of the **tachytelic process**

Cold tolerance: see **Cold hardiness**

Conditional polyphenism: see **Polyphenism**

Critical day length: see **Critical photoperiod**

Critical photoperiod: under field conditions or in the laboratory, **photoperiod** (i.e., **day length**) at which 50% of individuals of a particular population at particular temperature (especially in the laboratory) demonstrate clearly **photoperiodic response** (e.g., enter **diapause**). Synonyms: **Critical day length**, **Photoperiodic threshold**

Cryophase: lower-temperature phase of the **thermorhythm** in a laboratory experiment

Cryoprotective dehydration: one of three strategies of **cold hardiness**; survival of subzero temperatures by losing osmotic water to the surrounding environment, so resulting in an increase of the concentration of their body fluids and, thus, a decline in their melting point (to equilibration with the ambient temperature); as a result, they cannot freeze (Zachariassen 1985, Bale 2002, Sinclair et al. 2003)

Crystallization temperature: see **Supercooling point**

Day length: duration (in hours and minutes) of the light part of a daily cycle (i.e., **photophase**). Synonym: **Photoperiod** (note that **day length** usually refers to the field situation, whereas **photoperiod** to laboratory experiment). Antonym: **Night length** (i.e., **Scotophase**). Laboratory photoperiod is usually indicated as, e.g., L:D 16:8, where L is light period, or **photophase** (16 hours), and D is dark period, or **scotophase** (8 hours)

Day-length sensitive stage: see **Sensitive stage**

Decreasing day length: see **Changing day length**

Decreasing photoperiod: see **Changing day length**

Degree-days: a method of estimation of thermal (i.e., temperature) requirements of organisms (populations, species) or resources of particular locations or regions; total degree-days from an appropriate starting date or temperature level are used to understand **voltinism** of species or develop pest control strategy; computed as the integral of a function of time that generally varies with temperature. See **Sum of effective temperatures**

Development(al) threshold: see **Lower development threshold**

Diapause: profound, endogenously, and centrally mediated interruption that routes the developmental program away from direct morphogenesis into an alternative diapause program of succession of physiological events; the start of diapause usually precedes the advent of adverse conditions, but the end of diapause need not coincide with the end of adversity (Koštál 2006)

Diapause, forms of: diapause can be of two forms – **facultative diapause** and **obligate diapause**

Diapause, seasonal classes of: diapause can be of two seasonal classes – **winter diapause** and **summer diapause**

Diapause, types of: diapause can be linked to four (in Heteroptera – three) ontogenetic (i.e., developmental) stages and, thus, be of four (in Heteroptera – three) types – **embryonic** (i.e., **egg**) **diapause**, **nymphal** (i.e., **larval**) **diapause**, pupal diapause (not in Heteroptera), and **adult** (i.e., **reproductive**, or **imaginal**) **diapause**

Diapause development: slow and dynamic changes (i.e., physiological processes) in internal state of diapausing individual leading to **diapause termination**

Diapause induction: in species with **facultative diapause**, such **diapause** needs to be induced (i.e., initiated) by an environmental cue and, thus, this cue needs to be perceived, transmitted, and

interpreted by the neurohormonal system of the individual; this cue switches the ontogenetic pathway from **active physiological state** to **diapause**

Diapause phase: central phase of **diapause**; consists of three subphases: **initiation**, **maintenance**, and **termination**

Diapause syndrome: complex of morphological, physiological, and behavioral traits associated with **diapause** (Tauber et al. 1986); often used as a synonym of **diapause**

Diapause termination: end of **diapause**; gradual changes that occur during **diapause development** and result in its ending

Diapausing stage: ontogenetic (i.e., developmental) stage at which diapause occurs. In pentatomoids, it can be the egg (i.e., embryonic), nymphal, or adult stages

Direct development: individual **active physiological state** without interruption for physiological **dormancy**; opposite to **diapause** or any other form of **dormancy**. Synonym: **Nondiapause development**. Antonym: **Diapause**, **Diapause development**

Dispersal: general term for movement of insects; scattering or spreading of members of one population in space, with different purposes, usually resulting in increasing of mean distance among members of the population (see Dingle 1996)

Dormancy: general term covering any state of suppressed development (i.e., developmental arrest) that is adaptive (that is ecologically or evolutionarily meaningful and not just artificially induced) and usually accompanied with metabolic suppression (Koštál 2006)

Ecological polymorphism: see **Polyphenism**

Egg diapause: see **Embryonic diapause**

Embryonic diapause: diapause at the embryonic (i.e., egg) stage of ontogenesis; typically manifests itself as arrested embryogenesis (i.e., postponed hatching of nymphs). Synonym: **Egg diapause**

Endogenous processes: processes that originate from within an organism; internal. Antonym: **Exogenous processes**

Endogenous univoltinism: pattern of **univoltinism** based on **obligate diapause**; seasonal development with completion of strictly only one **generation** during the **vegetative season** or year. See **Univoltine seasonal cycle**

Environmental polymorphism: see **Polyphenism**

Estivation: see **Summer diapause.** Alternative spelling: **Aestivation**

Estivation quarters: microhabitats used by insects to survive during **summer diapause** (i.e., **estivation**). Synonyms: **Estivation sites**

Estivation sites: see **Estivation quarters**

Exogenous processes: processes that originate from outside of an organism, from its environment; external. Antonym: **Endogenous processes**

Exogenous univoltinism: pattern of **univoltinism** in species or populations that potentially can have **multivoltine seasonal cycles**, but whose **seasonal development** is limited by completion of strictly only one **generation** during the **vegetative season** or year; such pattern is controlled by external factors. See **Univoltine seasonal cycle**

Facultative: optional or discretionary, something that must be induced. See, for example, **Facultative diapause.** Antonym: **Obligate**

Facultative diapause: **diapause** that is not obligate but induced in particular **generation** by external factors (e.g., **day length**, temperature, food, humidity); it can, but does not necessarily, occur in each **generation**

Food-mediated diapause: **facultative diapause** that is induced by trophic factor (i.e., food or diet) – seasonal change of quality or availability of food. Synonym: **Trophic diapause**

Freeze avoidance: see **Freeze intolerance**

Freeze intolerance: one of three strategies of **cold hardiness**; the freeze intolerant species cannot survive the formation of ice within their bodies and, thus, have evolved a set of biochemical, physiological, behavioral, and ecological measures/adaptations aimed at prevention of ice formation. Synonyms: **Freeze avoidance**, **Freeze susceptibility**

Freeze susceptibility: see **Freeze intolerance**

Freeze tolerance: one of three strategies of **cold hardiness**; the freeze tolerant insects can withstand ice formation, usually only in the extracellular fluids, and have a set of characteristics that enables them to survive such ice formation

Generation: (1) all individuals of the population living and developing at the same time (i.e., started development approximately at the same time) and usually existing in the same physiological state (i.e., **active physiological state** or **diapause**); **(2)** a period of time necessary for completion of development of a full **life cycle**

Genetic polymorphism: case of **polymorphism** in which two or more different phenotypes (i.e., morphs or forms) are produced by different genotypes. Also see **Polyphenism**

Growing season: see **Vegetative season**

Heterodynamic seasonal cycle: **seasonal cycle** that corresponds to **heterodynamic seasonal development**

Heterodynamic seasonal development: type of **seasonal development** in which periods of **active seasonal development** alternate with periods of seasonal **dormancy** of varying duration and intensity (e.g., **winter diapause** or **summer diapause**). Also see **Heterodynamic seasonal cycle**

Hibernacula (singular: **Hibernaculum):** see **Hibernation quarters**

Hibernaculum (plural: **Hibernacula):** see **Hibernation quarters**

Hibernation: see **Winter diapause**

Hibernation quarters: microhabitats used by insects to survive during **winter diapause** (i.e., **hibernation**). Synonyms: **Hibernaculum** (plural: **Hibernacula), Hibernation sites, Overwintering sites**

Hibernation sites: see **Hibernation quarters**

Homodynamic seasonal cycle: seasonal cycle that corresponds to **homodynamic seasonal development**

Homodynamic seasonal development: type of **seasonal development** in which **active seasonal development** is not interrupted by periods of seasonal **dormancy**; it is typical only for very stable and warm environmental conditions (e.g., tropical and subtropical regions, caves, subterranial microhabitats, artificial constructions such as grain storage barns). See **Homodynamic seasonal cycle**

Horotelic process: slow, spontaneous, and endogenous internal physiological processes of **diapause development** that proceeds under stable environmental conditions (i.e., when there are no dramatic changes of environmental conditions) and leads to **spontaneous diapause termination**. See **Tachytelic process**

Imaginal diapause: see **Adult diapause**

Increasing day length: see **Changing day length**

Increasing photoperiod: see **Changing day length**

Induced diapause termination: diapause termination based on physiological processes induced by external conditions (i.e., exogenous, nonspontaneous); it is equivalent and the result of **tachytelic process**; can proceed only under influence of changes in environmental conditions

Induction subphase: only in the case of **facultative diapause**, subphase of **prediapause phase** during which the ontogenetic pathway is switched from **direct development** to **diapause**

Initiation subphase: subphase of **diapause phase** during which direct development ceases, deep physiological preparations take place, and intensity (or deepness) of diapause may increase

Larval diapause: see **Nymphal diapause**

Life cycle: sequence of life stages (in Heteroptera – egg, nymphal, and adult stages) that an organism undergoes from birth to reproduction and death. Compare to **Seasonal cycle**

Long day: for a particular population and conditions (first of all temperature), daily cycle with **photophase** longer than the **critical photoperiod**

Long-day conditions: day-length (i.e., **photoperiodic) conditions** with **photophase** longer than **critical photoperiod**; for majority of insect in the Northern Hemisphere, the conditions with **photophase** that induces **active physiological state** (i.e., **nondiapause development**). Antonym: **Short-day conditions**

Long-day diapause: facultative summer diapause induced under **long-day conditions** in early or mid-summer in the Northern Hemisphere. In laboratory, such **diapause** usually can be induced under **photoperiodic conditions** with **photophase** longer than 12 hours of light

Long-day photoperiodic response: see **Long-day type photoperiodic response of diapause induction**

Long-day type photoperiodic response of diapause induction: photoperiodic response that induces **active physiological state** under **long-day conditions** and **facultative diapause** under **short-day conditions**; a typical **photoperiodic response** in populations that have facultative **winter diapause** and **multivoltine seasonal development**. Synonym: **Long-day photoperiodic response**

Long-winged adults: adults with fully developed wings. Wing length may be controlled genetically (see **Wing polymorphism**) or environmentally (see **Wing polyphenism**). Synonym: **Macropterous adults, Macroptery**. Antonyms: **Short-winged adults, Brachypterous adults, Brachyptery**

LDT: see **Lower development threshold**

Lower development threshold: species- or ontogenetic-stage-specific temperature below which growth and development (i.e., morphogenesis) do not take place. Synonym: **Development(al) threshold**. Abbreviation: **LDT**

Macropterous adults: see **Long-winged adults**

Macroptery: see **Long-winged adults**

Maintenance subphase: subphase of **diapause phase** during which the endogenous developmental arrest persists regardless of environmental conditions

Maternal care: see **Parental care**

Maternal instinct: see **Parental care**

Migration: complex form of movement of individuals and populations characterized by the following parameters: (1) it is persistent; (2) it is straightened out; (3) it is undistracted by resources that would ordinarily halt it; (4) there are distinct departing and arriving behaviors; and (5) energy is reallocated to sustain it; not all migrants display all of these characteristics all of the time, but most will display most of them at least part of the time during which they are migrating; migrations often happen seasonally (Dingle 1996). See **Seasonal migrations**

Monovoltine seasonal cycle: see **Univoltine seasonal cycle**

Monovoltinism: see **Univoltinism**

Multivoltine seasonal cycle: seasonal cycle typical for **multivoltine seasonal development**. Synonym: **Polyvoltine seasonal cycle**

Multivoltine seasonal development: type of **seasonal development** with completion of two or more **generations** during the **vegetative season** or year; in the last seasonal **generation,** facultative **winter diapause** is formed

Multivoltinism: type of **seasonal development** with **multivoltine seasonal cycle**. See **Multivoltine seasonal development**

Night length: duration (in hours and minutes) of the night (i.e., dark) part of daily cycle (i.e., **scotophase**). Antonym: **Day length**

Nondiapause development: see **Direct development**, **Active physiological state**, and **Active seasonal development**

Nymphal diapause: diapause at the nymphal (i.e., larval) stage, typically manifests itself as arrested metamorphosis (i.e., absence of molting to the next nymphal or adult stage). Synonym: **Larval diapause**

Obligate: by necessity; genetically determined; something that should not be induced. See **Obligate diapause**. Synonym: **Obligatory**. Antonym: **Facultative**

Obligate diapause: diapause in which initiation needs no external signal or cues because it represents a fixed component of the ontogenetic program that is realized regardless of the environmental conditions in each **generation**; one of two forms of **diapause**. Antonym: **Facultative diapause**

Obligatory: see **Obligate**

Oligopause: form of **dormancy** with less intensive suppression of development than **diapause**

Overwintering: process of passing winter season with all associated unfavorable conditions (e.g., cold and/or subzero temperatures, ice, snow, and limited food availability)

Overwintering quarters: see **Hibernation quarters**

Overwintering sites: see **Hibernation quarters**

Packet of photoperiodic information: number of photoperiodic cycles (**short days** or **long days**) triggering **diapause** or **active physiological state**. Synonym: **Required day number**

Parental care: complex of behavioral traits that enhance the fitness of offspring. Synonyms: **Maternal care**, **Care behavior**, **Care behavior**, **Maternal instinct**

Partial generation: fairly common pattern in which, at the end of the appropriate **season**, some part of the population gives rise to the subsequent **generation** whereas the other part (usually the one that completed development somewhat later) enters **diapause**

Perennial seasonal cycle: see **Semivoltine seasonal cycle**

Phenology: (1) study of periodic plant and animal **seasonal cycle** events and how these events are influenced by seasonal and interannual variations in climate, as well as habitat factors (such as elevation); **(2) seasonal development** of a population in a particular year

Phenophase(s): particular phase(s) of **seasonal development** of a local population

Photoperiod: see **Day length**

Photoperiodic conditions: important characteristic of natural (i.e., field) conditions or laboratory regime in terms of light; usually understood as a ratio between **day length** (i.e. **photophase**) and **night length** (i.e., **scotophase**), but also might refer to intensity of light, its specter, duration of cycle (in laboratory), etc.

Photoperiodic control (i.e., regulation) of the nymphal growth rate: type of **photoperiodic response** that manifests itself as different rates of nymphal growth under different **photoperiodic conditions** (e.g., acceleration of growth under **short-day conditions** and retardation of growth under **long-day conditions**); note that some species do not have such **photoperiodic response**

Photoperiodic diapause termination: diapause termination that happens in response to change in **photoperiodic conditions**; often considered as a result of the **tachytelic process**

Photoperiodic refractoriness: period of insensitivity of insects to **day length**; usually after **overwintering**

Photoperiodic response: physiological reaction of an organism to the experienced **photoperiodic conditions** (e.g., **photoperiodic response of diapause induction**). Abbreviation: **PhPR**

Photoperiodic response of diapause induction: (1) physiological reaction of an organism to the experienced **photoperiodic conditions** that manifests itself in induction of one of two alternative physiological states – **facultative diapause** or **active physiological state**; **(2)** total of reactions of a particular population or laboratory cohort

Photoperiodic threshold: see **Critical photoperiod**

Photophase: light part of daily cycle. Antonym: **Scotophase**

PhPR: see **Photoperiodic response**

Polymorphism: presence in a population of two or more distinct phenotypes (i.e., morphs, forms) at the same ontogenetic stage (discontinuous variation). See **Genetic polymorphism**, **Polyphenism**

Polyphenism: special case of **polymorphism** when changes in frequencies of phenotypes are controlled by environmental conditions. Synonyms: **Environmental polymorphism**, **Ecological polymorphism, Conditional polyphenism**

Polyvoltine seasonal cycle: see **Multivoltine seasonal cycle**

Polyvoltinism: see **Multivoltinism**

Postdiapause phase: final phase of **diapause**; follows **termination subphase**; during this phase, insect often experience **postdiapause quiescence**

Postdiapause quiescence: quiescence that insects often experience in late winter and/or early spring when **active development** and metabolism are exogenously (i.e., externally) inhibited

Prediapause phase: first phase of **diapause** during which **direct development** (morphogenesis) continues and **diapause** is induced (in species with **facultative diapause**) or formed (in species with **facultative diapause** as well as **obligate diapause**)

Preparation subphase: subphase of **prediapause phase** during which individuals undergo behavioral and/or physiological change (e.g., acquire energy resources such as lipids), void digestive

system (gut), migrate and/or simply look for protective microhabitats (i.e., **hibernaculum**), sometimes change body color and so on

Pyrrhocoris-**like response:** insensitivity to **day length** when, in response to prolonged exposure to cold, some insects lose the ability to measure or respond to **day length** and, thus, develop without entering **diapause** under any **day-length conditions**

Qualitative photoperiodic response: photoperiodic response in which each individual responds in an "All or None" (i.e., "Yes or No") manner by choosing one of two alternative pathways (e.g., in the case of **adult diapause – diapause** or **direct development** [i.e., reproduction]). Antonym: **Quantitative photoperiodic response**

Qualitative PhPR: see **Qualitative photoperiodic response**

Quantitative photoperiodic response: photoperiodic response that controls quantitative parameters such as size, duration of a particular stage, or degree of pigmentation, etc. Antonym: **Qualitative photoperiodic response**

Quantitative PhPR: see **Quantitative photoperiodic response**

Quasi-natural experimental conditions: experimental set up in which insects are reared/maintained outdoors under conditions as much as possible mimicking the wild environmental conditions; for example, insect are reared in captivity in containers (e.g., Petri dishes, cages), but the containers are placed outdoors in such a way that insects can experience natural **day length**, temperature, and humidity, usually being only protected from direct sun light, rain, large predators, and parasitoids

Quiescence: an immediate response (without complex preceeding central neuroendocrine regulation) to a decline of any limiting environmental factor(s) below the physiological thresholds with immediate resumption of the processes if the factor(s) rise above them (Koštál 2006)

Recurrent response: see *Aelia*-**like response**

Reproductive diapause: see **Adult diapause**

Required day number: see **Packet of photoperiodic information**

Scotophase: night (i.e., dark) part of daily cycle. Antonym: **Photophase**

SCP: see **Supercooling point**

Seasonal adaptations: ability of organisms (in the form of physiological, biochemical or behavioral responses) to survive, take advantage in utilization of resources and form a specific and stable pattern of **seasonal development** (i.e., **seasonal cycle**) under seasonally changing local environmental conditions

Seasonal body color change: see **Seasonal body color polyphenism**

Seasonal body color polyphenism: example of **seasonal polyphenism** when during the season, two or more forms exist of the same ontogenetic stage (e.g., nymphs [larvae], pupae, or adults) with difference in body coloration. These different body color forms can be in different generations or coloration of one particular individual can change during its life (e.g., diapausing individuals change body color from green to russet and, then, upon diapause termination after overwintering, the body color changes back to green). Synonym: **Seasonal body color change**

Seasonal camouflage: ability an organism to avoid observation or detection by other organisms; passive protection from predators

Seasonal changes of degree of development of wing muscles: example of **seasonal polyphenism** when during the season, two or more forms of adults exist with difference in degree of development of wing muscles (e.g., a form with fully developed wing muscles and capable of flight and a form with weakly developed or reduced wing muscles and incapable of flight). Also see **Seasonal changes of wing size**

Seasonal changes of reproductive allocation: refers to the seasonal changes in the proportion of an organism's energy budget (or investment of resources) allocated to reproduction

Seasonal changes of wing size: example of **seasonal polyphenism** when during the season, two or more forms of adults exist with difference in degree of development of wings (in some species, can range from winglessness to fully developed wings, or **macroptery**). See **Long-winged adults**, **Short-winged adults**, and **Seasonal changes of degree of development of wing muscles**

Seasonal cycle: specific and stable pattern of realization of the **life cycle** of a species or population against the background of seasonally changing local environmental conditions; might either include or not periods of seasonal **dormancy**, **migrations** or other **seasonal adaptations**. Synonym: **Annual cycles**

Seasonal development: consecutive realization (i.e., completion) of **generation(s)** against the background of seasons in a particular location. **Active seasonal development** might alternate with periods of seasonal **dormancy** (i.e., **heterodynamic seasonal development**) or might go without such alteration (i.e., **homodynamic seasonal development**)

Seasonal food plant change: situation when during the **vegetative season** individuals of the same or different **generations** of a particular local population consequently use different plants as food plants (e.g., one plant species as a primary food plant in the early summer and then another plant species as a primary food plant in the late summer)

Seasonal forms: categories of individuals in a population that look differently as a result of **seasonal morphological polyphenism**; representation of **seasonal morphological polyphenism**. Synonym: **Seasonal morphs**

Seasonal migrations: strictly regular (seasonal) **migrations** linked to particular stages of **life cycle** and **seasonal cycle**, usually between breeding habitats and **hibernation quarters** and/or **estivation quarters**; as a rule, an essential part of the **seasonal cycle** of a population

Seasonal morphological polyphenism: example of **seasonal polyphenism** when during the season, two or more forms of the same ontogenetic stage (e.g., nymphs [larvae], pupae, or adults) exist and differ in morphology (e.g., differ in shape, size) of the whole body or particular organs

Seasonal morphs: see **Seasonal forms**

Seasonal polyphenism: special case of **polyphenism** when changes in frequencies of phenotypes are regular (i.e., annual, seasonal) and controlled by environmental conditions

Seasonal variation of microhabitat selection: situation when during the **vegetative season**, individuals of the same or different **generations** of a particular local population use different microhabitats (e.g., one microhabitat is preferred in summer and then another microhabitat is preferred in winter)

Semivoltine seasonal cycle: seasonal cycle typical for **semivoltine seasonal development**

Semivoltine seasonal development: seasonal development with completion of one **generation** over a period that is longer than one **vegetative season** or year

Semivoltinism: type of seasonal development with **semivoltine seasonal cycle**. See **Semivoltine seasonal development**

Sensitive stage: developmental (i.e., ontogenetic) stage(s) during which individuals of a particular species are sensitive to external signals (e.g., to **day length**). See **Sensitivity to day length**

Sensitivity to day length: ability of individuals to measure **day length** and discriminate **short days** from **long days**

SET: see **Sum of effective temperatures**

Short day: for a particular population and conditions (first of all temperature), daily cycle with **photophase** shorter than the **critical photoperiod**

Short-day conditions: photoperiodic conditions with **photophase** shorter than **critical photoperiod**; for majority of insect in the Northern Hemisphere, the conditions that induce **winter diapause**

Short-day diapause: facultative winter diapause induced under **short-day conditions** in late summer or autumn in the Northern Hemisphere; in laboratory, such **diapause** usually can be induced under **short-day conditions**

Short-day photoperiodic response: see **Short-day type photoperiodic response of diapause induction**

Short-day type photoperiodic response of diapause induction: photoperiodic response which induces **active physiological state** under **short-day conditions** and **facultative diapause** under **long-day conditions**; a typical **photoperiodic response** in populations that have facultative **summer diapause** and **bivoltine or univoltine seasonal development**. More common in insects living in tropical and subtropical regions; rare in the Temperate Zone. Synonym: **Short-day photoperiodic response**

Short-winged adults: adults with small (i.e., reduced in size, undeveloped) wings usually unsuitable for flight. Wing length may be controlled genetically (see **Wing polymorphism**) or

environmentally (see **Wing polyphenism**). Synonym: **Brachypterous adults, Brachyptery**. Antonyms: **Long-winged adults**, **Macropterous adults**, **Macroptery**

Signal factor: see **Signal function of ecological factors**

Signal function of ecological factors: reflects dual mode of action of ecological factors (primarily temperature, but also light, food, etc.) on living organisms; some ecological factors (e.g., day length, thermorhythm, quality of food) can be used as signals that predict the coming seasonal environmental changes (Tyshchenko 1980). See **Vital function of ecological factors**

Spontaneous diapause termination: diapause termination based on spontaneous (i.e., not induced by external conditions, endogenous) physiological processes; equivalent and result of **horotelic process**; can proceed without changes of environmental conditions

Sum of effective temperatures: sum of **degree-days** above the **lower development threshold** required for an insect stage or the ontogenesis to complete development. Abbreviation: **SET**

Summer diapause: diapause that takes place in summer; one of two seasonal classes of **diapause**. Synonym: **Estivation**. Alternative spelling: **Aestivation**

Summer–winter diapause: diapause that is formed in summer but does not end in autumn and instead lasts until the end of winter. In some cases, it is likely to consist of two diapauses (i.e., summer and winter ones) with short and hardly detectable period between them

Supercooling: the process of lowering the temperature of a liquid (i.e., water or any body liquids) below its freezing point without it becoming a solid (i.e., ice)

Supercooling point: the temperature at which spontaneous freezing occurs in a supercooled liquid. Synonym: **Crystallization temperature**. Abbreviation: **SCP**

Tachytelic process: fast and induced physiological process that evolves at a rate faster than in the case of **horotelic process**; internal physiological process of **diapause development** that proceeds under influence of change of environmental conditions and lead to **induced diapause termination** (see Hodek 1983, 1996, 2002). See **Horotelic process**

Temperature optimum of photoperiodic response: range of temperatures under which a particular **photoperiodic response** manifests itself adequately and is not suppressed by too low or too high suboptimal temperatures (e.g., in the case of **long-day diapause**, clear **active physiological state** is observed under **long-day conditions** and apparent **diapause** is induced under **short-day conditions**)

Termination subphase: final subphase of central **diapause phase** during which the intensity of **diapause** decreases and by the end of this subphase, a usual **active physiological state** is mostly reached

Thermoperiod: one of characteristics of **thermorhythm**; ratio between duration of **thermophase** (i.e., phase with higher temperature) and duration of **cryophase** (i.e., phase with lower temperature) in daily temperature cycle

Thermophase: higher-temperature phase of the **thermorhythm** in laboratory experiment

Thermoregulation: ability of an organism to utilize special behavioral or physiological adaptations in order to keep its body temperature within certain boundaries, even when the surrounding temperature is different

Thermorhythm: (1) under field conditions, a sinusoid changes of ambient temperature during daily cycle; **(2)** under laboratory conditions, experimental regime of temperature mimicking the natural dynamics of ambient temperature during daily cycle; in a simple case, **thermorhythm** (similar to **photoperiod**) consists of two phases (i.e., parts) – **thermophase** (with higher temperature) and **cryophase** (with lower temperature), which might (or might not) coincide with **photophase** and **scotophase**, respectively

Trivoltinism: special case of **multivoltinism**, characterized by development of three **generations** per **vegetative season** or year

Trophic diapause: see **Food-mediated diapause**

Univoltine seasonal cycle: seasonal cycle typical for **univoltine seasonal development**. Synonym: **Monovoltine seasonal cycle**

Univoltine seasonal development: seasonal development with completion of strictly only one **generation** during the **vegetative season** or year

Univoltinism: type of **seasonal development** with **univoltine seasonal cycles**. Synonym: **Monovoltinism**. See **Univoltine seasonal development**

Vegetation season: see **Vegetative season**

Vegetative season: period of time in a year when the climate is prime for plants to experience the most growth. Synonyms: **Growing season**, **Vegetation season**

Vital factor: see **Vital function of ecological factors**

Vital function of ecological factors: reflects dual mode of action of ecological factors (primarily temperature, but also light, food, etc.) on living organisms; determines a range within which a particular species can live (Tyshchenko 1980). See **Signal function of ecological factors**

Voltinism: term used to indicate the number of **generations** realized/produced by a population during a year

Wing muscle seasonal polyphenism: special case of **polyphenism** when degree of development of wing muscles change during a **vegetative season** or year; strongly linked to flight ability

Wing polymorphism: special case of **polymorphism** when within a population two or more discrete genetically controlled morphs (or forms) exist with wings of different length or degree of development (e.g., with fully developed, reduced, or totally absent wings). See, for example, **Long-winged adults**, **Short-winged adults**, and **Apterous adults**

Wing polyphenism: special case of **polyphenism** when, within a population, two or more discrete phenotypes (i.e., forms) with wings of different length or degree of development (e.g., with fully developed, reduced, or totally absent wings) are produced by one genotype under different environmental conditions. See, for example, **Long-winged adults**, **Short-winged adults**, and **Apterous adults**

Winglessness: see **Aptery**

Winter diapause: diapause that takes place in winter; one of two seasonal classes of **diapause**. Synonym: **Hibernation**