

# Summer Diapause as a Special Seasonal Adaptation in Insects: Diversity of Forms, Control Mechanisms, and Ecological Importance

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**Abstract**—Insects living in the temperate climate include summer diapause, or aestivation, in their seasonal cycle to solve various problems related to adaptation to unfavorable seasons. Unlike winter diapause, summer diapause occurs in summer and is usually terminated in autumn when active feeding, development, and/or reproduction are restored. Typically, high temperature and long day induce summer diapause and then maintain it, whereas short day and low temperature prevent induction of this diapause or terminate it. The summer diapause syndrome is basically similar to that of winter diapause; it includes prior development of large fat body, decreased level of metabolism, increased general resistance to unfavorable abiotic and biotic conditions, etc. Inhibition of morphogenesis and gametogenesis is under the control of the endocrine system. The onset of summer diapause is often accompanied by migrations to varying, sometimes significant distances to the sites of aestivation. The selective factors responsible for evolution of summer diapause vary between insect species. Climatic factors and, consequently, availability and abundance of food, as well as pressure of predators and parasites are likely to be the main factors that stimulate its occurrence. In some species, prolonged diapause begins in spring or early summer and ceases only after overwintering. When studied in detail, such prolonged diapause often turns out to be a sequence of two independent diapauses, summer and winter ones, occurring in succession without detectable external changes.

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The existence of organisms under the conditions of annual climate rhythms would be impossible without special adaptations to seasonal changes in the environment. In the course of evolution, insects have acquired different forms of dormancy varying in intensity for survival of the adverse periods of the year. Such dormancy increases general resistance of the organism to the damaging environmental factors. Regardless of its form, physiological dormancy of insects can solve various ecological tasks. It facilitates survival of both winter colds and hot and dry seasons as well as the seasonal shortage of food, ensures synchronization of interspecific and intraspecific relations, and may also perform some other functions. One of the forms of physiological dormancy is summer diapause, or aestivation. Summer dormancy is particularly frequently observed in insects living in the tropical and subtropical belts and is very pronounced in the inhabitants of deserts and semi-deserts, but it is also

fairly common in representatives of the temperate faunas.

Analysis of the published data shows that winter dormancy of insects, mostly aimed at their survival at low temperatures, has been much better studied than summer dormancy. Much progress has been made as to both the scope of the taxa studied and the profundity of understanding of the processes occurring during winter physiological dormancy in insects (Danilevsky, 1961; Vinogradova, 1984, 1991; Zaslavsky, 1984; Tauber et al., 1986; Danks, 1987; Bale, 2002; Denlinger, 2002; Hodková and Hodek, 2004; Numata, 2004; Saulich and Volkovitsh, 2004; Košťál, 2006; Belozerov, 2007, 2009, 2012; Kipyatkov and Lopatina, 2007; Saulich and Musolin, 2007; Volkovitsh, 2007; Denlinger and Lee, 2010; Goto and Numata, 2015; Rogers, 2015; Storey and Storey, 2015; Musolin and Saulich, 2018; Saulich and Musolin, 2018).

The summer dormancy of insects has been less comprehensively studied, partly due to the fact that this kind of dormancy is not as common. For example, our recent study of the distribution of different seasonal classes of diapause (summer and winter) among shield bugs (Heteroptera, Pentatomoidea) in the temperate climate showed that winter diapause occurred in almost all the species included in analysis whereas summer diapause was observed only in about 10% of the species (Musolin, 2017; Musolin and Saulich, 2018).

Three large reviews of the available data on summer diapause have been published (Masaki, 1980; Denlinger, 1986; Ushatinskaya, 1987). There are also papers devoted to the ecological and physiological aspects of summer dormancy by the example of different insect species (Spieth and Schwarzer, 2001; Xue et al., 2001; 2002; Tanaka et al., 2002; Liu et al., 2006; Wu et al., 2006; Yamamura et al., 2008, etc.; see also *References*). New experimental data were recently obtained (Loomis, 2010; Storey and Storey, 2015, etc.) which improve our understanding of the properties and significance of summer dormancy in the life of insects and allow us to analyze from a new perspective the phenological schemes which were previously believed to be based on obligate summer-autumn-winter diapause.

The goal of this paper is to reflect the current state of knowledge of summer diapause as one of the seasonal adaptations playing an important role in the annual cycles of many species and populations of insects.

The summer dormancy of insects is referred to by three largely synonymous terms: *summer diapause*, *aestivation*, and *oversummering* (Ushatinskaya, 1987). These terms were evidently proposed as antonyms of the terms *winter diapause*, *hibernation*, and *overwintering*. At the very least, such terminological difference emphasizes the seasonal timing of the corresponding states. However, summer in the temperate climate belt differs significantly from summer in the tropical and subtropical areas, not only in the range and seasonal dynamics of temperatures but also in the fact that it is not temperature per se but expressed seasonal rains, droughts, and hurricanes that may constitute the primary adverse factors in the tropics. Since the ecophysiological features of summer diapause in the tropics are still insufficiently studied, this work will be mostly focused on the species inhabiting the temperate climate belt.

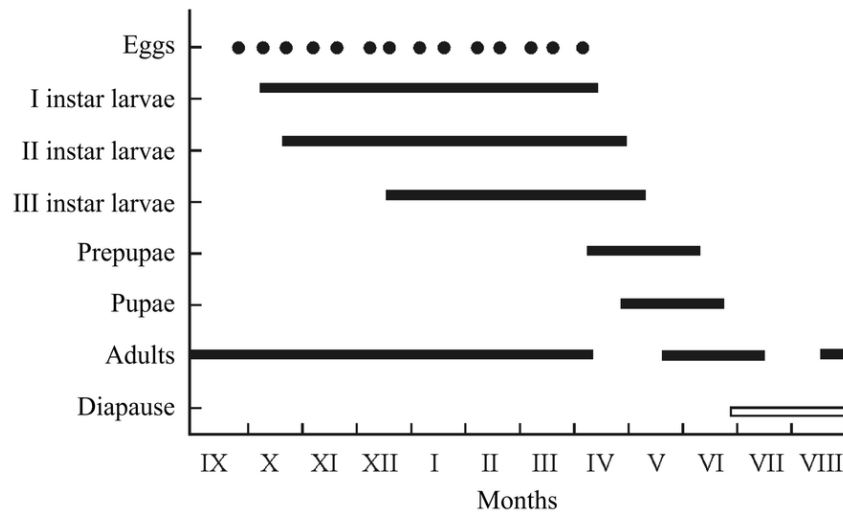
## 1. SPECIFIC ECOLOGICAL FEATURES OF SUMMER DIAPAUSE

In insects living in temperate latitudes, summer diapause usually occurs in summer and performs a great variety of functions. By analogy with winter diapause, summer diapause may be related to unfavorable temperatures (in this case, higher than optimal ones), but its formation is more frequently determined by the absence, deficiency, or low quality of food which, in turn, is determined by the effects of the abiotic component of the environment onto the trophic resources. In many cases, the factors determining the development of summer diapause in insects are not evident; they may be clarified only by a thorough study of their biology, seasonal development, and inter- and intra-specific relations.

The timing of onset and duration of summer dormancy vary greatly between species. Usually summer dormancy covers a short period of time in summer and is terminated when conditions become suitable closer to the end of summer or the beginning of autumn. However, there are cases of summer dormancy extending over the whole vegetation season and activity of the insects being completely shifted onto late autumn or winter. For example, such prolonged summer diapause is typical of many Palaearctic round fungus beetles (Coleoptera, Leiodidae: Cholevinae) and rove beetles (Coleoptera, Staphylinidae: Omaliinae) which, despite the relatively severe natural conditions within their ranges, have annual cycles with reproduction in autumn, larval development in winter, and adult diapause in summer (Topp, 1990, 2003).

Insects living in temperate latitudes show few examples of active development being shifted onto winter. Mention may be made of the unusual seasonal cycle of the cabbage stem flea beetle *Psylliodes chrysocephala* (Linnaeus, 1758) (Coleoptera, Chrysomelidae) in which, as opposed to most inhabitants of the temperate climate, oviposition and larval development in the southwest of Hungary take place not in summer but in winter, extending from September to April (Fig. 1; Sáringer, 1984).

The adult diapause in this species occurs during the hottest and driest period of the year. It begins in July and lasts about two months regardless of the external conditions, such as the day length, temperature, humidity, and food quality. Diapause is terminated at the end of August, as spontaneously as it starts. It is followed by the period of active development of adult



**Fig. 1.** Phenology of the population of the cabbage stem flea beetle *Psylliodes chrysocephala* (L.) in the southwest of Hungary (after Sáringer, 1984).

beetles that includes feeding, maturation, and oviposition; the latter continues over the whole winter and may occur at very low temperatures, from +4 to +12°C. In mild winters, oviposition was observed even in December and January. The cabbage stem flea beetle always completes only one generation per year (Sáringer, 1984).

An inverted seasonal cycle with active development during the colder period of the year is more characteristic of insects living in the mild subtropical and tropical climates. For example, *Abraxas miranda* Butler, 1878 (Lepidoptera, Geometridae) under the conditions of subtropical climate on Honshu Island (Japan, 34°N) also survives the hot season in pupal diapause, whereas in winter its larvae feed on the evergreen Japanese spindle tree *Euonymus japonicus* (Celastraceae) (Masaki, 1957, 1958).

Summer diapause is quite often observed only in part of the population, as in the American fall webworm *Hyphantria cunea* (Drury, 1773) (Lepidoptera, Arctiidae) (Masaki, 1977); or it may be totally absent in some years, as in some lacewings (Neuroptera, Chrysopidae) (Volkovitsh, 2007) and other predatory insects. In some species summer diapause occurs in one sex only; such situations are also known for winter diapause (Tauber et al., 1986; Teraoka and Numata, 1995). For instance, only females aestivate in the dryad butterfly *Minois dryas* Scopoli, 1763 (Lepidoptera, Satyridae) (Kida et al., 1997) and the encyrtid wasp *Blastothrix longipennis* Howard, 1881 (= *B. confusa*) (Hymenoptera, Encyrtidae) which is a parasite of

soft scale insects (Homoptera, Coccidae) (Sugonyaev, 1963; Danilevsky and Sheldeshova, 1968). By contrast, a higher percentage of aestivating males was observed, for example, in flies of the genera *Sarcophaga* (Diptera, Sarcophagidae) (Denlinger, 1981) and *Lucilia* (Diptera, Calliphoridae) (Ring, 1971), and also in the tobacco budworm *Heliothis virescens* (Fabricius, 1777) (Lepidoptera, Noctuidae) (Butler et al., 1985).

Summer diapause may be formed at any stage of insect development but it is relatively rare in eggs or early-instar larvae (Falkovitsh, 1979; Masaki, 1980; Oku, 1983). Summer dormancy of prepupae, pupae, and adults seems to be related to a better adaptation of these stages to elevated temperatures. It is known that prepupae and pupae of many species usually survive the hot season in soil chambers protecting them from both desiccation and overheating, while adults of the species having an adult diapause can migrate over long distances in search of places with more favorable conditions.

Although summer diapause may be formed at different stages, its position in the ontogenesis, as well as that of winter diapause, is strictly species-specific. In particular, according to the data of Masaki (1980), of a total of 179 aestivating species from 12 orders of insects, 6.1% aestivate at the egg stage, 17.4% at the larval stage, 29% at the pupal stage, and 47.5% of species have summer diapause at the adult stage. By now, the number of the species studied in this respect has grown considerably but the relative occurrence of

summer diapause with respect to ontogenetic stages has remained approximately the same.

Summer diapause has been more thoroughly studied in representatives of the orders Coleoptera and Lepidoptera. It was found that insects of different taxa might be characterized by the prevalence of different types of diapause (embryonic, larval, pupal, and adult diapauses). For example, according to the available data, species aestivating as adults clearly prevail among the shield bugs (Heteroptera, Pentatomoidea) having a summer diapause. So far, aestivation at the nymphal stage has been found in this superfamily only in members of the genus *Coptosoma* Laporte (Heteroptera, Plataspidae) (Saulich and Musolin, 2014a; Musolin, 2017; Musolin and Saulich, 2018).

Winter and summer diapauses occur at the same ontogenetic stage in some species, and at different stages in other species (Tauber et al., 1986; Danks, 1987). Representatives of Lepidoptera more often hibernate as larvae (44%) or pupae (49%), whereas aestivation more frequently occurs in pupae (53%) or adults (34%). In Coleoptera and Diptera both diapauses usually occur at the same stage of development (Masaki, 1980). In the few species of shield bugs having two diapauses in the seasonal cycle, aestivation is usually observed in adults and hibernation, at different stages depending on the species, more often in nymphs than in eggs (Saulich and Musolin, 2014a; Musolin, 2017).

The formation of summer and winter dormancy in insects is not correlated with phylogenetic closeness of species. For instance, summer diapause in the swallowtail *Luehdorfia puziloi* Erschoff, 1872 (Lepidoptera, Papilionidae) occurs at the pupal stage, and winter diapause, at the stage of the pharate adult (Kimura, 1975). By contrast, the closely related *Luehdorfia japonica* Leech, 1889 has only summer pupal diapause and overwinters at the stage of a developing pupa that undergoes imaginal morphogenesis (Ishii and Hidaka, 1979, 1982).

It is evident that the main ecological function of summer diapause is to facilitate survival of the period of limiting conditions in summer. However, of no less importance is its synchronizing function, which may serve different purposes in different species and may be differently manifested according to the specific traits of their seasonal cycle. For example, many species whose larvae feed on fruits and seeds have to time their seasonal cycles with the beginning of the specific phenological stage of their host plants. Females of

such species aestivate during a certain part of summer, which allows them to synchronize the hatching of the larvae with the ripening of fruits or seeds of the host plant (Tanaka et al., 2002; Numata, 2004). In other species, summer dormancy shifts the formation of the overwintering stages closer to the exact season to which these stages are adapted. The later the potential diapausing stages appear, the more successful is their overwintering. This adaptation has been found in many insects from different orders, characterized by a univoltine seasonal cycle with a weak winter diapause, for instance, *Spilosoma obliqua* (Walker, 1855) (= *Spilarctia obliqua*) (Lepidoptera, Arctiidae) (Li and Xue, 1991) or *Picromerus bidens* Amyot et Serville, 1843 (Heteroptera, Pentatomidae) (Musolin and Saulich, 2000; Saulich and Musolin, 2007). In other cases, for example in the round fungus beetles *Catops nigricans* (Spence, 1815) (Coleoptera, Leiodidae) that are active in winter, the adult aestivation shifts the reproduction period onto the season most favorable for activity (Topp, 2003). In the crane fly *Tipula pagana* Meigen, 1818 (Diptera, Tipulidae), the timing of the onset of summer diapause is labile while its duration depends on external factors; these features ensure the synchronous emergence of adults, which is needed for successful reproduction at lower, more favorable temperatures in autumn (Butterfield, 1976).

The synchronizing function of summer diapause can be also demonstrated by the examples of coordinated seasonal development of parasitic insects and their hosts (Danilevsky and Sheldeshova, 1968; Spieth and Schwarzer, 2001; Sugonyaev and Voinovich, 2006). Such cases and the factors regulating the annual cycles in the host-parasitoid system will be specially considered below.

In most cases, inclusion of summer dormancy in the seasonal cycle is accompanied by transition of the species or some of its populations to univoltinism (Saulich and Musolin, 1996, 2014b; Saulich and Volkovitsh, 1996). This transition may be determined by different factors, such as shortage of suitable food or the absence of a suitable phenological stage of the host plant for phytophages, the absence of the infestable stage of the host for parasitic insects, etc. At the same time, there are species in which the presence of summer diapause does not lead to complete reduction of the annual cycle to a single generation per year. An example of this kind is the cabbage moth *Mamestra brassicae* (Linnaeus, 1758) (Lepidoptera, Noctuidae), which was studied in detail in Japan (Masaki,

1956; Masaki and Sakai, 1965). In the north of Japan (Hokkaido Island) the thermal resources can support the development of only one generation during the summer season. In more southern areas the amount of heat increases to the point where it can support the development of two annual generations: the spring and autumn ones, separated by the summer pupal diapause. The duration of this diapause increases from north to south, so that the summer diapause completely replaces the winter one in the extreme south of Japan (Amami Islands). Owing to geographic variation in the duration of summer diapause, two complete generations of *M. brassicae* can develop annually over almost the whole territory of Japan, regardless of the latitude.

A similar trend in the phenological development of this species can be observed in France: despite the summer pupal diapause, the cabbage moth has a bivoltine seasonal cycle in the south of the country (Sauer and Grüner, 1988).

## 2. PHYSIOLOGICAL FEATURES OF INSECTS IN THE STATE OF SUMMER DIAPAUSE

Summer diapause is largely similar to winter diapause in its specific physiological features. Preparation to summer diapause (both obligate and facultative one) takes place in advance and is accompanied by a considerable increase in the general resistance to adverse environmental actions. Preparation to both seasonal classes of diapause includes accumulation of reserve nutrients, usually in the form of fat deposits and glycogen. The reduced intensity of metabolism, which is one of the consequences of the onset of diapause, determines an increased resistance to such adverse factors as high or low temperatures, moisture deficit, and prolonged absence of food.

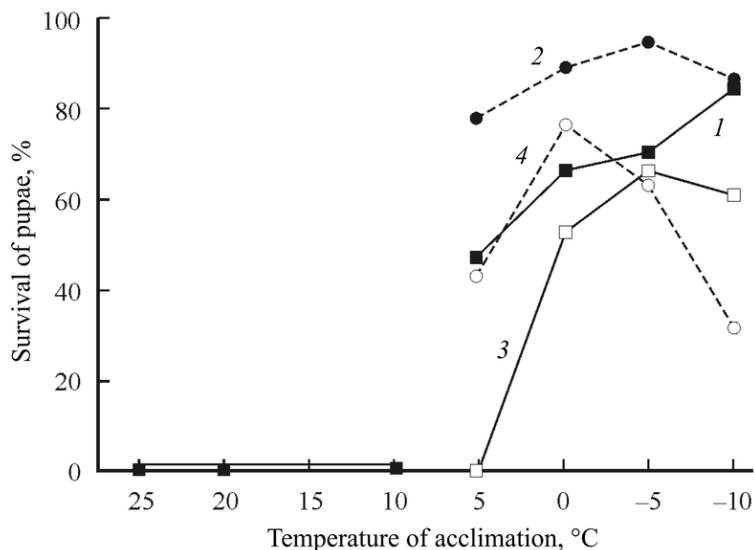
The specific physiological features of diapauses of different seasonal classes, adapted to different conditions, were analyzed by the example of a widespread and well studied species, the cabbage moth *Mamestra brassicae*. Both summer and winter diapauses in this moth occur at the same ontogenetic stage, namely the pupa. Facultative winter diapause is induced at the short day and low temperatures. These factors act efficiently on larvae from I to V instar. In the natural environment, winter dormancy is established in November–December and terminated at the end of December (Masaki and Sakai, 1965; Goryshin and Tyshchenko, 1973; Saulich, 1999). Facultative summer diapause is formed if VI instar larvae develop at the long day and

high temperatures (Masaki and Sakai, 1965; Goto and Hukushima, 1995; Goto et al., 2001). Similar results were obtained in the study of the conditions of summer diapause induction in the cotton bollworm *Helicoverpa armigera* (Hübner, [1809]) (Lepidoptera, Noctuidae) (Liu et al., 2006).

In the ecophysiology of insects, the state of diapause is usually described using two criteria. Regardless of its type (embryonic, larval, pupal, or adult), form (obligate or facultative), and seasonal class (winter or summer) (Musolin, 2017; Musolin and Saulich, 2018), diapause can be characterized by such parameters as *duration* and *intensity* (Tauber et al., 1986; Danks, 1987; Topp, 1990; Masaki, 2002). The duration of diapause may be assessed by (1) the actual duration of this state under the conditions facilitating diapause, (2) the width of the ranges of photoperiods and temperatures capable of inducing reactivation, and (3) the rate of reactivation under the conditions terminating the diapause. The diapause intensity is usually interpreted as the degree of metabolism suppression (Zaslavsky, 1984).

According to the data of Maslennikova and co-authors (1976), the winter and summer pupal diapauses in the cabbage moth *M. brassicae* from Belgorod Province of Russia (50°N) differed in both duration and intensity. In particular, winter pupal diapause formed at the short day and 25°C lasted on average for 8 months at 18°C, whereas the mean duration of summer diapause induced at the same temperature but at the long day was only 1.5 months under the same experimental conditions of reactivation. Later it was shown that termination of winter diapause in the cabbage moth from Tsuruoka (Japan, 39.4°N) required 4 months, whereas its summer diapause was terminated in 1 month under the conditions favoring reactivation (Ding et al., 2003). Different duration of summer and winter diapauses was also observed in the cotton bollworm *Helicoverpa armigera* from China (Liu et al., 2006). Although the intensity of both diapauses was lower in the latter species than in the cabbage moth, the termination of the winter pupal diapause, which was detected by the timing of retention of pigmented eye spots, still required 37 days, whereas the summer diapause was terminated in 10 days.

A reliable indicator of diapause intensity in insects is the concentration of the molting hormone ecdysone. A high titer of ecdysone is known to ensure active development while the state of diapause is determined by low concentration or complete absence of this hor-



**Fig. 2.** Survival of diapausing and post-diapause pupae of the cabbage moth *Mamestra brassicae* (L.) from Tsuruoka (Japan; 38°N) with different seasonal classes of diapause after 24 h of exposure to  $-15^{\circ}\text{C}$  following acclimation at different temperatures (after Goto et al., 2001): 1, pupae in winter diapause; 2, pupae after winter diapause; 3, pupae in summer diapause; 4, pupae after summer diapause (for detailed description of the experiment, see Goto et al., 2001).

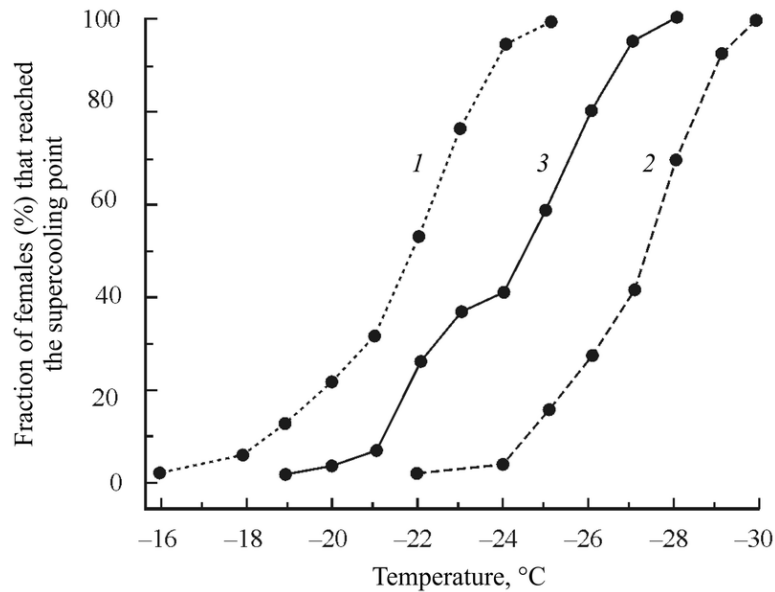
more. Analysis of ecdysone titer in the cabbage moth pupae, determined by the so-called “Calliphora test” and measured in Calliphora units (C.u.) per 1 g of body weight (Karlson and Shaaya, 1964), yielded values of 0.7–1.0 C.u./g during winter diapause (Maslennikova et al., 1976). The corresponding value during the less intense summer diapause was within the range of 2.3–3.0 C.u./g, i.e., three times as great as in the hibernating pupae, whereas the maximum ecdysone titer in the actively developing pupae reached 8.5 C.u./g. Simultaneously with ecdysone titer, the metabolism intensity (assessed by the weight loss rate) was analyzed in the pupae during active development and both seasonal classes of diapause. In this parameter, summer diapause was found to be intermediate between active development and winter diapause. Thus, ecdysone titer was correlated with the metabolism level during active development and diapause of cabbage moth pupae: the more intensive metabolism corresponded to a higher ecdysone titer. A histological study of the neurosecretory brain cells of the aestivating pupae showed them to be in an intermediate state between that of active pupae and that of hibernating individuals (Kind, 1977). Similar data were obtained later for the cabbage moth population from Japan (Endo et al., 1997).

Despite the paucity of data on the physiology and biochemistry of aestivation, most researchers believe that the changes preceding and accompanying summer

diapause differ from those typical of winter diapause only in the degree of manifestation (Maslennikova et al., 1976; Masaki, 1980; Ushatinskaya, 1981; Endo et al., 1997; Košťál et al., 1998; Ishikawa et al., 2000; Goto et al., 2001; Liu et al., 2006; Xiao et al., 2006).

Regardless of the seasonal class of diapause (summer or winter), diapausing individuals show considerable resistance to low temperatures. This property is usually assessed either by the supercooling temperature (cold hardiness) or by the survival rate under the prolonged action of low temperatures (cold resistance). According to the data of Japanese researchers (Goto et al., 2001; Ding et al., 2003), nonspecific cold hardiness determined by the thermoelectric method was only weakly different in the aestivating and hibernating cabbage moth pupae. Their supercooling point was  $-21.9^{\circ}\text{C}$  in winter diapause and  $-19.5^{\circ}\text{C}$  in summer diapause. At the same time, resistance to prolonged action of low temperatures was found to be much higher in hibernating pupae and noticeably increased after cold acclimation. In particular, the survival rate of such pupae after 24 h of exposure to  $-15^{\circ}\text{C}$  following acclimation at  $-5^{\circ}\text{C}$  reached 94.7%, whereas the highest survival rate of aestivating pupae after acclimation at  $0^{\circ}\text{C}$  was only 76.7% (Fig. 2).

Individuals in the state of diapause of different seasonal classes (summer or winter) share a number of physiological properties but at the same time reveal



**Fig. 3.** Supercooling temperature in females of the spider mite *Tetranychus urticae* Koch depending on their physiological state (after Geispits and Orlovskaya, 1971): 1, physiologically active females; 2, females in winter diapause; 3, females in summer diapause.

some specific features (for detail, see Saulich and Volkovitch, 2004). For example, the oxygen consumption rate and resistance to desiccation in active females of the spider mite *Tetranychus urticae* Koch, 1836 (Acari, Tetranychidae) were compared with the same parameters in hibernating and aestivating mites. Of these three groups, the aestivating females had the lowest oxygen consumption rate and the highest resistance to desiccation. The hibernating females were the most resistant to low temperatures, and physiologically active (non-diapausing) individuals were found to be the least adapted to these limiting factors (Fig. 3; Geispits and Orlovskaya, 1971). These data demonstrate the difference between summer and winter diapauses and emphasize the significance of each of these two variants of physiological dormancy.

In some cases, survival of adverse conditions in summer requires more profound physiological transformations than overwintering. For example, in the seven-spot ladybird *Coccinella septempunctata brucki* Mulsant, 1866 (Coleoptera, Coccinellidae) in the south of Japan, the characteristics of summer dormancy (such as arrest of oogenesis, a low level of gas exchange, reduction of the wing muscles, and low hormonal activity of the corpora allata) are more consistent with true and intensive diapause, whereas simple quiescence is sufficient for survival during winter (Sakurai et al., 1986).

### 3. FACTORS CONTROLLING THE ONSET OF FACULTATIVE SUMMER DIAPAUSE

At all latitudes within the temperate climatic belt, summer dormancy of insects occurs during the warmest months. Similar to hibernation, summer dormancy may be induced in all or some individuals of the population, either independently of external conditions or under the action of external cues. On the whole, the processes of induction of summer diapause are studied much worse than the responses controlling the onset of winter diapause.

In many species summer diapause is genetically determined for each generation and begins inevitably at a certain, species-specific stage of development. The inclusion of obligate diapause usually determines the formation of a univoltine seasonal cycle, when under the pressure of some external conditions the seasonal activity of the insect gets reduced to only one generation a year. Such reduction of the number of generations may be often observed over the whole species range.

Summer diapause is very often considered to be obligate, although in reality this property needs to be experimentally confirmed in each particular case. The formation of summer diapause independently of external conditions was proved by special experiments for some species, for instance, the winter moth *Opero-*

*phtera brumata* (Linnaeus, 1758) (Geometridae) (Kozhanchikov, 1950a, 1950b; Bonnemaïson, 1971; Holliday, 1983), the autumnal shade *Exapate congelatella* (Clerck, 1739) (Tortricidae) (Glinyayana, 1972), the swallowtails *Luehdorfia puziloi* (Kimura, 1975) and *L. japonica* (Ishii and Hidaka, 1982), the owl moths *Euxoa sibirica* (Boisduval, [1837]) (Oku, 1982) and *Dichagyris flammata* ([Denis et Schiffermüller], 1775) (= *Ochropleura flammata*) (Sukhareva, 1999) (Noctuidae), and also the cabbage stem flea beetle *Psylliodes chrysocephala* (Sáringer, 1984) (Chrysomelidae), various species of ground beetles (Carabidae) (Thiele, 1977), and many other insects.

The examples of external control of the onset of summer diapause are much more numerous, and in these cases aestivation is considered to be facultative. The principal cues controlling the induction of facultative summer diapause are the temperature, photoperiod, food, and some other external stimuli. These are practically the same cues that are involved in formation of facultative winter diapause, but the effects of individual components of the environment may be manifested in different ways.

### 3.1. Temperature

The temperature is rarely used by insects as a cue inducing facultative diapause, because this factor is not anticipatory under natural conditions and therefore lacks the principal quality of a good inductor: a valid cue should appear a considerable time in advance of the actual worsening of living conditions, so as to give the insects sufficient time for physiological preparation. Still, there are some species which mainly respond to high temperatures during induction of summer diapause, whereas the other factors play minor roles, merely enhancing or reducing the principal signal action of the temperature. The species experimentally studied in this respect include the tobacco budworm *Heliothis virescens* (Butler et al., 1985) and the cotton bollworm *Helicoverpa armigera* (Liu et al., 2006) (Lepidoptera, Noctuidae), in which summer pupal diapause is formed in response to very high temperatures (above 32–33°C), and also *Pegomyia bicolor* (Wiedemann, 1817) (Diptera, Anthomyiidae), in which summer pupal diapause is induced by high temperatures regardless of the photoperiod (Xue et al., 2001). The timely onset of summer dormancy, characterized by low metabolism and increased resistance to adverse conditions, allows the insects to survive the extreme temperatures of the southern latitudes.

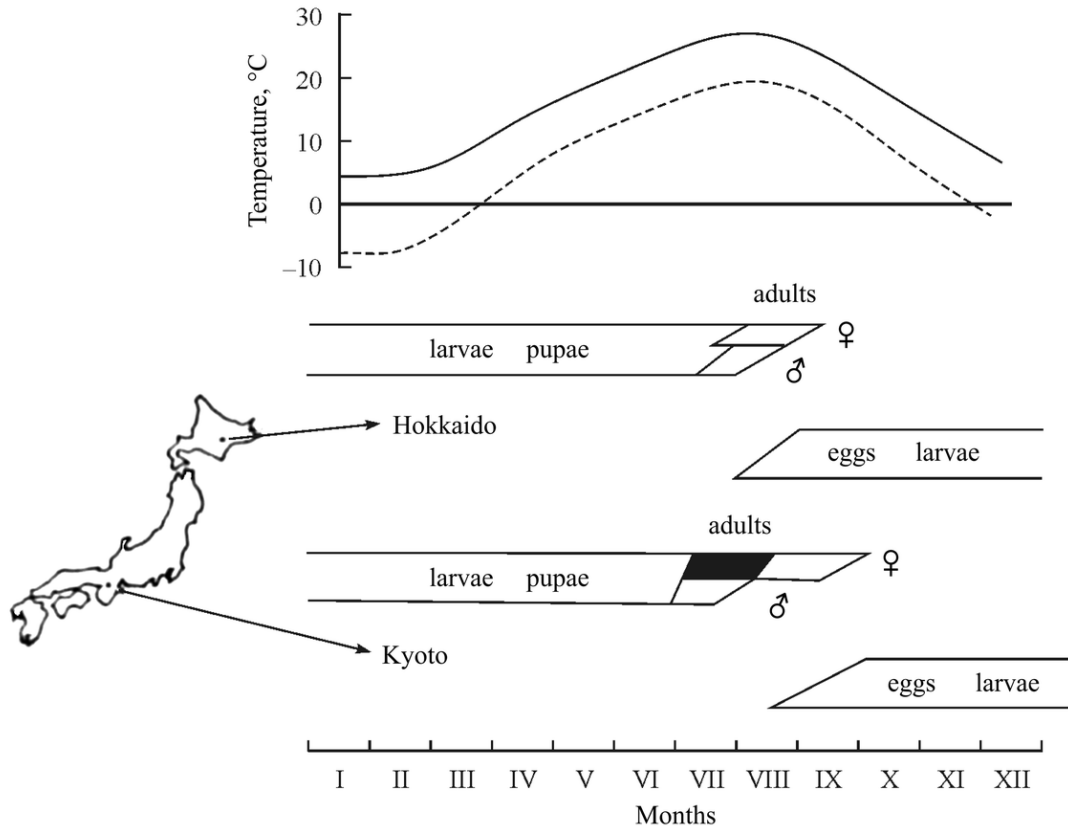
Larval summer diapause of the univoltine leaf beetle *Pyrrhalta humeralis* (Chen, 1942) (Coleoptera, Chrysomelidae) is also induced by the temperature and to a lesser extent, by the day length (Ogata and Sasaki, 1983; Nakai and Takeda, 1995). Studies carried out in Japan have shown that adults of *P. humeralis* emerge at the beginning of June but their feeding and reproduction remain inhibited until mid-September. In the second half of September the beetles lay eggs in the bases of winter buds of the evergreen Chindo arrowwood *Viburnum awabuki* (Caprifoliaceae) where they overwinter. Oviposition starts only at temperatures lower than 15°C. The ecological function of summer diapause consists in shifting the reproduction onto a later period of autumn, when the conditions are optimal for the diapausing eggs.

Under the natural conditions, it is difficult to isolate the action of one out of the whole complex of external factors. This is especially true of the temperature and day length because these two factors change almost concurrently in the nature. In order to determine which of them more efficiently controls summer diapause, field observations and special experiments were carried out with dryad butterflies *Minois dryas* from two localities in Japan differing in climatic conditions: the more northern Hokkaido Island (42°N) and the more southern Kyoto (34°N) (Kida et al., 1997). *Minois dryas* is a widespread Palearctic species with a univoltine seasonal cycle. Its larvae feed on various grasses. On Hokkaido, females mature soon after the imaginal molt and show no indication of summer diapause. Several characteristics were used as criteria of the onset of aestivation: the stage of egg maturation, the size of the fat body, the wing pattern, and the number of spermatophores in the bursa copulatrix. No aestivation was detected in the males.

In Kyoto, females of *M. dryas* emerge at the beginning of July and immediately enter summer diapause which lasts till mid-August (Fig. 4). Oviposition starts only in autumn, and the hatched larvae overwinter. Unlike those from Hokkaido Island, the females of *M. dryas* from Kyoto show all the features of a true summer diapause. Thus, the seasonal cycles of the two studied populations (the northern and southern ones) are different.

The mean temperature of July and August in Kyoto is approximately 25°C whereas on Hokkaido it is less than 20°C. The summer diapause in the Kyoto population, which is formed only in females, seems to in-





**Fig. 4.** The seasonal cycle of the dryad butterfly *Minois dryas* Scop. in Kyoto (34°N) and on Hokkaido Island (42°N), Japan (after Kida et al., 1997). The black area marks the summer period of females' aestivation. The upper diagram shows the seasonal dynamics of mean monthly air temperatures in Kyoto (solid line) and on Hokkaido (dashed line).

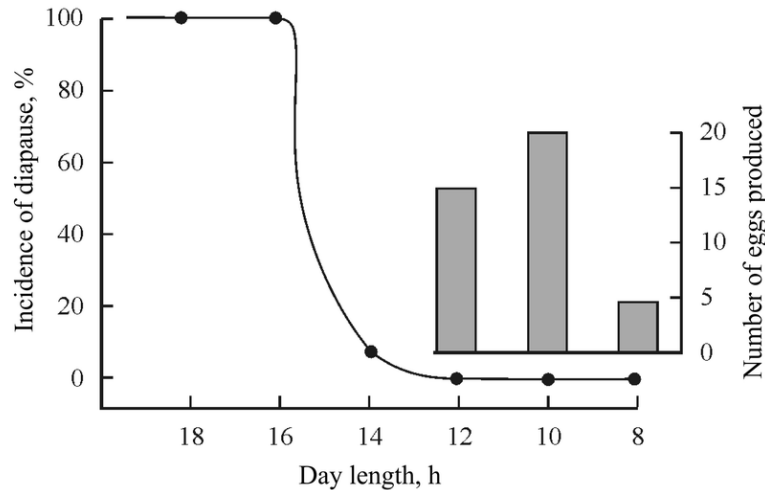
crease the resistance of *M. dryas* to the conditions of long and hot summer. At the same time, the development of this species cannot be limited by excessively dry air, because the relative air humidity in Kyoto in June is no less than 72%, and that in August, 69%. Therefore, it is not air humidity but high temperatures that determine the induction of summer diapause in *M. dryas* in Kyoto. The experimental laboratory study of the role of photoperiod yielded a negative result, which additionally confirms the principal role of the temperature in induction of summer diapause in this butterfly (Kida et al., 1997).

### 3.2. Day Length

The day length, or photoperiod, is used by many insect species as an aestivation-inducing cue much more frequently than the other external factors, no matter what adverse influence determines the need for diapause. The ecophysiological response is formed on the basis of a short-day photoperiodic response (PhPR) that determines the onset of diapause at the long day

(often combined with elevated temperatures). This was clearly demonstrated by the example of the leaf beetle *Galeruca tanacetii* (Linnaeus, 1758) (Coleoptera, Chrysomelidae) (Figs. 5, 6): at the short day the adults were reproductively active while at the long day they formed summer diapause. The seasonal development of *G. tanacetii* was studied in detail under the natural conditions of Southern England (Siew, 1966) and of Belgorod Province of Russia (Saulich and Volkovitsh, 1996) (Fig. 7).

Winter embryonic diapause is induced in *G. tanacetii* irrespective of the external conditions. Larvae hatch in spring; young adults emerge at the end of June and form summer diapause based on a short-day PhPR with a threshold of about 15 h 30 min in adults from Belgorod Province and 14 h 30 min in those from Southern England (Figs. 5, 6). Under long-day conditions, all the beetles form a short summer diapause whose termination is also controlled by the day length: as the photoperiod decreases to the threshold value, the diapause ends and the females start laying eggs.



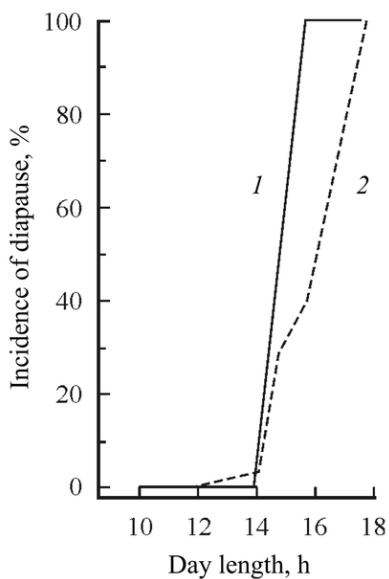
**Fig. 5.** Influence of the day length on aestivation in the leaf beetle *Galeruca tanacetii* (L.) (population from Southern England, Great Britain) at 20°C: photoperiodic control of diapause induction (curve) and reproduction intensity (histogram) (after Siew, 1966).

Although the two studied populations live at similar latitudes, the critical photoperiods inducing and terminating the summer adult diapause are slightly (by about 1 h) higher in the forest-steppe population from Belgorod Province; correspondingly, the onset and termination of summer diapause in this population are shifted towards the middle of summer (Fig. 7).

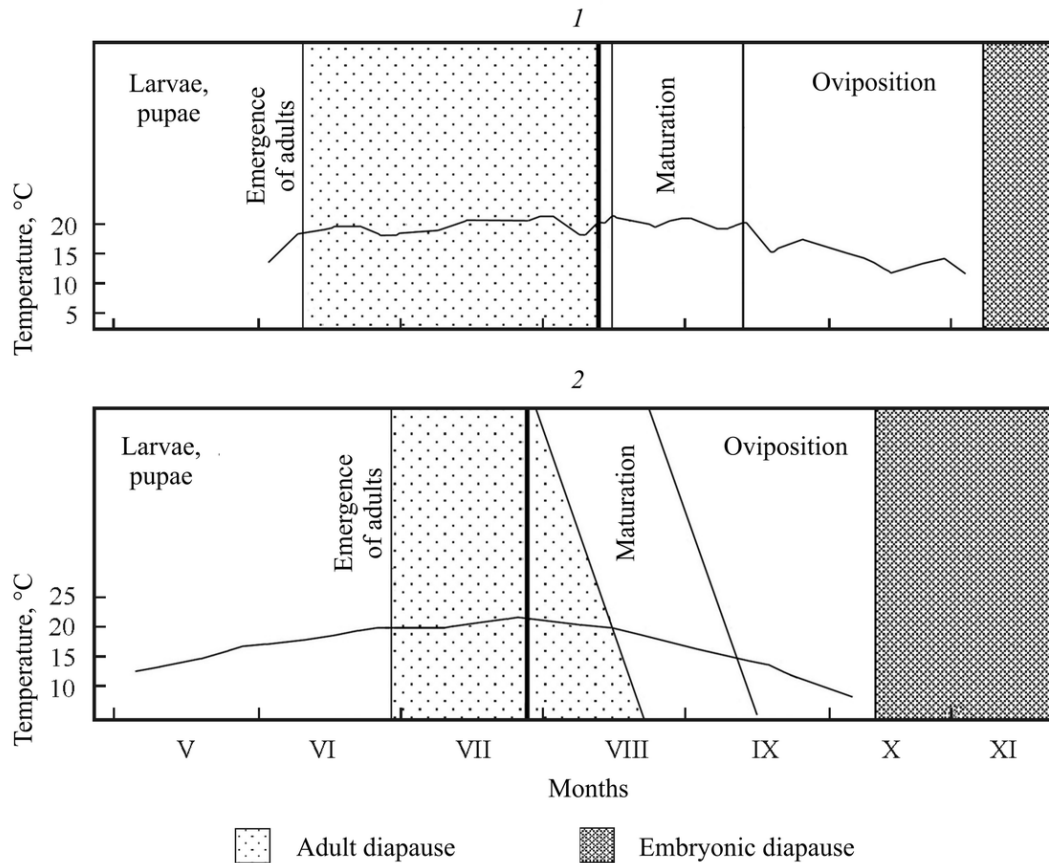
The ecological significance of adult aestivation in this species is not exactly clear since the external con-

ditions of the temperate climate do not limit its development; however, the studied populations of *G. tanacetii* show identical patterns of development (Fig. 7). The minor differences in the timing of onset and termination of diapause are determined by the differences in the PhPR parameters which, in turn, are adapted to the local climatic conditions. It was suggested that aestivation might be aimed at avoiding the adverse action of not physical but biotic factors, namely the pressure of predators and parasites (Siew, 1966). However, it is more probable that adult aestivation in *G. tanacetii*, resembling that in the predatory spiny shield bug *Picromerus bidens* which has a similar seasonal cycle (Musolin and Saulich, 2000), facilitates the timing of oviposition with the thermal conditions of late autumn, which are more favorable to the overwintering eggs. *Picromerus bidens* has a very weak embryonic diapause, so that in case of early oviposition at moderate temperatures, the hatching of its nymphs starts already in autumn (Musolin and Saulich, 2000). Unfortunately, the details of winter embryonic diapause in *G. tanacetii* remain unstudied.

The short-day PhPR inducing summer diapause has been studied in many species from different orders of insects. It controls the onset of aestivation at different development stages, for instance, in the nymphs of *Carbula humerigera* Uhler, 1860 (Heteroptera, Pentatomidae) (Kiritani, 1985a, 1985b), in the eonymphs of the sawflies *Neodiprion sertifer* (Geoffroy, 1785) (Hymenoptera, Tenthredinidae) (Sullivan and Wallace, 1965, 1967) and *Neodiprion taedae linearis* Ross, 1955 (Hymenoptera, Diprionidae) (Wigfield and Warren, 1972), in the pupae of many Lepidoptera,



**Fig. 6.** Photoperiodic control of induction of adult aestivation in the leaf beetle *Galeruca tanacetii* (L.) at 20°C: 1, population from Southern England, Great Britain (after Siew, 1966); 2, population from Belgorod Province, Russia, 50°N (after Saulich and Volkovitsh, 1996).



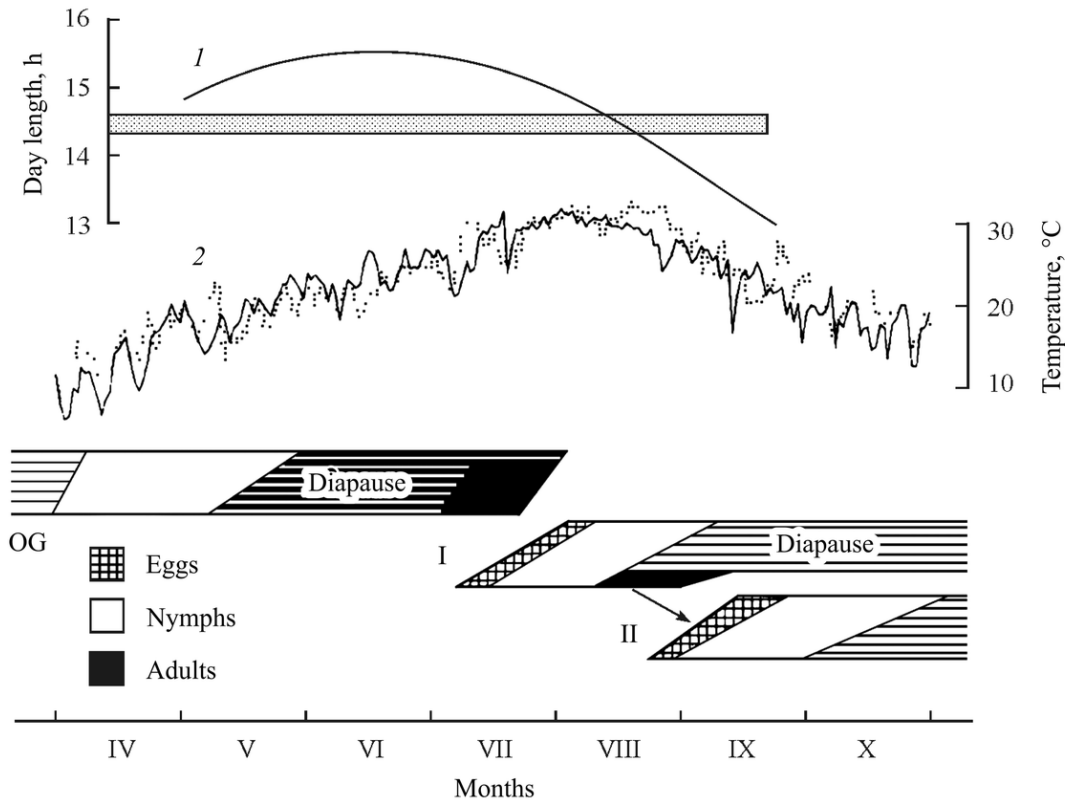
**Fig. 7.** Seasonal cycles of two populations of the leaf beetle *Galeruca tanacetii* (L.): (1) Southern England, Great Britain (after Siew, 1966); (2) the forest-steppe zone of Russia (Belgorod Province, 50°N) (after Saulich and Volkovitsh, 1996).

such as *Pieris melete* Ménériés, 1857 (Xiao et al., 2006), *Pieris brassicae* (Linnaeus, 1758) (Pieridae) (Spieth, 2002), *Mamestra brassicae* (Linnaeus, 1758) (Masaki, 1956), *Helicoverpa armigera* (Hübner, [1808]) (Murray and Wilson, 1991), and other insects; in the adults of the weevils *Hypera postica* (Gyllenhal, 1813) (Bland, 1971; Witt and Armbrust, 1972; Schroder and Steinhauer, 1976a, 1976b) and *Hypera brunneipennis* (Boheman, 1834) (Coleoptera, Curculionidae) (Madubunyi, 1978), the ground beetles *Nebria brevicollis* (Fabricius, 1792) and *Patrobis atrorufus* (Stroem, 1768) (Coleoptera, Carabidae) (Thiele, 1969), the meadow spittlebug *Philaenus spumarius* (Linnaeus, 1758) (Homoptera, Cercopidae) (Witsack, 1975), and the spiny shield bug *Picromerus bidens* Amyot et Serville, 1843 (Heteroptera, Pentatomidae) (Musolin and Saulich, 2000).

Summer adult diapause of some Lepidoptera is associated with migrations to the places of aestivation. In these cases, diapause induction is also controlled by the short-day PhPR. This was demonstrated in many

owlet moths (Lepidoptera, Noctuidae), for example, *Chorizagrotis auxiliaris* Grote, 1873 in America (Pruess, 1967), species of the genus *Noctua* Linnaeus, 1758 in Central Europe (Novák and Spitzer, 1975), *Euxoa sibirica* (Boisduval, [1837]) (Oku and Kobayashi, 1978; Oku, 1982, 1983) and *Amphipyra corvina* Motschulsky, 1866 (Tsugane, 1975) in Japan, and *Amphipyra pyramidea* (Linnaeus, 1758) in Central Europe (Sukhareva, 1999).

Some species of insects respond not only to the absolute day length but also to its changes. For example, larval aestivation of the stonefly *Capnia bifrons* (Newman, 1839) (Plecoptera, Capniidae) is induced by the increasing day length and temperatures below 9°C and is terminated by a constant photoperiod of 12 h 30 min (Khoo, 1968). In the shield bug *Carbula humerigera* (Uhler, 1860) adult aestivation is formed under the influence of increasing day length in late spring and early summer, while oviposition starts only after the summer solstice, when the day length begins to decrease (Kiritani, 1985a). This summer delay

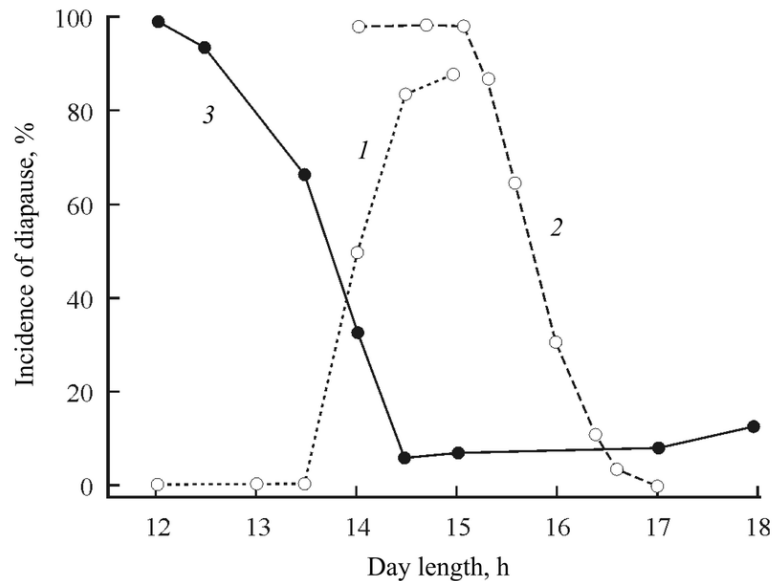


**Fig. 8.** Seasonal development of the jewel bug *Poecilocoris lewisi* Dist. in Osaka, Japan (34.6°N) (after Tanaka et al., 2002): 1, day length (including 1 h of civil twilights); 2, air temperature in 1995 (dotted line) and 1996 (solid line). The shaded strip in 1 corresponds to the critical day length inducing summer adult diapause and winter nymphal diapause. Lower diagram: OG, overwintering generation; I, the first (complete) generation; II, the second (partial) generation; dark hatching, adult diapause; light hatching, nymphal diapause; arrow indicates the origin of the second (partial) generation from the non-diapausing part of the first (complete) generation.

of oviposition was regarded by the cited author as an adaptive mechanism shifting the development of nymphs onto a later period of summer, when photoperiodic conditions would induce their hibernation. Thus, two facultative diapauses occurring at different ontogenetic stages of *C. humerigera* participate in formation of a strictly univoltine seasonal cycle.

As mentioned above, inclusion of summer diapause in the seasonal cycle usually facilitates transition from multi- and bivoltine cycles to univoltinism. However, there are species in which the presence of summer diapause does not limit the number of annually completed generations. For instance, the life cycle of the jewel bug *Poecilocoris lewisi* Distant, 1883 (Heteroptera, Scutelleridae) in Japan includes two diapauses, both controlled by the photoperiod with thresholds close to 14 h 30 min: the short day induces winter diapause in the V instar nymphs whereas the long day induces a short adult diapause, with gonad development delayed by approximately 20 days (Tanaka et al., 2002). Nymphs of *P. lewisi* feed on seeds of the giant

dogwood *Cornus controversa* (Cornaceae), which ripen only by the beginning of July. Since the final molt of the overwintered nymphs takes place in May under the long-day conditions, all the females enter summer diapause and lay eggs only after its termination, in July (Fig. 8). In this way, the development of the nymphs of the first (complete) summer generation can be synchronized with ripening of seeds of the host plant. The early nymphs of this generation reach the V instar at the beginning of August (when the day length still exceeds 14 h 30 min) and molt to adults without nymphal diapause. These adults soon mature and lay eggs (Fig. 8, arrow) because the day is already short enough (< 14 h 30 min) for reproduction without diapause. Therefore, despite the presence of summer adult diapause, *P. lewisi* has time to produce the partial second generation. The later or more slowly developing nymphs of the first (complete) summer generation reach the V instar after the middle of August, when the day is already short (< 14 h 30 min), and form winter nymphal diapause in response to this



**Fig. 9.** Photoperiodic control of pupal diapause induction in different populations of the cabbage white *Pieris brassicae* (L.) at 21°C (after Spieth et al., 2011): 1, Lisbon (Portugal, 38.5°N); 2, Horsens (Denmark, 55.9°N); 3, hybrids obtained by crossing of individuals from Lisbon and Horsens.

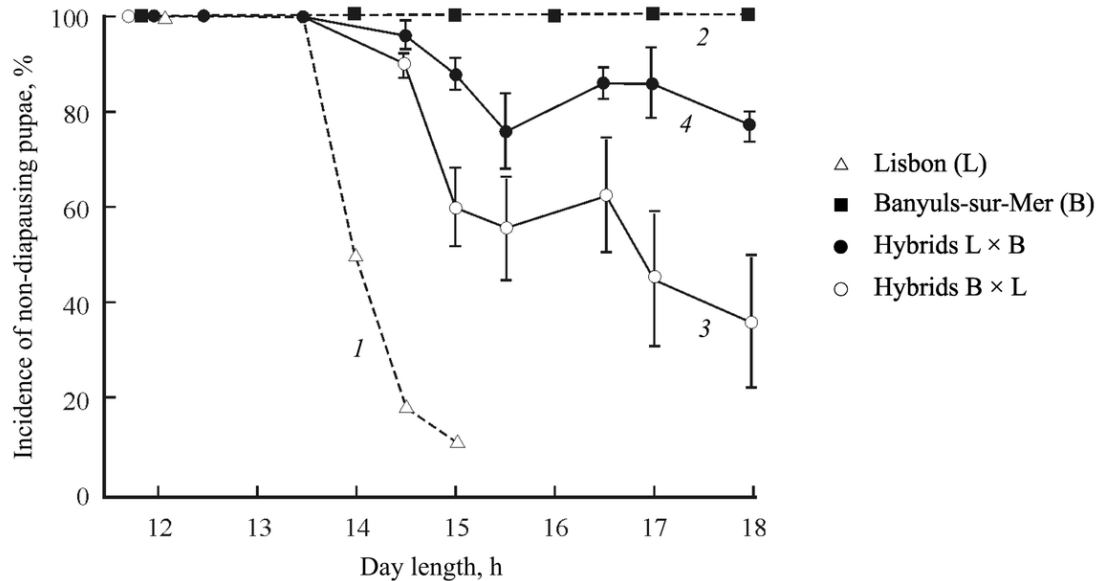
photoperiod. All individuals of the partial second generation also diapause at the nymphal stage (Fig. 8). Thus, adult aestivation in *P. lewisi* eliminates the critical pressure of the trophic factor by shifting the onset of reproduction onto the period when food is available to the offspring, and does not prevent development of the partial second generation.

### 3.2.1. Photoperiodically Controlled Summer Diapause as a Way of Avoiding Parasites

Among the various seasonal adaptations of the cabbage white *Pieris brassicae*, two are well studied: the winter pupal diapause, aimed at survival of the unfavorable winter conditions, and long-distance migrations of the adults, allowing them to avoid adverse conditions during summer (Roer, 1959; Danilevsky, 1961; Goryshin et al., 1981). However, one more peculiar feature was recently discovered in this species. It was found that southern populations of the cabbage white possessed not only the winter but also the summer pupal diapause (Spieth et al., 2011). Among the 25 studied populations from the south of France and Italy, and also from Israel, India, and other southern territories, only in 3 populations from the south coast of the Iberian Peninsula (36.5–40°N) all the 100% of individuals formed summer diapause; in 3 more populations from slightly more northern areas (41–43°N) summer diapause was observed only in some individuals. The northern boundary of the region within which

aestivation is formed in this species passes along the southern slopes of the Pyrenees. The cabbage white pupae do not aestivate to the north of this line, whereas the zone to the south of it is inhabited by populations varying in the degree of manifestation of summer diapause. This zone is about 200 km wide, and the fraction of aestivating individuals in it varies from year to year. For example, according to the laboratory data, the incidence of aestivation fluctuated from 7 to 100% in the offspring of 35 females (Spieth et al., 2011).

An attempt was made to emulate the processes taking place in nature and to estimate the influence of the parental generation on the incidence of aestivation in the offspring. For this, individuals from Lisbon (Portugal, 38.5°N; Fig. 9, 1), which did not form winter diapause at 21°C but aestivated at a day length exceeding 15 h, were crossed with individuals from Horsens (Denmark, 55.9°N; Fig. 9, 2), which hibernated at a day length shorter than 15 h. It was found that the PhPR of the hybrids was generally the same as that of the northern parents but their critical photoperiod was almost 2 h 30 min shorter, and about 10% of the pupae diapaused in all the long-day regimes. Therefore, the properties of the Lisbon population exerted strong influence on the induction of short-day diapause, which shifted onto considerably later dates in the offspring due to a shorter critical photoperiod (Spieth et al., 2011).



**Fig. 10.** Photoperiodic control of pupal diapause induction in the cabbage white *Pieris brassicae* (L.): 1, aestivating population from Lisbon (Portugal, 38.5°N); 2, non-aestivating population from Banyuls-sur-Mer (France, 42.5°N); 3, hybrids obtained by crossing of males from Banyuls-sur-Mer and females from Lisbon; 4, hybrids obtained by crossing of males from Lisbon and females from Banyuls-sur-Mer (after Spieth et al., 2011). The temperature was 21°C. Standard errors are given for 3 and 4.

In the next experiment, the aestivating individuals from the Lisbon population were crossed with non-aestivating ones from the environs of Banyuls-sur-Mer (42.5°N) in the southwest of France (Fig. 10). In this case, the PhPR of the hybrids was intermediate between the responses of the parental generation. However, the acquired ability to form summer diapause was lost completely after 4 or 5 generations.

A question arises, why only the populations from the south of the Iberian Peninsula can form summer diapause? The cited authors proposed two hypotheses to explain this phenomenon. First, summer diapause may synchronize the seasonal development of individuals in the population (which has 6 annual generations, 3 in spring and 3 in autumn); second, it may allow the cabbage white to avoid the deadly activity of parasitoids, the most important of which is the braconid wasp *Cotesia glomerata* (Linnaeus, 1758) (Hymenoptera, Braconidae).

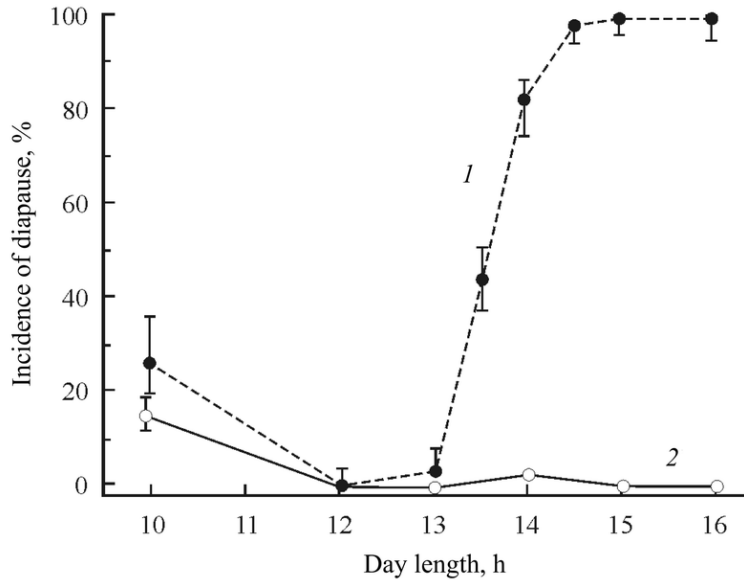
On the Iberian Peninsula, the cabbage white aestivates for three months, from the end of May to approximately the end of August, all the 100% of pupae forming summer diapause. No summer diapause was found in *C. glomerata* (Spieth and Schwarzer, 2001; Fig. 11), whereas the maximum lifespan of its females does not exceed one month (Moiseeva, 1960). Therefore, in the absence of the cabbage white larvae, the

parasitoid has to infest other, less favorable hosts, such as the larvae of *Pieris rapae* Linnaeus, 1758, *P. napi* Linnaeus, 1758, and *Aporia crataegi* Linnaeus, 1758 (Lepidoptera, Pieridae), in which its development is less successful (Maslennikova, 1958; Brodeur et al., 1996).

### 3.3. Food

The importance of food as a cue inducing summer diapause has been studied in a few species, despite the fact that the main function of summer diapause seems to be adaptation of the life cycle to the seasonal changes in the availability of food (regardless of the mode of feeding). Moreover, in the opinion of Masaki (1980, p. 18), “the food supply is a priori the most critical selecting factor for the evolution of diapause. Other factors, both biotic and abiotic, may exert modifying influences on the framework of seasonal adaptation set by the food supply.”

The role of food in summer diapause induction was experimentally demonstrated both for many predatory insects, for example ladybirds (Coleoptera, Coccinellidae) (Zaslavsky, 1984; Hodek and Honěk, 1996) and lacewings (Neuroptera, Chrysopidae) (Tauber and Tauber, 1982; Volkovitsh, 2007), and for phytophages, such as leaf beetles (Coleoptera, Chrysomelidae) (Ogata and Sasakawa, 1983; Nakai and Takeda, 1995)



**Fig. 11.** Photoperiodic responses in the cabbage white *Pieris brassicae* (L.) and its parasitoid, the braconid wasp *Cotesia glomerata* (L.) from Lisbon (Portugal, 38.5°N) at 21°C (after Spieth and Schwarzer, 2001): 1, *Pieris brassicae* (induction of summer pupal diapause; 95% confidence interval is shown); 2, *Cotesia glomerata* (no summer diapause).

and shield bugs (Heteroptera, Pentatomidae) (Nakamura and Numata, 1997; Numata, 2004). The formation of summer diapause in parasitic insects (entomophages) in the absence of their oviposition substrate, i.e., the infestable host stage, may be also regarded as a response to the trophic factor.

The distinct role of food as an ecological cue of summer diapause induction is a characteristic adaptive feature of aphidophages reflecting the ephemeral presence of living aphids that constitute their trophic resource. The most convincing examples of the signal function of the trophic factor can be found among the aphidophagous lacewings (Neuroptera, Chrysopidae) and ladybirds (Coleoptera, Coccinellidae). For instance, the lacewing *Chrysoperla mohave* (Banks, 1938) (= *Chrysoperla downesi* [Smith, 1932]), unlike the closely related *Chrysoperla plorabunda* (Fitch, 1855), is predaceous not only at the larval but also at the adult stage (Tauber and Tauber, 1973a, 1973b, 1982). The Californian population of *Ch. mohave* is characterized by two adult diapauses: the winter one, which begins in autumn and is induced by the short day, and the summer one, triggered by the absence of prey combined with high temperatures. This trophic diapause is terminated when aphids appear in sufficient numbers. The winter diapause is an integral element of the seasonal cycle of *Ch. mohave* while the summer diapause is not. Its ecological significance is evident, considering that in July–September, when the

day length does not prevent reproduction of the lacewing, California typically has hot and dry weather at which the abundance of aphids noticeably decreases or varies from year to year. Later studies showed that the population of *Ch. mohave* was polymorphic with respect to both photoperiod and prey (i.e., trophic preferences), while the seasonal cycle of the species might be multivoltine, univoltine, or mixed (Tauber and Tauber, 1982; Volkovitsh, 2007).

Similar to the lacewings, a very strong influence of food on the induction of summer diapause can be observed in ladybirds, in which the trophic factor also acts as a cue (Stewart et al., 1967; Ipert and Hodek, 1974; Hodek and Honěk, 1996). For example, both food and the day length were shown to be powerful cues for the seven-spot ladybird *Coccinella septempunctata* (Linnaeus, 1758) (Coleoptera, Coccinellidae): non-diapause development was possible only when it was supported by both factors, i.e., the long day and the presence of aphids. Even under the conditions of long day, high temperature, and available carbohydrate and protein food, in the absence of aphids the ladybirds quickly stopped laying eggs and formed summer diapause, which was terminated when aphids reappeared. Similar to the situation with lacewings, the trophic factor acted primarily as a cue, since the absence of aphids caused rapid induction of diapause, rather than starvation and emaciation (Zaslavsky,

1984; Hodek and Honěk, 1996; Zaslavsky and Vaghina, 1996; Hodek, 2012a, 2012b).

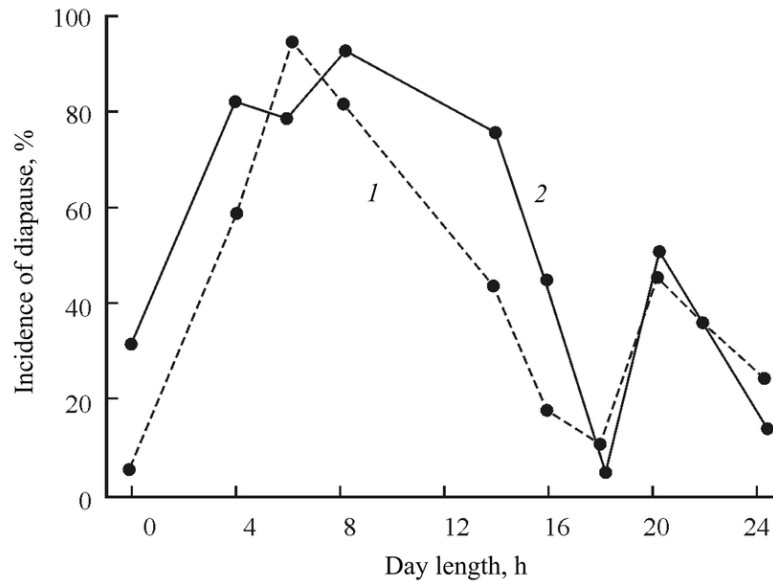
All populations of the seven-spot ladybird from Northern and Central Europe have winter diapause and complete one generation a year. In Southern Europe and the Mediterranean region, the seasonal pattern of the species is shaped by inclusion of two dormancy periods, the summer and the winter one (Hodek and Okuda, 1997). Judging by its physiological characteristics, the summer dormancy may be regarded as a true diapause. The aestivating females have immature eggs, abundant fat reserves, and a long pre-oviposition period. Their winter dormancy, which is formed in response to lowering temperatures, should probably be interpreted as consecutive quiescence, since it is terminated immediately upon the return of favorable conditions, namely elevated temperatures and abundant aphids (Hodek and Okuda, 1997). Regardless of the diapause-inducing factor (food or photoperiod), the diapausing beetles show the same properties: they enter a migratory state, their metabolism rate is lowered, and after the end of the migratory state they reduce mobility and acquire thigmotaxis, manifested in the tendency to find shelters and assemble in groups (Semyanov, 2002).

It is interesting that after the establishment of high farming with irrigation, which maintained high humidity and indirectly supported high abundance of aphids during the whole summer in the agricultural areas of California, the aestivating lacewing *Chrysoperla mohlave* was replaced there by the non-aestivating species *Ch. plorabunda* (Neuroptera, Chrysopidae) (Tauber and Tauber, 1982). By contrast, in the ladybird *Hippodamia convergens* Guérin-Ménéville, 1842 (Coleoptera, Coccinellidae), which also forms summer adult diapause in response to scarcity of aphids, the appearance of abundant aphid colonies in irrigated areas caused changes in the seasonal cycle. In particular, summer diapause was lost from the seasonal cycle of this ladybird because the period of food shortage, which determined the need for this diapause, had disappeared (Stewart et al., 1967). Thus, the anthropogenic action which changed the humidity conditions caused different responses in the populations of different predatory insects: in lacewings one aphidophagous species was replaced by another, and in ladybirds the structure of the seasonal cycle was modified by elimination of summer dormancy which was no longer needed.

Aestivation of the encyrtid wasp *Blastothrix longipennis* (= *B. confusa*) was also acquired as an adaptation for surviving the critical period of absence of the infestable stage of its host, the brown apricot scale *Parthenolecanium corni* (Bouché, 1844) (Homoptera, Coccidae), and not for surviving adverse climatic conditions. This parasitoid overwinters as I instar larvae inside the diapausing II instar larvae of the host. In Leningrad Province of Russia and in the north of Moldova, where *P. corni* has one annual generation, females of the overwintered generation of the wasp mature by the moment of emergence and immediately infest young and ovipositing females of the scale, in which the first summer generation of the parasitoid develops. Females of this generation emerge approximately a month later, when only I instar larvae of *P. corni* are present in the nature. The summer females of the parasitoid always emerge while immature and remain in the state of adult diapause until the end of August or the beginning of September, when the II instar larvae of the host appear; only then the females quickly mature and infest them. By the end of September, most females of *B. longipennis* perish while the larvae do not develop beyond the I instar. It should be noted that males of the summer generation of *B. longipennis*, unlike females, have no summer adult diapause; they always mature before emergence and die soon after mating (Sugonyaev, 1963; Danilevsky and Sheldeshova, 1968; Sugonyaev and Voinovich, 2006).

Summer diapause in females of *B. longipennis* is induced by the short-day PhPR. If the larvae and pupae develop at the short day (12 h), the females mature by the time of emergence, whereas at the long day (over 14 h) they emerge with still undeveloped gonads. The adult diapause can be easily terminated by the short day (Sugonyaev, 1963), the parameters of PhPR inducing and terminating the diapause being very similar. The duration of diapause and the physiological state of females are also affected by the thermal conditions. An increase in temperature (up to 25 or 30°C) acts in the same manner as the long day, inhibiting the gonad development. On the contrary, lower temperatures (15 and 17°C) stimulate the oocyte development. One important feature of this parasitoid deserves special attention: the inhibitory action of the day length and temperature was clearly manifested only in the absence of the infestable host, when the female wasps fed on glucose or honey solution. However, if the diapausing females of *B. longipennis* were kept together





**Fig. 12.** Photoperiodic control of induction of adult aestivation in two geographic populations of the fruit fly *Drosophila phalerata* Meig. at 18°C (after Geispits and Simonenko, 1970): 1, Abkhazia (Sukhumi, 42°N); 2, Leningrad Province (60°N).

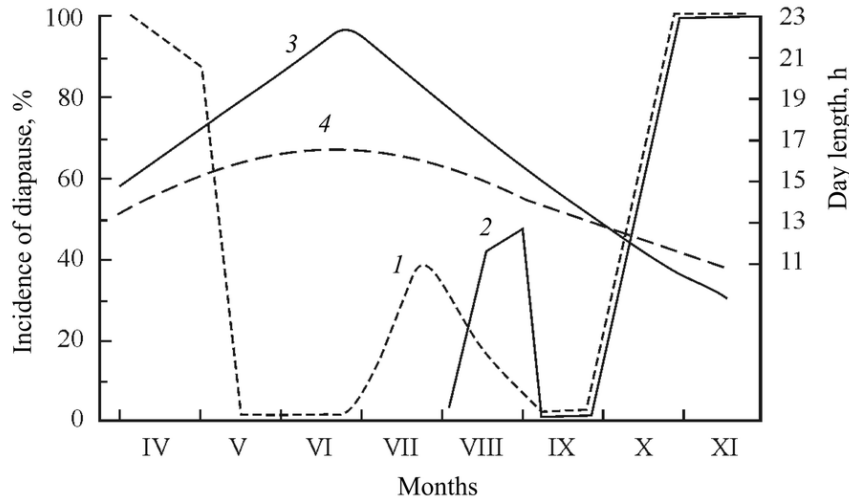
with II instar larvae or young females of the brown apricot scale on whose hemolymph they could feed, they matured even at the long day, i.e., the action of the photoperiod was neutralized. In the areas where *P. corni* completes two annual generations and its II instar larvae and young females are available almost during the whole summer, for example on black locust trees in the south of Moldova, the parasitoid forms no summer diapause (Sugonyaev, 1963; Danilevsky and Sheldeshova, 1968).

Laboratory experiments with the fruit fly *Drosophila phalerata* Meigen, 1830 (Diptera, Drosophilidae) revealed a bimodal PhPR curve in two studied populations: one from Abkhazia (Sukhumi, 42°N), the other from Leningrad Province (60°N). Adult diapause was formed both at the long day (20 h of light a day), and at the short day (8–14 h) (Fig. 12; Geispits and Simonenko, 1970).

Experiments carried out under the natural conditions of Leningrad Province with the local and Abkhazian populations showed that this species, besides the winter adult diapause formed at the short day, also has a development delay at the long day. Not all the females entered diapause in summer, the fraction of diapausing individuals during this season being 39% for the Leningrad population and 48% for the Abkhazian population. Also different was the timing of summer diapause under the natural conditions of Leningrad Province: individuals from the Leningrad

population diapaused in July, and those from the Abkhazian population, in August. This delay of development was not long: females from both populations resumed development in August and became reproductively active already at the beginning of September (Fig. 13).

The cited authors explain the origin of summer diapause in *D. phalerata* in terms of adaptation to the shortage of mushrooms serving as oviposition substrate. This shortage leads to diapause induction in a considerable fraction of females of the first generation. The flies that remain active probably find suitable substrates and lay eggs from which the second generation develops. In autumn, starting with September when mushrooms become abundant, females of the first generation reactivate from the short summer diapause and start laying eggs simultaneously with females of the second generation. Thus, the second and third generations develop concurrently in August, and the emerging adults of both generations form winter diapause under the action of the short day in autumn. Both induction and termination of summer diapause in females of the Abkhazian population are shifted onto earlier dates, according to the parameters of their PhPR. The annual cycle as a whole is regulated by two (summer and winter) facultative adult diapauses. The aestivating part of the population produces two generations per season, while the part developing without a summer delay produces three generations (Geispits and Simonenko, 1970).



**Fig. 13.** Seasonal dynamics of adult diapause in two populations of *Drosophila phalerata* Meig. kept under the natural conditions of Leningrad Province, Russia (60°N) (after Geispits and Simonenko, 1970): 1, incidence of diapause (%) in females of the local population under the natural conditions of Leningrad Province; 2, the same, for the Abkhazian (Sukhumi) population maintained in Leningrad Province; 3, day length in Leningrad Province; 4, day length in Sukhumi (Abkhazia, 42°N).

#### 4. FACTORS CONTROLLING TERMINATION OF SUMMER DIAPAUSE

The factors inducing summer diapause are usually considered together with the factors terminating it; it is interesting that the latter are much better studied. Similar to induction of summer diapause, in most cases its termination is related to the influence of the temperature and photoperiod: reactivation is stimulated by the decreasing temperature and the shortening day. Since these two factors act in a concerted manner, it is usually very difficult to assess the action of either factor separately. However, in some species of insects the temperature was shown to independently affect the termination of summer diapause. For instance, in the north of Japan the diapausing pupae of the summer cabbage fly *Delia floralis* (Fallén, 1824) (= *Hylemyia floralis*) (Diptera, Anthomyiidae) do not reactivate after overwintering in response to high temperatures but remain in summer diapause for the whole summer. Their morphogenesis starts only in autumn in response to a decrease in temperature, and reproduction is thus shifted onto September (Ishitani and Sato, 1981). A similar type of termination of summer diapause was also observed in the cotton bollworm *Heliothis armigera* in Sudan, where its post-diapause development starts only after the drop of temperature from 34 to approximately 26°C (Hackett and Gatehouse, 1982).

The role of short-day conditions in termination of summer diapause has been demonstrated for many species aestivating at different stages: the egg in the

range crane fly *Tipula simplex* Doane, 1901 (Diptera, Tipulidae) (Hartman and Hynes, 1980); the larva in the lacewing *Nineta pallida* (Schneider, [1846]) (Neuroptera, Chrysopidae) (Canard, 1988); the eonymph in the sawfly *Neodiprion sertifer* (Sullivan and Wallace, 1965, 1967; Minder, 1980); the pupa in the owlet moths *Diloba coeruleocephala* Linnaeus, 1758 (Lepidoptera, Noctuidae) (Tzanakakis and Koveos, 1983) and *Heliothis virescens* (Butler et al., 1983), the Japanese oak silkworm *Antheraea yamamai* Guérin-Méneville, 1861 (Lepidoptera, Saturniidae) (Kato and Sakate, 1981), and the root maggot fly *Pegomyia bicolor* (Xue et al., 2001); the adult in the lacewing *Nineta flava* (Scopoli, 1793) (Volkovitch, 2007), the diving beetle *Agabus disintegratus* (Leach, 1817) (Coleoptera, Dytiscidae) (Garcia and Hagen, 1987), the leaf beetles *Galeruca tanacetii* (Siew, 1966; Saulich and Volkovitch, 1996) and *Colaphellus bowringi* Baly, 1865 (Coleoptera, Chrysomelidae) (Xue et al., 2002), the ladybirds *Epilachna admirabilis* Dejean, 1835 (Coleoptera, Coccinellidae) (Imai, 2004) and *Hippodamia undecimnotata* (Schneider, 1792) (= *Semiadalia undecimnotata*) (Katsoyannos et al., 2005), the fruit fly *Drosophila phalerata* (Geispits and Simonenko, 1970), and many other species.

In most cases, the principal cue is the absolute day length, which is assessed relative to the photoperiodic threshold (i.e., whether it is greater or smaller than the threshold value). At the same time, similar to diapause induction, there are species in which post-aestivation

activity is induced or enhanced not by constant but by decreasing photoperiod, or aestivation is terminated spontaneously. For example, larvae of the crane fly *Tipula pagana* remain in diapause for over 200 days at the long day (L : D 18 : 6)<sup>1</sup> but pupate after approximately 100, 54, and 48 days in shorter photoperiods: L : D 16 : 8, 14 : 10, and 12 : 12, respectively. Therefore, the shorter the light day, the shorter is summer diapause in this species (Butterfield, 1976). The summer pronymphal diapause in the moth *Elcysma westwoodi* Vollenhoven, 1863 (Lepidoptera, Zygaenidae) gradually shortens from 83 to 30 days as the photoperiod changes from the typical long (L : D 16 : 8) to the typical short one (L : D 12 : 12) (Ishii and Tsuneyoshi, 1977). The summer diapause of the leaf beetle *Galeruca tanacetii* was more efficiently terminated by the decreasing day length than by the constant short-day conditions (Siew, 1966).

Summer diapause may sometimes be terminated by certain unusual stimuli. For example, diapause was terminated when aestivating flies *Drosophila moriwakii* Okuda et Kurokawa, 1957 (Diptera, Drosophilidae) were kept in small cages, i.e., under congested conditions (Ichijō et al., 1992). The same effect was produced by mechanically pricking the diapausing pupae of the Japanese oak silkmoth *Antheraea yama-mai* (Kato and Sakate, 1983).

##### 5. PROLONGED SUMMER-WINTER DIAPAUSE OR TWO CONSECUTIVE DIAPAUSES?

Prolonged diapause induced in the height of summer and terminated only in spring of the following year is often observed in insects whose trophic resources are only available in spring and early summer (Masaki, 1980; Danks, 1987). Such annual cycles occur in univoltine species reproducing in early spring, such as the gypsy moth *Lymantria dispar* (Linnaeus, 1758) (Lepidoptera, Erebididae), the green oak moth *Tortrix viridana* (Linnaeus, 1758) (Lepidoptera, Tortricidae), and many others. This seasonal cycle was studied, in particular, in the shield bugs *Dybowskyia reticulata* (Dallas, 1851) and *Eurydema rugosum* Motschulsky, 1861 (Heteroptera, Pentatomidae) which feed on the early ripening seeds of umbellates in Japan (Nakamura and Numata 1997; Numata, 2004). Many representatives of other insect taxa also have to adapt

to the expressed seasonality and food shortage during the middle and end of summer by entering an early and prolonged diapause which may be called summer-winter diapause. This diapause occurs at one ontogenetic stage and can be identified only by its seasonal timing. Regardless of its form, this inhibition of development is usually referred to as *dormancy*, a more general term than *diapause*.

For example, under the conditions of Transcarpathian Ukraine, some adults of the first generation of the Colorado potato beetle *Leptinotarsa decemlineata* Say, 1824 (Coleoptera, Chrysomelidae), developing in May–June at the long day and high temperatures, burrow into the soil and remain there to overwinter. Therefore, their aestivation continues into winter diapause. Moreover, some beetles remain in the soil for 2–3 years, i.e., their summer diapause after the first overwintering is transformed into the many-year superdiapause (Goryshin et al., 1986; Ushatinskaya, 1987). Similarly, in experiments with the ragweed leaf beetle *Zygogramma suturalis* (Fabricius, 1775) (Coleoptera, Chrysomelidae) in Stavropol Territory, a half of the adults of the first summer generation formed an obligate summer-winter diapause (Kovalev et al., 1986; Vinogradova and Bogdanova, 1988). The white *Euchloe belia* (Stoll, 1782) (Lepidoptera, Pieridae) in Central Asia develops in one annual generation and has summer diapause continuing into winter diapause (Shchetkin, 1965). The seasonal cycles of insects living in semi-arid and arid climates are probably controlled in the same way. Summer diapause with transition to overwintering allows one generation to develop under the conditions of excessively long summer season and synchronizes the appearance of the feeding stages with the relatively short vegetation period of their host plants. This type of diapause was described in many desert-dwelling Lepidoptera (Shchetkin, 1965; Falkovitsh, 1979; Kaplin, 1994). If diapause is formed in summer and insects remain dormant without any visible changes till the spring of the following year, this diapause is usually described as summer-winter or summer-autumn-winter one, according to its seasonal timing.

However, it has been found that in many cases, such a vague description merely reflects the lack of knowledge of the externally undetectable physiological processes. In reality, according to Masaki (1980), this type of prolonged physiological dormancy often corresponds to two consecutive diapauses (summer and winter), sometimes occurring at the same ontogenetic

<sup>1</sup> Here and below, the photoperiod is described as the daily duration of light and darkness (L : D), or the photophase and scotophase, in hours.

stage but always separated by at least a short period of activity. Depending on the species, this period may be differently manifested and involve different processes, from brief resumption of locomotion and feeding to reproduction and morphogenesis (for example, molting onto the next instar or transition to the next ontogenetic stage).

The true summer diapause can be identified by several criteria. Its termination is most easily detected by the resumption of locomotion. For example, in the sunn pest *Eurygaster integriceps* Puton, 1881 (Heteroptera, Scutelleridae) the summer and winter diapauses are separated by a period of activity during which the adults migrate from the places of oversummering to those of overwintering. Obligate summer diapause is formed in young adults in June–July, i.e., by the moment of harvesting of spiked cereals with which this species is tropically associated. After a brief but intensive pre-diapause feeding, the bugs migrate to the places of aestivation. In the plain terrain such places are forest belts, forest edges, clearings, and even parks and gardens. In the mountains, the bugs ascend to altitudes of up to 2500–2800 m above sea level. Aestivation lasts about two months, during which the bugs lose about 20% of the nutrient reserves stored during the pre-diapause feeding period (Ushatinskaya, 1955). In autumn, with abatement of heat, they migrate downhill and overwinter in the state of obligate winter adult diapause. The bugs living on plains also have a period of activity between the summer and winter diapauses, during which they fly over short distances into the forest belts and may also feed on wild grasses and other plants. This active period lasting about two weeks marks a clear boundary between the summer and winter diapauses (Arnoldi, 1947; Saulich and Musolin, 2018).

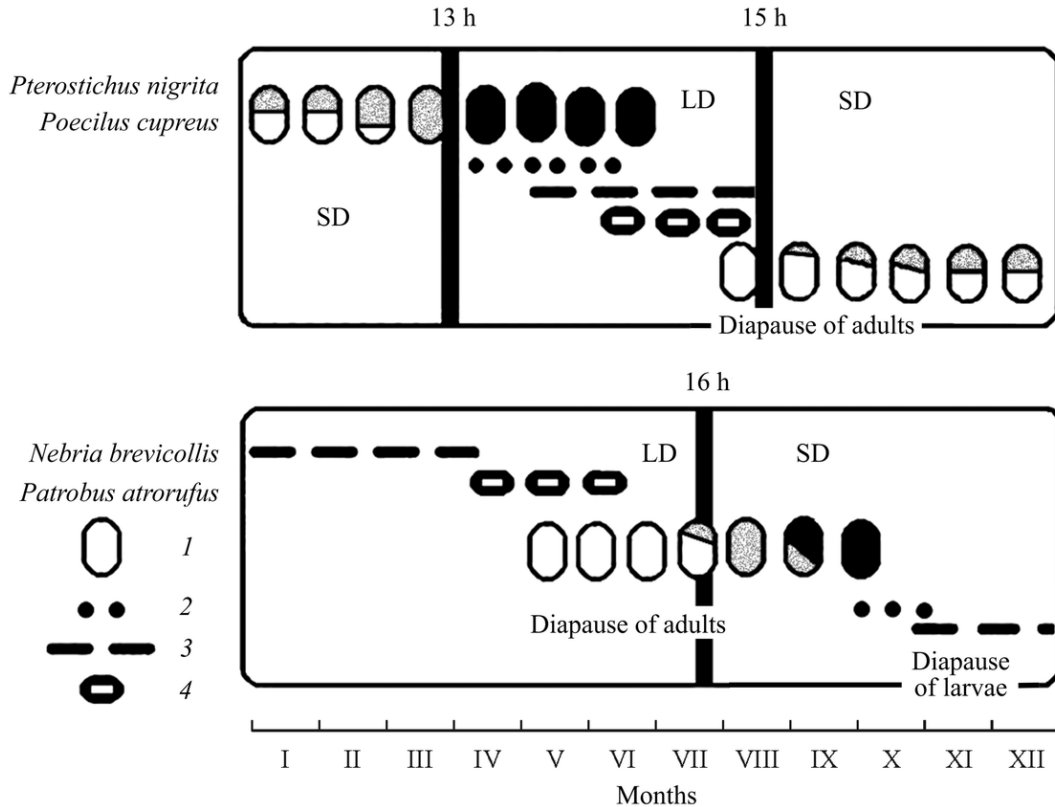
However, such a distinct boundary between the two diapauses cannot be observed if transition from one form of physiological dormancy to the other is not accompanied by resumption of mobility, in particular, in the cases of embryonic or adult diapauses when both diapauses occur at the same ontogenetic stage and their transition is related only to inconspicuous changes in the phases of embryogenesis or oogenesis. The latter case is considered in detail below by the example of the seasonal cycles of ground beetles.

It is known that ground beetles are subdivided into two groups: species reproducing in spring and those reproducing in autumn (Thiele, 1971; Ferenz, 1977).

*Pterostichus nigrita* (Paykull, 1790) (Coleoptera, Carabidae) is a typical representative of species with spring reproduction. Young adults which appear in the middle of summer, at the long day and favorable temperatures, do not reproduce but form a prolonged diapause that is terminated only in the spring of the following year. It was found that the delay in their gonad development could be eliminated only by a two-step change in the day length, from long to short day and back to long day. The first step of reproductive maturation, namely previtellogenesis, is controlled by a short-day PhPR. In the nature (Fig. 14, upper diagram), the short-day induction of previtellogenesis takes place in autumn, at the day length less than 15 h. The beetles overwinter at this stage; therefore, the action of the short day terminates summer diapause which is followed by winter diapause. The second step is that of vitellogenesis (accumulation of yolk by the developed oocytes), which is controlled by a long-day PhPR with a threshold of 13 h. Maturation of females and oviposition start in April, when the day length exceeds the threshold value. Pre-adult stages develop in May–July, and the young adults that appear in the middle of summer form obligate summer diapause (Thiele, 1971; Ferenz, 1977).

The two-step response in *P. nigrita* controls only the maturation of females, whereas males can mature at the short day and probably overwinter in the mature state. This pattern, referred to as the short-long-day control, is typical of most of the studied species of the genus *Pterostichus* Bonelli (Coleoptera, Carabidae) (Thiele, 1971; Ferenz, 1977).

Differentiation of diapauses in the ground beetles reproducing in autumn (such as *Nebria brevicollis* and *Patrobus atrorufus*) is quite obvious. Such species have two diapauses occurring at different ontogenetic stages: the summer adult and the winter larval diapause (Fig. 14, lower diagram). As opposed to the species with spring reproduction, in the ground beetles reproducing in autumn previtellogenesis is unblocked by the long day in summer and vitellogenesis is unblocked by the short day in autumn. As a result, the females mature in August and reproduce in autumn; the larvae overwinter. Thus, the so-called two-step control consists in consecutive realization of two elementary responses controlling the consecutive phases of ontogenesis. The second step (formation of winter diapause) is possible only after the completion of the first step (in species reproducing in spring, this is termination of summer diapause). In ground beetles re-



**Fig. 14.** Seasonal cycles of some ground beetles (Coleoptera, Carabidae) in Cologne (Germany, 51 N) (after Thiele, 1971; Ferenz, 1977): 1, adults (white, reproductively immature; gray, during vitellogenesis; black, during vitellogenesis); 2, eggs; 3, larvae; 4, pupae; LD, long day (photoperiod longer than the critical value); SD, short day (photoperiod shorter than the critical value). Bold vertical lines show the seasonal timing of critical photoperiods inducing gonad maturation.

producing in autumn, oviposition is impossible until summer diapause has been terminated (Thiele, 1969).

Similar examples of identical external manifestations of summer and winter diapauses can be found in insects from other orders as well. For instance, adults of the swallowtail *Luehdorfia puziloi* emerge and lay eggs in early spring. Larvae pupate at the end of spring and the beginning of summer. The imaginal morphogenesis (i.e., formation of the adult inside the pupal sheath) starts in autumn as the temperature decreases and is almost completed before winter, but adults emerge only after winter cooling (Kimura, 1975). Therefore, the first (summer) diapause occurs in the pupa, and the second (winter) one, at the stage of the pharate adult. A similar pattern is observed in moths of the genus *Orthosia* Ochsenheimer (Lepidoptera, Noctuidae) associated with woody plants: most of them have one annual generation and belong to the group of species with early spring reproduction activity. The flight starts early in spring; even in Leningrad Province the adults appear as early as in April. The

summer generation proceeds rapidly, and the pupae diapause at the beginning of summer. Laboratory experiments showed that pharate adults of *Orthosia cerasi* Fabricius, 1775 overwintered in the state of winter diapause inside the pupal sheaths (Saulich and Sokolova, 2002).

Very similar patterns seem to occur in the Douglas fir cone moth *Barbara colfaxiana* Kearfott, 1907 (Lepidoptera, Olethreutidae) (Sahota et al., 1983), the pine beauty *Panolis flammea* (Denis et Schiffermüller, 1775) (Lepidoptera, Noctuidae) (Klyuchko, 2006; Meshkova, 2009), and other univoltine species reproducing in early spring. The seasonal development of the looper moth *Cheimoptena pennigera* Danilevsky, 1969 (Lepidoptera, Geometridae), described by Danilevsky (1969), may be also classified under this type. This moth inhabits saxaul sand dunes in the deserts of South Kazakhstan and Turkmenistan and appears to be widely distributed in Central Asia, as indicated by its records from two localities positioned more than 1000 km apart. The adults of *Ch. pennigera* have

a habitus uncharacteristic of the representatives of the taxon, and the systematic position of the new species could be determined only after a thorough study of its seasonal development. The annual cycle of *Ch. pennigera* is typical of looper moths reproducing in early spring and includes a prolonged pupal diapause extending over the whole summer, autumn, and winter. Adults emerge after cooling in January, at the mean temperature of about 0°C in Turkmenistan and about -8°C in Kazakhstan. The moths are active only in the daytime and their activity is completely determined by the intensity of insolation. The males fly while the females only crawl on the sand (Danilevsky, 1969). The seasonal development of the species was later clarified by Falkovitsh (1979). It was found that by the late autumn, the pupal sheaths already contained completely formed adults. Thus, pupal aestivation seems to be terminated at the end of summer when the temperature drops, and morphogenesis is resumed in autumn. Adults emerge in December–February and reproduce despite very low temperatures; this is possible due to their diurnal activity. The eggs laid during this period do not develop until early spring because of low temperatures. Larvae hatch in early spring (March), feed actively on saxauls, and pupate in mid-May; the pupae aestivate. Correspondingly, the seasonal development of *Ch. pennigera* may be described as univoltine with two diapauses: summer pupal diapause and winter diapause of the pharate adult inside the pupal sheath. Active larval development in early spring is an adaptation to the desert conditions and seems to be typical of many species of Lepidoptera forming a peculiar winter faunal complex of the desert zone. In such cases, the period of activity separating the summer and winter diapauses may be hard to detect due to the inconspicuous nature of the physiological processes involved.

Good indicators of the seasonal class of diapause are the factors of its induction and termination. It is known that facultative winter diapause is usually induced by the short day and low temperatures; by contrast, summer diapause is induced by the long day and high temperatures. Termination of winter diapause occurs as the result of prolonged action of cold (usually at temperatures below the development threshold) and less frequently, of the short day, while summer diapause is most frequently terminated at somewhat lowered but moderate temperatures (about 15°C) and the short day. Prolonged summer-winter diapause probably consists of two separate processes, each requiring special cues for termination. It was shown

under the laboratory conditions that the termination effect could be achieved by two consecutive actions: first the short day (SD), corresponding to autumn and terminating summer diapause, and then the long day (LD), corresponding to spring and terminating winter diapause. Based on this consecutive action of SD and LD, Zaslavsky (1984) made a conclusion about the existence of a separate category of two-step photoperiodic responses: SD-LD and LD-SD. Still, under the natural conditions the principal factor terminating winter diapause in insects is exposure to temperatures below the active development threshold.

Identification of some atypical exogenous states observed in insect larvae may be very difficult. For example, the delay of larval development of the pale tussock moth *Calliteara pudibunda* (Linnaeus, 1758) (= *Dasychira pudibunda*) (Lepidoptera, Erebidae) under the long-day conditions in summer was regarded as a special category of quantitative PhPR (Tyshchenko, 1983; Musolin and Saulich, 1997), because the locomotion and feeding of the larvae did not stop completely but only became less intensive. However, some facts suggest that such development delays may have much in common with aestivation. This is indicated, in particular, by occurrence of these delays at specific larval instars (starting with the VI or VII), an abrupt simultaneous decrease in the feeding intensity and gut content, the histological structure of the fat body, and the existence of geographic forms varying in the degree of manifestation of this response; the latter was confirmed by experiments with parallel acclimation of the northern and southern populations of *C. pudibunda* under the natural conditions of Leningrad Province (Geispits and Zarankina, 1963).

Such manifestations of summer diapause proved to be quite common in insects. For example, the growth of the I instar larvae of the lacewing *Nineta pallida* in the Pyrenees is slowed down under the influence of the short day in autumn; in the laboratory this effect occurred at 12 h of light a day. The overwintered larvae molt to the next instar in April. However, under the long day conditions of spring and early summer the development of the II and III instar larvae is delayed till July; correspondingly, adults reproduce only at the end of summer (Canard, 1988, 1990).

The larval growth rates of the North American lacewing *Ceraeochrysa placita* Banks, 1908 (Neuroptera, Chrysopidae) are also controlled by the day length. The short day slows down the development of

the I instar larvae and induces diapause at the II instar (Tauber et al., 1998). Similar responses are typical of almost all the lacewings of the genus *Dichochrysa* Yang (Neuroptera, Chrysopidae), in which the short day induces a labile (i.e., relatively weak) diapause at the III larval instar and slows down the development of the preceding instars (I and II) (Volkovitsh, 2007).

The same form of summer diapause, namely a delay of larval development during the summer season, occurs in the Japanese emperor *Sasakia charonda* (Hewitson, 1863) (Lepidoptera, Nymphalidae) (Kato and Hasegawa, 1984; Kato, 1989), the brown apricot scale *Parthenolecanium corni* (Sheldeshova and Stekolnikov, 1965), and many other insects.

During the study of seasonal development of the shield bug *Coptosoma scutellatum* (Geoffroy, 1785) (Heteroptera, Plataspidae) from the forest-steppe zone of Russia (Belgorod Province, 50°N), we obtained experimental data indicating that nymphal development was always suppressed at the middle (III and IV) instars regardless of the conditions (Musolin, 1997; Saulich and Musolin, 2014a). It was assumed that nymphs of this species overwintered at this particular ontogenetic phase. None of the tested laboratory conditions aimed at promoting active development, including different exposures to constant photoperiods at two temperatures (24.5 and 28°C) or changing day lengths in different combinations, resulted in continuation of metamorphosis: the nymphs inevitably formed diapause at the middle instars. Their metamorphosis ended only in the spring of the following year, when the nymphs passed the IV and V instars and molted to adults (Musolin, 1997; Saulich and Musolin, 2014a).

The adaptive significance of such a seasonal strategy of *C. scutellatum* in the forest-steppe zone is not clear. The early onset of nymphal diapause (in mid-July) is ecologically inexpedient, because in this case the vegetation season is only partly used while the diapausing nymphs (which are usually less protected from the adverse biotic and abiotic conditions than adults) are affected by the hottest period of summer. It was hypothesized that early dormancy might be composed of the consecutive summer and winter nymphal diapauses. This assumption is indirectly supported by observations both in the nature and in the laboratory. In particular, under the natural conditions of Ukraine, the first two nymphal instars complete development in 25–30 days while the development of the III instar takes about a month (Putshkov, 1961). According to the experimental data (Musolin, 1997), at a tempera-

ture of 24.5°C and a photoperiod of L : D 18 : 6, corresponding to the maximum day length in the study region, the development time of the III instar nymphs was twice as long as that at a shorter photoperiod of L : D 15 : 9. In this case, it may indeed be assumed that the seasonal cycle of *C. scutellatum* actually includes two diapauses: aestivation in III instar nymphs and hibernation in IV instar nymphs, with an inconspicuous gap between them, manifested externally as a prolonged summer-winter diapause of III and IV instar nymphs. This phenomenon has been described for many species, in which the prolonged diapause formed at the beginning or in the middle of summer was characterized merely by its seasonal timing.

Each similar case of expressed delay at a certain stage of larval development requires special experimental study, without which it cannot be reliably interpreted as a specific type of seasonal adaptation.

## CONCLUSIONS

Insects living in the temperate climate belt include summer diapause in their seasonal cycle for solving various problems related to adaptation to adverse seasonal conditions. Unlike winter diapause, summer diapause is induced in summer and terminated in autumn when active feeding, development, and/or reproduction are resumed. Its induction and maintenance are usually facilitated by high temperatures and the long day, whereas the short day and low temperatures prevent its induction or terminate summer diapause. The summer diapause syndrome is largely similar to that of winter diapause; it includes prior hypertrophy of the fat body, lowering of the metabolism rate, increased resistance to adverse biotic and abiotic conditions, etc. Inhibition of morphogenesis and gametogenesis is under the control of the endocrine system. The onset of summer diapause is often accompanied by migrations to varying, sometimes significant distances to the places of aestivation.

The selection factors responsible for evolution of summer diapause vary between species. The principal factors stimulating the development of summer diapause are probably climatic ones, which determine the availability and abundance of food, and also the pressure of predators and parasites. The prolonged diapause, which starts in spring or early summer and ends only after overwintering, is often composed of independent summer and winter diapauses, with inconspicuous transition between them.

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## REFERENCES

- Arnoldi, K.V., "The Sunn Pest (*Eurygaster integriceps*) in the Natural Biotopes of Central Asia: Ecological and Biocenological Aspects," in *The Sunn Pest Eurygaster integriceps Put., Vol. 1*, Ed. by D.M. Fedotov (USSR Academy of Sciences, Moscow, 1947), pp. 136–269 [in Russian].
- Bale, J.S., "Insect and Low Temperatures: from Molecular Biology to Distributions and Abundance," *Philosophical Transactions of the Royal Society of London. B. Biological Sciences* **357** (1423), 849–862 (2002).
- Belozero, V.N., "The Position of Dormant Stages in the Life Cycles of Acarines (Chelicerata: Arachnida: Acari), as Compared with Those of Mandibulata (Insecta; Crustacea)," in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions (Proceedings of the Biological Research Institute, Vol. 53)*, Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 193–233 [in Russian].
- Belozero, V.N., "New Aspects in Investigations of Diapause and Non-Diapause Dormancy Types in Insects and Other Arthropods," *Entomologicheskoe Obozrenie* **88** (1), 3–15 (2009) [*Entomological Review* **89** (2), 127–136 (2009)].
- Belozero, V.N., "Dormant Stages and Their Participation in Adjustment and Regulation of Life Cycles of Harvestmen (Arachnida, Opiliones)," *Entomologicheskoe Obozrenie* **91** (1), 180–216 (2012) [*Entomological Review* **92** (6), 688–714 (2012)].
- Bland, R.G., "Photoperiod-Diapause Relationship in the Alfalfa Weevil *Hypera postica*," *Annals of the Entomological Society of America* **64**, 1163–1166 (1971).
- Bonnemaison, L., "Particularites de la croissance embryonnaire et de la diapause nymphale chez le chematobie (*Operophtera brumata* L.) (Lepidoptera, Geometridae)," *Bulletin de la Societe Entomologique de France* **76** (5–6), 123–130 (1971).
- Brodeur, J., Geervliet, J.B.F., and Vet, L.E.M., "The Role of Host Species, Age and Defensive Behaviour on Ovipositional Decisions in a Solitary Specialist and a Gregarious Generalist Parasitoid (*Cotesia* Species)," *Entomologia Experimentalis et Applicata* **81**, 125–132 (1996).
- Butler, G.D. Jr., Henneberry, T.J., and Bartlett, A.C., "*Heliothis virescens* (Lepidoptera: Noctuidae): Termination of Summer Diapause," *Journal of Economic Entomology* **78** (6), 1287–1292 (1983).
- Butler, G.D. Jr., Wilson, L.T., and Henneberry, T.J., "*Heliothis virescens* (Lepidoptera: Noctuidae): Initiation of Summer Diapause," *Journal of Economic Entomology* **78**, 320–324 (1985).
- Butterfield, J., "Effect of Photoperiod on a Winter and on a Summer Diapause in Two Species of Crane-fly (Tipulidae)," *Journal of Insect Physiology* **22**, 1443–1446 (1976).
- Canard, M., "Seasonal Change in Photoperiodic Response of the Larvae of the Lacewing *Nineta pallida*," *Entomologia Experimentalis et Applicata* **47**, 153–159 (1988).
- Canard, M., "Effect of Photoperiod on the First-Instar Development in the Lacewing *Nineta pallida*," *Physiological Entomology* **15**, 137–140 (1990).
- Danilevsky, A.S., *Photoperiodism and Seasonal Development of Insects* (Leningrad State University, Leningrad, 1961) [in Russian].
- Danilevsky, A.S., "Two New Remarkable Species of Winter Moths from Central Asian Deserts: *Dasyethmia hiemalis*, gen. et sp. n. (Lepidoptera, Ethmiidae) and *Cheimoptena pennigera*, gen. et sp. n. (Lepidoptera, Geometridae)," *Entomologicheskoe Obozrenie* **48** (1), 179–189 (1969).
- Danilevsky, A.S. and Sheldeshova, G.G., "The Adaptive Significance of Photoperiodic and Cold Reactivation," in *Photoperiodic Adaptations in Insects and Acarines*, Ed. by A.S. Danilevsky (Leningrad State University, Leningrad, 1968), pp. 80–99 [in Russian].
- Danks, H.V., *Insect Dormancy: An Ecological Perspective* (Biological Survey of Canada, Ottawa, 1987).
- Denlinger, D.L., "The Physiology of Pupal Diapause in Flesh Flies," in *Current Topics in Insect Endocrinology and Nutrition*, Ed. by G. Bhaskaran et al. (Plenum, New York, 1981), pp. 131–160.
- Denlinger, D.L., "Dormancy in Tropical Insects," *Annual Review of Entomology* **31**, 239–264 (1986).
- Denlinger, D.L., "Regulation of Diapause," *Annual Review of Entomology* **47**, 93–122 (2002).
- Denlinger, D.L. and Lee, R.E. Jr. (Eds.), *Low Temperature Biology of Insects* (Cambridge University Press, New York, 2010).
- Ding, L., Li, Y., and Goto, M., "Physiological and Biochemical Changes in Summer and Winter Diapause and Non-Diapause Pupae of the Cabbage Armyworm, *Mamestra brassicae* L. during Long-Term Cold Acclimation," *Journal of Insect Physiology* **49**, 1153–1159 (2003).
- Endo, K., Fujimoto, Y., Kondo, M., Yamanaka, A., Watanabe, M., Weihua, K., and Kumagai, K., "Stage-Dependent Changes of the Prothoracicotropic Hormone (PTTH) Activity of Brain Extracts and of the PTTH Sensitivity of the Prothoracic Glands in the Cabbage Armyworm, *Mamestra brassicae*, before and during Winter and Aestival Pupal Diapause," *Zoological Science* **14**, 127–133 (1997).
- Falkovitsh, M.I., "Seasonal Development of Central Asian Desert Lepidoptera and Its Historical and Faunistic



- tic Analysis,” *Entomologicheskoe Obozrenie* **58** (2), 260–281 (1979).
25. Ferenz, H.J., “Two-Step Photoperiodic and Hormonal Control of Reproduction in the Female Beetle, *Pterostichus nigrita*,” *Journal of Insect Physiology* **23**, 671–676 (1977).
  26. Garcia, R. and Hagen, K.S., “Summer Dormancy in Adult *Agabus disintegratus* (Crotch) (Coleoptera: Dytiscidae) in Dried Ponds in California,” *Annals of the Entomological Society of America* **80** (2), 267–271 (1987).
  27. Geispits, K.F. and Orlovskaya, E.E., “Specific Physiological Features of the Two Types of Diapause in the Two-Spotted Spider Mite *Tetranychus urticae* Koch (Acarina, Tetranychidae),” in *Cold Tolerance in Insects and Acarines: Proceedings of a Symposium* (Tartu, 1971), pp. 16–20.
  28. Geispits, K.F. and Simonenko, N.P., “Experimental Analysis of Seasonal Changes in the Photoperiodic Response of *Drosophila phalerata* Meig. (Diptera, Drosophilidae),” *Entomologicheskoe Obozrenie* **49** (1), 83–96 (1970).
  29. Geispits, K.F. and Zarankina, A.I., “Specific Features of the Photoperiodic Response in the Pale Tussock Moth *Dasychira pudibunda* L. (Lepidoptera, Orgyidae),” *Entomologicheskoe Obozrenie* **42** (1), 29–38 (1963).
  30. Glinyanaya, E.I., “The Role of Photoperiodic Conditions in Reactivation after Winter and Summer Diapause,” in *Problems of Photoperiodism and Diapause of Insects*, Ed. by N.I. Goryshin (Leningrad State University, Leningrad, 1961), pp. 88–102 [in Russian].
  31. Goryshin, N.I. and Tyshchenko, G.F., “On Accumulation of Photoperiodic Information in the Cabbage Moth *Barathra brassicae* (Lepidoptera, Noctuidae) during Diapause Induction,” *Entomologicheskoe Obozrenie* **52** (2), 249–255 (1973).
  32. Goryshin, N.I., Saulich, A.Kh., and Volkovitsh, T.A., “A Study of the Ecological Significance of Photoperiodic Response in Three Species of Lepidoptera,” in *Photoperiodic Control of Seasonal Phenomena in Arthropods and Plants (Proceedings of the Biological Research Institute, Vol. 31)*, Ed. by V.P. Tyshchenko and N.I. Goryshin (Leningrad State University, Leningrad, 1981), pp. 60–81 [in Russian].
  33. Goryshin, N.I., Volkovitsh, T.A., Saulich, A.Kh., and Shakhova, N.N., “Experimental Analysis of Seasonal Development of the Colorado Potato Beetle in the Forest-Steppe Zone. II. Field Experiments and Phenological Observations,” *Zoologicheskii Zhurnal* **65** (4), 528–535 (1986).
  34. Goto, M. and Hukushima, H., “Factors Affecting the Induction of Summer and Winter Diapause and Diapause Sensitive Larval Stage of Cabbage-Armypworm Moth *Mamestra brassicae* (Lepidoptera: Noctuidae),” *Journal of Yamagata Agriculture and Forestry Society* **52**, 17–24 (1995).
  35. Goto, M., Li, Y.-P., Kayaba, S., Outani, S., and Suzuki, K., “Cold Hardiness in Summer and Winter Diapause and Post-Diapause Pupae of the Cabbage Armyworm, *Mamestra brassicae* L. under Temperature Acclimation,” *Journal of Insect Physiology* **47**, 709–714 (2001).
  36. Goto, S.G. and Numata, H., “Insect Photoperiodism,” in *Insect Molecular Biology and Ecology*, Ed. by K.H. Hoffmann (CRC Press, Boca Raton, 2014), pp. 211–238.
  37. Hackett, D.S. and Gatehouse, A.G., “Diapause in *Heliothis armigera* (Hübner) and *H. fletcheri* (Hardwick) (Lepidoptera: Noctuidae) in the Sudan Gezira,” *Bulletin of Entomological Research* **72**, 409–422 (1982).
  38. Hartman, M.J. and Hynes, C.D., “Embryonic Diapause in *Tipula simplex* and the Action of Photoperiod in Its Termination (Diptera: Tipulidae),” *Pan-Pacific Entomology* **56** (3), 207–212 (1980).
  39. Hodek, I., “Adult Diapause in Coleoptera,” *Psyche*, Art. ID 249081 (2012a). <http://dx.doi.org/10.1155/2012/249081>.
  40. Hodek, I., “Diapause/Dormancy,” in *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae)*, Ed. by I. Hodek, H.F. van Emden, and A. Honěk (Blackwell, Chichester, 2012b), pp. 275–342.
  41. Hodek, I. and Honěk, A. (with contributions from P. Ceryngier and I. Kovár), *Ecology of Coccinellidae* (Kluwer Academic Publishers, Dordrecht, 1996).
  42. Hodek, I. and Okuda, T., “Regulation of Adult Diapause in *Coccinella septempunctata* and *C. septempunctata brucki* from Two Regions of Japan (a Minireview),” *Entomophaga* **42**, 139–144 (1997).
  43. Hodková, M. and Hodek, I., “Photoperiod, Diapause and Cold-Hardiness,” *European Journal of Entomology* **101**, 445–458 (2004).
  44. Holliday, N.J., “Effects of Temperature on Winter Moth Pupae, *Operophtera brumata* (Lepidoptera, Geometridae),” *The Canadian Entomologist* **115** (3), 243–249 (1983).
  45. Ichijō, N., Beppu, K., and Kimura, M.T., “Aestivo-Hibernal Reproductive Diapause in *Drosophila moriwakii*: Flight as a Controlling Factor,” *Entomologia Experimentalis et Applicata* **62**, 23–28 (1992).
  46. Imai, C., “Photoperiodic Induction and Termination of Summer Diapause in Adult *Epilachna admirabilis* (Coleoptera: Coccinellidae) from a Warm Temperature Region,” *European Journal of Entomology* **101**, 523–529 (2004).
  47. Iperiti, G. and Hodek, I., “Induction alimentaire de la dormance imaginaire chez *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae) pour aider à la conservation des Coccinelles élevées au laboratoire avant une utilisation ultérieure,” *Annales de Zoologie, Écologie Animale* **6** (1), 45–51 (1974).
  48. Ishii, M. and Hidaka, T., “Influence of Photoperiod on the Adult Differentiation in the Pupae of the Univoltine

- Papilionid *Luehdorfia japonica*,” Applied Entomology and Zoology **14**, 360–361 (1979).
49. Ishii, M. and Hidaka, T., “Characteristics of Pupal Diapause in the Univoltine Papilionid, *Luehdorfia japonica* (Lepidoptera, Papilionidae),” Kontyû (Tokyo) **50** (4), 610–620 (1982).
  50. Ishii, M. and Hidaka, T., “The Second Pupal Diapause in the Univoltine Papilionid *Luehdorfia japonica* (Lepidoptera: Papilionidae) and Its Terminating Factor,” Applied Entomology and Zoology **18**, 456–463 (1983).
  51. Ishii, M. and Tsuneyoshi, Y., “Termination of Prepupal Diapause in *Elcysma westwoodi*,” Tyo to Ga **28**, 170 (1977) [in Japanese].
  52. Ishikawa, Y., Yamashita, T., and Nomura, M., “Characteristics of Summer Diapause in the Onion Maggot, *Delia antiqua* (Diptera: Anthomyiidae),” Journal of Insect Physiology **46**, 161–167 (2000).
  53. Ishitani, M. and Sato, N., “The Life Cycle and a Method of its Control of the Turnip Maggot *Hylemyia floralis* Fallén (Diptera: Anthomyiidae) in Aomori Prefecture,” Bulletin of the Aomori Field Crops and Horticultural Experiment Station **4**, 1–16 (1981).
  54. Kaplin, V.G., “Seasonal Rhythms of Openly Living Insects Associated with Seed Plants in the Karakum,” Zhurnal Obshechi Biologii **55** (6), 716–736 (1994).
  55. Karlson, P. and Shaaya, S., “Der Ecdysontiter während der Insectenentwicklung. I. Eine Methode zur Bestimmung des Ecdysongehalts,” Journal of Insect Physiology **10**, 797–804 (1964).
  56. Kato, Y., “Role of Photoperiod in Larval Growth of *Sasakia charonda* (Lepidoptera, Nymphalidae),” Japanese Journal of Entomology **57** (1), 221–230 (1989).
  57. Kato, Y. and Hasegawa, Y., “Photoperiodic Regulation of Larval Diapause and Development in the Nymphalid Butterfly *Sasakia charonda* (Lepidoptera, Nymphalidae),” Kontyû (Tokyo) **52** (3), 363–369 (1984).
  58. Kato, Y. and Sakate, S., “Early Termination of Summer Diapause by Mechanical Shaking in Pupae of *Antheraea yamamai* (Lepidoptera: Saturniidae),” Applied Entomology and Zoology **18**, 441–443 (1983).
  59. Katsoyannos, P., Kontodimas, D., and Stathas, G., “Summer Diapause and Winter Quiescence of *Hippodamia (Semiadalia) undecimnotata* (Coleoptera: Coccinellidae) in Central Greece,” European Journal of Entomology **102**, 453–457 (2005).
  60. Khoo, S.G., “Experimental Studies on Diapause in Stoneflies. I. Nymphs of *Capnia bifrons* (Newman),” Proceedings of the Royal Society of London. Series A. General Entomology **43**, 40–48 (1968).
  61. Kida, Y., Numata, H., and Fujii, H., “Summer Diapause in Females of *Minois dryas* (Lepidoptera: Satyridae),” Environmental Entomology **26** (2), 201–206 (1997).
  62. Kimura, T., “*Luehdorfia* Butterflies Waiting for Emergence in Spring,” Insectarium **12**, 76–79 (1975) [in Japanese].
  63. Kind, T.V., “Dynamics of Endocrine Brain Activity during Reactivation of the Diapausing Pupae and Subsequent Imaginal Development of the Cabbage Moth *Barathra brassicae*,” Zoologicheskii Zhurnal **54** (6), 884–893 (1977).
  64. Kipyatkov, V.E. and Lopatina, E.B., “Seasonal Cycles and Strategies in Ants: Structure, Diversity, and Adaptive Traits,” in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions (Proceedings of the Biological Research Institute, Vol. 53)*, Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 107–192 [in Russian].
  65. Kiritani, Y., “Timing of Oviposition and Nymphal Diapause under the Natural Daylength in *Carbula humerigera* (Heteroptera: Pentatomidae),” Applied Entomology and Zoology **20**, 252–256 (1985a).
  66. Kiritani, Y., “Effect of Stationary and Changing Photoperiods on Nymphal Development in *Carbula humerigera* (Heteroptera: Pentatomidae),” Applied Entomology and Zoology **20**, 257–263 (1985b).
  67. Klyuchko, Z.F., *Noctuid Moths of Ukraine* (Vidavnistvo Raevskogo, Kiev, 2006) [in Ukrainian].
  68. Košťál, V., “Eco-Physiological Phases of Insect Diapause,” Journal of Insect Physiology **52**, 113–127 (2006).
  69. Košťál, V., Šula, J., and Šimek, P., “Physiology of Drought Tolerance and Cold Hardiness of the Mediterranean Tiger Moth *Cymbalophora pudica* during Summer Diapause,” Journal of Insect Physiology **44**, 165–173 (1998).
  70. Kovalev, O.V., Reznik, S.Ya., and Vinogradova, E.B., *Guidelines for Dispersal and Production Testing of Zygogramma Leaf Beetles in Biological Control of Common and Perennial Ragweeds* (Nauka, Leningrad, 1986) [in Russian].
  71. Kozhanchikov, I.V., “Development Cycle and Geographic Distribution of the Winter Moth (*Operophtera brumata* L.),” Entomologicheskoe Obozrenie **31** (1–2), 178–197 (1950a).
  72. Kozhanchikov, I.V., *The Tussock Moths (Orgyidae). Insecta, Lepidoptera (Fauna of the USSR. New Series, Vol. 42, Issue 12)* (Nauka, Moscow, 1950b) [in Russian].
  73. Li, L.X. and Xue, F.S., “The Life History and Diapause of *Spilarctia obliqua* (Walker),” Acta Agriculturae Universitatis Jiangxiensis **13** (3), 264–267 (1991).
  74. Liu, Zh., Gong, P., Wu, K., Sun, J., and Li, D., “A True Summer Diapause Induced by High Temperatures in the Cotton Bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae),” Journal of Insect Physiology **52**, 1012–1020 (2006).
  75. Loomis, S.H., “Diapause and Estivation in Sponges,” Progress in Molecular and Subcellular Biology **49**, 231–243 (2010).
  76. Madubunyi, L.C., “External Environmental Factors Regulating Imaginal Diapause in *Hypera brunneipen-*

- nis,” *Annals of the Entomological Society of America* **71**, 37–39 (1978).
77. Masaki, S., “The Local Variation in the Diapause Pattern of the Cabbage Moth, *Barathra brassicae* Linnaeus, with Particular Reference to the Aestival Diapause (Lepidoptera, Noctuidae),” *Bulletin of the Faculty of Agriculture, Mie University* **13**, 29–46 (1956).
  78. Masaki, S., “Ecological Significance of Diapause in the Seasonal Cycle of *Abraxas miranda* Butler,” *Bulletin of the Faculty of Agriculture, Mie University* **15**, 15–24 (1957).
  79. Masaki, S., “The Response of a ‘Short-Day’ Insect to Certain External Factors: the Induction of Diapause in *Abraxas miranda* Butler,” *Japanese Journal of Applied Entomology and Zoology* **2** (4), 285–294 (1958).
  80. Masaki, S., “Life Cycle Programming,” in *Adaptation and Speciation in the Fall Webworm*, Ed. by T. Hidaka (Kodansha Ltd., Tokyo, 1977), pp. 31–60.
  81. Masaki, S., “Summer Diapause,” *Annual Review of Entomology* **18**, 1–25 (1980).
  82. Masaki, S., “Ecophysiological Consequences of Variability in Diapause Intensity,” *European Journal of Entomology* **99**, 143–154 (2002).
  83. Masaki, S. and Sakai, T., “Summer Diapause in the Seasonal Life Cycle of *Mamestra brassicae* Linne (Lepidoptera: Noctuidae),” *Japanese Journal of Applied Entomology and Zoology* **9** (3), 191–205 (1965).
  84. Maslennikova, V.A., “On the Conditions of Diapause of the Parasitic Wasps *Apanteles glomeratus* L. (Hymenoptera, Braconidae) and *Pteromalus puparum* (Hymenoptera, Chalcididae),” *Entomologicheskoe Obozrenie* **37** (3), 538–545 (1958).
  85. Maslennikova, V.A., Abdel Nabi, A.A., and Chernysh, S.I., “The Ecdysone Titer during Induction of Summer and Winter Diapause in the Cabbage Moth *Barathra brassicae* L. (Lepidoptera, Noctuidae),” *Entomologicheskoe Obozrenie* **55** (4), 768–776 (1976).
  86. Meshkova, V.L., *Seasonal Development of Needle- and Leaf-Eating Forest Pests* (Novoe Slovo, Kharkiv, 2009) [in Russian].
  87. Minder, I., “Photoperiodic Reactivation of Eonymphs of *Neodiprion sertifer* Geoffr. (Hymenoptera: Diprionidae),” *Doklady Akademii Nauk SSSR* **248**, 1075–1077 (1980).
  88. Moiseeva, T.S., “Specialization of *Apanteles glomeratus* L. and Its Role in Reducing the Abundance of Whites of the Genus *Pieris*,” *Trudy Vsesoyuznogo Instituta Zashchity Rastenii* **14**, 51–56 (1960).
  89. Murray, D.A.H. and Wilson, A.G.L., “Methods for Studying Diapause,” in *Heliothis: Research Methods and Prospects*, Ed. by M.P. Zalucki (Springer, New York, 1991), pp. 102–108.
  90. Musolin, D.L., *Candidate’s Dissertation in Biology* (St. Petersburg, 1997).
  91. Musolin, D.L., *Doctoral Dissertation in Biology* (St. Petersburg, 2017).
  92. Musolin, D.L. and Saulich, A.Kh., “Photoperiodic Control of Nymphal Growth in True Bugs (Heteroptera),” *Zoologicheskii Zhurnal* **76** (5), 530–540 (1997) [*Entomological Review* **77** (6), 768–780 (1997)].
  93. Musolin, D.L. and Saulich, A.H., “Summer Dormancy Ensures Univoltinism in the Predatory Bug *Picromerus bidens* (Heteroptera, Pentatomidae),” *Entomologia Experimentalis et Applicata* **95**, 259–267 (2000).
  94. Musolin, D.L. and Saulich, A.Kh., “Diapause in Pentatomoidea,” in *Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management*, Ed. by J.E. McPherson (CRC Press, Boca Raton, 2018), pp. 497–564.
  95. Nakai, T. and Takeda, M., “Temperature and Photoperiodic Regulation of Summer Diapause and Reproduction in *Pyrrhalta humeralis* (Chen) (Coleoptera: Chrysomelidae),” *Applied Entomology and Zoology* **30** (2), 295–301 (1995).
  96. Nakamura, K. and Numata, H., “Effects of Environmental Factors on Diapause Development and Postdiapause Oviposition in a Phytophagous Insect, *Dybowskyia reticulata*,” *Zoological Science* **14**, 1021–1026 (1997).
  97. Novák, I. and Spitzer, K., “Adult Dormancy in Some Species of the Genus *Noctua* (Lepidoptera, Noctuidae) in Central Europe,” *Acta Entomologica Bohemoslovaca* **72** (5), 215–221 (1975).
  98. Numata, H., “Environmental Factors that Determine the Seasonal Onset and Termination of Reproduction in Seed-Sucking Bugs (Heteroptera) in Japan,” *Applied Entomology and Zoology* **39**, 565–573 (2004).
  99. Ogata, T. and Sasakawa, M., “Effect of the Aestivation on the Feeding and Reproductive Activities of the Viburnum Leaf Beetle *Pyrrhalta humeralis* Chen (Coleoptera: Chrysomelidae),” *Japanese Journal of Applied Entomology and Zoology* **27** (4), 276–279 (1983).
  100. Oku, T., “Overwintering of Eggs in the Siberian Cutworm, *Euxoa sibirica* Boisduval (Lepidoptera: Noctuidae),” *Applied Entomology and Zoology* **17** (2), 244–252 (1982).
  101. Oku, T., “Aestivation and Migration in Noctuid Moths,” in *Diapause and Life Cycle Strategies in Insects*, Ed. by M. Brown and I. Hodek (Junk, the Hague, 1983), pp. 219–231.
  102. Oku, T. and Kobayashi, T., “Migratory Behaviour and Life Cycle of Noctuid Moths (Insecta, Lepidoptera), with Notes on the Recent Status of Migrant Species in Northern Japan,” *Bulletin of Tohoku National Agricultural Experimental Station (Morioka)* **58**, 97–209 (1978) [in Japanese].
  103. Pruess, K.P., “Migration of the Army Cutworm *Chorizagrotis auxillaris*. I. Evidence for Migration,” *Annals of the Entomological Society of America* **60** (5), 910–920 (1967).
  104. Putshkov, V.G., *Fauna of Ukraine*, Vol. 21: *Pentatomidae, Issue 1* (Ukrainian SSR Academy of Sciences, Kiev, 1961) [in Ukrainian].

105. Ring, R.A., "Variation in the Photoperiodic Reaction Controlling Diapause Induction in *Lucilia caesar* L. (Diptera, Calliphoridae)," *Canadian Journal of Zoology* **49** (2), 137–142 (1971).
106. Roer, H., "Über die Flug- und Wandergewohnheiten von *Pieris brassicae*," *Zeitschrift für Angewandte Zoologie* **44**, 272–309 (1959).
107. Rogers, S.M., "Mechanisms of Polyphenism in Insects," in *Insect Molecular Biology and Ecology*, Ed. by H. Hoffmann (CRC Press, Boca Raton, 2015), pp. 1–38.
108. Sahota, T.S., Farris, S.H., and Ibaraki, A., "Timing of Initiation of Pharate Adult Development in *Barbara colfaxiana* (Kft.) (Lepidoptera, Olethreutidae)," *Canadian Journal of Zoology* **61** (10), 2305–2306 (1983).
109. Sakurai, H., Hirano, T., and Takeda, S., "Physiological Distinction between Aestivation and Hibernation in the Lady Beetle *Coccinella septempunctata brucki* (Coleoptera: Coccinellidae)," *Applied Entomology and Zoology* **21**, 424–429 (1986).
110. Sáringer, Gy., "Summer Diapause in Cabbage Stem Flea Beetle *Psylliodes chrysocephala* L. (Coleoptera, Chrysomelidae)," *Zeitschrift für Angewandte Entomologie* **98** (1), 50–54 (1984).
111. Sauer, K.P. and Grüner, C., "Aestival Dormancy in the Cabbage Moth *Mamestra brassicae* L. (Lepidoptera: Noctuidae). 2. Geographical Variation in Two Traits: Day Length Thresholds Triggering Aestival Dormancy and Duration of Aestival Dormancy," *Oecologia* **76**, 89–96 (1988).
112. Saulich, A.Kh., *Seasonal Development and Dispersal Potential of Insects* (St. Petersburg State University, St. Petersburg, 1999) [in Russian].
113. Saulich, A.Kh. and Musolin, D.L., "Univoltinism and Its Regulation in Some Temperate True Bugs (Heteroptera)," *European Journal of Entomology* **93** (3), 507–518 (1996).
114. Saulich, A.Kh. and Musolin, D.L., "Times of the Year: the Diversity of Seasonal Adaptations and Ecological Mechanisms Controlling Seasonal Development of True Bugs (Heteroptera) in the Temperate Climate," in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions (Proceedings of the Biological Research Institute, Vol. 53)*, Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 25–106 [in Russian].
115. Saulich, A.Kh. and Musolin, D.L., "Seasonal Development of Shield Bugs of the Family Plataspidae (Heteroptera: Pentatomoidea)," *Vestnik Moskovskogo Gosudarstvennogo Universiteta Lesa – Lesnoy Vestnik* **18** (6), 193–201 (2014a).
116. Saulich, A.Kh. and Musolin, D.L., "Seasonal Cycles in Stink Bugs (Heteroptera, Pentatomidae) from the Temperate Zone: Diversity and Control," *Entomologicheskoe Obozrenie* **93** (2), 263–302 (2014b) [*Entomological Review* **94** (6), 785–814 (2014)].
117. Saulich, A.Kh. and Musolin, D.L., "Seasonal Cycles of Pentatomoidea," in *Invasive Stink Bugs and Related Species (Pentatomoidea): Biology, Higher Systematics, Semiochemistry, and Management*, Ed. by J.E. McPherson (CRC Press, Boca Raton, 2018), pp. 565–607.
118. Saulich, A.Kh. and Sokolova, I.V., "Seasonal Adaptations in Noctuid Moths (Lepidoptera, Noctuidae)," *Entomologicheskoe Obozrenie* **81** (3), 529–546 (2002) [*Entomological Review* **82** (9), 1127–1141 (2002)].
119. Saulich, A.Kh. and Volkovitsh, T.A., "Univoltinism and Its Control in Insects," *Entomologicheskoe Obozrenie* **75** (2), 244–258 (1996).
120. Saulich, A.Kh. and Volkovitsh, T.A., *Ecology of Photoperiodism in Insects* (St. Petersburg State University, St. Petersburg, 2004) [in Russian].
121. Schroder, R.F.W. and Steinhauer, A.L., "Effects of Photoperiod and Temperature Regimens on the Biology of European and United States Alfalfa Weevil Populations," *Annals of the Entomological Society of America* **69**, 701–706 (1976a).
122. Schroder, R.F.W. and Steinhauer, A.L., "Studies of Cross-Mating Strains of the Alfalfa Weevil from the United States and Western Europe," *Proceedings of the Entomological Society of Washington* **78**, 1–5 (1976b).
123. Semyanov, V.P., "Obligate and Facultative Diapauses in Aphidophagous Ladybirds (Coleoptera, Coccinellidae): Similarities and Differences," in *Abstracts of Papers of the XII Congress of the Russian Entomological Society, St. Petersburg, August 19–24, 2002* (St. Petersburg, 2002), pp. 313–314.
124. Shchetkin, Yu.L., *Higher Lepidoptera of the Vakhsh Valley Sands* (Tajik SSR Academy of Sciences, Dushanbe, 1965) [in Russian].
125. Sheldeshova, G.G. and Stekolnikov, A.A., "On the Change of the Photoperiodic Response Type during Development of the Brown Apricot Scale *Parthenolecanium corni* Bouché (Homoptera, Coccidae)," *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **36**, 26–30 (1965).
126. Siew, Y.C., "Some Physiological Aspects of Adult Reproductive Diapause in *Galeruca tanacetii* L. (Coleoptera: Chrysomelidae)," *Transactions of the Entomological Society of London* **118**, 359–374. 1966.
127. Spieth, H.R., "Estivation and Hibernation of *Pieris brassicae* (L.) in Southern Spain: Synchronization of Two Complex Behavioral Patterns," *Population Ecology* **44**, 273–280 (2002).
128. Spieth, H.R. and Schwarzer, E., "Aestivation in *Pieris brassicae* (Lepidoptera: Pieridae): Implications for Parasitism," *European Journal of Entomology* **98**, 171–176 (2001).
129. Spieth, H.R., Pörschmann, U., and Teiwes, C., "The Occurrence of Summer Diapause in the Large White Butterfly *Pieris brassicae* (Lepidoptera: Pieridae):

- a Geographical Perspective,” *European Journal of Entomology* **108**, 377–384 (2011).
130. Stewart, J.W., Whitcomb, W.H., and Bell, K.O., “Aestivation Studies of the Convergent Lady Beetle in Arkansas,” *Journal of Economic Entomology* **60**, 1730–1735 (1967).
  131. Storey, K.B. and Storey, J.M., “Insects in Winter: Metabolism and Regulation of Cold Hardiness,” in *Insect Molecular Biology and Ecology*, Ed. by H. Hoffmann (CRC Press, Boca Raton, 2015), pp. 245–270.
  132. Sugonyaev, E.S., “On the Cyclic Seasonal Adaptations of the Parasite *Blastothrix confusa* Erd. (Hymenoptera, Chalcidoidea) to Its Host, *Parthenolecanium corni* Bouché,” *Zoologicheskii Zhurnal* **42** (11), 1732–1735 (1963).
  133. Sugonyaev, E.S. and Voinovich, N.D., *Adaptations of Chalcid Wasps (Hymenoptera, Chalcidoidea) to Parasitism on Soft Scales (Hemiptera, Sternorrhyncha, Coccidae) at Different Latitudes* (KMK Scientific Press, Moscow, 2006) [in Russian].
  134. Sukhareva, I.L., “Family Noctuidae,” in *Insects and Acarines as Agricultural Pests*, Vol. 3: *Lepidoptera*, Part 2, Ed. by V.I. Kuznetsov (Nauka, St. Petersburg, 1999), pp. 332–376 [in Russian].
  135. Sullivan, C.R. and Wallace, D.R., “Photoperiodism in the Development of the European Pine Sawfly, *Neodiprion sertifer* (Geoff.),” *Canadian Journal of Zoology* **43** (2), 233–245 (1965).
  136. Sullivan, C.R. and Wallace, D.R., “Interaction of Temperature and Photoperiod in the Induction of Prolonged Diapause in *Neodiprion sertifer*,” *The Canadian Entomologist* **99** (8), 834–850 (1967).
  137. Tanaka, S.I., Imai, C., and Numata, H., “Ecological Significance of Adult Summer Diapause after Nymphal Winter Diapause in *Poecilocoris lewisi* (Distant) (Heteroptera: Scutelleridae),” *Applied Entomology and Zoology* **37** (3), 469–475 (2002).
  138. Tauber, C.A. and Tauber, M.J., “Diversification and Secondary Intergradation of Two *Chrysopa carnea* Strains,” *The Canadian Entomologist* **105**, 153–167 (1973a).
  139. Tauber, C.A. and Tauber, M.J., “Evolution of Seasonal Adaptations and Life History Traits in *Chrysopa*: Response to Diverse Selective Pressures,” in *Evolution and Genetic of Life Histories*, Ed. by H. Dingle and J.P. Hegmann (Springer, New York, 1982), pp. 51–72.
  140. Tauber, C.A., de León, T., López-Arroyo, J.I., and Tauber, M.J., “*Ceraeochrysa placita* (Neuroptera: Chrysopidae): Generic Characteristics of Larvae, Larval Descriptions, and Life Cycle,” *Annals of the Entomological Society of America* **91**, 608–618 (1998).
  141. Tauber, M.J. and Tauber, C.A., “Nutritional and Photoperiodic Control of the Seasonal Reproductive Cycle in *Chrysopa mohave* (Neuroptera),” *Journal of Insect Physiology* **19** (4), 729–736 (1973b).
  142. Tauber, M.J., Tauber, C.A., and Masaki, S., *Seasonal Adaptations of Insects* (Oxford University Press, New York, 1986).
  143. Teraoka, T. and Numata, H., “Induction of Adult Diapause in a Parasitoid Wasp, *Ooencyrtus nezarae* under Natural Conditions,” *Entomologia Experimentalis et Applicata* **76**, 329–332 (1995).
  144. Thiele, H.-U., “The Control of Larval Hibernation and Adult Aestivation in the Carabid Beetles *Nebria brevicollis* F. and *Patrobus atrorufus* Stroem,” *Oecologia (Berlin)* **2**, 347–361 (1969).
  145. Thiele, H.-U., “Die Steuerung der Jahresrhythmik von Carabiden durch exogene und endogene Faktoren,” *Zoologische Jahrbücher Systematik* **98** (3), 341–371 (1971).
  146. Thiele, H.-U., “Measurement of Daylength as a Basis for Photoperiodism and Annual Periodicity in the Carabid Beetle *Pterostichus nigrita* F.,” *Oecologia (Berlin)* **30** (4), 331–348 (1977).
  147. Topp, W., “Selection for the Optimal Monovoltine Life Cycle in an Unpredictable Environment. Studies on the Beetle *Catops nigricans* Spence (Coleoptera: Catopidae),” *Oecologia (Berlin)* **84**, 134–140 (1990).
  148. Topp, W., “Phenotypic Plasticity and Development of Cold-Season Insects (Coleoptera: Leiodidae) and Their Response to Climatic Change,” *European Journal of Entomology* **100**, 233–243 (2003).
  149. Tsugane, R., “The Life Cycle of *Amphipyra livida corvina* Motschulsky with Special Reference to the Termination of Aestivation in the Adult Stage,” *Japanese Journal of Applied Entomology and Zoology* **19**, 169–175 (1975).
  150. Tyshchenko, V.P., “Evolution of Seasonal Adaptations in Insects,” *Zhurnal Obshchei Biologii* **44** (1), 10–22 (1983).
  151. Tzanakakis, M.E. and Koveos, D.S., “Duration of Aestival Diapause of *Diloba coeruleocephala* L. under Various Photoperiods and Temperatures,” *Entomologia Experimentalis et Applicata* **34** (3), 343–346 (1983).
  152. Ushatinskaya, R.S., “Physiological Features of the Sunn Pest *Eurygaster integriceps* Put. during Winter Dormancy in the Mountains and on the Plains,” in *The Sunn Pest Eurygaster integriceps Put.*, Vol. 3, Ed. by D.M. Fedotov (USSR Academy of Sciences, Moscow, 1955), pp. 134–170 [in Russian].
  153. Ushatinskaya, R.S. (Ed.), *The Colorado Potato Beetle Leptinotarsa decemlineata Say* (Nauka, Moscow, 1981) [in Russian].
  154. Ushatinskaya, R.S., “Summer Dormancy (Aestivation) in Insects,” in *Problems of Ecological Physiology of Insects*, Ed. by R.S. Ushatinskaya (Nauka, Moscow, 1987), pp. 140–173 [in Russian].
  155. Vinogradova, E.B., “The Blue Blowfly *Calliphora vicina* as a Model Object in Physiological and Ecological Research,” *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **118**, 1–272 (1984).

156. Vinogradova, E.B., "Diapause in Flies and Its Control," *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **214**, 1–254 (1991).
157. Vinogradova, E.B. and Bogdanova, T.P., "Reproduction and Diapause Formation in the Ragweed Leaf Beetle *Zygogramma suturalis* F. in Stavropol Region," *Entomologicheskoe Obozrenie* **67** (3), 468–478 (1988).
158. Volkovitsh, T.A., "Diapause in the Life Cycles of Lacewings (Neuroptera, Chrysopidae)," in *Strategies of Adaptations of Terrestrial Arthropods to Adverse Environmental Conditions (Proceedings of the Biological Research Institute, Vol. 53)*, Ed. by A.A. Stekolnikov (St. Petersburg State University, St. Petersburg, 2007), pp. 234–304 [in Russian].
159. Wigfield, M. and Warren, L.O., "The Effect of Photoperiod on Development of the Sawfly *Neodiprion taeda linearis*," *Journal of the Kansas Entomological Society* **45**, 1–6 (1972).
160. Witsack, W., "Experimentell-ökologische Untersuchungen über Dormanz-Formen von Zikaden 2. Zur Ovarial-Parapaus und obligatorischen Embryonal-Diapause von *Philaenus spumarius* (L.)," *Zoologische Jahrbücher Systematik* **100**, 517–562 (1975).
161. Witt, J.R. and Armbrust, E.J., "Photoperiodic Sensitivity of the Alfalfa Weevil during Larval Development," *Journal of Economic Entomology* **65**, 1289–1292 (1972).
162. Wu, S.-H., Yang, D., Lai, X.-T., and Xue, F.S., "Induction and Termination of Prepupal Summer Diapause in *Pseudopidorus fasciata* (Lepidoptera: Zygaenidae)," *Journal of Insect Physiology* **52**, 1095–1104 (2006).
163. Xiao, H.-J., Yang, D., and Xue, F.-S., "Effect of Photoperiod on the Duration of Summer and Winter Diapause in the Cabbage Butterfly, *Pieris melete* (Lepidoptera: Pieridae)," *European Journal of Entomology* **103** (3), 537–540 (2006).
164. Xue, F.S., Zhu, X.F., and Shao, Z.Y., "Control of the Summer and Winter Diapause in the Leaf-Mine Fly *Pegomyia bicolor* Wiedemann (Diptera, Anthomyiidae)," *Journal of Applied Entomology* **125**, 181–187 (2001).
165. Xue, F.S., Spieth, H.R., Li, A.Q., and Hua, A., "The Role of Photoperiod and Temperature in Determination of Summer and Winter Diapause in the Cabbage Beetle *Colaphellus bowringi* (Coleoptera: Chrysomelidae)," *Journal of Insect Physiology* **48**, 279–286 (2002).
166. Yamamura, S., Ikarashi, M., and Sasaki, M., "Dual Photoperiodic Regulation to Enable Univoltine Life Cycle in Alpine Silver-Y Moth, *Syngrapha ottolenguii* (Noctuidae: Plusiinae) without Obligatory Diapause," *Applied Entomology and Zoology* **43** (1), 105–112 (2008).
167. Zaslavsky, V.A., "Photoperiodic and Temperature Control of Insect Development," *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **120**, 1–180 (1984).
168. Zaslavsky, V.A. and Vaghina, N.P., "Joint and Separate Effects of Alimentary and Photoperiodic Induction of Diapause in *Coccinella septempunctata* (Coleoptera, Coccinellidae)," *Zoologicheskii Zhurnal* **75** (10), 1474–1482 (1996) [*Entomological Review* **76** (8), 1025–1031 (1996)].