Seasonal Development and Ecology of Anthocorids (Heteroptera, Anthocoridae)[1]

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Received December 22, 2008

Abstract—Seasonal development and ecology of Anthocoridae are reviewed. Most of 500–600 species in the family are predacious or zoo-phytophagous, and a few other species are exclusively phytophagous or myrmecophilous. Some anthocorids are (and many others can potentially be) used as biological control agents in the Integrated Pest Management (IPM). Overwintering at the adult stage is typical of anthocorid bugs from the temperate zone (especially for the subfamily Anthocorinae). The known exceptions are the embryonic diapause in *Tetraphleps abdulghanii*, *Temnostethus pusillus*, and *T. gracilis* (Anthocorinae) and continuous development through all seasons (a homodynamic seasonal cycle) in *Lyctocoris campestris* and some species of *Xylocoris* (Lyctocorinae). In a number of species, especially in the genera *Anthocoris* and *Orius*, copulation occurs before overwintering and only females survive winter, a feature very unusual for Heteroptera and insects in general. Many anthocorid species are multivoltine in the temperate zone, producing several (up to 8 in some cases) generations per year. The number of generations typically decreases to 1 per year towards the north. Seasonal development of multivoltine species is chiefly controlled by daylength and temperature. All multivoltine anthocorids of the temperate zone studied to date have photoperiodic response of a long-day type: the females reproduce under the long-day conditions, but enter diapause under the short-day conditions. Towards the south, the photoperiodic response gradually becomes weaker: some populations do not enter diapause even under the short-day conditions, especially at higher temperatures. Termination of diapause is poorly understood in anthocorids, but a number of species require low-temperature treatment for a few weeks prior to the start of oviposition. Alary and color polymorphism are rare in the family, and they have never been shown to be seasonal or environmentally controlled. Pronounced seasonal migrations and aggregation behavior also have never been reported in Anthocoridae. Summer diapause appears to be very unusual for the family, having been reported only in *Tetraphleps abdulghanii*. The seasonal change of host plants, known in some populations of *Anthocoris nemorum* and *A. nemoralis*, is also a seasonal adaptation unusual for Heteroptera. Seasonality of tropical and subtropical species is poorly studied, but anthocorids developing without winter diapause are considered promising agents for the biological control of arthropod pests. Further studies of ecophysiology of Anthocoridae will optimize application and mass rearing of these predators in IPM programs.

DOI: 10.1134/S0013873809050017

An increasing number of species of predacious and parasitic insects are now being used as agents of biological control of forest and agricultural pests (van Lenteren et al., 1997; Glenister, 1998; Yano, 2004). New species are being tested in the search for the most efficient and cost-effective methods of plant protection (primarily considering the costs of their application, rearing, and storage). Much more attention is now focused on the guarantees of biological safety of introducing new species into the practical pest control (Simberloff and Stiling, 1996; van Lenteren, 1997;

Blum et al., 2003; van Lenteren et al., 2003, 2006). However, before establishing laboratory cultures of a particular species, one should find out how this species acts under natural conditions, which factors control its onthogeny and seasonal development, what limits its distribution, and many other aspects.

This communication summarizes the available data on seasonal development and ecology of certain species of the family Anthocoridae Fieber, 1836 (Heteroptera). Most of them are predacious or zoo-phytophagous, although some members of this family are exclusively phytophagous or myrmecophilous (Péricart, 1996; Lattin, 1999, 2000). Anthocorid bugs can be regarded as promising agents of biological pest control owing to some of their properties, such as high

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[1] This paper is dedicated to the memory of Izyaslav Moiseevich Kerzhner (1936–2008), the eminent Russian expert in Heteropterans.

Table 1. Composition of the faunas of Anthocoridae of the Palaearctic and Russia (number of species; after Péricart, 1996)

Subfamilies	Palaearctic	Russia		
		total	European part	Asian part
Anthocorinae Fieber, 1836	118	40	28	31
Lyctocorinae Reuter, 1884	62	23	15	17
Lasiochilinae Carayon, 1972	1	–	–	–
Total	181	63	43	48

efficiency of prey seeking, the ability to concentrate in the areas of the highest density of the potential prey, rapid population growth in case of abundant food, etc. (Hodgson and Aveling, 1988).

The family includes about 100 genera with 500–600 species presently described in the world fauna; they are distributed approximately from 70°N to 56°S. (Péricart, 1996; Lattin, 2000). It should be noted that some authors (Schuh and Slater, 1995) subdivide Anthocoridae into three independent families (Anthocoridae, Lyctocoridae, and Lasiochilidae). However, in this communication we follow the system accepted for the Palaearctic, in which these taxa are regarded as subfamilies (Péricart, 1972, 1996). The Palaearctic fauna comprises 28 genera with 181 species and 7 subspecies (Aukema and Rieger, 1996; Péricart, 1996); the fauna of Russia includes 63 species (43 in the European part of the country and 48 in the Asian part; Table 1; Péricart, 1996).

The representatives of Anthocoridae are small bugs (1.4–6 mm) living on flowers, shrubs, on and under the bark of living and dead trees, often covered with moss and lichens, in the galls of aphids, nests of ants, birds, and mammals, in food storage facilities, etc. (Sands, 1957; Hodgson, Aveling, 1988; Schuh and Slater, 1995; Lattin, 1999, 2000). They are mostly predacious forms feeding on aphids, psyllids, scale insects, thrips, small caterpillars, insect eggs, and spider mites. Some of the species inhabit a broad range of plants and feed on any suitable prey, while some occur only on certain plant species and feed on the insects associated exclusively with those plants. For example, *Anthocoris minki* Dohrn occurs only on the common ash *Fraxinus excelsior* L., *A. sarothamni* Douglas et Scott is associated with the Scotch broom *Cytisus sco-*

parius (L.) Link, and *A. confusus* Reuter prefers a restricted set of deciduous plant species (Anderson, 1962b). However, it was shown that most species of this family could be reared on unusual insect prey under laboratory conditions (Anderson, 1962c; Hodgson and Aveling, 1988).

Many species of anthocorid bugs have several generations per year. This fact indicates a facultative nature of diapause in these species, which is essential for their mass rearing for the purpose of pest control. Under natural conditions, all the anthocorid bugs living in the temperate climate appear to overwinter as adults, finding shelters under fallen leaves, in the litter, under the tree bark, or in plant stems. In nearly all the species of the subfamily Anthocorinae, copulation takes place in late summer or in autumn. Only the fertilized females enter diapause and can overwinter successfully, while the males usually do not survive until spring. It was recently shown by the example of three species of the genus *Orius* that mating in autumn increased considerably the survival rates of the females during wintering. The authors assumed that the females could have obtained some nutritive substance from the males during mating, or that the very act of copulation could have some positive effect on the behavior or diapause of the females (Kobayashi and Osakabe, 2009).

At least one species, *Orius insidiosus* (Say), did not stop feeding during diapause under laboratory conditions, even though the intensity of feeding was low. The absence of food considerably decreased the probability of successful wintering. This species probably overwinters in such microstations in which some food is available during winter as well (Ruberson et al., 1998).

The openly living species (*Orius*, *Anthocoris*) lay eggs in plant tissues, while other forms (*Xylocoris*, *Scoloposcelis*; Lattin, 1999) place them under the bark or in soil. The larvae of the vast majority of anthocorid bugs develop with 5 instars, although some species, such as *Temnostethus gracilis* Horváth (Péricart, 1972; Štys and Davidová-Vilimová, 1989) and *Orius maxidentex* Ghauri (Thontadarya and Rao, 1987), have only 4 larval instars. This may be true only for the brachypterous morph of *T. gracilis* (Štys and Davidová-Vilimová, 1989). The duration of larval development depends primarily on the temperature and the quantity and quality of food (Hodgson and Aveling, 1988), and in some species also on the photoperiodic conditions (Musolin and Ito, 2008).
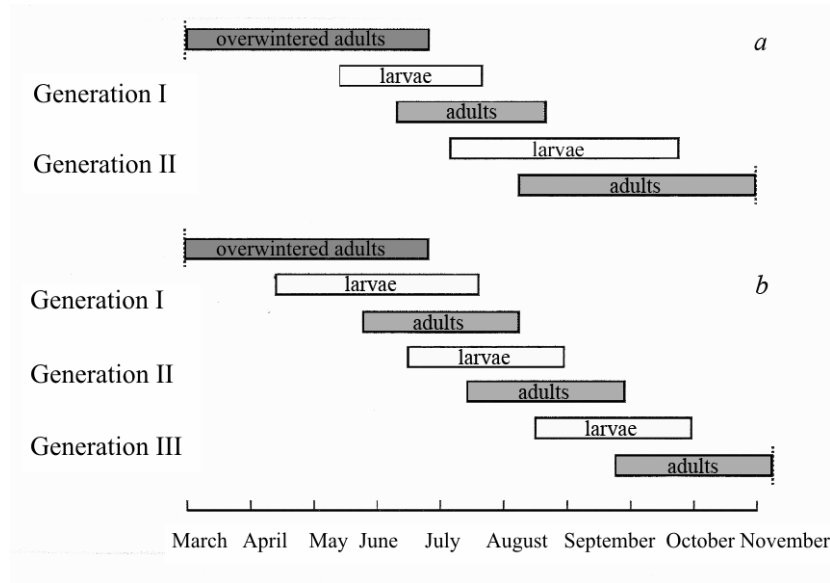
Fig. 1. The seasonal cycle of *Anthocoris nemorum* in the south of England (51.4°N, 0.6°E) (*a*) and in the north of France (48.6°N, 1.9°E) (*b*) (after Anderson, 1962b; Herard and Chen, 1985).

Although most species of the family have only one (alate) morph, several cases of wing polymorphism have been described. For example, bugs of the genera *Brachystekes*, *Elatophilus*, *Temnostethus*, and *Xylocoris* have two morphs: macropterous and brachypterous (Péricart, 1972; Štys and Davidová-Vilimová, 1989; Lattin, 1999, 2000). In *Orius retamae* (Noualhier) 2 alary morphs have been described in males and 3 in females (Wagner, 1952). A very few species, mostly those occurring in sheltered habitats, include only apterous morphs (Lattin, 1999). Neither the seasonal aspect of alary polymorphism nor its dependence on external ecological factors has been demonstrated in any representative of the family, even though such relations are known for many other heteropteran families (Musolin and Saulich, 1996; Saulich and Musolin, 2007a, 2007b).

The anthocorid bugs used in biological pest control mostly belong to two Holarctic genera, *Anthocoris* and *Orius*.

The genus ***Anthocoris*** Fallén (Anthocorinae) comprises about 70 species described in the world fauna, most of which are associated with trees and shrubs (Lattin, 2000).

Anthocoris nemorum (L.) is a Euro-Siberian species extending as far northward as Scandinavia; it often occurs on flowers (Péricart, 1972, 1996).

The principal overwintering group includes the females fertilized in autumn (Anderson, 1962d; Collyer,

1967; Herard and Chen, 1985), although the males may also survive until spring in regions with a mild climate (Hill, 1957; Von Lauenstein, 1977; Herard and Chen, 1985). According to the observations made in the south of England, the sex ratio in spring varies considerably both from year to year and among the populations (Collyer, 1967). An additional copulation after wintering noticeably increases the fecundity of females (Von Lauenstein, 1977).

The time of emergence in spring depends both on the climate and on the weather conditions. In Norway (30 km S of Oslo) the bugs become active in mid-May. The populations of *A. nemorum* are the most abundant in June–July, when they are represented by larvae of various instars. The last larvae of the season can usually be found in mid-August. The adults of the new generation first appear in late July or early August. The males are more numerous than the females during the autumn; however, the males die gradually during wintering, and sometimes already in the autumn, after copulation. The bug populations in spring consist only of females, and the first males of the new generation appear in July. In Scandinavia, *A. nemorum* always has only one generation per season (Austreng and Sømme, 1980).

Under the conditions of northwestern Russia, *A. nemorum* reveals a distinct trend towards univoltinism (Saprykin, 2008).

On the British Isles, the bugs emerge after wintering in the end of March or the beginning of April; the
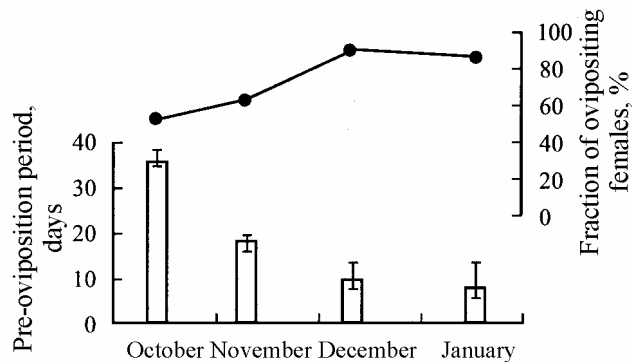
Fig. 2. Diapause termination in *Anthocoris nemorum* females transferred from their natural wintering places in the north of France (48.6°N, 1.9°E) into the laboratory conditions (+21°C, 16L : 8D, 70% humidity) (after Herard and Chen, 1985). The mean values and ranges are shown.

same timing is observed in Scotland (Hill, 1957, 1977) and in the south of England (Anderson, 1962b; Collyer, 1967). According to the light-trap capture data from the Rothamsted Experimental Station in the south of England, the first individuals of *A. nemorum* appeared in early April, when the maximum daily temperature rises to +18° (Hodgson and Mustafa, 1984, cited after Hodgson and Aveling, 1988).

Early in spring, the bugs concentrate on the flowering willows, where they find plenty of both animal food and pollen. Two or three weeks later they migrate onto other flowering shrubs or herbaceous vegetation, seeking prey and places for oviposition, and show no preference for any particular plant species (Hill, 1957, 1977; Anderson, 1962b).

Oviposition of *A. nemorum* starts in spring 2–3 weeks after emergence of females from their wintering shelters and lasts for a long time (Anderson, 1962b). According to the observations made in Poland and in the south of England, overwintered ovipositing females can be found until mid-June, and in Scotland, until early July (Hill, 1957). The embryonic development under the conditions of southern England takes from 22 days in April, at an average temperature of +9.9°, to 7.5 days in August, at +17.9° (Collyer, 1967).

In the south of England, the larvae of *A. nemorum* hatch in May (Anderson, 1962b; Collyer, 1967). The duration of their development is mostly determined by the temperature and the availability of food, varying on average from 30 to 40 days (Collyer, 1967). The peak of abundance of the larvae of the first generation occurs in June. The adults of the first (summer) generation appear in mid-June, and those of the second

generation, in August (Fig. 1*a*). The generations often overlap owing to the extended reproduction period, so that individuals of both generations and all the development stages of *A. nemorum* can be found in nature since July.

A third generation of the species was sometimes recorded in Central Europe during especially warm years. In case of a warm and prolonged autumn, its individuals may reach the adult stage in late October or November. However, all the larvae of this generation perish in case of an early cold spell (Southwood and Scudder, 1956; Collyer, 1967).

Active migrations of the bugs accompanied by changes of their host plants are observed during the vegetation season. For example, in abandoned orchards in the south of England (Collyer, 1967), the overwintered adults and the first generation larvae were abundant on the trees occupied by aphid and psyllid colonies, whereas the second generation larvae mostly occurred on herbaceous vegetation, especially on the nettle *Urtica dioica* L. Later, the bugs moved back onto the arboreal vegetation.

In the end of September and in October, the adult bugs find wintering shelters in bark fissures, litter, dense herb patches, and other protected places. Under different conditions, the females were observed to lose about 16–27% of live weight during wintering (Anderson, 1962d; Herard and Chen, 1985).

The fertilized females of *A. nemorum* overwinter in the state of diapause. This is indicated by studying the physiological state of the wintering females transferred from the nature into the laboratory conditions (+15°). The females that emerged after the beginning of August were able to reproduce only in the spring of the following year, after a prolonged exposure to a low temperature. The females which were brought into the laboratory in January or later, when the diapause had come to an end and oviposition was blocked solely by a low temperature, started laying eggs with mere several days of delay (Collyer, 1967).

The role of external factors in the regulation of seasonal development of *A. nemorum* was experimentally studied in two populations from the British Isles: one from the south of England (51.4°N, 0.6°E) and the other from Scotland (56.7°N, 4.4°E). The onset of diapause in the southern population was determined by the photoperiodic response (PPR) with a threshold of about 17 h at +17°. Since the females of the northern
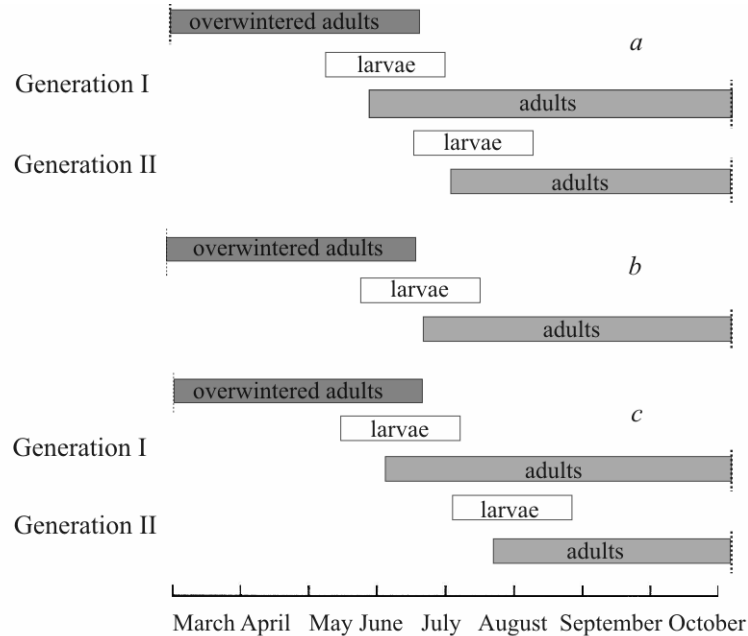
Fig. 3. The seasonal cycle of *Anthocoris nemoralis* (*a*), *A. gallarumulmi* (*b*), and *A. sarothamni* (*c*) in the south of England (51.4°N, 0.6°E) (after Anderson, 1962b).

population did not lay eggs even at a very long day (22 h) and a temperature of +25°, the diapause in the northern population may be regarded as obligatory. The main factor of diapause termination is low temperature maintained for no less than one month and a half (Parker, 1975).

Owing to the obligatory onset of diapause, the northern population in Scotland always develops in a single generation. The cited author believed the different seasonal strategies of the two populations to be related to the differences in their geographic origin; however, the existence of different ecological types cannot be excluded.

According to the observations made in Germany (51.5°N, 9.9°E), the first generation of *A. nemorum* comprises two fractions of females, differing in their physiological state (Von Lauenstein, 1977). Most of the females (80%) enter diapause soon after emergence, regardless of the external conditions, and return to the active state only after a sufficiently long exposure to low temperature. A smaller fraction of the females (20%) can reproduce in the same vegetation season without a diapause.

In France (the environs of Paris; 48.6°N, 1.9°E), the studied populations of *A. nemorum* occurred in fruit orchards on pear trees and surrounding herbaceous vegetation (Herard and Chen, 1985). The overwintered adults become active in mid-March, during the period

of pear flowering (Fig. 1*b*). This time coincides with the beginning of oviposition of their prey, *Psylla pyri* (L.). Three generations are completed in this region during summer (Bonnemaison and Missonnier, 1956, cited after Herard and Chen, 1985). The first generation develops from mid-March to the end of July, the second, from mid-June to the end of September, and the third, from mid-August to the end of October, when the fertilized females find wintering shelters (Fig. 1*b*; Herard and Chen, 1985).

Having studied the oviposition dynamics in the females overwintering in nature and transferred into the long-day laboratory conditions, the cited authors concluded that *A. nemorum* in France develops without diapause. The life activity and reproduction proceed all the year round, only decelerating in the winter months owing to the low temperatures (Herard and Chen, 1985).

However, the results reported in the above work may (and should) be interpreted in a different way. The females collected late in the autumn were in the state of diapause. Since diapause is the strongest in its initial phase, only 52.9% of the females collected in mid-October and transferred into the comfort conditions started ovipositing, and their average pre-oviposition period (35.7 days) was much longer than that of the active females (Fig. 2). During winter, the hibernating insects undergo gradual changes (diapause

development) which result in weakening of the dia-pause and finally in resumption of activity (Hodek, 1971; Honek and Hodek, 1973; Saulich and Volk-ovich, 2004; Koštál, 2006; Saulich and Musolin, 2007a). The females collected later (during the first half of November) were already in a somewhat more advanced phase of diapause development, therefore their pre-oviposition period was shortened to 17.7 days and the fraction of ovipositing individuals increased to 64.3%. In the subsequent period (December–January), as the diapause development proceeded further and probably came to an end, the fraction of active females increased to nearly 100% and the time interval before the onset of oviposition was reduced to 10 days (Fig. 2). All these facts indicated the termination of diapause by the end of winter, after which activity could potentially be resumed, but was blocked by the low temperature under natural conditions. The data obtained agree quite well with the recent concepts describing the termination of winter diapause in in-sects in general and heteropterans in particular (Koštál, 2006; Saulich and Musolin, 2007a).

Thus, *A. nemorum* reveals the usual latitude-related variability of voltinism, determined by the genetically fixed capacities of the populations and their living conditions. In the northern part of the distribution range (Norway, Finland, Scotland, and northwestern Russia) the species develops in a single generation, in most areas of Central Europe (England, Germany, Holland, Austria, Poland, etc.) it has two generations, and in more southern areas (for example, in France), three generations. The onset of winter diapause in bivoltine and multivoltine populations is controlled by the daylength, even though a fraction of the population may have a genetically determined obligatory diapause induction (Von Lauenstein, 1977). The diapause is terminated by exposure to low temperatures.

Anthocoris nemoralis (F.) is a Palaearctic species commonly occurring in the Western Europe and the north of Africa (Péricart, 1996).

The seasonal development of the species was stud-ied in the most detail in the south of England (Ander-son, 1962b). The first overwintered adults were ob-served in the second half of March. The sex ratio at that time was approximately 1 : 1, but mortality rates at the beginning of the season were noticeably higher in males than in females. The peak of abundance of the overwintered individuals was recorded in mid-April, most of the bugs occurring on the flowering willows.

Mass oviposition takes place since the end of April or beginning of May, even though some females ma-ture already in early April. The females lay eggs on various plants infested with psyllids, which are the favorite food of *A. nemoralis*. During this period of the year, the largest colonies of psyllids can be found on willows, apple trees, and the broom (*Cytisus* spp.); the females of the predator migrate onto these plants and lay most of their eggs on them. The first generation larvae hatch in early May and develop on the plant species mentioned above.

Occasional adults of the first generation appear al-ready in late May, and mass emergence takes place in mid-June, simultaneously with that of the psyllids. However, since the psyllids are univoltine and migrate to their wintering places in July, the mass migration of the bugs also begins in that moment. A part of the population forms diapause and migrates to the winter-ing places. The remaining individuals, developing by the multivoltine type, move onto new host plants (ma-ples and linden trees) infested by various species of aphids, and form there a sparse second generation, whose adults enter diapause in August (Fig. 3*a*).

At the same time, there exist populations (or sub-populations) of the bugs that live permanently on one plant (usually hawthorn) and complete the seasonal cycle without changing the host plant species. In this case, the overwintered females lay eggs on hawthorn, and their offspring develops on the psyllids infesting this shrub. When the psyllids leave the plant to hiber-nate, the non-migrating bugs also form diapause and overwinter simultaneously with the psyllids. These bugs have a univoltine seasonal cycle (Anderson, 1962b).

Thus, *A. nemoralis* may realize two parallel types of seasonal development, depending on the habitat and the kind of prey. If the seasonal cycle includes a change of the host plant, one fraction of the bugs has a univoltine cycle, and the other fraction, migrating onto the alternative host plant, has a multivoltine cycle. If the entire development is exclusively associated with hawthorn, the population demonstrates a univoltine seasonal cycle.

The factors regulating the seasonal cycle of *A. ne-moralis* have not been experimentally studied.

Anthocoris nemoralis was introduced into North America to control the pear psylla *Cacopsylla pyricola* (Foerster). This is the only one of the 7 anthocorid bug species introduced which was able to colonize the vast

territory from California to British Columbia (southern Canada) and to compete successfully with the local species. Within its new distribution range, the predator has been found on plants from 13 genera, some of which are absent in the Old World (Horton et al., 2004).

Anthocoris gallarumulmi (De Geer) is a mostly Western Palaearctic species (Péricart, 1996), which appears to be univoltine over most of its distribution area. The species overwinters as adults, mostly females. The female-to-male ratio in spring may reach 13 : 1 (Parker, 1984).

The overwintered bugs appear in different time of spring, depending on the latitude. They occur singly on various trees. In Holland (Cobben, 1958, cited after Anderson, 1962b) and the south of England (Anderson, 1962b) they become active in early April (Fig. 3*b*). In mid-May, the bugs start to concentrate on elms, and their subsequent life cycle is closely coordinated with the phenology of the dioecious aphids *Eriosoma ulmi* (L.) and *E. patcher* Börner et Blunk, which form leaf galls where the bugs live and reproduce. The single generation of *A. gallarumulmi* develops in the galls, and its adults emerge from the end of June to August. At the same time, the aphid colonies produce the alate individuals that migrate onto the roots of currant or gooseberry bushes. The bugs leave the elm trees, following the aphids. Accumulation of fat reserves before wintering takes 2–3 months, during which the bugs appear to feed on various small arthropods.

The populations of *A. gallarumulmi* studied in Great Britain overwinter in the state of obligatory reproductive diapause that starts in each generation regardless of the external conditions (Anderson, 1962b; Parker, 1984). Termination of this diapause requires exposure to a low temperature for at least 75 days (Parker, 1984), which undoubtedly confirms the presence of a true diapause in *A. gallarumulmi*.

The bugs from a more southern population (Göttingen, 51.0°N, 9.0°E) may have a facultative diapause (Ruth and Dwumfour, 1989).

This species is scarce within the most part of his distribution range, which is the result of this highly specialized predator being strongly dependent not only on its direct prey (aphids) but also on the galls formed on only one plant species (elm), in which a considerable part of its life cycle takes place.

Anthocoris sarothamni Douglas et Scott occurs in Central and Southwestern Europe and Northern Africa (Péricart, 1996).

The most detailed data on the biology and ecology of the species were obtained by studying the populations from Southern England (Anderson, 1962b) and Scotland (Hill, 1961). The activity and reproduction of the bugs are mostly associated with the Scotch broom *Cytisus scoparius*, and their diet consists of two species of psyllids, *Arytaina genistae* (Latr.) and *Psylla spartiophila* Foerster, and one species of aphids, *Acyrthosiphon pisum* (Harris) (Anderson, 1962b). In the north, the principal food objects of the species may be the aphids *A. pisum* and *Trioza urticae* (L.) (Hill, 1961). Experiments showed, however, that in the absence of their usual prey the bugs could feed on the insects not associated with the Scotch broom (Hill, 1961).

The adults overwinter in the dry Scotch broom seedpods that remain attached to the branches (Anderson, 1962b). The bugs can be found in small numbers all the year round, including the winter months. During this period, *A. sarothamni* may feed on the eggs of psyllids, plant bugs (Miridae), and aphids, adult psyllids, and other insects overwintering in the seedpods. The abundance of the predator increases noticeably in mid-March, probably indicating the onset of spring activity. In cold years the bugs emerge from their wintering places later, in the end of March or in April (Hill, 1961).

In the south of England, oviposition starts in late March and lasts until early May (Anderson, 1962b); in Scotland it proceeds from April to early June (Hill, 1961).

The time of development of individual larval instars is determined by the temperature and the availability of food. In the south of England, all the phenological phases take place slightly earlier than in Scotland. For example, the mass hatchment of the larvae in the south can be observed in mid-May (Fig. 3*c*), adults of the first generation emerge in the beginning of June, and those of the second generation appear since the middle of July and can be found until the end of August. Most of the females (up to 70%) of the first generation, collected in 20.VI–18.VII from the Scotch broom and nettle, contained mature eggs, whereas the females collected from elm trees were in diapause (Anderson, 1962b).
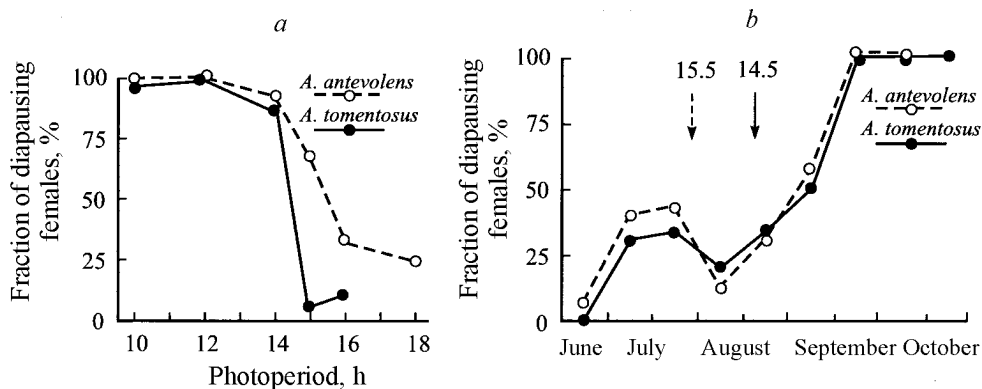
Fig. 4. Photoperiodic diapause induction (*a*) and seasonal dynamics of the physiological state (*b*) of females of *Anthocoris antevolens* and *A. tomentosus* under natural conditions (Yakima, US, 46.5°N, 120.5°W) (after Horton et al., 1998). The photoperiodic response (*a*) was determined by dissecting the females on the 21st day after the imaginal molt at +22°C (averaged data; all females without eggs were regarded as diapausing). In the natural samples (*b*), young females of undiagnosable reproductive status (teneral females) were excluded from analysis. *Arrows* in (*b*) indicate the photoperiodic thresholds of diapause induction (including half the civil twilight period; after Beck, 1980).

In the north, the first adults on the summer genera-tion appear at the end of July, and those of the second generation, in mid-September (only after a very warm summer). The second generation may be very scarce. The populations occurring in Scotland are practically univoltine (Hill, 1961).

Examination of the physiological state of the fe-males collected in nature at the end of the vegetation season showed that all the females were fertilized in autumn but did not lay eggs, resting in the state of reproductive diapause. The diapausing females laid eggs only after a prolonged (nearly 2 months) expo-sure to a temperature of about +4°C. The control fe-males kept at room temperature gradually died out without reproduction (Hill, 1961).

Anthocoris antevolens White has a broad North American distribution range. The principal overwinter-ing stage, as in the rest of anthocorid bugs, is that of fertilized females. The female-to-male ratio in late autumn is 8 : 1. In the northwest coast of North Amer-ica (British Columbia, Washington, Oregon, and Idaho), the overwintered females become active in late March and often form large aggregations on the wil-low goslings (Anderson, 1962a). Oviposition starts in mid-April. One generation is completed in approxi-mately 5–6 weeks. Since the adult lifespan may be as long as 50 days, the generations of *A. antevolens* over-lap. The species appears to have three generations per year. The females enter diapause during the last third of August, after which neither eggs nor young larvae of *A. antevolens* were found in nature (Anderson, 1962a).

The role of photoperiod in induction of reproductive diapause was experimentally studied in *A. antevolens* and ***Anthocoris tomentosus*** Péricart (populations from Yakima, US, 46.5°N, 120.5°W; Horton et al., 1998). At +22°, the number of diapausing females of both species increased as the daylength decreased (Fig. 4*a*). The critical photoperiod value for *A tomentosus* was between 14 and 15 h, whereas in *A. antevolens*, over 20% of the females diapaused even at 18L, and even more (about 30%) diapaused at 16L. Examination of the females dissected on the 21st day after emergence showed that, besides the reproductively active and diapausing individuals, there was a small fraction of females that did not participate in reproduction and had neither eggs nor a well developed fat body. These individuals may have been determined to diapause but could not for some reason accumulate fat reserves in due time (Fig. 4*a*); they were regarded as diapausing.

The fractions of diapausing females in the samples collected in nature in different periods of the season are shown in Fig. 4*b*. A relatively large fraction of diapausing females was observed in the earliest sam-ples (July), where it reached 40% for *A. antevolens* and more than 30% for *A. tomentosus*. These data indicate that diapausing individuals are present already in the first generation, even though both species com-pete 2 or three generations per year in the study area (Anderson, 1962a; Horton et al., 1998).

Diapausing individuals were also recorded in both species under the long-day laboratory conditions, al-though their fractions were considerably smaller than in the natural samples. The females forming diapause

at long day did not differ from short-day diapausing females in their physiological parameters: they had well developed fat body and contained no mature eggs. It may be hypothesized that a fraction of the population forms a summer diapause under the conditions of high temperature and a long day (even though this is uncharacteristic of anthocorid bugs), or that the trend toward diapause in some individuals may be stronger than in the rest of the population. It is difficult to explain why the relative number of diapausing individuals under natural conditions increases much later in the autumn than it could be expected from the experimental data (Fig. 4a). It is also still not clear why the difference in the PPR threshold in the two species, reaching 1 h under constant laboratory conditions, does not manifest itself in nature, where the numbers of diapausing females of these species increase synchronously. The species-specific reproductive traits may play a certain role in this phenomenon. For example, maturation of the females of *A. antevolens* takes 3–4 days longer than that of *A. tomentosus* (Horton et al., 1998). A slightly overestimated fraction of diapausing individuals in summer and an underestimated value for the autumn period may result from the fact that the diapause induction curve in Fig. 4a did not include the newly molted females whose reproductive status could not be determined. However, the fraction of such individuals was small in most samples and could not significantly affect the shape of the curve describing the diapause dynamics under natural conditions.

In general, even though not all the results obtained can now be adequately explained, they clearly indicate that the multivoltine seasonal cycle of *A. antevolens* and *A. tomentosus* in northwestern North America is controlled by the daylength.

Bugs of the genus ***Orius*** Wolff (Anthocorinae) are most intensively used for biological pest control. The world fauna of this genus includes about 75 described species (Lattin, 2000). They are very small bugs (up to 3 mm in length) whose larvae and adults actively attack spider mites, thrips, and other small arthropods. These bugs are broad polyphages; however, like many other polyphagous forms, they still prefer certain species of prey. For example, *O. niger* (Wolff) prefers spider mites, while *O. laevigatus* (Fieber) feeds on thrips. Some species of this genus readily consume pollen. In particular, the survival rate of *O. insidiosus* (Say) under experimental conditions was 91.2% on the diet consisting solely of pollen, 96.2% on thrips and
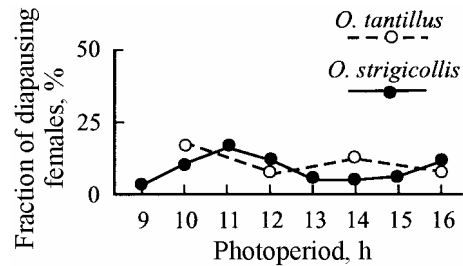

Fig. 5. Photoperiodic diapause induction in *Orius strigicollis* and *O. tantillus* from Okinawa (26.0°N, 128.0°E) at +20° (after Shimizu and Kawasaki, 2001).

pollen, and only 68% when the diet consisted only of thrips (Izhevskii and Akhatov, 1999).

Orius niger (Wolff) is a broadly distributed Palaearctic species occurring on trees and herbaceous plants. It mostly feeds on mites and thrips, and also consumes aphids, whiteflies, eggs and larvae of lepidopterans, and eggs of shield bugs (Péricart, 1972; Akramovskaya, 1978; Ramakers, 1978; Lykouressis and Perdikis, 1997). In the laboratory, the species developed successfully on spider mites (Chelnokova, 1977), larvae of the cabbage moth *Mamestra brassicae* (L.) (van de Veire and Degheele, 1992), and eggs of *Ephestia kuehniella* Zeller with the addition of pollen (Baniameri et al., 2005).

In England, bugs of this species usually occur on heather (*Calluna* spp.) but may also be found on various herbaceous plants, in particular wormwood (*Artemisia* spp.). The eggs are laid on the flowers. The species overwinters as adults, and is believed to have two generations per year (Southwood and Leston, 1959).

Different authors reported *O. niger* to have 2–5 generations per year in European Russia (Péricart, 1972), 2–3 in Kazakhstan (Asanova and Iskakov, 1977), 4–5 in the south of Ukraine (the Crimea) (Bogachev, 1951), and 7–8 generations per year in Tajikistan (Elov, 1976).

In the Middle Volga area, these bugs often occur on the flowers of alfalfa, clover, mustard, buckwheat, and dill. Emergence of the overwintered individuals was recorded in late April, and oviposition, in May. The first generation develops in May, and the second, in June–July. Three or four generations per season can develop in this region. The maximum abundance of the bugs was recorded in July–August. The duration of the larval stage was about 12 days in June–July (at +23–27°C) and 23 days in October (at +18–20°C) (Chelnokova, 1977).
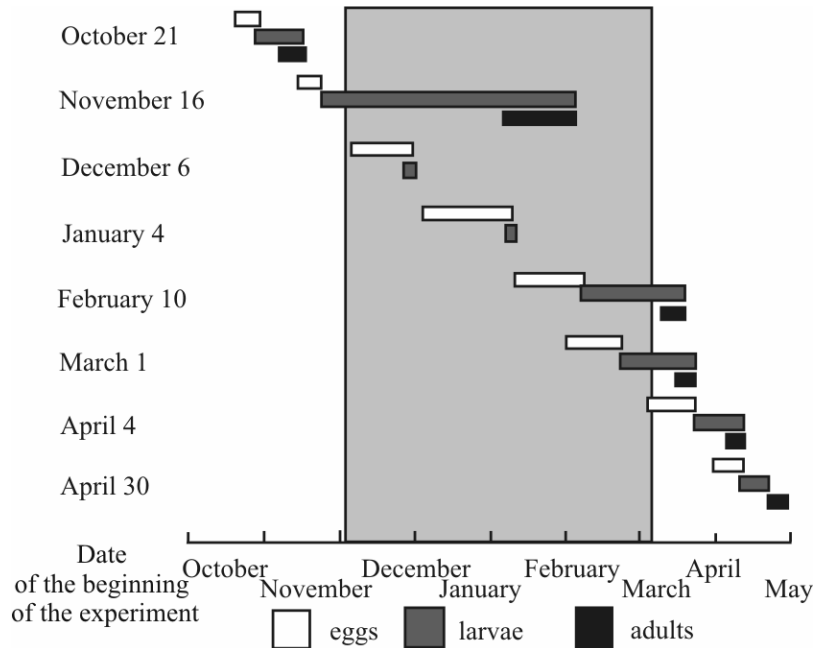
Fig. 6. Development of *Orius albidipennis* under near-natural experimental conditions in Israel in 1992–1993 (Bet Dagan; 32.0°N, 34.8°E) (after Chyzik et al., 1995). The shaded area marks the period during which the mean daily temperatures fell below +15°.

In the cotton fields of Greece, *O. niger* is the most abundant of the 7 representatives of the genus. The maximum abundance was recorded in August–September (Lykouressis and Perdikis, 1997). According to the observations made in Turkey, this bug actively exterminates the thrips *Frankliniella occidentalis* (Pergande) and *F. intosa* (Trybom) in cotton fields (Atakan, 2006). In Iran, the species is regarded as the most promising agent of biological control of the onion thrips *Thrips tabaci* Lind (Baniameri et al., 2005). Of special interest are the reports of this predator attacking the lacebug *Stephanitis pyri* (F.) (Carayon and Steffan, 1959, cited after Lattin, 2000). Owing to its high ecological plasticity, the species is considered to hold much promise for use in protected grounds under the conditions of northwest Russia (Saprykin, 2008).

The factors regulating the seasonal development of *O. niger* are still poorly known. The effects of daylength and temperature were studied in a population of the species from Antalya (Turkey; 36.9°N, 30.7°E) (Bahşi and Tunç, 2008). In all the experimental regimes (daylength 9L, 11L, and 13L; temperature +26°), the females continued to lay eggs and revealed the same duration of the pre-oviposition period. Based on these data, the cited authors concluded that the photoperiodically induced diapause was absent in the population studied. However, this conclusion appears to be premature since no experiments at a lower tem-

perature were carried out. At least in the more northern populations, *O. niger* has a multivoltine seasonal cycle and overwinters only at the adult stage, which suggests the presence of some regulatory mechanisms controlling both the onset of hibernation and the general structure of the seasonal cycle. The lesser significance of daylength in the onset of hibernation and the lesser significance of diapause itself as a form of prospective dormancy are the general trends of the southern populations of *Orius* bugs. Such trends can be clearly observed, for example, in *Orius strigicollis* (Poppius) and *O. tantillus* (Motschulsky) in the south of Japan (Fig. 5; Shimizu and Kawasaki, 2001), even though more northern populations of *O. strigicollis* (from central Japan) demonstrate a common PPR of the long-day type (Musolin et al., 2004). This phenomenon will be discussed below in greater detail.

Orius albidipennis (Reuter) is distributed in Western and Eastern Europe and the Mediterranean region, and is also known from Central Asia and Pakistan. The bugs feed on aphids, spider mites, thrips, and other small arthropods (Kiranova, 1954; Lattin, 2000).

The species overwinters at the adult stage. In the temperate zone of Russia, the bugs emerge from their wintering places in the end of March (Korinek, 1940).

In Uzbekistan, the bugs become active in late March or early April, and their maximum abundance in cotton

fields was recorded in early August. The adults hibernate in October. No less than 6 generations develop in one vegetation season (Kiranova, 1954). In Israel (Bet Dagan; 32.0°N, 34.8°E), oviposition of the species stops only in January–February, when the minimum temperatures fall to +5–0°. The females that molted in November–December stop ovipositing due to reproductive diapause and resume reproduction only in spring, when the temperature rises above +15° (Chyzik et al., 1995). The possibility of development of the species during the winter months was revealed by experiments carried out under the conditions resembling the natural conditions of the region (Fig. 6). Embryonic development and hatchment of larvae are possible even in the coldest months (December–February), probably because of higher daytime temperatures. However, the larvae hatched during this period die within the first several hours (Fig. 6, variants of 6.XII and 4.I). Successful development is possible only in the larvae that hatch no earlier than in the end of February, when the mean daily temperature rises above +15°. The larvae of older instars may develop during the winter months as well; even though their development was strongly retarded by low temperatures, it still completed successfully by the final molt.

The role of daylength in the control of seasonal cycle in this population was not studied. However, the cited authors assumed that the reproductive diapause was induced by a low temperature rather than a short day (Chyzik et al., 1995). This conclusion was indirectly confirmed by the studies of an *O. albidipennis* population from the Canary Islands (28.1°N, 15.4°W; van den Meiracker, 1994). Adult bugs can be found on the Canary Islands nearly all the year round, and the annual cycle of the species appears to have no distinct dormancy period (Carnero et al., 1993). However, in the laboratory experiments, at all photoperiodic regimes and at +18°, a small fraction of the females (no more than 10%) entered reproductive diapause (Fig. 7). This fraction increased to 25% only in the photoperiodic regime 12L, in which the temperature was somewhat lower (+17°). Such a weak photoperiodic control of diapause in populations from relatively warm regions allows one to conclude that diapause is mostly controlled by temperature. It is also possible that diapause itself is weak in individuals from these populations. As mentioned above, a lesser significance of daylength in winter dormancy induction is characteristic of the southern populations of *Orius* bugs.
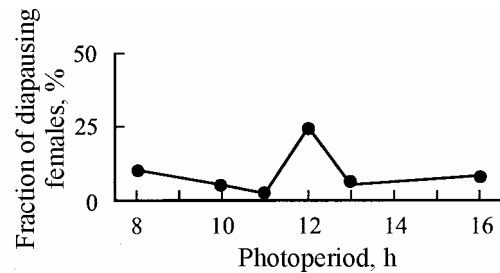

Fig. 7. The effect of photoperiod on diapause induction in *Orius albidipennis* from the Canary Islands (28.1°N, 15.4°W) at +17–18°C (after van den Meiracker, 1994).

Orius minutus (L.) is a Palaearctic species distributed from Western Europe to China and Japan (Péricart, 1972, 1996). In 1939, the species was recorded as an introduced form on the Pacific coast of North America (Tonks, 1953, cited after Anderson, 1962a), after which it extended over the entire continent (Lattin et al., 1999). *O. minutus* can be often found in berry fields and on fruit trees, where it destroys thrips, mites, psyllids, aphids, plant bugs, and leafhoppers.

The seasonal development of the species was observed in apple orchards in Poland (Niemczyk, 1978). The first occasional individuals appear on trees during the first half of April. Their abundance increases abruptly during the blossoming of the apple trees, to which the bugs migrate from the nearby vegetation, being attracted by large colonies of aphids. Mass oviposition was recorded in the first half of May. Adults of the first generation appear in late June, and those of the second generation can be commonly found since the beginning of August. Since the periods of development of individuals from different generations overlap considerably, all the stages of the species can be observed simultaneously in summer. The highest abundance was observed from mid-August to mid-October, after which the fertilized females moved to wintering places.

Experimental studies were carried out on *O. minutus* from the Japan islands, where the species is a common one. The facultative winter diapause was found to be regulated by PPR of the long-day type: diapause is formed under short-day conditions, and at a long day, the females lay eggs (Figs. 8*b*, 8*d*; Musolin and Ito, 2008). It is interesting that PPR of *O. minutus*, unlike those of many other species, is practically independent of the temperature: changes of the temperature within the range of +20–28° had almost no influence on the fraction of diapausing females and on the position of the threshold. At the same time, the species
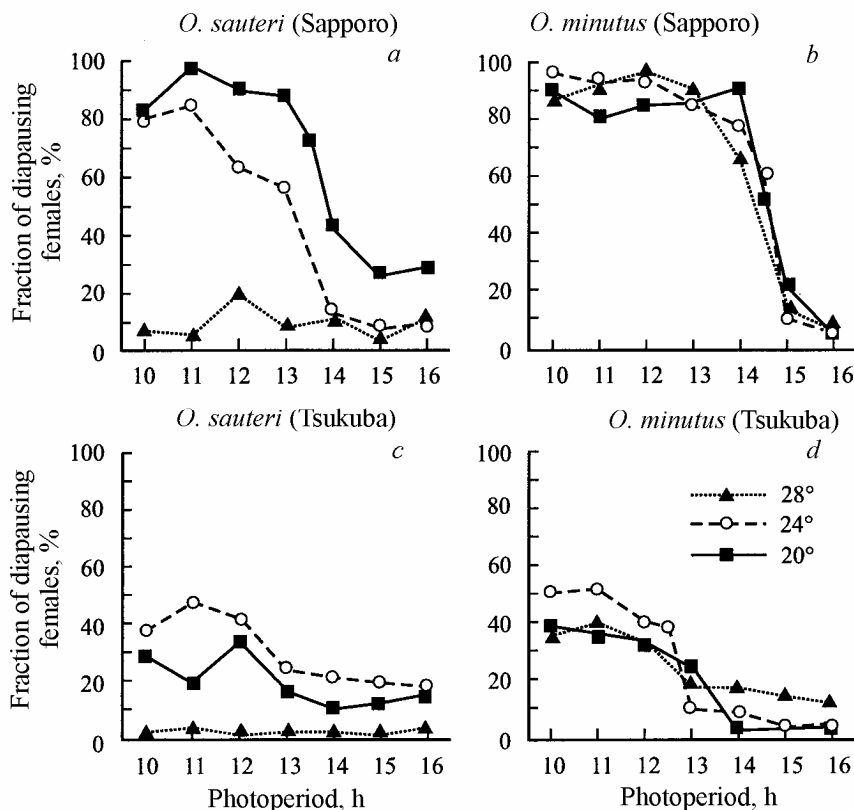
Fig. 8. Photoperiodic diapause induction in the females of *Orius sauteri* (*a*, *c*) and *O. minutus* (*b*, *d*) from Sapporo (Japan; 43.0°N, 141.4°E) and Tsukuba (Japan; 36.1°N, 140.1°E) at different temperatures (after Musolin and Ito, 2008).

clearly demonstrated the typical geographic trend: the southern population revealed a suppressed potential for diapause, so that only half of the females entered diapause even under short-day conditions (Fig. 8*d*). Similar results were reported by other authors (Shimizu and Kawasaki, 2001).

Orius sauteri (Poppius) occurs in Korea, Japan, China, and the Far East of Russia (Yasunaga, 1993; Péricart, 1996).

In Korea, *O. sauteri* prevails over the rest of anthocorid bugs in the plantations of soybeans, red pepper, and watermelons. The overwintered bugs appear in the end of May on the flowering red clover. In early June, they migrate onto the cultured plants which at this time enter the flowering phase. The flowering plants strongly attract all insects, including anthocorids, and the plant phenophase was shown to determine the seasonal population dynamics of predaceous bugs on various cultivars. The first abundance peak was observed in July on buckwheat, red pepper, and white clover, and the second, in August–September on soybeans (Kim et al., 2001).

In Japan, *O. sauteri* was shown to be effective against the inadvertently introduced *Thrips palmi* Karny on eggplants in the open (Nagai, 1993) and protected ground (Yano, 1996).

The factors regulating seasonal development of *O. sauteri* were experimentally studied in Japan. The principle factors of diapause induction are the photoperiod and temperature. The parameters of the long-day PPR (Figs. 8*a*, 8*c*) show distinct temperature-related and geographic variability. In experiments, high temperature (+28°) almost completely suppressed diapause even under the extreme short-day conditions (Musolin and Ito, 2008; see also Kohno, 1998). Striking differences were observed between the northern and the southern populations: the great majority of females from the northern population entered diapause at low (+20°) and moderate (+24°) temperatures, whereas the fraction of diapausing females in the southern population did not exceed 50% even at extreme short-day photoperiods (Fig. 8*a*, 8*c*).

Comparison of the threshold PPR values in several geographic populations of *O. sauteri*, occurring in the

north of the Japan Islands between 34.0 and 45.4°N, revealed an almost linear relation between the threshold value and the latitude (Ito and Nakata, 2000). The PPR threshold changed approximately by 1 h per 5 degrees of latitude (Fig. 9), which agreed well with the recent concepts of the geographic variability of PPR in insects (Saulich and Volkovich, 2004). The populations also differed in the shape and inclination of their PPR curves.

In the bugs of more northern origin, a 1-h change in daylength near the critical photoperiod value induced transition into the alternative physiological state. The trend towards diapause development decreased gradually in the southern populations. In the southernmost population from Kochi (Japan; 33.5°N), PPR did not disappear completely but the fraction of diapausing females did not exceed 10–12% even under the typical short-day conditions (9–12L); at the same time, some females entered diapause in the long-day regimes as well (Fig. 10; Shimizu and Kawasaki, 2001). In general, the geographic PPR variability in *O. sauteri* is distinctly clinal. It should be noted, however, that different authors reported different parameters of the same geographic populations examined (Kohno, 1998; Ito and Nakata, 2000; Shimizu and Kawasaki, 2001; Musolin and Ito, 2008), which may be related to certain methodological differences.

The seasonal cycles of the species with a facultative diapause and a long-day PPR are very similar. The bugs form winter diapause in autumn, after the daylength decresed below the critical value. The PPR parameters are usually adapted to the living conditions of each local population. For example, the critical photoperiod of diapause induction in *O. sauteri* from Sapporo (43.0°N, 141.4°E) at +20° was slightly shorter than 14 h (Musolin and Ito, 2008). In the study area, such a daylength value can be observed in mid-August. The larvae developing during this period accumulate short-day photoperiodic signals, and the adults form diapause. Development of a complete generation of *O. sauteri* requires approximately 300 grad.-days, whereas the climatic conditions of Sapporo allow about 480 grad.-days to be accumulated (above the development threshold for the species, estimated at +12.7°); therefore only one complete generation can develop in the region. Development of the second generation is possible only in part of the population and/or in exceptionally warm years (Musolin and Ito, 2008).
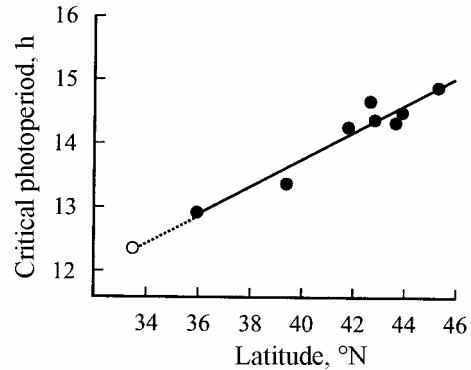

Fig. 9. The relation between the critical PPR threshold and the latitude in *Orius sauteri* females in the north of Japan (after Ito and Nakata, 2000). The temperature was +22°C. The line of regression is shown together with the accessory data (data taken from Kohno, 1997 are designated by an empty circle).
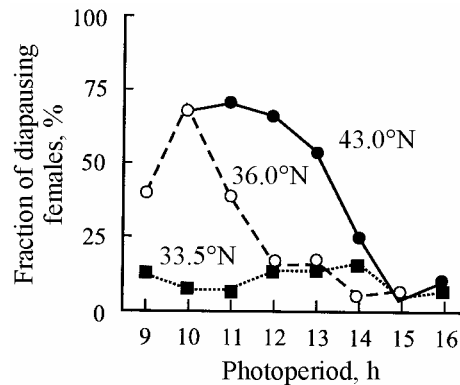

Fig. 10. Geographic variability of photoperiodic response in *Orius sauteri* females in Japan (after Shimizu and Kawasaki, 2001). Populations from Obihiro (43.0°N, 143.2°E), Tsukuba (36.1°N, 140.2°E), and Kochi (33.5°N, 133.5°E). The temperature was +20°C.

The populations of *O. sauteri* from more southern geographic regions have PPRs with smaller threshold values or a weak response; they are of little importance for survival and may even be adaptive in the mild climate. In such regions diapause is formed much later, after the development of several generations (Kohno, 1997; Shimizu and Kawasaki, 2001).

In case of adult diapause, perception of the photoperiodic signals often starts in the middle larval instars and continues during the adult stage (Saulich and Volkovich, 2004; for heteropterans, see Saulich and Musolin, 2007b). The sensitivity of adults to daylength allows them to switch between the main and alternative photoperiodic responses depending on the photoperiod affecting the adult stage. Therefore in autumn, even the individuals determined for active development gradually stop oviposition and enter diapause under the influence of short-day conditions. This is the
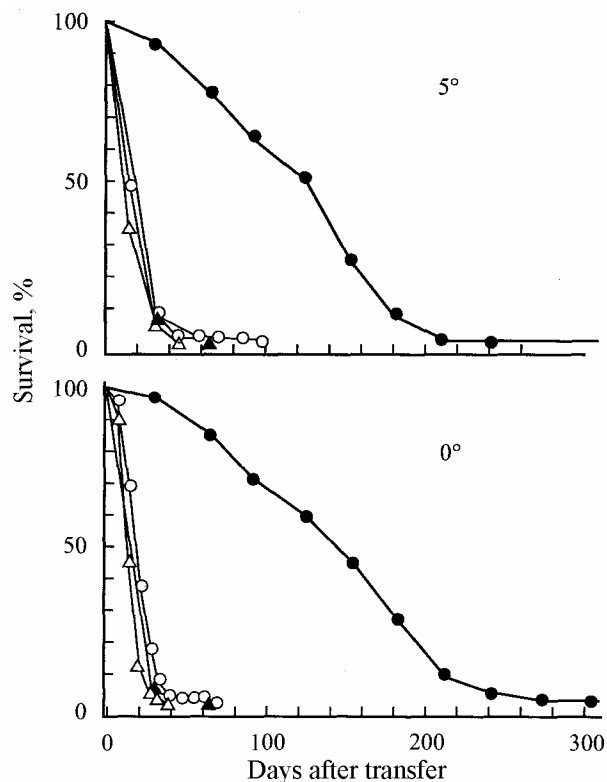
Fig. 11. Survival rates of *Orius sauteri* from Sapporo (Japan; 43.0°N, 141.4°E) at the temperatures 0 and +5°C (after Ito and Nakata, 1998a). The larvae, and then adults, were kept for one week at +22°C and the specified daylength, and then transferred into 0 or +5°C at the same daylength. Females reared at short day (11L : 13D) are designated by dark circles; males reared at short day, by dark triangles; females reared at long day (16L : 8D), by empty circles; males reared at long day, by empty triangles.

case, for example, in *O. insidiosus* (Ruberson et al., 1998). The adults of *O. sauteri* and *O. minutus* do not react to daylength, and the final response is determined by the conditions under which the larvae have developed (Ito and Nakata, 1998b). This feature accounts for the fact that ovipositing females of these two species can sometimes be found in nature even after the daylength has decreased far below the threshold level. A very important consequence of this trait is that the bugs reared under long-day conditions will reproduce in greenhouses during late autumn and winter, despite the short day.

The field observations carried out in autumn revealed both sexes of *O. minutus* and *O. sauteri*; however, no males were found in spring (Yasunaga, 1993; Ito and Nakata, 1998a). This feature is typical of many anthocorid bugs, as was discussed above. Detailed biochemical and physiological studies were performed to understand this phenomenon, quite uncharacteristic of most insects. The bugs were reared under long- and

short-day conditions, and their survival rates at low temperatures (0 and +5°) were compared (Ito and Nakata, 1998a).

All the females reared under long-day conditions and determined towards reproduction, died at low temperatures approximately within a month, whereas 50% of the diapausing females reared at short day remained alive even after a 4-month exposure to low temperatures (Fig. 11). The males died at low temperatures as quickly as non-diapausing females, regardless of the preceding photoperiodic conditions.

The lipid content (Fig. 12) was much higher in the diapausing females reared under short-day conditions than in the non-diapausing females reared under long-day conditions. The lipid content of the males remained at a low level, close to that of non-diapausing females, regardless of the rearing conditions.

Thus, the males of *O. sauteri* and *O. minutus* cannot enter diapause and accumulate the energy reserves needed for wintering, therefore they die already in early winter (Ito and Nakata, 1998a). Mating takes place in autumn. Contrary to what is observed in other bugs, and insects in general, these two *Orius* species copulate actively under any photoperiod conditions (Ito and Nakata, 1998b). Only the females in the state of winter diapause can survive winter; they are fertilized in autumn but have immature gonads.

The diverse seasonal adaptations of insects are not limited to winter adults diapause. Many insect species, including heteropterans, possess special adaptations that allow them to survive unfavorable periods in other seasons of the year (for example, extreme high temperatures in summer, seasonal droughts, floods, and absence of food) and optimize the use of seasonal resources provided by the environment (for heteropterans, see Saulich and Musolin, 2007a, 2007b). For example, in laboratory experiments at +20°, the larvae from the northern populations of *O. sauteri* and *O. minutus* developed more slowly at the photoperiod 14L : 10D than at longer or shorter photoperiods. Faster larval development under short-day conditions may have a certain adaptive significance: the shorter is the day in autumn, the sooner will the larvae complete development, and the adults will have more time to copulate and prepare themselves for wintering. In addition, the development rates of the larvae were shown to be less dependent on the temperature under short-day conditions than under long-day ones; this feature might also have an adaptive significance in autumn
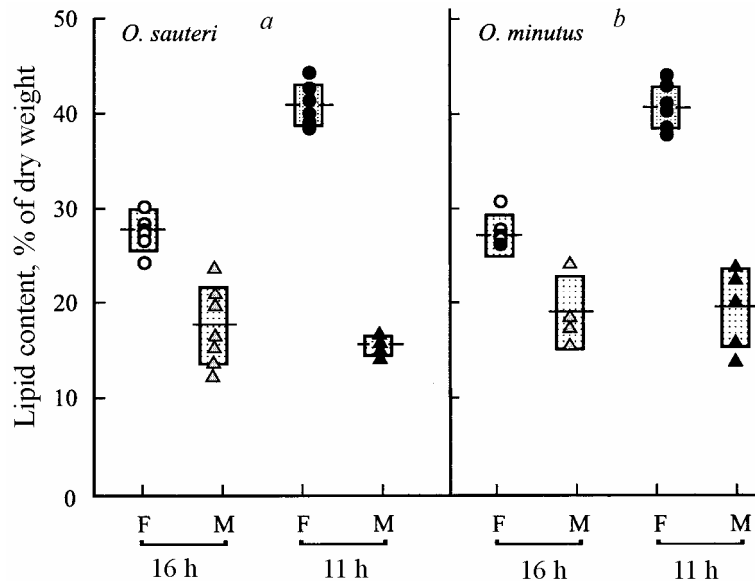
Fig. 12. Comparative lipid content in the adults of *Orius sauteri* (*a*) and *O. minutus* (*b*) from Sapporo (Japan; 43.0°N, 141.4°E), reared under long- or short-day conditions at +22°C (after Ito and Nakata, 1998a): females (*F*) and males (*M*).

(Musolin and Ito, 2008). In general, however, the eco-logical value of such adaptations is not as great for the rapidly developing anthocorid bugs as it is for the species with longer development cycles.

Orius strigicollis (Poppius) occurs in central and southeastern Japan, southern China, Korea, and Taiwan (Yasunaga, 1997). The species is used for controlling *Thrips palmi*, *Frankliniella occidentalis*, and many other small arthropods in the open and protected grounds (Song et al., 2101; Wang et al., 2001).

The number of generations of *O. strigicollis* varies depending on the geographic zone. As in many other anthocorid species, the adults of the last generation of the vegetation season mate in autumn; the females of this generation, however, do not start laying eggs but enter a winter reproductive diapause, while the males usually die before or during wintering.

The winter reproductive diapause is induced by long-day PPR, whose parameters vary depending on the temperature. In the populations from central Japan (Tsuchiura, 36.1°N, 140.2°E), the critical photoperiod at +20° is close to 13L, that at +24° is close to 12.5L, while a temperature of +28° strongly suppresses diapause induction, so that no more than 50% of females enter diapause even under very short-day conditions of 10L (Fig. 13; Musolin et al., 2004).

As shown by the examples of *O. sauteri* and *O. minutus* (Figs. 8–10), the geographic variability of PPR is usually manifested in suppression of diapause

in the southern populations, under both long-day and short-day conditions. The same phenomenon can be observed in *O. strigicollis*: in the population from Okinawa (26.0°N, 128.0°E) the fraction of diapausing females did not exceed 20% even at the most extreme diapause inducing regimes of 9L and 10L (see Fig. 5; Shimizu and Kawasaki, 2001). Similar data were obtained for the population from Kagoshima (Japan; 31.7°N, 130.7°E; Kakimoto et al., 2003). At the same time, diapause induction was possible only at temperatures not exceeding +20°; at +22° all the females remained active even under short-day conditions (Furubayashi et al., 2003).

The daylength-sensitive stage of *O. strigicollis* was identified in a population from South Korea (37.3°N, 127.0°E; Cho et al., 2005). For diapause to be induced in all the individuals, both the larvae (starting from the IV instar) and the adults should be subjected to the short-day conditions (Table 2, var. 6). Exposure to short-day conditions of only V instar larvae and adults (Table 2, var. 5) induced diapause only in a fraction of the individuals (72.7%).

The temperature requirements of development were determined for a southern (Kagoshima) population of *O. strigicollis*. The lower temperature threshold of development was +10.0°, while the sum of effective temperatures was 281.9 degree-days (Kakimoto et al., 2003). These experimental data are consistent with the reports according to which the species may have up to 8 generations per season in this region. The diapause
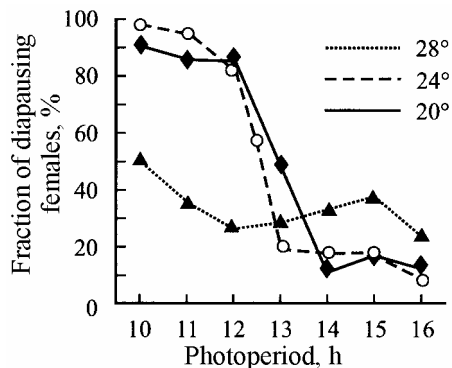
Fig. 13. Photoperiodic diapause induction in *Orius strigicollis* females from Tsuchiura (Japan; 36.1°N, 140.2°E) at different temperatures (after Musolin et al., 2004).

under natural conditions is formed in the individuals that develop in October–November: up to 70% of females enter diapause, even though the air temperature in this period is still high enough to suppress diapause induction, according to the experimental data. It was assumed that the process of diapause formation in *O. strigicollis* might be affected not only by the absolute daylength value but also by its seasonal dynamics (Furubayashi et al., 2003).

The number of generations developing annually in a particular region is usually determined by the required sum of effective temperatures and the availability of food. The number of generations that can be completed within the vegetation season decreases gradually towards the north, and near the northern distribution boundary the species usually has only one generation; in other words, the population or its part becomes univoltine (by an exo- or endogenous mechanism). *O. strigicollis*, however, revealed unusual geographic variability of voltinism. The northern distribution boundary of the species appears to be determined by the minimum temperature of January (the mean daily minimum is –1.0°) and number of cold days with temperatures below 0° (50 days during winter; Shimizu et al., 2001). In Tsuchiura (Japan), near the northern boundary of the species, where these parameters are close to the critical values, not one but 4–5 overlapping generations develop in the period from April to September (Musolin et al., 2004). Reproductive diapause in the females starts to develop in the first half of September, when the natural daylength is reduced to a near-critical PPR value (12.5–13 h) and the mean air temperature falls to +20–24°. Thus, the number of annual generations is determined by temperature conditions of wintering, rather than the sum of effective temperatures. Further northward distribu-

tion seems to be restricted by the relatively cold winter which this species cannot survive. It may appear only in human settlements where the climate is warmer (the "warm island" effect; Shimizu et al., 2001).

Orius insidiosus (Say) is distributed in North and South America (Herring, 1966) and occurs in various natural and anthropogenic landscapes. The diet of this polyphagous predator comprises over 20 insect species from different orders, including such major agricultural pests as *Thrips tabaci* Lind., *Trialeurodes vaporariorum* Westw., *Corythucha ciliata* (Say), *Spodoptera frugiperda* (J.E. Smith), *Ostrinia nubilalis* Hbn., *Helicoverpa zea* Boddie, and *Heliothis virescense* (F.) (Barber, 1939). Under experimental conditions, all the vital parameters of the bugs reared exclusively on maple pollen were similar to those of the insects consuming animal food (Kiman and Yeargan, 1985).

Among the predacious bugs, *O. insidiosus* is the species most extensively used in the biological pest management; it is commercially available to farmers in the US and Europe. The species was introduced into Europe to control the thrips *F. occidentalis* in protected grounds (van den Meiracker, 1994). This predator is also likely to be efficient against the lacebug *C. ciliata*, a North American species which was inadvertently introduced into Europe and became a serious pest of ornamental trees, such as maples and sycamores (Horn et al., 1983).

The adults of *O. insidiosus* can be found in great numbers in March–April on flowering herbaceous plants, where they find abundant prey. In early June, the abundance of bugs on wild plants decreased noticeably owing to intensive migration onto the cultural plants (corn, cotton, soybeans, etc.) that start flowering at this time. The bugs are most strongly attracted by the flowering corn plants, which host abundant prey. In addition, the silky filaments of female flowers, positioned in the leaf axils, serve as shelters for the larval and adult bugs and provide favorable humidity conditions, whereas the male flowers provide pollen (Isenhour and Marston, 1981; Elkassabany et al., 1996). The phenology of flowering of the preferred host plants determines not only an increase of *O. insidiosus* abundance in the fields but also its decline, because after the end of flowering the bugs migrate back onto wild herbaceous plants.

The adults overwinter in the state of reproductive diapause (Kingsley and Harrington, 1982; Ruberson et al., 1991). The females have better chances of over-

Table 2. Sensitivity of different development stages of *Orius strigicollis* to daylength (after Cho et al., 2005)

Variant	Eggs	Larval instars					Adults	Fraction of diapausing females, %
		I	II	III	IV	V		
1	S	L	L	L	L	L	L	0.0
2	L	S	S	S	L	L	L	0.0
3	L	L	L	L	S	S	L	45.5
4	L	L	L	L	L	L	S	11.2
5	L	L	L	L	L	S	S	72.7
6	L	L	L	L	S	S	S	100.0
7	L	L	L	S	S	S	S	100.0
8	L	L	S	S	S	S	S	100.0
9	L	S	S	S	S	S	S	100.0

Note: Population from South Korea (37.3°N, 127.0°E). S is short day (8L : 16D), L is long day (16L : 8D). The temperature was +18°C. The physiological state of the females was determined on the 20th day after the imaginal molt. The variants in which the fraction of diapausing females exceeded 50% are shown in bold.

wintering than males; in some regions (and probably in colder winters) male mortality reaches 100%, so that the natural populations in spring consist mostly of fertilized females (Elkassabany et al., 1996; Ruberson et al., 1998). The diapausing females contain no mature eggs and have a hypertrophic fat body (see photo in Ruberson et al., 1998).

The number of generations of *O. insidiosus* varies in different parts of its distribution range: two generations in Wisconsin (Kingsley and Harrington, 1982), and 2–3 (sometimes 4) in Virginia (Barber, 1936).

In the south of the US (Arkansas), the overwintered bugs appear in early spring on clover, vetch, buttercups, and other early flowering herbaceous plants, where they feed on thrips, plant bugs, and other small insects. At least one generation is completed on these early plants. Later the bugs migrate onto other plants, seeking not only animal food but also flowering vegetation. The population of the predator decreases as the flowering plants become scarce. Finally, in the second half of October, at temperatures about +20° and short day, the bugs leave the plants and find wintering shelters in the litter or under the bark, where they diapause forming no aggregations (Elkassabany et al., 1996; Ruberson et al., 1998).

The onset of diapause in *O. insidiosus* is regulated by daylength and temperature. This species has PPR of the long-day type. Nearly all the females in the Arkansas population (36.1°N, 94.3°W) entered diapause under short-day conditions of 10 h of light (Fig. 14). At a longer day the fraction of diapausing females decreased, and at photoperiods exceeding 14 h all the

females reproduced actively. The critical daylength at +20° lay between 12 and 13 h (Ruberson et al., 1991). Under the natural conditions of the region, such daylength values can be observed approximately since mid-October. Indeed, field sampling indicated that by the beginning of November all the females of *O. insidiosus* had entered diapause (Elkassabany et al., 1996). The highest sensitivity to daylength was manifested by V instar larvae and adults during the first several days after molting (Table 3). The action of a short day only at the adult stage was not sufficient for diapause induction in all the females (variant 19; Ruberson et al., 2000).

In a more southern population from Georgia (approximately 31.5°N, 83.5°W), the PPR threshold at +18° was slightly lower: between 11 and 12 h (van den Meiracker, 1994). Diapause could be easily terminated when the adults were transferred into long-day conditions and/or a temperature of +25°. Nearly all the females began ovipositing 2 weeks after the change of conditions; the effect of the high temperature manifested itself faster than that of the long day (Fig. 15).

The daylength affected the duration of the pre-oviposition period as well. The females reared under long-day conditions (15L : 9D) started oviposition on average 6 days after the final molt. At the short day, only 2 out of 46 females were active; they laid eggs only 17 days after the molt.

O. insidiosus appears to need food during wintering. At least at a moderate temperature (+18°), the diapausing adults showed the same mortality rates in the ab-
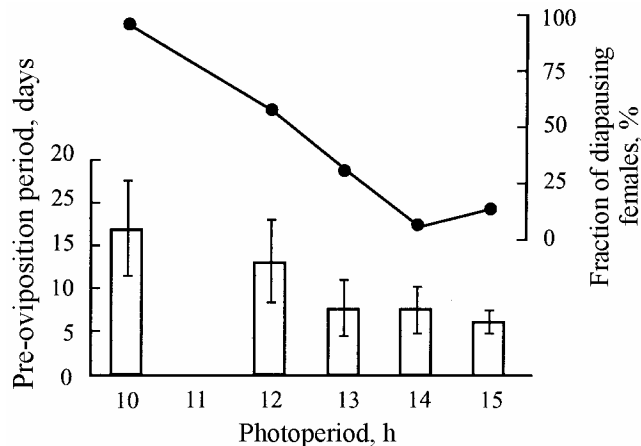
Fig. 14. Photoperiodic diapause induction (upper curve) and duration of the pre-oviposition period (histogram, mean ± *SE*) in *Orius insidiosus* females from Arkansas (36.1°N, 94.3°W) at +20°C (after Ruberson et al., 1991).

sence of food as did non-diapausing adults also deprived of food (Ruberson et al., 1998).

Orius tristicolor (White) is a species having much in common with *O. insidiosus*, in both morphological and biological aspects. The two species are so similar that at the beginning of the last century they were regarded as color morphs of a single species (Parshley, 1919, cited after Anderson, 1962a).

O. tristicolor is distributed in North and South America (Lattin, 2000) and has a multivoltine seasonal cycle. In the US, this species may have up to 3–4 generations (Anderson, 1962a). Like most anthocorid bugs, *O. tristicolor* overwinters at the stage of females fertilized in autumn; nearly all males die in winter (Anderson, 1962a).

The onset of diapause in females is controlled by daylength (Gillespie and Quiring, 1993). The available data demonstrate geographic variability of PPR in *O. tristicolor*. Under identical temperature conditions, the critical photoperiod of the Californian population (Davis; 38.5°N, 121.8°W) was between 12 and 13 h, whereas that of a northern population (Agassiz, British Columbia, Canada; 49.2°N, 121.8°W) was between 14 and 16 h (Fig. 16).

In the study area of Canada, a daylength of 15 h without the civil twilight can be observed in the first 10 days of August, and considering the civil twilight, in late August. The adult bugs collected in nature in early August were reproductively active and gave rise to the following generation. The adults of this generation molted in early September and were in the state of

diapause: the females did not contain mature eggs and had well developed lipid reserves. In a warmer climate of California, the daylength reaches the threshold values later (in late September or early October), considerably prolonging the reproductive season.

The PPR parameters of *O. tristicolor* from California varied greatly depending on the temperature conditions during the experiments. In particular, under the conditions of daily thermorhythm +25° (day) : +15° (night), the PPR threshold was close to 12L (Fig. 16; Gillespie and Quiring, 1993), whereas at a constant temperature of +18° about 50% of the females did not start reproducing even at the longest photoperiod examined (16L : 8D; Fig. 17; van den Meiracker, 1994). These data indicate that the trend towards diapause induction is more distinct at a relatively low constant temperature than at a thermorhythm resembling the natural daily temperature dynamics.

The seasonal development of anthocorid bugs in the Southern Hemisphere is very poorly known. One of the few species studied in this respect is *Orius vicinus* Ribaut, inadvertently introduced from Europe to New Zealand late in the XX century. In Otago (New Zealand; 45.5°S, 169.0°E) *O. vicinus* has two generations per season, although a third generation may partially develop in very warm years (Fig. 18). The bugs are usually active since October (spring in the Southern Hemisphere) to early April (autumn), when the fertilized females do not start oviposition but find wintering shelters in the litter or fissures in the bark of the trees on which they have fed during the summer (Wearing and Attfield, 2002).

Orius thyestes Herring, distributed in the Neotropical Region (Colombia, Mexico, and Brazil), appears to have no diapause (at least of the kind induced by a short day). In experiments carried out at +28° and various short-day photoperiods, the females of *O. thyestes* from Lavras (Brazil; 21.2°S, 45.0°W) laid eggs under any conditions, their reproductive parameters being the same in different regimes (Carvalho et al., 2006). It is essential that *O. insidiosus* from this region also revealed no PPR at +25°, its females continuing to reproduce in all short-day photoperiods (Argolo et al., 2002; Silveira and Bueno, 2003). The climate of southern Brazil appears to be mild enough for these species to overwinter without diapause.

The non-diapausing populations and specially selected strains of anthocorid bugs are now actively tested in Japan for efficiency and ecological safety of

Table 3. Sensitivity of different development stages of *Orius insidiosus* to daylength (after Ruberson et al., 2000)

Variant	Larval instars					Adults			Fraction of dia-pausing females, %
	I	II	III	IV	V	days 1–5	days 6–14	after day 14	
1	L	L	L	L	L	L	L	L	8.7
2	S	L	L	L	L	L	L	L	0.0
3	S	S	L	L	L	L	L	L	0.0
4	S	S	S	L	L	L	L	L	0.0
5	S	S	S	S	L	L	L	L	8.3
6	S	S	S	S	S	L	L	L	**54.2**
7	S	S	S	S	S	S	L	L	**100.0**
8	L	S	S	S	S	S	S	S	**100.0**
9	L	L	S	S	S	L	L	L	**91.7**
10	L	L	S	S	S	S	L	L	**100.0**
11	L	L	S	S	S	S	S	L	**100.0**
12	L	L	S	S	S	S	S	S	**100.0**
13	L	L	L	S	S	L	L	L	**90.9**
14	L	L	L	S	S	S	L	L	**95.8**
15	L	L	L	S	S	S	S	L	**100.0**
16	L	L	L	L	S	L	L	L	**52.6**
17	L	L	L	L	S	S	L	L	**82.4**
18	L	L	L	L	S	S	S	L	**100.0**
19	L	L	L	L	L	S	S	S	**54.4**
20	S	S	S	S	S	S	S	S	**100.0**

Notes: Population from Arkansas (36.1°N, 94.3°W). S is short day (10L : 14D), L is long day (14L : 10D). The temperature was +20°C. The fraction of diapausing females was determined as the number of females that start ovipositing on the 14th day after the imaginal molt or earlier, related to the total number of females in each variant. The variants in which the fraction of diapausing females exceeded 50% are shown in bold.

transportation and application in protected and open grounds. According to the preliminary data, this group includes *Orius tantillus* and *Wollastoniella rotunda*.

Orius tantillus Motschulsky is known from the tropical and subtropical zones of India and Southeast Asia (Yasunaga and Miyamoto, 1993). Experimental studies were carried out with a population from Okinawa prefecture (Japan; 26.2°S, 127.7°E). The adults collected in nature in the middle of a warm subtropical winter contained mature eggs. The natural winter populations, subjected to a relatively low temperature of +15.8° and a short day (about 10 h), contained larvae, indicating that *O. tantillus* overwintered in an active state. Under the laboratory conditions resembling those of the Okinawa winter, the females formed no diapause but continued oviposition. Finally, the adults reared at a long (16L) and short (10L) days at +25°, started oviposition equally fast: on average 2.9 and 2.5 days after molt, respectively (Nakashima and

Hirose, 1997). All these facts indicate the absence of diapause at least in this southern population of *O. tantillus*.

Wollastoniella rotunda Yasunaga et Miyamoto, belonging to a small genus ***Wollastoniella*** Reuter (Orinae), is an effective predator of *T. palmi*. The species was first described from Thailand (Yasunaga and Miyamoto, 1993). According to laboratory and field studies, *W. rotunda* has no diapause (Shima, 1997, cited after Nakashima et al., 2004), while the lower temperature threshold of development of its preimaginal stages is lower than the mean daily temperatures maintained in greenhouses in winter. This means that the predator can be efficiently used in protected groups during the winter months as well (Shima and Hirose, 2002). Observations carried out on a *W. rotunda* population (originally from Thailand) kept in greenhouses in the south of Japan (33.6°N, 130.4°E) showed that within the period from October till March one genera-
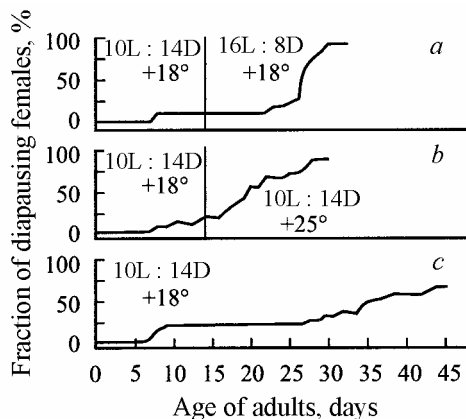
Fig. 15. Diapause termination in *Orius insidiosus* females from Georgia (US; about 31.5°N, 83.5°W) (after Van den Meiracker, 1994). The diapause was induced at the photoperiod 10L : 14D and +18°. The curves show the cumulative fraction of ovipositing females (%) at daylength increasing to 16L : 8D on the 14th day after the final molt (*a*); at temperature rising to +25°C on the 14th day after the final molt (*b*); and under the initial conditions preserved (*c*).
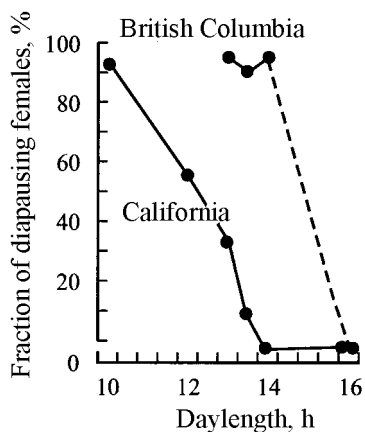

Fig. 16. Photoperiodic diapause induction in females of two populations of *Orius tristicolor* from California (Davis; 38.5°N, 121.8°W) and British Columbia (Agassiz, Canada; 49.2°N, 121.8°W), at a daily thermorhythm +25°C (day): +15°C (night) (after Gillespie and Quiring, 1993).

tion was successfully completed and the larvae of the second generation appeared. The predator proved to be very efficient against the thrips (Nakashima et al., 2004).

Representatives of other anthocorid genera have been less extensively studied, even though some of their species may have unusual seasonal cycles.

The Eurasian species ***Temnostethus gracilis*** Horváth and ***T. pusillus*** (Herrich-Schaeffer) from the genus ***Temnostethus*** Fieber (Anthocorinae) were previously thought to overwinter at the adult stage. However, dissection of females collected in France and the

Netherlands in July–August showed that each of the 14 ovarioles examined contained only one egg and not several eggs, which is characteristic of reproductively active females of Anthocoridae. Even though the eggs had already passed the first stages of embryogenesis, oviposition did not start in autumn at any combination of temperature and daylength (Cobben, 1968). It was assumed that *T. gracilis* had two simultaneous winter diapauses: 1) reproductive diapause of the females which do not lay mature eggs, and 2) embryonic diapause of the eggs in the ovarioles. Oogenesis may be resumed in spring, and the females may lay some non-diapausing eggs in addition to the overwintered ones. A somewhat different situation was observed in *T. pusillus*: the females collected in September contained many mature eggs in their ovarioles; these eggs were laid in autumn and entered diapause (Cobben, 1968; pp. 295–296). Special studies are needed to characterize the seasonal cycles of these species.

Representatives of the genus ***Tetraphleps*** Fieber (Anthocorinae) feed on aphids and adelgid plantlice (Homoptera). ***Tetraphleps latipennis*** Van Duzee in British Columbia (Canada) appears to have two generations and overwinter at the adult stage (Anderson, 1962a). ***Tetraphleps raoi*** Ghauri in India is multivoltine, and also seems to overwinter at the adult stage (Chacko, 1973). However, ***Tetraphleps abdulghanii*** Ghauri in Pakistan develops as a univoltine form and overwinters at the egg stage. Active development of this species proceeds from early spring to mid-May. Under laboratory conditions at room temperature (+14.5–28.0°), its larvae hatched only after 307–310 days of incubation; the long summer-winter diapause could not be artificially terminated (Krishnaswamy and Yaseen, 1972). ***Tetraphleps galchanoides*** Ghauri, distributed in China and India, probably overwinters at the larval stage, its adults appearing only in late winter or in spring. The larvae of this species successfully fed and developed in the laboratory even at such low temperatures as +5 and +8° (McAvoy et al., 2007).

Representatives of the genus ***Lyctocoris*** Hahn (Lyctocorinae) are primarily distributed in the Northern Hemisphere (Chu, 1969; Lattin, 2000). They mostly occur under the tree bark and feed on small arthropods. ***Lyctocoris campestris*** (F.) was inadvertently introduced from Europe into other continents, where it adapted itself to living in grain and food storage facilities, agricultural and dwelling buildings, and nests of birds and mammals. Under natural conditions

in England the species probably has two generations. Adults of the second generation appear in August–September (Southwood and Leston, 1959) and overwinter under the tree bark, together with the V instar larvae (Anderson, 1962a). The reported light-trapping data were insufficient for a complete reconstruction of the seasonal cycle of this species (Parajulee and Phillips, 1995). In granaries and other habitats with more or less constant temperatures, *L. campestris* is likely to be homodynamic, having no distinct seasonal dormancy. Development may take place at rather high temperatures, at least up to +30° (Parajulee and Phillips, 1992).

Seasonal development of **Lyctocoris beneficus** (Hiura) was studied in detail in a population from Saga (Japan; 33.3°N, 130.0°E). This species feeds on many small arthropods and is regarded as a potential control agent of the rice stem borer *Chilo suppressalis* (Walker) (Chu, 1969). *L. beneficus* occurs on herbaceous vegetation, in stacks of straw, piles of timber, and harvested cultivars. It is essential that the temperature in many of these habitats considerably exceeds that of the environment and may reach +70–80°. Field observations and simple experiments showed that *L. beneficus* in southwestern Japan developed in three generations and overwintered at the adult stage (Fig. 19*a*). The adults appeared on the haystack surface in early May, and the females examined since mid-May contained mature eggs (Chu, 1969). The reproductively active females were found even in November; during this period the bugs concentrated in the center of the haystack, where the temperature was much higher than on its surface. In synanthropic habitats, where the temperature is high enough even in winter, this species may have no distinct dormancy period.

Representatives of the genus **Xylocoris** Dufour (Lyctocorinae) are broadly distributed, especially in the Northern Hemisphere (Lattin, 2000). They occur under the tree bark and in the radical zone of plants and feed on small arthropods, especially lepidopteran and coleopteran larvae. Some species have two wing morphs: brachypterous and macropterous (Sands, 1957; Lattin, 2000). The most widespread and the best studied species is **Xylocoris flavipes** (Reuter), which is regarded as a promising agent of biological control of stored food pests (Hodgson and Aveling, 1988). Its natural distribution range appears to be limited to the warm climatic zone; now, however, this species inhabits granaries over practically the entire temperate and
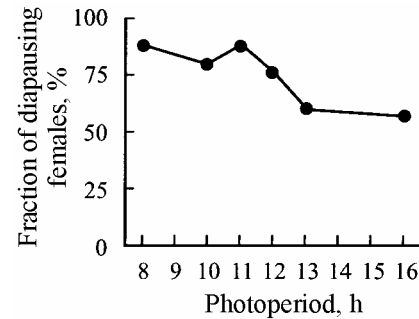

Fig. 17. Photoperiodic diapause induction in *Orius tristicolor* females from California (38.5°N, 121.8°W) at +18°C (after van den Meiracker, 1994).

tropical zones (Péricart, 1972, 1996; Lattin, 2000). Although *X. flavipes* can develop at high temperatures (up to +35°), the optimum values are +29–31° (Arbogast, 1975; Abdel-Rahman et al., 1977; Russo et al., 2004). Exactly these temperatures are usually observed in granaries during the summer season. The seasonal development and the factors controlling it in nature are unknown, and in the granaries the species appears to be homodynamic.

Xylocoris galactinus (Fieber) has an almost ubiquitous distribution, most probably the result of food transportation (Chu, 1969; Lattin, 2000). Under natural conditions, these bugs occur on or under the bark of oaks and beeches, in swamped areas, manure heaps, stacks of straw, and in synanthropic ecosystems such as stables and granaries (Hall, 1951; Chu, 1969). Many of the natural and synanthropic habitats of *X. galactinus* are characterized by high temperatures caused by fermentation or decomposition. *X. galactinus* can tolerate high temperatures up to +42° but is sensitive to humidity (Southwood and Leston, 1959). The diet comprises many small arthropods, including mites (Chu, 1969). The seasonal development of *X. galactinus* was studied in detail in Saga (Japan, 33.3°N, 130.0°E). It should be noted, however, that, according to I.M. Kerzhner and E.S. Elov (1976), the bugs occurring in Japan and studied by Y. Chu (1969) actually belong to the species **Xylocoris hiurai** Kerzhner et Elov. Field observations and experiments carried out in southwestern Japan showed this species to have up to 5 generations per year and to overwinter at the adult stage (Fig. 19*b*). The adults appeared on the surface of haystacks in late April, the females already containing mature eggs (Chu, 1969). The reproductively active females were found even in November; the bugs then concentrated in the center of the haystack, where the temperature was much higher than
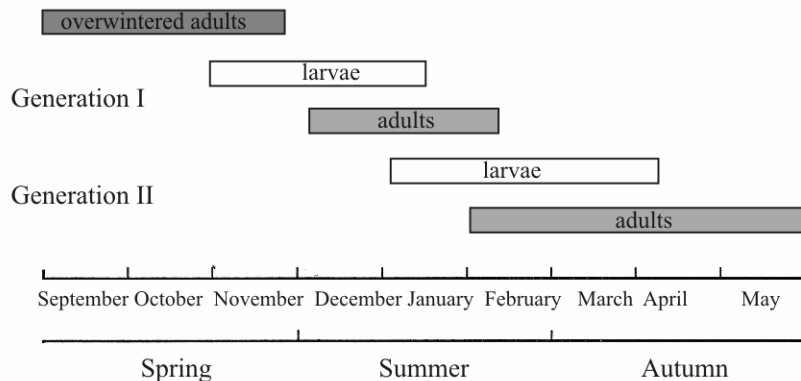
Fig. 18. The seasonal cycle of *Orius vicinus* in Otago (New Zealand; 45.5°S, 169.0°W) (after Wearing and Attfield, 2002).
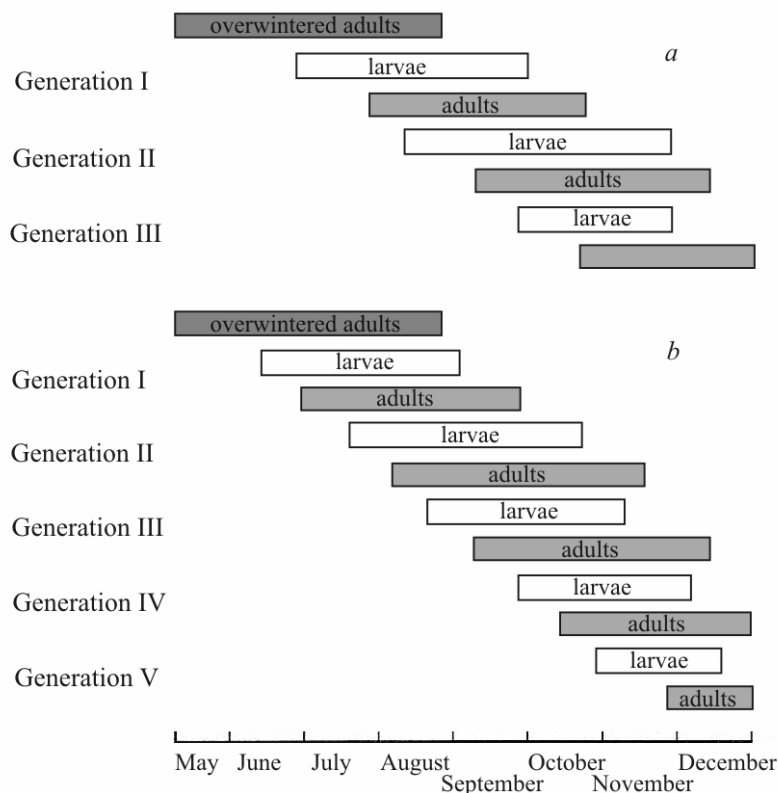

Fig. 19. The seasonal cycles of *Lyctocoris beneficus* (*a*) and *Xylocoris galactinus* (= *X. hiurai*) (*b*) in Saga (Japan; 33.3°N, 130.0°E) (after Chu, 1969).

on its surface. In synanthropic habitats with constant high temperatures, this species (like *L. beneficus*) may have no distinct dormancy period.

Xylocoris sordidus (Reuter) is distributed in the Western Hemisphere, and also inhabits agricultural storage facilities. Although the biology and ecology of the species are poorly studied, the bugs are known to prefer places with high humidity. Their lower development threshold lies between +15 and +20°, and the upper one, between +35 and +40° (Arbogast et al., 1983), which is higher than in the most heteropteran species studied in this respect.

All the larval instars and the adults of **Xylocoris cursitans** (Fallen) were found in early spring under the bark of decomposing trees in England. In view of these findings, it was assumed that this species had no distinct seasonal cycle but developed homodynamically, depending only on the temperature (Sands, 1957).

The larvae and adults of the obligatory myrmecophilous species **Xylocoris formicetorum** (Boheman) were found in the nests of the ant *Formica* sp. in Bulgaria from April to November (Simov, 2002), which may also indicate homodynamic development.

CONCLUSION

The above review demonstrates that anthocorid bugs living in the temperate climate typically overwinter at the adult stage in the state of reproductive diapause. Even though this feature is characteristic of heteropterans as a whole (from 68.5 to 92.6% species of bugs overwinter as adults; see Hertzel, 1982; Ruberson et al., 1998; Saulich and Musolin, 2007a), the fraction of species with adult diapause is much higher among Anthocoridae, primarily due to the subfamily Anthocorinae. Unusual exceptions are the embryonic diapause in *Tetrapleps abdulghanii*, *Temnostethus pusillus*, and *Temnostethus gracilis* (Anthocorinae) and homodynamic development in *Lyctocoris campestris* and several species of the genus *Xylocoris* (Lyctocorinae). Wintering at the adult stage provides the best opportunities for finding wintering places (usually sheltered microstations under the tree bark and in the radical zone of plants). A characteristic feature of anthocorid bugs (mostly the genera *Anthocoris* and *Orius*), rarely observed in heteropterans as a whole, is copulation in autumn, after which the fertilized females overwinter, whereas the males of many species in the temperate climate cannot survive winter. The vast majority of anthocorid bugs in the temperate climate are characterized by a multivoltine seasonal cycle, which in some species may comprise up to 8 generations per year. The number of generations decreases gradually towards the north, usually to a single generation per year. All the species studied in sufficient detail were shown to have a photoperiodically controlled adult diapause. The long-day PPR of diapause induction is more pronounced in the northern populations than in the southern ones; the southern populations may have almost no response to daylength and a very weak trend towards diapause induction. Termination of adult diapause has been studied less extensively and in a small number of species. The available data indicate that cold reactivation is required to terminate the diapause. Alary polymorphism is rarely found in the family. Not a single anthocorid species revealed seasonal alary polymorphism or polymorphism regulated by external ecological factors, which typically occurs in many other heteropteran taxa. Pronounced seasonal migrations and aggregation behavior also seem to be absent in Anthocoridae, although some species may form small groups before wintering. Summer diapause has not been observed in the family, except for the prolonged summer-winter embryonic diapause in *Tetrapleps abdulghanii*

(Anthocorinae; Krishnaswamy and Yaseen, 1972). No cases of seasonal polymorphism with respect to coloration, have been described so far, except for an assumption that color variants of *Orius sauteri* adults (paler or darker elytra and legs) might be related to the temperature conditions (Yasunaga, 1997). The seasonal change of host plants, known, for example, in *Anthocoris nemorum* and *A. nemoralis*, is a feature unusual for heteropterans in general. The ecology and physiology of Anthocoridae have been very unevenly studied both on the taxonomic and the geographic scale, the tropical species being especially poorly known. Further studies of Anthocoridae, especially their seasonal development and its regulation, and development of methods of mass rearing and prolonged storage of the bugs, will undoubtedly optimize their large-scale application in modern agriculture and forestry.

REFERENCES

1. Abdel-Rahman, H.A., Shaumar, N.F., Soliman, Z.A., and El-Agoze, M.M., "Biological Studies on the Anthocorid Bug, *Xylocoris flavipes* (Reut.)," Bull. Soc. Entomol. d'Egypte, No. 61, 45–51 (1977).

2. Akramovskaya, E.G., "On the Biology of Some Predaceous Bugs of the Family Anthocoridae in the Ararat Depression, Armenia," Biol. Zh. Armenii **31** (9), 959–964 (1978).

3. Anderson, N.H., "Anthocoridae of the Pacific Northwest with Notes on Distribution, Life Histories, and Habits (Heteroptera)," Canad. Entomol. **94**, 1325–1334 (1962a).

4. Anderson, N.H., "Bionomics of Six Species of *Anthocoris* (Heteroptera: Anthocoridae) in England," Trans. R. Entomol. Soc. London **114** (3), 67–95 (1962b).

5. Anderson, N.H., "Growth and Fecundity of *Anthocoris* spp. Reared on Various Prey (Heteroptera: Anthocoridae)," Entomol. Exp. Appl. **5**, 40–52 (1962c).

6. Anderson, N.H., "Studies on Overwintering of *Anthocoris* (Hem., Anthocoridae)," Entomol. Mon. Mag. **98** (1), 13 (1962d).

7. Arbogast, R.T., "Population Growth of *Xylocoris flavipes*: Influence of Temperature and Humidity," En-

viron. Entomol. **4** (5), 825–831 (1975).

8. Arbogast, R.T., Flaherty, B.R., and Press, J.W., "Demography of the Predaceous Bug *Xylocoris sordidus* (Reuter), Amer. Midland Naturalist **109** (2), 398–405 (1983).

9. Argolo, V.M., Bueno, V.H.P., and Silveira, L.C.P., "Influência do fotoperíodo na reprodução e longevidade de *Orius insidiosus* (Say) (Heteroptera: Anthocoridae), Neotrop. Entomol. **31** (2), 257–261 (2002).

10. Asanova, R.B. and Iskakov, B.V., *Harmful and Beneficial Heteropterans of Kazakhstan* (Kainar, Alma-Ata, 1977) [in Russian].

11. Atakan, A., "Associations between *Frankliniella* spp. and *Orius niger* Populations in Cotton," Phytoparasitica **34** (3), 221–234 (2006).

12. Aukema, B. and Rieger, C., "Preface," in *Catalogue of the Heteroptera of the Palaearctic region. Vol. 2. Cimicomorpha*, Ed. by B. Aukema and C. Rieger (The Netherlands Entomological Society, Wageningen, 1996), p. 7.

13. Austreng, M.P. and Sømme, L., "Fauna of Predatory Bugs (Heteroptera, Miridae and Anthocoridae) in Norwegian Apple Orchards," Fauna Norv. Ser. B **27**, 3–8 (1980).

14. Bahşi, S.Ü. and Tunç, I., "Development, Survival and Reproduction of *Orius niger* (Hemiptera: Anthocoridae) under Different Photoperiod and Temperature Regimes," Biocontrol Sci. Tech. **18** (8), 767–778 (2008).

15. Baniameri, V., Soleiman-Nejadian, E., and Mohaghegh, J., "Life Table and Age-Dependent Reproduction of the Predatory Bug *Orius niger* Wolff (Heteroptera: Anthocoridae) at Three Constant Temperatures: a Demographic Analysis," Appl. Entomol. Zool. **40** (4), 545–550 (2005).

16. Barber, G.W., "*Orius insidiosus* (Say), an Important Natural Enemy of the Corn Ear Worm," U.S. Dep. Agric. Tech. Bull. **504**, 1–24 (1936).

17. Beck, S.D., *Insect Photoperiodism*, 2nd ed., (Acad. Press, N.Y., 1980).

18. Blum, B., Ehlers, R., Haukeland-Salinas, S., et al., "Biocontrol Agents: Safety and Regulatory Policy," BioControl **48**, 177–184 (2003).

19. Bogachev, A.V., "Predators and Parasites of the American Bollworm," Trudy Krymskogo Filiala Akad. Nauk SSSR **2**, 31–60 (1951).

20. Bonnemaison, L. and Missonnier, J., "Le psylle du Poirier (*Psylla pyri* L.). Morphologie et biologie. Méthodes de lutte," Ann. Epiphyt. **7** (2), 263–331 (1956).

21. Carayon, J. and Steffan, J.R., "Observations sur le régime alimentaire des *Orius* et particuliérement d'*Orius pallidicornis* (Reuter) (Heteroptera: Anthocoridae)," Cah. Nat. Bull. Nat. Parisiens (N.S.) **15**, 53–63 (1959).

22. Carnero, A., Pena, M.A., Perez-Padron, F., et al., "Bionomics of *Orius albidipennis* and *Orius limbatus*," IOBC Bull. Integrated Control in Glasshouses **16** (2), 27–30 (1993).

23. Carvalho, A.R., Bueno, V.H., Pedroso, E.C., et al., "Influence of Photoperiod on *Orius thyestes* Herring (Hemiptera: Anthocoridae) Reproduction and Longevity," Neotrop. Entomol. **35** (4), 489–492 (2006).

24. Chacko, J., "Observations on Some Natural Enemies of *Pineus* sp. (Hem.: Adelgidae) at Shillong (Meghalaya), India, with Special Reference to *Tetraphleps raoi* Ghauri (Hem.: Anthocoridae)," Commonwealth Inst. Biol. Contr. Tech. Bull., No. 16, 41–46 (1973).

25. Chelnokova, T.A., "Biology of the Predaceous Bug *Orius niger* (Wolff) of the Family Anthocoridae (Hemiptera–Heteroptera) in the Middle Volga Area," Nauch. Trudy Kuibyshevsk. Gos. Ped. Inst. **199**, 81–87 (1977).

26. Cho, J.R., Kim, J.H., Lee, M., and Kim, H.S., "Induction and Termination of the Reproductive Diapause in the Minute Pirate Bug *Orius strigicollis* Poppius (Hemiptera: Anthocoridae)," J. Asia-Pacific Entomol. **8** (2), 167–174 (2005).

27. Chu, Y., "On the Bionomics of *Lyctocoris beneficus* (Hiura) and *Xylocoris galactinus* (Fieber) (Anthocoridae, Heteroptera)," J. Fac. Agric. Kyushu Univ. **15** (1), 1–136 (1969).

28. Chyzik, R., Klein, M., and Ben-Dov, Y., "Overwintering Biology of the Predatory Bug *Orius albidipennis* (Hemiptera: Anthocoridae) in Israel," Biocontrol Sci. Tech. **5** (3), 287–296 (1995).

29. Cobben, R.H., "Biotaxonomische Einzelheiten über Niederlandische Wanzen (Hemiptera, Heteroptera)," Tijdschr. Entomol. **101**, 1–46 (1958).

30. Cobben, R.H., *Evolutionary Trends in Heteroptera. Part I. Eggs, Architecture of the Shell, Gross Embryology and Eclosion* (Centre for Agricultural Publishing and Documentation, Wageningen, 1968).

31. Collyer, E., "On the Ecology of *Anthocoris nemorum* (L.) (Hemiptera—Heteroptera), Proc. R. Entomol. Soc. London. Ser. A. Gen. Entomol. **42** (7–9), 107–118 (1967).

32. Elkassabany, N., Ruberson, J.R., and Kring, T.J., "Seasonal Distribution and Overwintering of *Orius insidiosus* (Say) in Arkansas," J. Entomol. Sci. **31** (1), 76–88 (1996).

33. Elov, E.S., "Biology of the Predaceous Bug *Orius niger*," Izv. Akad. Nauk Tadzh. SSR Biol. Nauki, No. 2, 37–44 (1976).

34. Furubayashi, Y., Kakimoto, K., and Noda, T., "Effect of Temperature on Reproductive Diapause of *Orius strigicollis* (Poppius) (Heteroptera: Anthocoridae), Kyushu Plant Prot. Res. **49**, 101–105 (2003) [in Japanese].

35. Gillespie, D.R. and Quiring, D.M.J., "Extending Seasonal Limits on Biological Control," IOBC/WPRS Bull. **16** (2), 43–45 (1993).

36. Glenister, C.S., "Predatory Heteropterans in Augmentative Biological Control: an Industry Perspective," in *Predatory Heteroptera: Their Ecology and Use in Biological Control*, ed. by M. Coll and J.R. Ruberson (En-

tomol. Soc. Amer., Lanham, 1998), pp. 199–208.

37. Hall, D.W., "Observations on the Distribution, Habits and Life History of the Bug *Piezostethus galactinus* (Fieb.) (Hem., Anthocoridae)," Entomol. Mon. Mag. **87**, 45–52 (1951).

38. Herard, F. and Cheng, K., "Ecology of *Anthocoris nemorum* (L.) (Het.: Anthocoridae) and Evaluation of Its Potential Effectiveness for Biological Control of Pear Psylla," Agronomie **5** (10), 855–863 (1985).

39. Herring, J.L., "The Genus *Orius* of the Western Hemisphere (Hemiptera: Anthocoridae)," Ann. Entomol. Soc. Amer. **59**, 1093–1109 (1966).

40. Hertzel, G., "Zur Phänologie und Fortpflanzungsbiologie einheimischer Pentatomiden-Arten (Heteroptera)," Entomol. Nachr. Ber. **26** (2), 69–72 (1982).

41. Hill, A.R., "The Biology of *Anthocoris nemorum* (L.) in Scotland (Hemiptera, Anthocoridae)," Trans. R. Entomol. Soc. London **109**, 379–394 (1957).

42. Hill, A.R., "The Biology of *Anthocoris sarothamni* Douglas and Scott in Scotland (Hemiptera: Anthocoridae)," Trans. R. Entomol. Soc. London **113** (3), 41–54 (1961).

43. Hill, A.R., "The Seasonal Distribution of *Anthocoris* spp. (Hem., Cimicidae) in a Deciduous Wood in West Central Scotland," Entomol. Mon. Mag. **113**, 139–146 (1977).

44. Hodek, I., "Termination of Adult Diapause in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae) in the Field," Entomol. Exp. Appl. **14** (2), 212–222 (1971).

45. Hodgson, C.J. and Aveling, C., "Anthocoridae," in *Aphids: Their Biology, Natural Enemies and Control. Vol. B*, Ed. by A.K. Minks and P. Harrewijn (Elsevier, Amsterdam, 1988), pp. 279–292.

46. Hodgson, C.J. and Mustafa, M.T., "Aspects of Chemical and Biological Control of *Psylla pyricola* Förster in England," SROP/WPRS Bull. **7** (5), 330–353 (1984).

47. Honek, A. and Hodek, I., "A Diapause of *Chrysopa carnea* (Chrysopidae, Neuroptera) Females in the Field," Věst. Čs. Spol. Zool. **37**, 95–100 (1973).

48. Horn, K.F., Farrier, M.H., and Wright, C.G., "Some Mortality Factors Affecting Eggs of the Sycamore Lace Bug, *Corythucha ciliata* (Say) (Hemiptera: Tingidae)", Ann. Entomol. Soc. Amer. **76**, 262–265 (1983).

49. Horton, D.R., Lewis, T.M., and Broers, D.A., "Ecological and Geographic Range Expansion of the Introduced Predator *Anthocoris nemoralis* (Heteroptera: Anthocoridae) in North America: Potential for Nontarget Effects?," Amer. Entomol. **50** (1), 18–30 (2004).

50. Horton, D.R., Lewis, T.M., Hinojosa, T., and Broers, D.A., "Photoperiod and Reproductive Diapause in the Predatory Bugs *Anthocoris tomentosus*, *A. antevolens*, and *Deraeocoris brevis* (Heteroptera: Anthocoridae, Miridae) with Information on Overwintering Sex Ratios," Ann. Entomol. Soc. Amer. **91** (1), 81–86 (1998).

51. Isenhour, D.J. and Marston, N.L., "Seasonal Cycles of *Orius insidiosus* (Hemiptera: Anthocoridae) in Missouri Soybeans," J. Kansas Entomol. Soc. **54** (1), 129–142 (1981).

52. Ito, K. and Nakata, T., "Diapause and Survival in Winter in Two Species of Predatory Bug, *Orius sauteri* and *O. minutus*," Entomol. Exp. Appl. **89**, 271–276 (1998a).

53. Ito, K. and Nakata, T., "Effect of Photoperiod on Reproductive Diapause in the Predatory Bugs, *Orius sauteri* (Poppius) and *O. minutus* (Linnaeus) (Heteroptera: Anthocoridae)", Appl. Entomol. Zool. **33** (1), 115–120 (1998b).

54. Ito, K. and Nakata, T., "Geographical Variation of Photoperiodic Response in the Females of a Predatory Bug, *Orius sauteri* (Poppius) (Heteroptera: Anthocoridae) from Northern Japan," Appl. Entomol. Zool. **35** (1), 101–105 (2000).

55. Izhevskii, S.S. and Akhatov, A.K., *Protection of Greenhouse Plants from Pests: Species Identification, Census Methods, Biology and Morphology, Harmfulness, and Control. A Reference Book* (KMK Scientific Press, Moscow, 1999) [in Russian].

56. Kakimoto, K., Hinomoto, N., and Noda, T., "Responses of Three *Orius* Species Collected in Kagoshima to Different Rearing Temperatures and Photoperiods," Japan. J. Appl. Entomol. Zool. **47**, 19–28 (2003).

57. Kerzhner, I.M. and Elov, E.S., "Bugs of the Genus *Xylocoris* Duf., Subgenus *Proxylocoris* Carayon (Heteroptera, Anthocoridae) in the Fauna of the USSR and Adjacent Countries," Entomol. Obozr. **55** (2), 364–368 (1976).

58. Kim, J.-H., Lee, G.-S., Kim, Y.-H., and Yoo, J.-K., "Species Composition of *Orius* spp. (Hemiptera: Anthocoridae) and Their Seasonal Occurrence on Several Plants in Korea," Korean J. Appl. Entomol. **40** (3), 211–217 (2001).

59. Kiman, Z.B. and Yeargan, K.V., "Development and Reproduction of the Predator *Orius insidiosus* (Hemiptera: Anthocoridae) Reared on Diets of Selected Plant Material and Arthropod Prey," Ann. Entomol. Soc. Amer. **78**, 464–467 (1985).

60. Kingsley, P.C. and Harrington, B.J., "Factors Influencing Termination of Reproductive Diapause in *Orius insidiosus* (Hemiptera: Anthocoridae)," Environ. Entomol. **11**, 461–462 (1982).

61. Kiranova, D.M., "Biology and Economic Significance of the Predatory Bug *Orius albidipennis* Reut.," Trudy Sredneaz. Gos. Univ. **53** (17), 149–164 (1954).

62. Kobayashi, T. and Osakabe, M., "Pre-Winter Copulation Enhances Overwintering Success of *Orius* Females (Heteroptera: Anthocoridae), Appl. Entomol. Zool. **44** (1), 47–52 (2009).

63. Kohno, K., "Photoperiodic Effect on Incidence of Reproductive Diapause in *Orius sauteri* and *O. minutus* (Heteroptera, Anthocoridae), Appl. Entomol. Zool. **32** (4), 644–648 (1997).

64. Kohno, K., "Thermal Effects on Reproductive Diapause Induction in *Orius sauteri* (Heteroptera: Anthocoridae),"

Appl. Entomol. Zool. **33** (4), 487–490 (1998).

65. Korinek, V.V., "Fauna of True Bugs—Hemiptera-Heteroptera of the Khoper State Reserve," Trudy Khoper. Gos. Zapov., No. 1, 174–218 (1940).

66. Koštál, V., "Ecophysiological Phases of Insect Diapause," J. Insect Physiol. **52**, 113–127 (2006).

67. Krishnaswamy, S. and Yaseen, M.I., "Hemiptera: Anthocoridae," in *Studies on Predators of Adelges spp. in the Himalayas* ed. by V. P. Rao and M. A. Ghani (Misc. Publ. Commonw. Inst. Biol. Control, 1972), No. 3, pp. 4–14.

68. Lattin, J.D., "Bionomics of the Anthocoridae," Ann. Rev. Entomol. **44**, 207–231 (1999).

69. Lattin, J.D., "Minute Pirate Bugs (Anthocoridae)," in *Heteroptera of Economic Importance*, ed. by C.W. Schaefer and A.R. Panizzi (CRC Press, Boca Raton, 2000), pp. 607–637.

70. Lattin, J.D., Asquith, A., and Booth, S., "*Orius minutus* (Linnaeus) in North America (Hemiptera: Heteroptera: Anthocoridae)," J. New York Entomol. Soc. **97**, 409–416 (1989).

71. Lukouressis, D.P. and Perdikis, D.C., "The Phenology and Abundance of Certain Species of *Orius* (Hemiptera: Anthocoridae) that Occur in Greece," Israel J. Entomol. **31**, 47–54 (1997).

72. McAvoy, T.J., Zilahi-Balogh, G.M.G., Salom, S.M., et al., "Development and Feeding of *Tetraphleps galchanoides*, a Predator of the Hemlock Woolly Adelgid," Biol. Control **52**, 339–350 (2007).

73. Musolin, D.L. and Ito, K., "Photoperiodic and Temperature Control of Nymphal Development and Induction of Reproductive Diapause in Two Predatory *Orius* Bugs: Interspecific and Geographic Differences," Physiol. Entomol. **33** (4), 291–301 (2008).

74. Musolin, D.L. and Saulich, A.Kh., "Photoperiodic Control of Seasonal Development in Bugs (Heteroptera)," Entomol. Obozr. **75** (3), 489–506 (1996) [Entomol. Review **76** (7), 849–864 (1996)].

75. Musolin, D.L., Tsytsulina, K., and Ito, K., "Photoperiodic and Temperature Control of Reproductive Diapause Induction in the Predatory Bug *Orius strigicollis* (Heteroptera: Anthocoridae) and Its Implications for Biological Control," Biol. Control **31**, 91–98 (2004).

76. Nagai, K., "Integrated Control of *Thrips palmi* Karny on Eggplants in Open Field with *Orius sauteri* (Poppius)," IOBC Bull. **16** (2), 117–120 (1993).

77. Nakashima, Y. and Hirose, Y., "Winter Reproduction and Photoperiodic Effects on Diapause Induction of *Orius tantillus* (Motschulsky) (Heteroptera: Anthocoridae), a Predator of *Thrips palmi*," Appl. Entomol. Zool. **32** (2), 403–405 (1997).

78. Nakashima, Y., Uefune, M., Tagashira, E., et al., "Cage Evaluation of Augmentative Biological Control of *Thrips palmi* with *Wollastoniella rotunda* in Winter Greenhouses," Entomol. Exp. Appl. **110**, 73–77

(2004).

79. Niemczyk, E., "*Orius minutus* (L.) (Heteroptera, Anthocoridae): the Occurrence in Apple Orchards, Biology and Effect of Different Food on the Development," Bull. Entomol. Pologne **48**, 203–209 (1978).

80. Parajulee, M.N. and Phillips, T.W., "Laboratory Rearing and Field Observations of *Lyctocoris campestris* (Heteroptera: Anthocoridae), a Predator of Stored-Product Insects," Anna. Entomol. Soc. Amer. **85** (6), 736–743 (1992).

81. Parajulee, M.N. and Phillips, T.W., "Seasonal Abundance and Spatial Patterns of the Predator *Lyctocoris campestris* in Stored Corn," Entomol. Exp. Appl. **75** (1), 33–42 (1995).

82. Parker, N.J.B., "An Investigation of Reproductive Diapause in Two British Populations of *Anthocoris nemorum* (Hemiptera: Anthocoridae)," J. Entomol. A **49** (2), 173–178 (1975).

83. Parker, N.J.B., "A Method for Mass Rearing the Aphid Predator *Anthocoris nemorum*," Ann. Appl. Biol. **99**, 217–223 (1981).

84. Parker, N.J.B., "Biology and Bionomics in Scotland of *Anthocoris gallarum-ulmi*," Ecol. Entomol. **9**, 55–67 (1984).

85. Parshley, H.M., "On Some Hemiptera from Western Canada," Univ. Michigan Occas. Papers Mus. Zool. **71**, 1–355 (1919).

86. Péricart, J., "Hémiptéres, Anthocoridae, Cimicidae et Microphysidae de l'Ouest Paléarctique," in *Faune de l'Europe et du Basin Méditerranéen, No. 7* (Paris, 1972).

87. Péricart, J., "Family Anthocoridae Fieber, 1836—Flower Bugs, Minute Pirate Bugs," in *Catalogue of the Heteroptera of the Palaearctic Region. Vol. 2. Cimicomorpha* ed. by B. Aukema and C. Rieger (The Netherlands Entomological Society, Wageningen, 1996), pp. 108–140.

88. Ramakers, P.M.J., "Possibilities for Biological Control of *Thrips tabaci* Lind. (Thysanoptera: Thripidae) in Glasshouse," Med. Fac. Landbouw. Rijksuniv. Gent **43**, 463–469 (1978).

89. Ruberson, J.R., Bush, L., and Kring, T.J., "Photoperiodic Effect on Diapause Induction and Development in the Predator *Orius insidiosus* (Heteroptera: Anthocoridae)," Environ. Entomol. **20**, 786–789 (1991).

90. Ruberson, J.R., Kring, T.J., and Elkassabany, N., "Overwintering and the Diapause Syndrome of Predatory Heteroptera," in *Predatory Heteroptera: Their Ecology and Use in Biological Control*, ed. by M. Coll and J.R. Ruberson (Entomol. Soc. Amer., Lanham, 1998), pp. 49–69.

91. Ruberson, J.R., Shen, Y.J., and Kring, T.J., "Photoperiodic Sensitivity and Diapause in the Predator *Orius insidiosus* (Heteroptera: Anthocoridae)," Ann. Entomol. Soc. Amer. **93** (5), 1123–1130 (2000).

92. Russo, A., Cocuzza, G.E., and Vasta, M.C., "Life Tables of *Xylocoris flavipes* (Hemiptera: Anthocoridae) Feeding on *Tribolium castaneum* (Coleoptera: Tenebrionidae)," J. Stored Products Res. **40** (1), 103–112 (2004).

93. Ruth, J. and Dwumfour, E.F., "Laboruntersuchungen zur Eignung einiger Blattlausarten als Beute der räuberischen Blumenwanze *Anthocoris gallarum-ulmi* (DeG.) (Het., Anthocoridae)," J. Appl. Entomol. **108** (4), 321–327 (1989).

94. Sands, W.A., "The Immature Stages of Some British Anthocoridae (Hemiptera)," Trans. R. Entomol. Soc. London **109** (10), 295–310 (1957).

95. Saprykin, A.A., "The Use of Predaceous Anthocorid Bugs in Biological Plant Protection," in *Phytosanitary Support of Steady Development of Agroecosystems: Proc. Int. Conf.* (Orel, 2008), pp. 286–288.

96. Saulich, A.Kh. and Musolin, D.L., "Times of Year. The Diversity of Seasonal Adaptations and Ecological Mechanisms Controlling Seasonal Development of Heteroptera in Temperate Climate," Trudy Biol. Nauchno-Issled. Inst. SPbGU **53**, 25–106 (2007a).

97. Saulich, A.Kh. and Musolin, D.L., *Seasonal Development of Aquatic and Semiaquatic Bugs (Heteroptera)* (St. Petersburg Univ., 2007b) [in Russian].

98. Saulich, A.Kh. and Volkovich, T.A., *Ecology of Insect Photoperiodism* (St. Petersburg Univ., 2004) [in Russian].

99. Schuh, R.T. and Slater, J.A., *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History* (Cornell Univ. Press, Ithaca, 1995).

100. Shima, K., *An Ecological Study on the Predator, Wollastoniella rotunda (Heteroptera: Anthocoridae) with Special Reference to Its Effectiveness as a Possible Control Agent of Thrips palmi (Thysanoptera: Thripidae) in Glasshouse in Japan during the Winter*, MSc Thesis, Kyushu University, 1997.

101. Shima, K. and Hirose, Y., "Effect of Temperature on Development and Survival of *Wollastoniella rotunda* (Heteroptera: Anthocoridae), a Predator of *Thrips palmi* (Thysanoptera: Thripidae), Appl. Entomol. Zool. **37**, 405–408 (2002).

102. Shimizu, T. and Kawasaki, K., "Geographic Variability in Diapause Response of Japanese *Orius* Species," Entomol. Exp. Appl. **98**, 303–316 (2001).

103. Shimizu, T., Kawasaki, K., and Hinomoto, N., "Factors Limiting the Northern Distribution in *Orius strigicollis* (Poppius) (Heteroptera: Anthocoridae)," Jap. J. Entomol. **4** (4), 129–141 (2001).

104. Silveira, L.C.P. and Bueno, V.H.P., "*Orius insidiosus* (Say) (Heteroptera: Anthocoridae): sensibilidade ao fotoperiodo e diapausa reprodutiva?," Revista Brasiliera Entomol. **47** (4), 631–635 (2003).

105. Simberloff, D. and Stiling, P., "How Risky is Biological Control?," Ecology **77** (7), 1965–1974 (1996).

106. Simov, N., "Distribution of *Xylocoris formicetorum* (Boheman, 1844) (Heteroptera: Anthocoridae) in Bulgaria," Acta Zool. Bulg. **54** (2), 55–58 (2002).

107. Song, J.-H., Kang, S.-H., Lee, K.-S., and Han, W.-T., "Effect of Minute Pirate Bug, *Orius strigicollis* (Hemiptera: Anthocoridae) on Control of Thrips on Hot Pepper in Greenhouse," Korean J. Appl. Entomol. **40** (3), 253–258 (2001).

108. Southwood, T.R.E. and Leston, D., *Land and Water Bugs of the British Isles* (Frederick Warne and Co., London, 1959).

109. Southwood, T.R.E. and Scudder, G.G.E., "Larvae and Biology of *Anthocoris* and Other Nettle Bugs," Entomol. Mon. Mag. **92**, 313–325 (1956).

110. Štys, P. and Davidová-Vilimová, J., "Unusual Numbers of Instars in Heteroptera: a Review," Acta Entomol. Bohemoslav. **86**, 1–32 (1989).

111. Thontadarya, T.S. and Rao, K.J., "Biology of *Orius maxidentex* Ghauri (Hemiptera: Anthocoridae), a Predator of the Sorghum Earhead Midge, *Contarinia sorghicola* (Coquillet)," Mysore J. Agric. Sci. **21** (1), 27–31 (1987).

112. Tonks, N.V., "Annotated List of Insects and Mites Collected on Brambles in the Lower Frazer Valley, British Columbia," Proc. Entomol. Soc. British Columbia **49**, 27–28 (1953).

113. van de Veire, V. and Degheele, D., "Biological Control of the Western Flower Thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), in Glasshouse Sweet Peppers with *Orius* spp. (Hemiptera: Anthocoridae). A Comparative Study between *O. niger* (Wolff) and *O. insidiosus* (Say)," Biocontrol Sci. Tech. **2**, 281–283 (1992).

114. van den Meiracker, R.A.F., "Induction and Termination of Diapause in *Orius* Predatory Bugs," Entomol. Exp. Appl. **73**, 127–137 (1994).

115. van Lenteren, J.C., "Benefits and Risks of Introducing Exotic Macrobiological Control Agents in Europe," Bulletin OEPP / EPPO Bulletin **27**, 15–27 (1997).

116. van Lenteren, J.C., Babendreier, D., Bigler, F., et al., "Environmental Risk Assessment of Exotic Natural Enemies Used in Inundative Biological Control," Biol. Control **48**, 3–38 (2003).

117. van Lenteren, J.C., Bale, J., Bigler, F., et al., "Assessing Risks of Releasing Exotic Biological Control Agents of Arthropod Pests," Ann. Rev. Entomol. **51**, 609–634 (2006).

118. van Lenteren, J.C., Roskam, M.M., and Timmer, R., "Commercial Mass Production and Pricing of Organisms for Biological Control of Pests in Europe," Biol. Control **10**, 143–149 (1997).

119. von Lauenstein, G., "Untersuchungen zu Fruchtbarkeit und Eiablage der räuberischen Blumenwanze *Anthocoris nemorum* L. (Hem.: Heteroptera)," Z. Angew. Entomol. **83**, 355–363 (1977).

120. Wagner, E., "Die Europäischen Arten der Gattung *Orius* Wolff (Hem. Het. Anthocoridae)," Notulae En-

tomol. **32**, 22–59 (1952).

121. Wang, C.-L., Lee, P.-C., and Wu, Y.-J., "Field Augmentation of *Orius strigicollis* (Heteroptera: Anthocoridae) for the Control of Thrips in Taiwan," in *Food and Fertilizer Technology Center, Taipei, ROC, Exten. Bull. Vol. 500* (2001), pp. 1–9.

122. Wearing, C.H. and Attfield, B., "Phenology of the Predatory Bugs *Orius vicinus* (Heteroptera: Anthocoridae) and *Sejanus albisignata* (Heteroptera: Miridae) in Otago, New Zealand, Apple Orchards," Biocontrol Sci. Tech. **12** (4), 481–492 (2002).

123. Yano, E., "Biology of *Orius sauteri* (Poppius) and Its Potential as a Biocontrol Agent for *Thrips palmi* Karny," IOBC/WPRS Bull. **19**, 203–206 (1996).

124. Yano, E., "Recent Development of Biological Control and IPM in Greenhouses in Japan," J. Asia-Pacific Entomol. **7**, 5–11 (2004).

125. Yasunaga, T., "A Taxonomic Study of the Subgenus *Heterorius* Wagner of the Genus *Orius* Wolff from Japan (Heteroptera, Anthocoridae)," Jpn. J. Entomol. **61** (1), 11–22 (1993).

126. Yasunaga, T., "The Flower Bug Genus *Orius* Wolff (Heteroptera: Anthocoridae) from Japan and Taiwan. Part II," Appl. Entomol. Zool. **32**, 379–386 (1997).

127. Yasunaga, T. and Miyamoto, S., "Three Anthocorid Species (Heteroptera: Anthocoridae), Predators of *Thrips palmi* (Thysanoptera) in Eggplant Gardens of Thailand," Appl. Entomol. Zool. **28**, 227–232 (1993).