

Global Change Biology



- Thematic Issue: “Impacts of Environmental Change on Insect Management and Conservation”
- Global change and invasive species risk assessments
- How does elevated CO₂ affect plant-herbivore interactions?
- A biological consequence of reducing Arctic ice cover



Global Change Biology

ISSN 1354-1013 (Print)
ISSN 1365-2486 (online)

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	Europe	The Americas	Rest of World
Premium*	£1869	\$3454	£2056

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Publisher. *Global Change Biology* is published by Blackwell Publishing Ltd, 9600 Garsington Road, Oxford, OX4 2DQ, UK. Tel: + 44 (0) 1865 776 868, Fax: + 44 (0) 1865 714 591

Production Editor: gcb@oxon.blackwellpublishing.com.

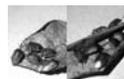
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Cover: Northward range expansion of the southern green stink bug, *Nezara viridula*, is stimulated by the climate warming. The image shows two forms of the species: green (reproductive) and russet (in winter diapause). Recent research demonstrated a vital importance of timing of diapause induction for winter survival and establishment at the edge of the range (see Musolin, Volume 13 Issue 8 pp. 1565-1585).



Thematic Issue "Impacts of Environmental Change on Insect Management and Conservation" (Organizers: Hefin Jones, Richard Harrington and Gregory Masters) a symposium of XXII International Congress of Entomology (see pp. 1823-1872 and the journal website).

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REVIEW

Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change

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Abstract

Focusing on the southern green stink bug, *Nezara viridula* (Pentatomidae), in central Japan the effects of climate change on true bugs (Insecta: Heteroptera) are reviewed. In the early 1960s, the northern edge of the species's distribution was in Wakayama Prefecture (34.1°N) and distribution was limited by the +5 °C coldest month (January) mean temperature isothermal line. By 2000, *N. viridula* was recorded 70 km further north (in Osaka, 34.7°N). Historical climate data were used to reveal possible causes of the northward range expansion. The increase of mean and lowest winter month temperatures by 1–2 °C in Osaka from the 1950s to the 1990s improved potential overwintering conditions for *N. viridula*. This promoted northward range expansion of the species. In Osaka, adult diapause in *N. viridula* is induced after mid-September, much later than in other local seed-feeding heteropterans. This late diapause induction results in late-season ineffective reproduction: some females start oviposition in autumn when the progeny have no chance of attaining adulthood and surviving winter. Both reproductive adults and the progeny die. A period from mid-September to early November represents a phenological mismatch: diapause is not yet induced in all adults, but it is already too late to start reproduction. Females that do not start reproduction but enter diapause in September have reduced postdiapause reproductive performance: they live for a shorter period, have a shorter period of oviposition and produce fewer eggs in smaller egg masses compared with females that emerge and enter diapause later in autumn. To some extent, *N. viridula* remains maladapted to Osaka environmental conditions. Ecological perspectives on establishment in recently colonized areas are discussed. A review of available data suggests that terrestrial and aquatic Heteroptera species respond to climate change by shifting their distribution ranges, changing abundance, phenology, voltinism, physiology, behaviour, and community structure. Expected responses of Heteroptera to further climate warming are discussed under scenarios of slight (<2 °C) and substantial (>2 °C) temperature increase.

Keywords: climate warming, diapause, dormancy, Hemiptera, life-history traits, *Nezara viridula* (Pentatomidae), overwintering, photoperiodic response, range expansion, seasonal adaptations

Received 22 October 2004; revised version received 25 August 2005 and accepted 27 September 2005

When our grandchildren write the history of global warming – how we discovered and debated it, and what we finally did about it – the stinkbugs . . . may not loom large . . . But our descendants may well decide that it was the long string of such close-to-home observations – the early springs, the shifting ranges of plants and animals, the mortal heat waves – that, more than any climatological data, convinced people that something needed to be done about global warming.

R. Kunzig (2005)

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Introduction

Since the early 20th century global surface temperature has increased by approximately 0.74 °C. The 1990s were

the warmest decade on record and 11 of the last 12 years (1995–2006) rank among the 12 warmest years in the instrumental record of global surface temperature started in 1850 (Houghton *et al.*, 2001; IPCC, 2007). Different scenarios of further climate warming provide best estimates of temperature increase of 1.8–4.0 °C by 2100 with likely ranges of 1.1–6.4 °C (IPCC, 2007). Observed and predicted climate change (mostly in air temperature, precipitation and atmosphere composition) is likely to have both direct and indirect effects on the physiology, ecology and adaptations of insects, as well as other biota (Hughes, 2000; Walther *et al.*, 2001; McLaughlin *et al.*, 2002; Schneider & Root, 2002; Parmesan & Yohe, 2003; Lawrence & Soame, 2004; Møller *et al.*, 2004; Hickling *et al.*, 2006).

Since 1990 many studies have focused on how insects respond to climate changes (e.g. Cammell & Knight, 1992; Harrington & Stork, 1995; Butterfield & Coulson, 1997; Bale *et al.*, 2002; Chown & Terblanche, 2006) and much has been learned about specific insect taxa (e.g. Harrington *et al.*, 1995; Parmesan *et al.*, 1999; Hill *et al.*, 2001; Ott, 2001; Reemer *et al.*, 2003; Hickling *et al.*, 2005). The responses of species from large taxon such as the Heteroptera (with some 37 000 described species worldwide; Schaefer & Panizzi, 2000), however, remain mostly unexplored and poorly understood.

Shifts in distribution ranges are the most often reported responses to climate change (Parmesan, 2001). But how much 'warm' is welcome in a world with a warmer climate? How difficult is it to adapt to new environmental conditions? Is increased temperature a sufficient condition to establish in a new location? Can successful colonization be predicted?

In an attempt to answer some of these questions, in this paper I review the results of a wide-scale ecological study of the southern green stink bug, *Nezara viridula* (L.) (Pentatomidae), conducted in central Japan in the 1960s before considering data from recent studies in a more northern area only recently occupied by *N. viridula*. After discussing possible ecological causes and consequences of range expansion in this species, I then review other reported cases of heteropteran responses to climate change and attempt to generalize what may be predicted to happen as climate continues to warm.

N. viridula in Japan

The 1960s: N. viridula vs. N. antennata

Two species of *Nezara* occur in Japan. The oriental green stink bug, *Nezara antennata* Scott, known to occur only in Asia (Hokkanen, 1986), is widely distributed in Japan, where its range covers Okinawa, Kyushu,

Shikoku, Honshu and Hokkaido Islands (Tomokuni *et al.*, 1993). The southern green stink bug, *N. viridula*, occurs in an ever-widening range throughout tropical and subtropical regions of Eurasia, Africa, Australia and the Americas (Yukawa & Kiritani, 1965; Todd, 1989; McPherson & McPherson, 2000; Panizzi *et al.*, 2000). Japan is at the northern margin of *N. viridula*'s Asian range. The species has long been distributed in the southern part of the archipelago (Okinawa, Kyushu, Shikoku and southern Honshu), mostly along the coastal belts (Oho & Kiritani, 1960; Yukawa & Kiritani, 1965; Tomokuni *et al.*, 1993). *N. viridula* is a major agricultural pest damaging soybean, rice, cotton and many other crops (Todd, 1989; Panizzi *et al.*, 2000). Within their respective ranges the two *Nezara* species occupy basically the same ecological niche and both species have been recorded sympatrically in mixed populations with inter-specific mating in the areas of overlapping distribution (Kiritani *et al.*, 1963; Kiritani, 1971; Yukawa *et al.*, 2007).

In the early 1960s, Kiritani and co-workers conducted a wide-scale field survey in central Honshu where both *Nezara* species occurred (Kiritani *et al.*, 1963; Kiritani & Hokyō, 1970). The northern limit of *N. viridula*'s distribution in central Japan occurred in Wakayama Prefecture (latitude approximately 34.1°N). *N. antennata* dominated in northern and central parts of the prefecture, whereas coastal and the southern parts of the prefecture were mostly or completely occupied by *N. viridula* (Fig. 1). The area of co-existence lay on the +5 °C isothermal line for mean temperature of the coldest month (usually January). *N. viridula* was found to occur sympatrically in warmer parts of the distribution range of *N. antennata* (Kiritani *et al.*, 1963). January temperature was proposed as the principal factor determining the northern limit of *N. viridula*'s distribution.

In areas of sympatric distribution *N. viridula* was able to replace *N. antennata* within a few years (Sameshima, 1960; Kiritani *et al.*, 1963). In Miyazaki Prefecture (southeastern Kyushu), for example, the proportion of *N. viridula* increased from 10% in 1951 to 70% in 1959 (Sameshima, 1960) and to 100% by the early 1970s (Kiritani, 1971). A similar pattern occurred in Wakayama Prefecture (Kiritani *et al.*, 1963; Kiritani & Hokyō, 1970; Fig. 2). Replacement was possible for a number of reasons: (1) voltinism (three to four generations per annum in *N. viridula* vs. two in *N. antennata*), (2) fecundity (*N. viridula* was two to three times more fecund than *N. antennata*), and (3) promotion of early-planting rice cultivation in the 1960s (first-generation adults of *N. viridula* successfully utilized this rice, whereas those of *N. antennata* did not) (Kiritani *et al.*, 1963). Furthermore, *N. antennata* has summer diapause (aestivation) and first-generation adults do not start reproduction until after mid-summer (Noda, 1984;

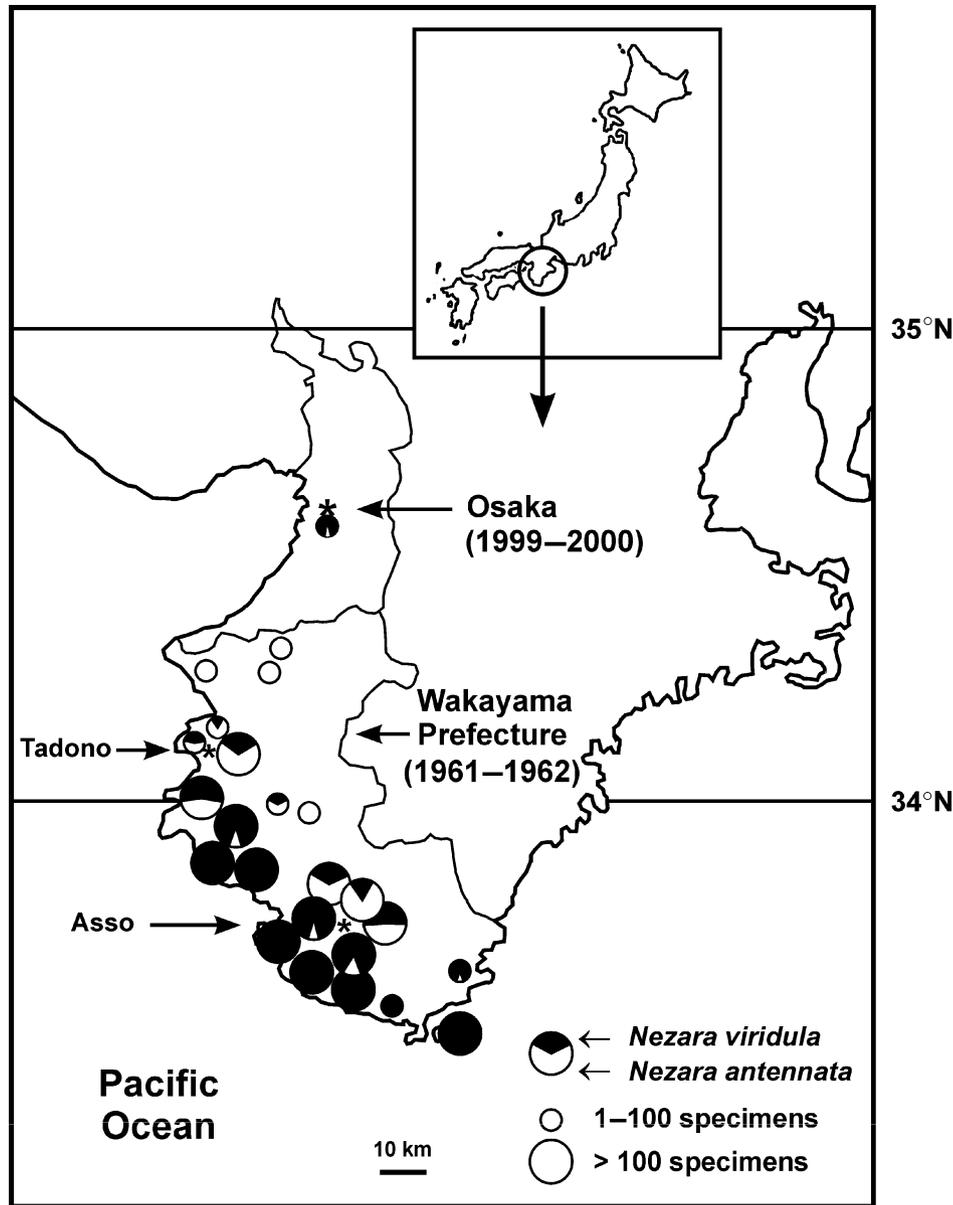


Fig. 1 Distribution and relative abundance of *Nezara viridula* and *N. antennata* in Wakayama Prefecture in the early 1960s (data from Kiritani *et al.*, 1963; Kiritani, 1971) and Osaka in 1999–2000 (data from Musolin & Numata, 2003b). Locations mentioned in the text are shown by asterisks.

Numata & Nakamura, 2002), while *N. viridula* is reproductive throughout the summer. Finally, in the areas where *N. antennata* became rare, most newly emerged females of this species were deprived of intraspecific mating by the presence of numerically dominant and sexually mature *N. viridula* males. Interspecific copulation was frequently observed and resulted in unfertilized eggs which further favoured dominance of *N. viridula* (Kiritani *et al.*, 1963; Kiritani, 1971; Kon *et al.*, 1994). *N. viridula* does, however, suffer higher overwintering mortality than *N. antennata*, especially during severe winters (Kiritani *et al.*, 1963).

40 years later

Mochida (1991) predicted climate change would cause a northward range expansion of *N. viridula*. In 1999–2000, a field study by Musolin & Numata (2003b) sampled the two *Nezara* species in Osaka (34.7°N, 135.5°E), 70 km further north than the northern limit of *N. viridula* in Wakayama Prefecture reported in the early 1960s by Kiritani *et al.* (1963) (Fig. 1). Not only was *N. viridula* found in Osaka, but the species was already strongly outnumbering *N. antennata*, following the pattern of the previously observed species replacement (43 *N. viridula*

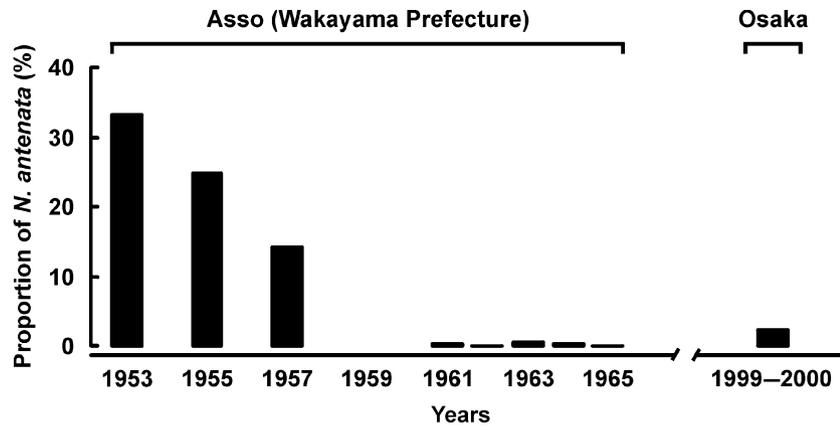


Fig. 2 Proportion of *Nezara antennata* in the total number of *N. antennata* and *N. viridula* collections (data from Kiritani *et al.*, 1963; Kiritani & Hokyo, 1970 for Asso and original for Osaka). $n = 4-7$ for Asso, 1953-1957 (laboratory preserved specimens), $n = 1038-8856$ for Asso, 1961-1965 (field collections) and $n = 44$ for Osaka, 1999-2000 (field collections).

adults: 1 *N. antennata* adult in 1999-2000; Fig. 2; Musolin & Numata, 2003b). Unpublished field records of *N. viridula* between Wakayama Prefecture and Osaka (A. Oe & H. Numata, 1988-1989; D. L. Musolin, 1999) suggest that the specimens of *N. viridula* collected in Osaka in 1999-2000 represent a continuous rather than an isolated population and that northward range expansion was a gradual process rather than a single event of long-distance migration. Absence of records of this species further north in central Japan indicates that Osaka is close to the current northern limit of the species range.

A series of questions associated with the northward range expansion of *N. viridula* in Japan remain unanswered: What factors have favoured the observed range expansion? Can *N. viridula* successfully overwinter in a recently colonized area? How well has the seasonal development of the species adapted to the new environment? Does the seasonal development of *N. viridula* differ from that of local Heteroptera species occupying similar ecological niches in the same region? How representative is *N. viridula* of heteropteran ecology under changing climate conditions?

What determines the northern limit of distribution in *N. viridula*?

Several abiotic and biotic factors are known to limit distribution ranges in insects (Uvarov, 1931; Cammell & Knight, 1992). Climate (mostly, thermal requirements), food and habitat availability are among the most important constraints. For *N. viridula* food and habitat availability are unlikely to be the principal limiting factors as the species, although exhibiting a preference for leguminous plants, is very polyphagous,

feeding on more than 145 species of both dicots and monocots (Oho & Kiritani, 1960; Panizzi *et al.*, 2000).

Seasonally available warmth does not appear to limit the species's range too. Close to the northern margin of *N. viridula*'s distribution (both in Wakayama Prefecture and Osaka) more than one generation are produced each year (Kiritani *et al.*, 1963; Musolin & Numata, 2003a, b). A similar multivoltine seasonal cycle close to the northern limit of the distribution range was reported in *Orius strigicollis* (Poppius) (Heteroptera: Anthocoridae) (Musolin *et al.*, 2004), although most heteropterans, as well as many other insects, are univoltine (or even semivoltine) towards the north of their ranges, even if bi- or multivoltine further south (Danks, 1987; Saulich & Musolin, 1996).

Measuring winter survival of *N. viridula* adults in 16 different habitats over six winter seasons (1961/1962-1966/1967) showed that survival rate differed between sexes, types of hibernacula (host tree species) and was affected by adult size and colouration (Kiritani *et al.*, 1962, 1966). Winter temperature appeared to be the principal factor determining adult mortality during the hibernation period. Only 2.5% of adults (1.5% of males, 3.5% of females) survived the very severe winter of 1962/1963 when the mean January temperature fell to $+2.9^{\circ}\text{C}$; survival during moderately cold winters was much higher (40-65%) (Fig. 3; Kiritani *et al.*, 1966; Kiritani, 1971). Overwintering mortality was negatively correlated with the mean January temperature, a decrease of 1°C resulting in approximately 15% increase in mean overwintering mortality (Fig. 3).

Mean temperatures in Tadono, located within *N. viridula*'s range in Wakayama Prefecture and within a few kilometers of the northern limit of the 1960s range (Fig. 1), fell below the critical level of $+5^{\circ}\text{C}$ only once (in 1962) in the 13 years preceding the survey and

averaged $+6.7^{\circ}\text{C}$ for 1950–1962 (Fig. 4b). During the same period, in Osaka, mean January temperature fell below $+5^{\circ}\text{C}$ often averaging $+4.8^{\circ}\text{C}$ for 1950–1962 (Fig. 4b; Central Meteorological Observatory, 1950, 1953–1964, 1955, 1960, 1965; Japan Meteorological Agency, 1969; National Astronomical Observatory, 2001). These results provide further support of the importance of the January isothermal line of $+5^{\circ}\text{C}$ in limiting the range of *N. viridula*: in the early 1960s, *N. viridula* occurred in Tadono where winters were warmer but was absent in Osaka where January temperatures were below $+5^{\circ}\text{C}$ (Figs 1 and 4).

Since the early 1950s, mean January air temperature (as well as that of December and February) and mean annual air temperature have shown an increasing trend in Osaka (Fig. 4). Mean temperature for each of three winter months and mean annual temperature were higher in Osaka by approximately $1\text{--}2^{\circ}\text{C}$ in the 1990s than in the 1950s. Furthermore, in 1987–2000, the mean January temperature always exceeded $+5^{\circ}\text{C}$ (Fig. 4b). Mean decadal temperatures for each of the winter months in 1950s–1960s were lower in Osaka than in Tadono during the decade before the survey of Kiritani *et al.* (1963), but had increased and become comparable, or even higher, in Osaka by the 1990s (Central Meteorological Observatory, 1950, 1953–1964, 1955, 1960, 1965; Japan Meteorological Agency, 1969, 2003).

Monthly lowest air temperature trends during the winter in Osaka were similar to those of mean temperatures: in the 1990s the monthly lowest temperatures were approximately 2°C higher than those in the 1950s–1960s. Decade means of the lowest temperatures were always higher in Osaka in the 1960s–1990s than in Tadono in the 1950s–1960s (Central Meteorological Observatory, 1950, 1953–1964, 1955, 1960, 1965; Japan Meteorological Agency, 1969, 2003).

These historical climate data indicate that the winter temperatures were higher, and thus overwintering conditions for *N. viridula* were less severe, in Osaka in the 1990s than they were within the northern margin of the species's range in Wakayama Prefecture in the 1950s–1960s. Climate warming is likely to have been an important factor favouring the northward range expansion of *N. viridula* in central Japan and allowing the species to reach Osaka (Musolin & Numata, 2003b). The wide distribution range of *N. viridula*, along with its strong ability to migrate over long distances and wide polyphagy (Todd, 1989; Panizzi *et al.*, 2000), are also likely to have contributed to its range expansion.

Diapause in *N. viridula*

Winter diapause is a hormonally mediated state of suppressed development and a vitally important

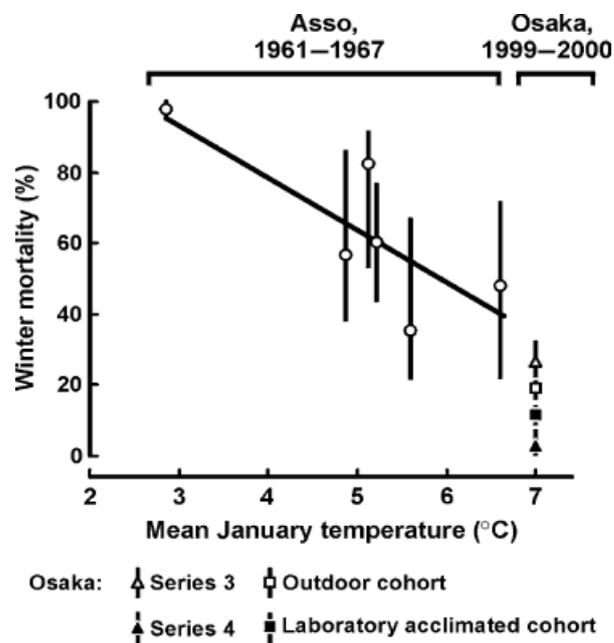


Fig. 3 Winter mortality of *Nezara viridula* adults. For Asso: mean mortality (all adults) and range (mortality in different types of hibernacula); $n = 284\text{--}1197$ per winter (data from Kiritani *et al.*, 1966; Kiritani, 1971); a linear regression trend line refers to the mean mortality ($F_{1,5} = 6.81$, $P = 0.06$). For Osaka: mean mortality (all adults) and range (mortality in two sexes); $n = 23\text{--}50$ per cohort (data from Musolin & Numata, 2003b, 2004). Note that Kiritani *et al.* (1966) measured mortality during the hibernation only and did so in the wild, whereas Musolin & Numata (2003b, 2004) also included prewinter mortality and reared the insects in containers, thus providing protection from predators and parasites. Temperature data: for Asso, grand mean of January temperature in the experimental site (Kiritani *et al.*, 1966) and the two nearest meteorological stations (Tanabe and Ichikano; Central Meteorological Observatory, 1953–1964, 1965; Japan Meteorological Agency, 1968a, b); for Osaka, mean January temperature in Osaka City Meteorological Station (National Astronomical Observatory, 2001).

element of the seasonal cycles of the majority of insects in the temperate zone (Tauber *et al.*, 1986; Danks, 1987). In *N. viridula*, diapause is relatively well understood (Ali & Ewiess, 1977; Harris *et al.*, 1984; Seymour & Bowman, 1994; Jones & Westcot, 2002; Musolin & Numata, 2003a, b, 2004). In temperate populations of the species, the adult reproductive diapause is facultative and its induction is controlled by a long-day photoperiodic response (Ali & Ewiess, 1977; Harris *et al.*, 1984; Musolin & Numata, 2003a). In Osaka, the critical photoperiod (i.e. at which 50% of the individuals enter diapause) is close to 12.5–13 h of light at $20\text{--}25^{\circ}\text{C}$; the response appears thermostable within this range of temperature, and day-length plays a leading role in diapause induction (Fig. 5). *N. viridula* also shows pronounced pattern of seasonal colour change

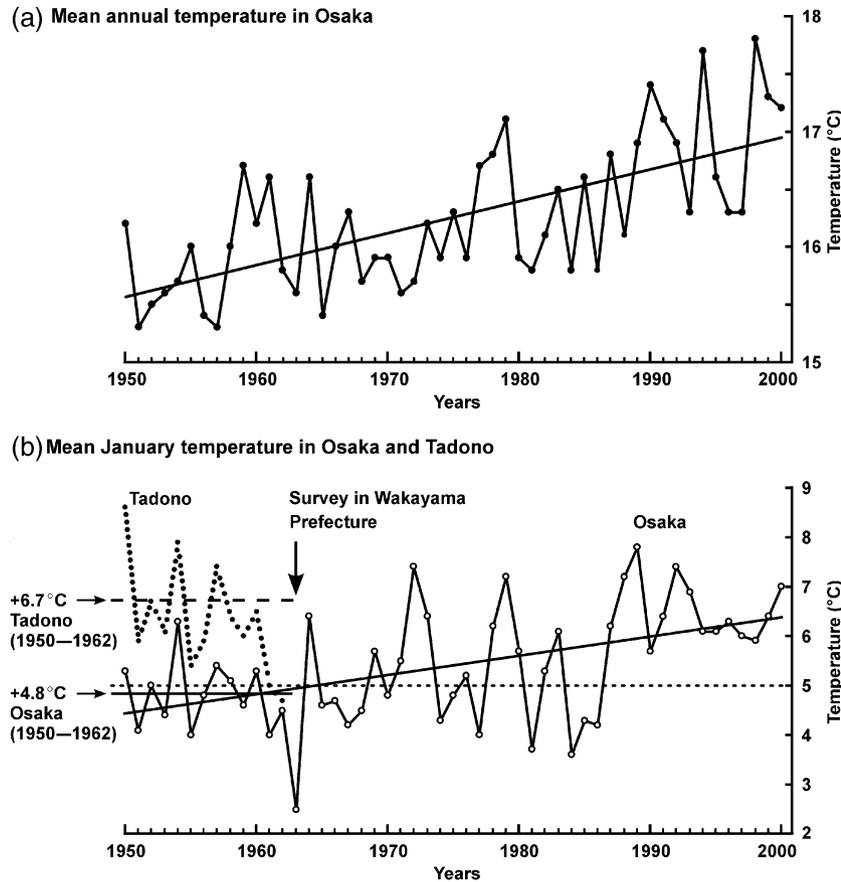


Fig. 4 Changes in air temperature in Tadono (1950–1962; within the range of *Nezara viridula* in the early 1960s) and Osaka (1950–2000) (Central Meteorological Observatory, 1950, 1953–1964, 1955, 1960, 1965; Japan Meteorological Agency, 1969; National Astronomical Observatory, 2001). Mean annual (a) and mean January (b) temperature for Osaka are shown with linear regression trend lines. For mean annual temperature, $F_{1,50} = 37.88$, $P < 0.01$; for mean January temperature, $F_{1,50} = 16.09$, $P < 0.01$ (ANOVA). Additional lines represent mean January temperatures in Tadono and Osaka for 13 years (1950–1962) preceding the range survey in Wakayama and temperature of $+5^{\circ}\text{C}$ suggested as critical for *N. viridula* overwintering (Kiritani *et al.*, 1963).

controlled by day-length; short-day photoperiods induce a gradual change from summer body colouration (typically green, but yellow in some genetic colour morphs) to overwintering (russet or brown) in adults (Fig. 6). The seasonal colour change is believed to be of adaptive value (as camouflage) and associated with diapause induction (Harris *et al.*, 1984; Musolin & Numata, 2003a). In summary, individuals reared under long-day summer conditions are reproductively active, start copulation and oviposition quickly, and remain green or yellow. Under short-day autumn conditions, reproductive development is arrested in both sexes, adults change body colour to russet and enter diapause.

Under natural environmental conditions in temperate regions, adults are reproductive and have summer colouration throughout the vegetative season. *N. viridula* can produce up to five or six generations per year, although the number of generations in a particular region may be limited by the availability and phenology

of food plants (Velasco *et al.*, 1995; Panizzi *et al.*, 2000). In late summer or early autumn, adults of the final generation do not start reproduction. They change body colour to russet, gain overwintering fat reserves, search for overwintering sites and enter diapause. Seasonal migrations (at least local) may occur (Gu & Walter, 1989). Neither nymphs nor eggs survive winter (Musolin & Numata, 2003b). In spring, adults change body colour back to green/yellow and start copulation and oviposition. Further south (e.g. in central India) the seasonal cycle of *N. viridula* includes a summer diapause that allows the population to survive hot and dry months (Singh, 1973); the eco-physiological basis of this dormancy remains unknown.

Critical photoperiod and timing of diapause induction

Critical photoperiod for diapause induction has important ecological significance in temperate zone insects: in

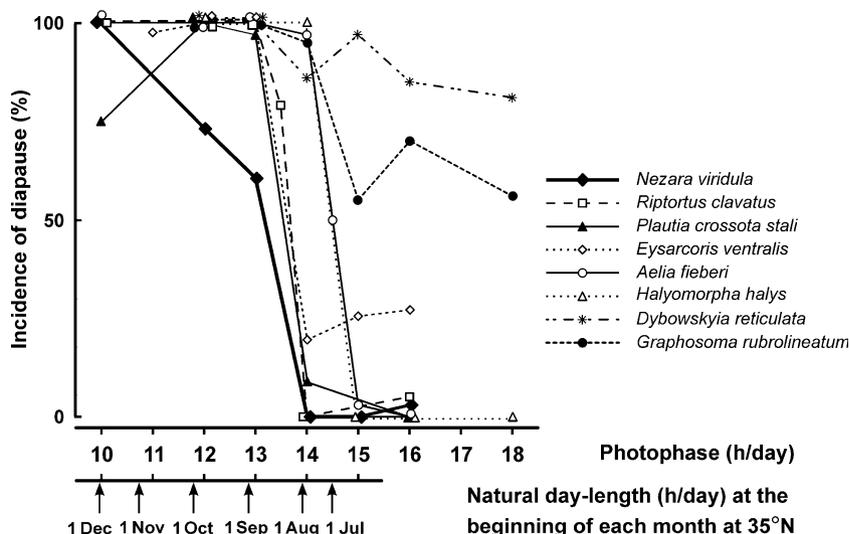


Fig. 5 Photoperiodic response curves for diapause induction in female adults of several seed-feeding heteropterans from Osaka and adjacent regions at 25 °C. Data from: *Nezara viridula* (Osaka, 34.7°N, 135.5°E; Musolin & Numata, 2003a), *Riptortus clavatus* (Kyoto, 35.1°N, 135.8°E; Kobayashi & Numata, 1993), *Plautia crossota stali* (Tawaramoto, 34.6°N, 135.8°E; Numata & Kobayashi, 1994), *Eysarcoris ventralis* (Izumo, 35.4°N, 132.8°E; Noda & Ishii, 1981), *Aelia fieberi* (Osaka, 34.7°N, 135.5°E; Nakamura & Numata, 1997), *Halyomorpha halys* (Kobe, 34.7°N, 135.3°E; Niva, 2003), *Dybowskyia reticulata* (Osaka, 34.7°N, 135.5°E; Nakamura & Numata, 1998), *Graphosoma rubrolineatum* (Osaka, 34.7°N, 135.5°E; Nakamura & Numata, 1999). An additional scale shows natural day-length at latitude 35°N (without twilight; Beck, 1980).

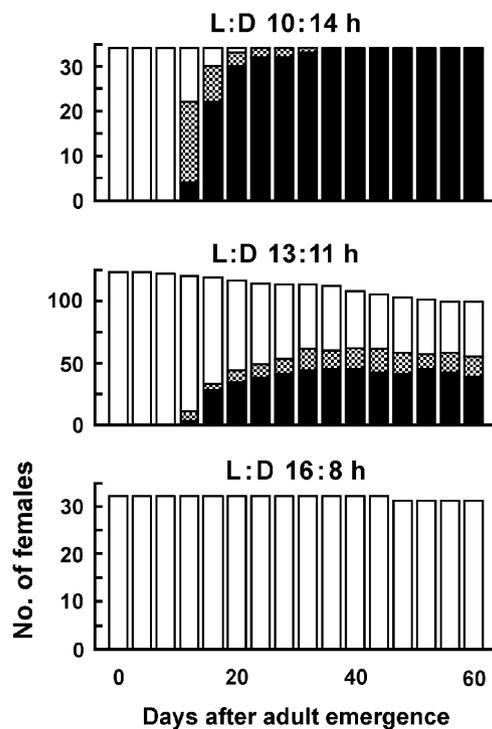


Fig. 6 Effect of day-length on adult body colour in females of *Nezara viridula* at 25 °C. Open, shaded, and black sections of the bars represent the proportion of adults with green, intermediately coloured, and russet bodies, respectively. Experimental photoperiods are shown above the corresponding graphs (taken from Musolin & Numata, 2003a; reproduced with permission from the Royal Entomological Society and Blackwell Publishing Ltd).

many species it determines the timing of the switch from a reproducing population to a diapausing one. In Osaka the critical photoperiod for *N. viridula* was close to 13 h at 25 °C (Fig. 5; Musolin & Numata, 2003a). In an outdoor experiment to determine the timing of diapause induction in *N. viridula* fresh egg-masses were placed sequentially (Series 1–6) outdoors during July–November 1999 and development was monitored until September 2000 (Fig. 7; Musolin & Numata, 2003b). Natural day-length in Osaka is 12 h 53 min on 1 September, 12 h 27 min on 15 September, and 11 h 48 min on 1 October (Fig. 5). Consistent with laboratory estimations of critical photoperiod, natural day-length led to reproduction in all females that emerged before 1 September (Fig. 7, Series 1), but only in approximately 40% of females that attained adulthood in the later half of September (Series 2 and 3). All females that attained adulthood later (in October, Series 4) entered diapause without starting reproduction. Nymphs in Series 5 and 6 failed to reach adulthood before winter cold and died during the winter.

When the photoperiodic response of *N. viridula* was compared with the responses of another seven local Heteroptera species exhibiting adult winter diapause *N. viridula* demonstrated the shortest critical photoperiod for diapause induction (Fig. 5): in *N. viridula* it is approximately 30 min shorter than that in the pentatomids *Plautia crossota stali* Scott (Numata & Kobayashi, 1994) and *Eysarcoris ventralis* (Westwood) (Noda & Ishii, 1981) and the alydid *Riptortus clavatus*

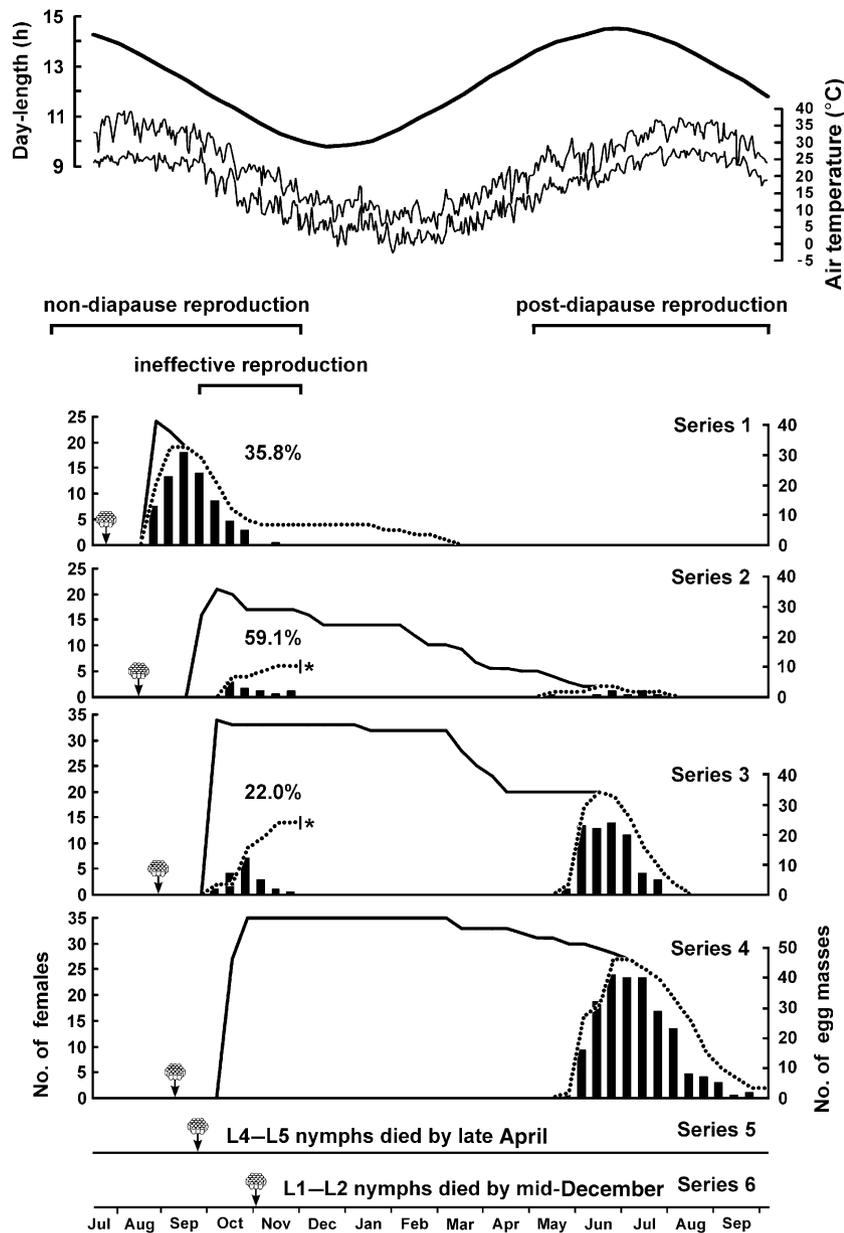


Fig. 7 Seasonal development of six series of *Nezara viridula* female adults under quasi-natural conditions (data partly from Musolin & Numata, 2003b). The symbol for egg mass shows the date when the series was initiated. Solid lines show total number of females; dotted lines show number of ovipositing females. Histograms show total number of egg masses produced per 10-day period. L1-L5 refer to nymphal instars. Asterisks show the dates when females were transferred from individual containers to group ones; this happened after cessation of oviposition. Percentage shows the proportion of egg masses produced during the period of ineffective reproduction in the total number of egg masses produced before and after overwintering in each series (see text for further explanation). Environmental conditions (at the top of the figure): thick line, natural day-length; thin lines, daily maximum and minimum air temperature.

(Thunberg) (Kobayashi & Numata, 1993); and almost 90 min shorter than that in the pentatomids *Aelia fieberii* Scott (Nakamura & Numata, 1997) and *Halyomorpha halys* Stål (Niva, 2003). The pentatomids *Graphosoma rubrolineatum* (Westwood) (Nakamura & Numata, 1999) and *Dybowskyia reticulata* (Dallas) (Nakamura & Numata, 1998) exhibit strong tendency towards dia-

pause in Osaka and most females entered diapause even under long-day conditions. *P. crossota stali* and *R. clavatus* produce three generations per annum in the Osaka region entering diapause in September; *E. ventralis* has two or three generations and enters diapause in August; and *A. fieberii* has two generations and enters diapause in August. The remaining three

species produce only one (*H. halys*) or generally one (*G. rubrolineatum* and *D. reticulata*) generation per year and enter diapause pre-August. The seasonal cycles of the two latter species are strongly influenced by the availability of specific host plants (Nakamura & Numata, 1998, 1999; Numata & Nakamura, 2002). Of these eight species, *N. viridula* has the shortest critical photoperiod. This results in the comparatively late induction of diapause: in the outdoor experiment, incidence of diapause reached 100% only among females emerging in early October (Series 4; Fig. 7), whereas some females that emerged during the last week of September were reproductive (Series 3). The late timing of diapause induction in *N. viridula* in Osaka has potential negative life-history consequences and entails various ecological costs.

Similar, comparatively late induction of diapause was reported in an interzonal transfer experiment with *R. clavatus*. When this species was transferred from Kyoto (35.0°N, 135.5°E) to Belgorod (Russia, 50.6°N, 36.0°E), and reared under outdoor conditions, adult diapause was induced in late August or September, when temperature was already too low for successful prediapause feeding. This timing of diapause induction was consistent with the photoperiodic response of the Kyoto population, but it was much later than the time the local Heteroptera species enter winter diapause. It was thought most likely that the progeny of the late nondiapause adults would fail to complete nymphal development and die in late autumn (Musolin *et al.*, 2001).

Late-season reproduction and overwintering of N. viridula

Females that initiated reproduction before winter laid eggs until late November (Series 1–3; Figs 7 and 8a). Data suggest that these females died by winter or early spring, being unable to switch from reproduction to diapause (Musolin & Numata, 2003b). Some females in Series 2 and 3, and all females in Series 4, did not start copulation or oviposition before winter, but changed body colour to russet and entered diapause (Musolin & Numata, 2003b).

Adults of *N. viridula* in Series 3 and 4 survived winter with low mortality (Fig. 3). Similar low mortality was recorded in a parallel experiment performed with laboratory-acclimated individuals (Fig. 3; Musolin & Numata, 2004). The mortality recorded in the Osaka experiments fits well with the pattern derived from records from the Wakayama survey: higher winter temperature in Osaka (mean temperature was +7°C in January, 2000) was favourable for overwintering and, thus, resulted in lower mortality (Fig. 3).

Postdiapause reproduction of N. viridula

In spring, all adult *N. viridula* that survived winter changed colour back to green, copulated and females produced eggs (Fig. 7). There was, however, a considerable difference in postdiapause reproductive performance between females from different series (Musolin & Numata, 2003b). Females in Series 4 lived longer, had a longer period of oviposition, produced more eggs and egg masses, and had larger size of egg masses than females in Series 3 (Fig. 8b–d). Females from Series 4 may have completely realized their reproductive potential, whereas females from Series 3 had not lived long enough to do so. Timing of adult emergence and diapause induction in autumn strongly affects life-history traits after overwintering.

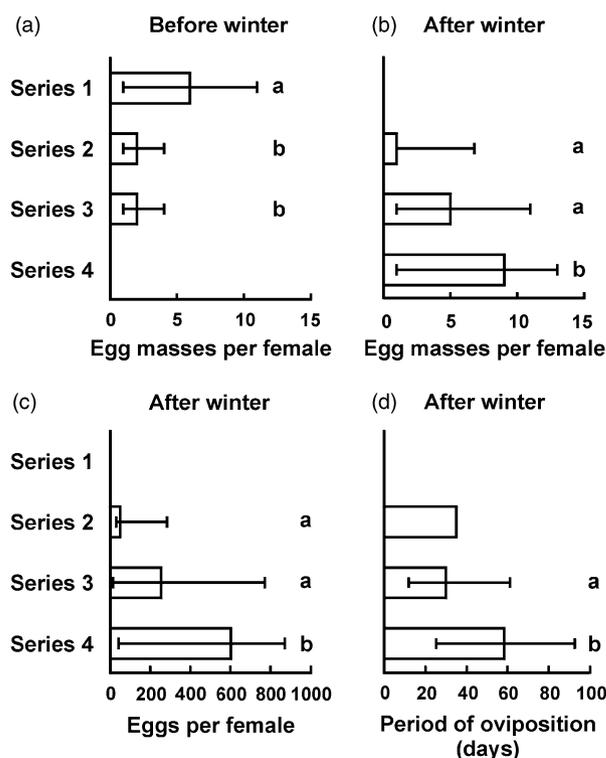


Fig. 8 Parameters of reproduction in different series of the field experiment before and/or after winter (December–February): number of egg masses per reproductive female before winter (a) and after winter (b); number of eggs per reproductive female after winter (c); and period of oviposition (from the first to the last oviposition; in females that produced more than one egg mass only) (d). Medians (with range) followed by the same letters within each histogram are not significantly different [$P > 0.05$ by the Kruskal–Wallis test followed by the Steel–Dwass test (a, b, c), or by Mann–Whitney *U*-test, $n > 2$ (d)]. Females $n = 6–19$ (a), $3–29$ (b), $3–29$ (c), $1–27$ (d) (this figure incorporates parts of figs 3 and 4 from Musolin & Numata, 2004; reproduced with permission from the Royal Entomological Society and Blackwell Publishing Ltd).

Ecological cost of range expansion

The results presented above and elsewhere (Musolin & Numata, 2003a, b, 2004) suggest that *N. viridula* is still, to a certain extent, maladapted to the environmental conditions in Osaka. The short critical photoperiod for diapause induction (Fig. 5) meant that the reproductive diapause was induced only in those adults that emerged in late September or early October (Fig. 7); this was later than in several other seed-feeding heteropterans native to Osaka (Fig. 5).

Nondiapause females in Series 1–3 oviposited until late November (Fig. 7). The late-season reproduction of adults that emerged in September or later is an ineffective allocation of resources, as the progeny from the egg masses produced after late September are destined to die, as it happened with all nymphs in Series 5 and 6 of the experiment (Fig. 7). During the period from late September (when Series 5 was initiated) to late November, 22.0–59.1% of the total number of egg masses was produced (Fig. 7), but the progeny had no chance of surviving winter.

Series 1 also differed from Series 2 and 3. In Series 1, all females started reproduction by 10 September and the progeny from at least the early egg masses had some chance of attaining adulthood and entering diapause before late autumn, to survive winter successfully in diapause and start reproduction in spring. In this case, reproduction before overwintering is justified even if the chances of progeny survival are low. Contrary, in Series 2 and 3, females emerged later in the season and some started oviposition only in October when the progeny were destined to die. Having initiated oviposition, these females most likely also died during the winter or early spring, failing to make any contribution to following year's population growth. The two month period from mid-September to early November appears to represent a phenological mismatch: diapause is not yet induced in all adults, but it is already too late to start reproduction.

For insects, the timing of seasonal development presents the most immediate impediment to range expansion into the temperate zone (Bradshaw *et al.*, 2000). The temporal mismatch in autumn, along with the reduced postdiapause reproductive performance in females entering diapause early in the season (as in Series 3), shows that *N. viridula* remains maladapted to Osaka environmental conditions and this may be considered the ecological cost of range expansion.

Perspectives of establishment in Osaka

To ensure a better adaptation to its new environmental conditions and complete establishment, the local population of *N. viridula* is likely to evolve a lengthening

of the critical photoperiod for diapause induction response and, consequently, advance the timing of diapause induction (Musolin & Numata, 2003b). This will allow adults to enter diapause earlier and, thus, avoid maladaptive reproduction after mid-September. Increased duration of diapause *per se* is unlikely to reduce significantly postdiapause reproductive output (Musolin *et al.*, 2007). Earlier induction of diapause under natural conditions will, however, perhaps entail additional costs, as it is known that prewinter high temperature may adversely affect overwintering success of diapausing insects (Han & Bauce, 1998; Gomi, 2000). Shifts in the timing of diapause induction are known to occur when selective pressures change (Hairston & Walton, 1986). Bradshaw & Holzapfel (2001), for example, showed that the critical photoperiod of diapause induction in an insect species can naturally shift towards shorter values under conditions of lengthening growing season caused by climate warming. In *N. viridula* in Osaka, however, high mortality associated with late-season reproduction should force selection for longer critical photoperiods indispensable for earlier diapause induction. A marked variation in the photoperiodic response recorded in *N. viridula* (Musolin & Numata, 2003a) can make such a shift feasible and quick; this type of physiological variation provides considerable scope for natural selection and rapid adaptation to climate change (Masaki, 1978; Pullin, 1986; Butterfield & Coulson, 1997). *N. viridula*, on the other hand, is a migratory species. If gene flow (e.g. from warmer regions) is persistent and intensive, the photoperiodic response and timing of diapause induction may remain variable and result in phenological mismatches and reproductive losses at least in a part of the Osaka population.

Can success of colonization be predicted?

The case study of *N. viridula* in Japan shows how detailed knowledge of a species's eco-physiology allows insight into responses to climate change. This raises the question of whether parameters of the photoperiodic response, such as critical photoperiod for diapause induction, may be useful generalized predictors of colonization success.

Insect colonization of new areas involves four stages: (1) introduction and survival, (2) establishment, (3) range expansion and adaptation to the new environment, and (4) divergence (Tauber *et al.*, 1986). Success of establishment greatly depends on inherited physiological characteristics and seasonal adaptations, and on physiological plasticity and genetic variability.

Whereas, a successful first stage mostly depends on the immigrant's ability to withstand seasonal physical factor extremes, the outcome of the second stage is, to

a great extent, determined by synchronization of the life cycle of the insect species with local seasonal physical and biological environments (Tauber *et al.*, 1986; Saulich, 1999). At this point, the role of critical photoperiod for diapause induction becomes vital: it should be sufficiently short to allow development to continue without diapause induction until the sensitive stage of the penultimate generation is completed while, at the same time, long enough to allow for diapause induction when remaining thermal units are insufficient for a complete generation (Tauber *et al.*, 1986).

A knowledge of a species's critical photoperiod and thermal requirements allows approximate prediction of timing of diapause induction and hence estimation of phenological (a) synchrony with, for example, food plants. The ecological costs of potential phenological mismatches are difficult to predict. In some species, too early diapause induction may result in a too long diapause period and consequently decreased winter survival and/or reduced postdiapause reproductive performance (Taylor, 1980). In other species this effect may be negligible. Comparison across taxonomically or ecologically closely related species has limited significance because all eco-physiological traits and adaptations are species- or population-specific (Danks, 1987; Saulich & Volkovich, 2004). Furthermore, prediction of microevolutionary adaptive changes is difficult because it is uncertain in which direction and how quickly physiological responses of the population will change after colonization. To adapt to local conditions and maximize fitness, some species evolve changes in photoperiodic responses comparatively quickly. The pitcher-plant mosquito, *Wyeomyia smithii* (Coquillett), for example, evolved detectable changes in critical photoperiod within 5–30 years, possibly in response to climate warming in eastern North America (Bradshaw & Holzapfel, 2001), and the Asian tiger mosquito, *Aedes albopictus* (Skuse), lost its diapause ability in southern United States but acquired it in southern Brazil within 15 years of initial establishment (Lounibos *et al.*, 2003). Other invading species may, however, be unable to modify their relict diapause responses so effectively as in the case of the Argentine stem weevil, *Hyperodes bonariensis* Kuschel, in New Zealand (Goldson & Emberson, 1980).

Critical photoperiod may be a useful generalized predictor of success in a new region, particularly in the early stages of colonization. Species with flexible photoperiodic responses (e.g. those in which temperature can modify diapause response, thus, allowing precise tuning of timing of diapause induction in the wild) have more chance to adapt successfully and quicker than those with less flexible responses (e.g. species with thermostable photoperiodic response or with obligate diapause).

Although detailed trait-based studies can significantly enhance understanding of colonization process, long-term prediction remains difficult, particularly taking into consideration that climate change is not a single event but a slow continuous process.

Responses to climate warming among other Heteroptera species

The Heteroptera is a generally thermophilic taxon (Honek & Kocourek, 1990; Yamamura & Kiritani, 1998; Kiritani, 2006) and many aspects of species physiology and population/community ecology depend on ambient temperature. Insect responses to climate warming may be divided into six categories: changes in distribution range, abundance, phenology, voltinism, physiology and behaviour, and community structure (see Table 1 for Heteroptera).

Distribution range

Range shift is the most easily observed and, consequently, most often reported response of insects to climate change (Parmesan, 2001; Musolin & Fujisaki, 2006). While, climate warming may not be involved in all reported cases of range expansion (e.g. *Anthocoris nemoralis* (F.) in North America and *Nysius huttoni* White in Europe; Horton *et al.*, 2004; Aukema *et al.*, 2005b; Scudder & Foottit, 2006), it remains an important determinant of range alteration. Recently, several South European Heteroptera species have been recorded as new in northern Europe (Nau, 1997; Kirby *et al.*, 2001; Aukema, 2003; Jones, 2004). Some of these colonists have apparently established themselves in northern European and climatic factors (along with the international trade and transportation of plant material) have likely contributed to the northward range expansion of these species (Kirby *et al.*, 2001; Aukema, 2003).

A recent comparison of distribution limits of southern aquatic Heteroptera species in the United Kingdom showed that from 1970–1980 to 1990–2000 the northern margins shifted northward by 64–84 km in average and altitudinal limits shifted uphill by 8.4–25.6 m in average (based on 10 km grid square recording; four to 14 species were included into analysis depending on the level of recording efforts; Hickling *et al.*, 2006).

Furthermore, while 45 years ago Southwood & Leston (1959) commented that *N. viridula* was 'unlikely to become established' in the British Isles, a few colonies of this species have already been reported breeding (Barclay, 2004; Shardlow & Taylor, 2004) and survived winter of 2003/2004 (M. V. L. Barclay, personal communication) in London.

Table 1 Responses of Heteroptera species and communities to climate change (recorded* and simulated)

Categories of responses and taxa	Response and location	References
Distribution range		
<i>Corythucha ciliata</i> (Say) and <i>C. arcuata</i> (Say) (Tingidae)	Both originally North American species. <i>C. ciliata</i> invaded Italy (probably with plant material) in 1960s, established there and then widely spread in southern and central Europe. Found in Bedfordshire (the United Kingdom) in 2006 and presumably had successfully overwintered there; <i>C. arcuata</i> arrived to Italy in 2000	d'Aguilar <i>et al.</i> (1977), Kozár & Dávid (1986), Bernardinelli & Zandigiacomo (2000), Rabitsch (2004), Malumphy <i>et al.</i> (2006)
<i>Brachycarenum tigrinus</i> (Schilling) (Rhopalidae), <i>Eurydema ornate</i> (L.) (Pentatomidae) and other species	South European species recently reported in the Netherlands for the first time	Aukema (1989, 1993, 2003), Aukema <i>et al.</i> (2005a)
<i>Leptoglossus occidentalis</i> Heidemann (Coreidae)	North America eastward range expansion augmented by humans, but probably promoted by climate change	Marshall (1991), Gall (1992), Ridge-O'Connor (2001)
<i>Calidea dregii</i> Germar (Scutelleridae)	Expanded range from northeastern to southwestern South Africa (Southern Hemisphere)	Giliomee (1997)
<i>Deraeocoris flavilinea</i> (Costa), <i>D. olivaceus</i> (F.) (Miridae), <i>Tuponia brevirostris</i> Reuter, <i>T. mixticolor</i> (Costa) (Miridae) and other species	South European species expanded range to and apparently established in the United Kingdom	Nau (1997), Kirby <i>et al.</i> (2001), Barclay & Nau (2003), Nau & Brooke (2003), Jones (2004)
<i>Ischnodemus sabuleti</i> (Fallen) and other seed bugs (Lygaeidae)	Northward range expansion; the United Kingdom	Judd & Hodkinson (1998)
<i>Pyrrhocoris apterus</i> (L.) (Pyrrhocoridae)	A colony first recorded in 1996 survived at least until 2003; Surrey, the United Kingdom	Hawkins (2003)
<i>Nezara viridula</i> (L.) (Pentatomidae)	Northward range expansion; Japan	Musolin & Numata (2003b), Yukawa <i>et al.</i> (2007)
<i>Nezara viridula</i> (L.) (Pentatomidae)	Several colonies reported breeding in 2003 in London, the United Kingdom; at least some survived winter 2003/2004	Barclay (2004), M. V. L. Barclay (personal communication), Shardlow & Taylor (2004)
<i>Orius strigicollis</i> (Poppius) (Anthocoridae)	Urban warming ('heat islands') allowed species to survive winters in areas where climate had been too cold; Honshu, Japan	Shimizu <i>et al.</i> (2001)
Aquatic Heteroptera (4–14 species)	Northward range expansion (in average 64–84 km) and altitudinal (in average 8.4–25.6 m uphill) shifts in range margins between 1970–1980 and 1990–2000 in a group of southern species; the United Kingdom	Eyre <i>et al.</i> (2005), Hickling <i>et al.</i> (2006)
Heteroptera fauna	Increases of local and national Heteroptera fauna lists in the United Kingdom, the Netherlands and Austria	Nau (1997, 2006), Kirby <i>et al.</i> (2001), Aukema (2003), Rabitsch (2004)
Abundance		
Grassland heteropteran species	Manipulated winter warming (+3 °C) decreased abundance of nymphs and adults; the United Kingdom	Roth & Masters (2000)
<i>Leptocoris chinensis</i> Dallas (Alydidae)	Southern species increased abundance and augmented damage to rice, perhaps due to higher summer temperature and earlier transplanting of rice; central Japan	Yokosuka (2001)
Aquatic Heteroptera community	Increased abundance of dominant species predicted by a simulation model based on climate change scenarios; Hungary	Hufnagel & Gaál (2005)

(contd.)

Table 1. (Contd.)

Categories of responses and taxa	Response and location	References
Rice pest true bugs (mostly Pentatomidae and Miridae)	A sharp increase in abundance from the mid-1970s to 1990s in Japan (a combined effect of climate warming, changes in land-use and agricultural practices)	Kiritani (2006)
Phenology		
Grassland heteropteran species	Manipulated winter warming (+3 °C) accelerated egg hatch and development, leading to earlier maturation and dispersal; the United Kingdom	Roth & Masters (2000)
<i>Plautia crossota stali</i> Scott and other fruit tree pests (Pentatomidae)	Warmer spring resulted in an earlier appearance (by approximately 1 month) of overwintered adults; Japan	Ohira (2003), Kiritani (2006)
Aquatic heteropteran species	Advance (up to 20–50 days) of early-season phenology and some delay of late-season phenology predicted by a simulation model based on climate change scenarios; Hungary	Hufnagel & Gaál (2005)
Voltinism		
Heteroptera (28 species)	Heteropteran species may exhibit one additional generation per annum under 2–3 °C climate warming; suggested by a model	Yamamura & Kiritani (1998)
Physiology and behaviour		
<i>Arocatus melanocephalus</i> (F.) (Lygaeidae)	Every summer from 1999, large numbers of adults enter urban buildings; northern Italy	Zandigiacomo (2003), Maistrello <i>et al.</i> (2006)
<i>Nezara viridula</i> (L.) (Pentatomidae)	Phenological mismatch in timing of diapause induction results in late-season ineffective reproduction in a recently colonized area in Japan	Musolin & Numata (2003b), this study
<i>Nezara viridula</i> (L.) and <i>Halyomorpha halys</i> Stål (Pentatomidae)	Increase of winter temperature causes decrease overwintering mortality (each 1 °C results in approximately 13.5–16.5% of mortality); Japan	Kiritani <i>et al.</i> (1966), Kiritani (1971, 2006), this study
<i>Aquarius paludum</i> (F.) (Gerridae)	Changes in photoperiodic responses of wing-form determination and diapause induction (shifts of the critical photoperiods and loss of sensitivity to decreasing daylength) from 1991 to 1999–2002; southern Japan	Harada <i>et al.</i> (2005)
Community structure		
Grassland heteropteran community	Manipulative field experiment showed that winter warming and/or summer drought or extra rainfall may affect abundance of nymphs and adults, altering phenology, and thus change community structure; the United Kingdom	Roth & Masters (2000)
Hemipteran community	Increase of species richness at temperate latitudes might be expected as a result of species migration in response to climate change and shifting climate zones	Andrew & Hughes (2005)

*In some cases, causal relationship between climate change and observed response is supposed but not proven.

In North America, the seed bug, *Leptoglossus occidentalis* Heidemann, was previously confined to the western third of the United States and Canada, but during the last 50–70 years has shown a strong eastward range expansion (Marshall, 1991; Gall, 1992; Ridge-O'Connor, 2001). This natural range expansion is suggested to be augmented by humans (Gall, 1992) but is also likely to have been promoted by climate change (Marshall, 1991). Recently, *L. occidentalis* arrived (most probably

with plant material) and became naturalized in northern Italy (Taylor *et al.*, 2001; Villa *et al.*, 2001; Rabitsch, 2004). As another example, the shield bug, *Calidea dregii* Germar, has expanded its range from northeastern to southwestern South Africa (note that in the Southern Hemisphere, responses modulated by climate change have an opposite geographic direction! Giliomee, 1997). Finally, constrained by low winter temperature the anthocorid *O. strigicollis* (Poppius) is mostly distributed

along the Pacific coast and urbanized areas of Japan. Urban warming ('heat islands') allows the species to survive winters in areas where climate was too cold in the first half of the 20th century (Shimizu *et al.*, 2001).

The expansion of distribution range of individual species can enrich local faunas, especially at higher latitudes, and climate change has accelerated this process. During a decade before 1996, additions to the Heteroptera list of Bedfordshire (southeast of the United Kingdom) averaged only 1.5 species per year; but in a single 1996 an additional 10 new, mostly xerophile, species were recorded (Nau, 1997). Such trends are becoming more and more obvious on a national scale too. Kirby *et al.* (2001) analysed changes in Heteroptera fauna of the United Kingdom during 1973–1998 and concluded that over this period 17 new species of terrestrial and aquatic true bugs (from five families) had arrived, established and perhaps further expanded in range and that another 15 native species (seven families) had appeared to expand their former ranges within the United Kingdom. Kirby *et al.* (2001) further emphasised that almost all the recorded changes in Heteroptera fauna (i.e. >60 species) were increases, compared with the Macrolepidoptera where there were many species in decline (Fox, 2001). Climate change, or at least the particular warm weather conditions experienced over recent years, was considered an obvious candidate for the cause of these changes (Kirby *et al.*, 2001; Southwood *et al.*, 2003).

In another research Nau (2006) compared the current UK Heteroptera list with that of the late 1950s, which included in total approximately 520 species (Southwood & Leston, 1959). He found that though nine species (from seven families) have not been recorded in the United Kingdom since 1959, new 43 species of mostly vagrants and colonizers (from 10 families) have been recorded for the first time and included in the country list since then.

A similar trend was recorded in the Netherlands. The national Heteroptera list increased from 119 recorded species in 1853 to 488 by 1951, and 610 by 2002 (Aukema, 2003; Fig. 9). Whereas, the early increase of the total species number is likely to represent an initial fauna inventory, the additions to the list since 1980 are most likely to be the consequence of anthropogenic effects and/or global warming. Appearance of 17 new species from eight terrestrial and aquatic families (i.e. 63.0% of new arrivals since 1980) is explained by range expansion of southern species, most likely stimulated by global warming (Fig. 10). This assumption is further supported by the fact that 70.2% of records of these species came from the 'continental' Dutch provinces (i.e. not northern or western ones; Fig. 10), where only two of the 17 new species have not been recorded (Aukema, 2003). Seven species formerly recorded in the country seem to have

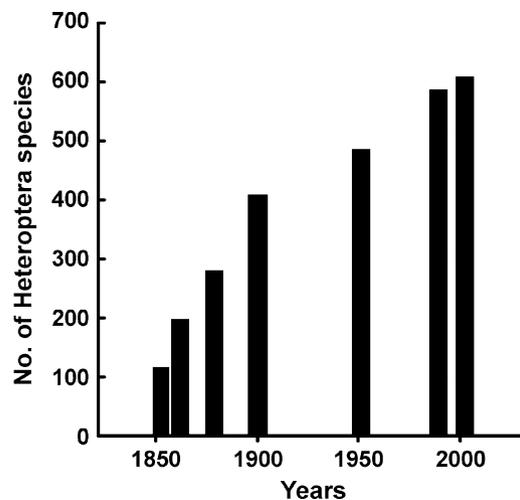


Fig. 9 Heteroptera fauna of the Netherlands: dynamics of the total number of species recorded (data from Aukema, 2003).

become extinct (Aukema, 2003). (The most recent update showed that the Holland national Heteroptera list had further increased to 618 by 2005; Aukema *et al.*, 2005a.)

Comparable increases of national Heteroptera fauna were recorded in Austria, with at least one new species arriving per year (in fact, 14 definite new arrival species in 1991–2004 along with another 10 species that have probably been overlooked). Such massive invasion of South European species was considered a 'Mediterranization' of the Austrian fauna (Rabitsch, 2004).

While an assumption that climate warming caused similar increases in Heteroptera faunas in the United Kingdom, the Netherlands and Austria lacks direct proofs, it is not groundless: in all these countries climate has changed in a similar way and temperature has risen by approximately 1 °C through the 20th century (Böhm *et al.*, 2001; Hulme *et al.*, 2002; Verbeek, 2003).

Abundance

Several pentatomid, mirid and alydid species have recently been reported to have increased in abundance and become serious agricultural pests in Japan, likely in response to increased summer temperatures and/or change in agricultural practices (Yokosuka, 2001; Kiritani, 2006). Increase in abundance of dominant species in an aquatic Heteroptera community in Hungary has been predicted by a simulation model, which mostly considered temperature dependence of seasonal population dynamics (Hufnagel & Gaál, 2005). Decrease in abundance of heteropteran nymphs and adults, however, was recorded in a long-term field experiment with manipulated winter warming (+3 °C; Roth & Masters, 2000) suggesting that species-specific responses are likely to occur.

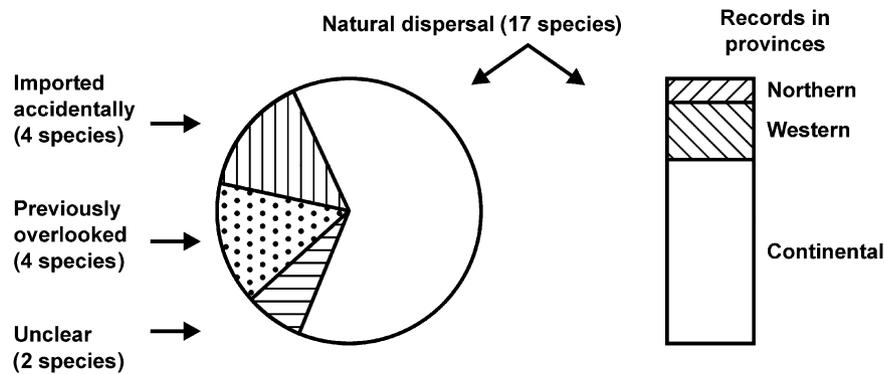


Fig. 10 Heteroptera species added to the fauna of the Netherlands in 1980–2002 (data from Aukema, 2003). A pie chart shows four categories of new species: successful accidental introductions related to international transportation or trade of plant material (i.e. passive dispersal); previously overlooked species; species extending their range in a natural way (i.e. active, or natural, dispersal); and species with unclear causes of appearance in the country. Bar sections represent all records of 17 naturally dispersed new species in 10 km survey squares in three groups of the Dutch provinces (northern, western, and continental). See text and Aukema (2003) for further details.

Phenology

Shifts in phenology in response to climate warming are well documented for several insect taxa (e.g. Harrington *et al.*, 1995; Stefanescu *et al.*, 2003). Surprisingly, there are no such records regarding Heteroptera in natural ecosystems except for one report of accelerated egg hatching and development leading to earlier maturation and dispersal of grassland Heteroptera species in response to artificial winter warming (Roth & Masters, 2000). In fruit orchards in Japan, light traps have recorded a 1-month advance in the spring appearance of overwintered adults of pentatomids *P. crossota stali* Scott, *Glaucias subpunctatus* (Walker) and *H. halys* Stål likely because of the high early spring temperature (Ohira, 2003; Kiritani, 2006).

Voltinism

A model based on a developmental zero (T_0) and a thermal constant (K) of >400 arthropod species (including 28 Heteroptera species) suggests that under conditions of 1 °C warming temperate Heteroptera will not increase their number of annual generations. If, however, temperature increases are higher (i.e. the total warming of 2–3 °C); Heteroptera may, on average, exhibit one additional annual generation (Yamamura & Kiritani, 1998). This model does not, however, take into account the fact that earlier initiation of postoverwintering growth and reproduction (reasonably expected under climate warming conditions) might advance all further seasonal development. In such case, in some species with nonobligatory diapause, a stage sensitive to diapause-inducing cues (e.g. day-length) might be advanced to a period when environmental conditions do not yet induce diapause and, thus,

such species might produce additional generation(s) (cf. Musolin & Saulich, 2001).

Physiology and behaviour

Eco-physiological responses to warming, similar to those studied in *N. viridula* above, have only once been reported in other Heteroptera species. Harada *et al.* (2005) compared photoperiodic responses of wing-morph determination and diapause induction obtained in 1999–2002 in a population of the water strider, *Aquarius paludum* (F.), from southern Japan with the results of a similar study conducted in the same location in 1991. After a decade of rising temperature, the population seems to have shifted the critical photoperiods and lost sensitivity to decreasing day-length which had strongly influenced both photoperiodic responses determining the late summer wing-morph and diapause incidence in 1991. In 1999–2002, *A. paludum* nymphs were likely to have failed to detect gradual decrease in natural day-length, probably because they grew faster under warmer environmental conditions. The 1999–2002 critical photoperiods were likely to have determined later induction of diapause and higher incidence of the macropterous morph which, in turn, should be advantageous for colonization of new habitats.

Behavioural responses of Heteroptera species to climate warming are also restricted to only one record. The seed bug, *Arocatus melanocephalus* (F.), began to demonstrate unusual behaviour in Italy and this was correlated with increased temperature: every summer large numbers of adult *A. melanocephalus* entered urban buildings apparently escaping from extremely high temperatures and in search of better conditions for aestivation (Maistrello *et al.*, 2006).

Table 2 Expected responses of Heteroptera species and communities under two scenarios of further climate change

Categories of responses	Climate change (warming) scenarios	
	Slight temperature increase (<2 °C)	Substantial temperature increase (>2 °C)
Distribution range	Likely to shift in some species, especially those capable of long-distance flights and associated with ornamental plants and/or urban habitats	Likely to shift in many species
Abundance	Likely to increase in multivoltine species with flexible life cycles	Likely to change, depending on the community response
Phenology	Slight to moderate advance of early-season events	Substantial advance of early-season and some delay of late-season events
Voltinism	An additional generation in some multivoltine species with flexible life cycles	One or more additional generation(s) in some multivoltine and univoltine species (with facultative diapause)
Physiology and behaviour	Slight/undetectable changes	Evident/detectable changes (e.g. in parameters of photoperiodic responses)
Community structure	Similar to currently observed	Increased species richness; substantial changes in structure

Community structure

Winter warming and/or summer increase or decrease in precipitation has been shown in a manipulative field experiment to directly and indirectly affect not only abundance of individual species, but also the structure of the whole Heteroptera community in a grassland ecosystem (Roth & Masters, 2000). Another study focusing on assemblage structure of Hemiptera along a latitudinal gradient suggests that increase of species richness at temperate latitudes might be expected as a result of species migration in response to further climate change and shifting climate zones (Andrew & Hughes, 2005).

Concluding remarks: what to expect?

A considerable body of information has already accumulated on the responses of insects and other biota to climate change (e.g. Harrington & Stork, 1995; Walther *et al.*, 2001, 2002; Bale *et al.*, 2002; Schneider & Root, 2002; Parmesan & Yohe, 2003; Reemer *et al.*, 2003; Møller *et al.*, 2004). Heteroptera species (Table 1) responded very similar to the general pattern (e.g. in rates of northward shifts of range margins – see: Hickling *et al.*, 2006). Many species have exhibited northward distribution range expansion, and this trend is particularly evident in northern Europe. Some species have improved winter survival and/or advanced spring phenology. Opposite changes in abundance have been recorded in different studies: abundance decreased in a grassland community and increased in agricultural ecosystems. More extensive study is likely to reveal an even wider range of responses including physiological responses, ecological trade-offs and

increases in the number of annual generations produced by Heteroptera species with flexible life cycles.

It is difficult to predict how any particular species or communities will respond to further climate warming. Possible scenarios are vague for most, if not all, climate change components and interactions between those factors will most probably affect species at all trophic levels in very different ways. Host plants, phytophagous insects, their competitors, symbionts, predators, parasites and pathogens will not only respond individually to climate changes, but also individual responses will further affect other responses making reliable prediction extremely complicated. Responses are expected to (1) be species- or population-specific, (2) concern basically all aspects of organism/species biology and ecology (individual physiology, population structure, abundance, local adaptations, phenology, voltinism and distribution) and (3) have scales ranging from an undetectable cell level to major distribution range shift or regional extinction. The scale of insect responses will depend on the extent and rate of climate warming. Slight to moderate warming might cause responses only in limited number of species with more flexible life cycles, whereas substantial temperature increase might do so in a greater number of different species and ecological groups (Table 2).

Warming will not necessarily have only favourable effect on all insect species (Chown & Terblanche, 2006). High summer temperatures exceeding species-specific optimal zones and tolerance limits will probably negatively affect growth, reproduction and/or survival.

The *N. viridula* study shows that during the early stages of establishment following climate-change-induced range expansion, a species may be maladapted

to new environmental conditions. Phenological mismatch between local climate pattern (mostly temperature and, perhaps, availability of host plants) and timing of diapause induction driven by the photoperiodic response inherited from migrated parents may markedly affect life-history traits and result in significant reproductive losses. Success of colonization will depend firstly on the ability of migrants to withstand the extremes of seasonal physical factors, and secondly on the ability to synchronize their seasonal cycle with the local physical and biological environments, and to optimise fitness.

Acknowledgements

I sincerely thank H. Numata and K. Ito for help with Japanese data, valuable advice and comments, B. S. Nau for permission to use unpublished data (Nau, 2006), C. C. Niva for permission to use data on *H. halys* (Fig. 5), M. V. L. Barclay, J. F. Esquivel, K. Fujisaki, H. T. Jones, K. Kiritani, K. Nakamura, N. Petrishcheva, A. H. Saulich and an anonymous referee for helpful criticism and comments on the manuscript. The research was supported by the Ministry of Education, Culture, Science, Sports and Technology of Japan (Grants-in-Aid for JSPS Fellows No. 98116, STA Fellows No 200141 and the 21st Century COE Program *Innovative Food and Environmental Studies Pioneered by Entomomimetic Sciences* at Kyoto University).

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