Some like it hot! Rapid climate change promotes changes in distribution ranges of *Nezara viridula* and *Nezara antennata* in Japan

Daisuke Tougou, Dmitry L. Musolin* & Kenji Fujisaki

Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan

Abstract

We compared past and current limits of the distribution range of the southern green stink bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae), in central Japan. In the early 1960s, the northern limit of the range was in Wakayama Prefecture and was limited by a +5 °C isothermal line for the mean January temperature. In 2006–2007, a new survey demonstrated that this northern limit had shifted northwards by 85 km (i.e., at a mean rate of 19.0 km per decade). The shift was most likely promoted by milder winter conditions. The mean January to February temperature in the region was 1.03–1.91 °C higher in 1998–2007 than in 1960–1969. The number of cold days (with the mean temperature below +5 °C) also significantly decreased, while the annual lowest temperature significantly increased. *Nezara viridula* was found mostly close to those locations where (i) the mean January temperature exceeded +5 °C, (ii) the mean number of cold days did not exceed 26 in January to February, and (iii) where the mean annual lowest temperature did not drop below –3.0 °C. The general linear model shows that the mean January temperature and number of cold days are the most important factors controlling the northern limit of distribution of *N. viridula*. All the climatic data suggest that over the last 45 years, environmental conditions have become more favourable for overwintering of *N. viridula* at many locations in central Japan. This has probably promoted the northward spread of the species, representing a direct response to climate warming. A sympatrically distributed congeneric, *Nezara antennata* Scott, seems to respond to the warming by a retreat from the ocean coast towards cooler elevated habitats, which might be a complex response to elevated temperature and interspecific mating with *N. viridula*. It is suggested that the range changes in both species will continue in response to further climate change.

Introduction

Global climate warming is unequivocal. Eleven of the last 12 years (1995–2006) rank among the 12 warmest years since 1850 and the linear warming trend over the last 50 years (0.13 °C per decade) is nearly double that of the last 100 years (Houghton et al., 2001; Intergovernmental Panel on Climate Change, 2007). There is now considerable attention directed to how global biota are and will be responding to global warming (e.g., Harrington & Stork,

1995; Walther et al., 2001; Bale et al., 2002; Reemer et al., 2003). Whereas there are obvious common trends such as shifts of distribution ranges and changes in phenology, responses of each species might be unique, as each species has a specific set of ecological requirements and range of physiological responses.

The southern green stink bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae), is apparently responding rapidly to climate warming (Musolin & Numata, 2003a,b, 2004; Kiritani, 2006, 2007; Musolin, 2007; Yukawa et al., 2007). It occurs in an ever-widening range throughout tropical and subtropical regions of Eurasia, Africa, Australia, and the Americas (Yukawa & Kiritani, 1965; Panizzi et al., 2000; Yukawa et al., 2007). Japan is at the northern margin

*Correspondence: E-mail: musolin@gmail.com
Daisuke Tougou and Dmitry L. Musolin contributed equally to this work.

Figure 1 Outline of the current distribution ranges of *Nezara viridula* and *N. antennata* in Japan and location of the field surveys (see Figure 2).

of *N. viridula*'s Asian range. This species has long been distributed in the southern part of the archipelago (Okinawa, Kyushu, Shikoku, and southern Honshu), largely along the coastal belts (Figure 1; Oho & Kiritani, 1960; Yukawa & Kiritani, 1965; Tomokuni et al., 1993). In the north, *N. viridula* is replaced by a congeneric species, the oriental green stink bug, *Nezara antennata* Scott, known to occur only in Asia (Hokkanen, 1986). In Japan, the range of *N. antennata* covers Okinawa, Kyushu, Shikoku, Honshu, and Hokkaido Islands (Figure 1; Tomokuni et al., 1993). Both species, and especially *N. viridula*, are major agricultural pests damaging soybean, rice, cotton, and many other crops (Todd, 1989; Tomokuni et al., 1993; Panizzi et al., 2000). Within their respective ranges, the two *Nezara* species utilize similar resources and both species have been recorded sympatrically in mixed populations with interspecific mating in the areas of overlapping distribution (Kiritani et al., 1963; Kiritani, 1971; Yukawa et al., 2007).

In the early 1960s, Keizi Kiritani and co-workers conducted a wide-scale field survey in central Honshu and mapped the northern limit of the range of *N. viridula* in central Japan (Figures 1 and 2A; Kiritani et al., 1963; Kiritani & Hokyo, 1970). They showed that this northern limit of the species' distribution in central Japan occurred in Wakayama Prefecture (latitude approximately 34.1°N).

Nezara 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* (Figure 2A). In general, *N. viridula* was found to occur sympatrically in warmer parts of the distribution range of *N. antennata*. The area of co-existence of the two species was shown to lay on the +5 °C isothermal line for the mean temperature of the coldest month (usually January) and, thus, January temperature was proposed as the principal factor determining the northern limit of *N. viridula*'s distribution (Kiritani et al., 1963).

In areas of sympatric distribution, *N. viridula* was able to replace *N. antennata* within a few years (Sameshima, 1960; Kiritani et al., 1963), although in some cases *N. antennata* was later able to re-establish populations (Goto, 2001; Yukawa et al., 2007). Replacement was possible because *N. viridula* produced more generations a year (3–4 vs. 2 in *N. antennata*), it was 2–3 times more fecund than *N. antennata*, and benefited from promotion of early-planted rice cultivation (first-generation adults of *N. viridula* successfully exploited early-planted 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; Numata & Nakamura, 2002), whereas *N. viridula* is reproductive throughout the summer. Finally, in 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 is frequently observed and results in unfertilised eggs, which further favoured dominance of *N. viridula* (Kiritani et al., 1963; Kiritani, 1971; Kon et al., 1994). *Nezara viridula* does, however, suffer higher overwintering mortality than *N. antennata*, especially during severe winters (Kiritani et al., 1963).

Since the 1960s, several records have been published documenting a presence of *N. viridula* at locations in central Japan further north from the previously established limit of the species' distribution (Musolin & Numata, 2003a,b; Ikeda, 2006; Kiritani, 2006; Musolin, 2007; Ohno & Nakamura, 2007; Yukawa et al., 2007). Isolated records, however, can neither reveal the current limit of the *N. viridula*'s range in the region nor show its dynamics. The objectives of this study were to determine the current northern limit of *N. viridula* in central Japan, compare it with the unique 45-year-old data available from the survey of the early 1960s, and assess, using historical climate information as well as recently published ecophysiological data on the overwintering of *N. viridula*, what factors could have promoted the change in the ranges of *N. viridula* and *N. antennata* in the region.

Materials and methods

Field survey

To determine the current northern limit of *N. viridula* and the relative abundance of both *Nezara* species in central Japan, an extensive field survey was conducted in Wakayama Prefecture and in five other prefectures from late June 2006 to late August 2007. We surveyed eight locations in Wakayama Prefecture very close to those sites where Kiritani and co-workers surveyed in 1960–1962 (Kiritani et al., 1963) and 42 locations in other prefectures situated further north and north-east in central Japan (Figure 2B).

Plains, lowlands, the coastal line of the Pacific Ocean, and bases of hills and mountains were surveyed. At each location we examined different types of vegetation on large industrial agricultural fields, small private fields, road-side vegetation, etc., although *Nezara* spp. were primarily concentrated on small private fields where little or no insecticides were used by growers (as we were informed on several occasions). At each location, 30–60 min were spent searching for adults and nymphs of both species on vegetation. Both *Nezara* species were found on and collected from maize (*Zea mays* L., Poaceae), soybean [*Glycine max* (L.) Merill, Fabaceae], okra [*Abelmoschus esculentus* (L.) Moench., Malvaceae], common bean (*Phaseolus vulgaris* L., Fabaceae), and tomato (*Solanum lycopersicum* L., Solanaceae). Only *N. viridula* was found on curly dock (*Rumex japonicus* Houttuyn, Polygonaceae), cabbage (*Brassica oleracea* var. *capitata* DC), and Chinese cabbage [*Brassica rapa* var. *chinensis* (L.) Hanelt] (both Brassicaceae), and only *N. antennata* on green shiso [*Perilla frutescens* (L.) Britt., Lamiaceae] and bitter melon (*Momordica charantia* Descourt, Cucurbitaceae). Collected adults were identified to species on site. Nymphs were taken to the laboratory, reared on soybean and raw peanuts (*Arachis hypogaea* L., Fabaceae) (see, for details, Musolin & Numata, 2003a), and identified upon emergence of adults.

Details of the field survey (exact locations, dates, and number of bugs of each species collected) are available upon request. Voucher specimens were deposited at the Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kyoto, Japan. Additionally, three field records from 1999–2003 were also included in the data set (see Figure 2B).

Climate data

Three data sets were used in the analysis of thermal conditions (Japan Meteorological Agency, 2007). First, we calculated averages of the monthly mean temperature from autumn to spring (October–March) at meteorological stations close to the capital cities of all six prefectures for the decade of the previous field survey (1960–1969)
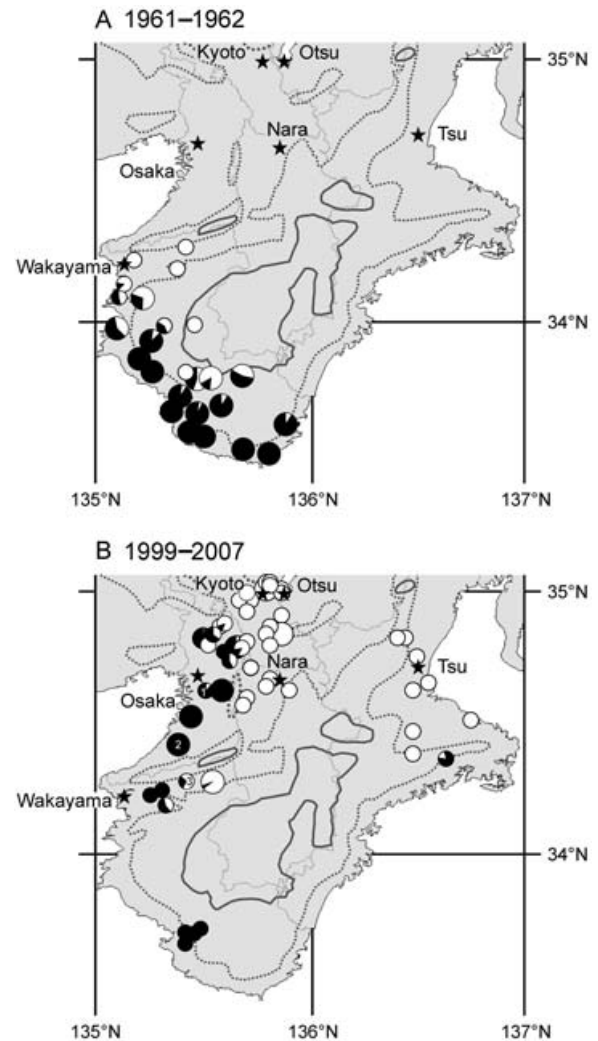

Figure 2 Distribution and relative abundance of *Nezara viridula* and *N. antennata* in central Japan in (A) the early 1960s (from Kiritani et al., 1963; Kiritani, 1971) and (B) 2006–2007 (this study). Symbols: black sections, *N. viridula*; white sections, *N. antennata*. Sample size: small circles, 1–50 specimens; large circles, > 50 specimens. Six prefectures in central Japan are outlined and their capital cities are indicated as stars. Elevation (simplified): dotted line, 500 m above sea level; solid black line, 1000 m above sea level. In addition to the data from the 2006–2007 field survey, the following data points are included (numbered on map B): (1) data from Musolin & Numata (2003a) and Musolin (2007) (collected in 1999); (2) data from Dr. H. Tanaka (collected in 2003; pers. comm.; see Yukawa et al., 2007); (3) data from Dr. M. Morishita (collected in 2002; pers. comm.; see Yukawa et al., 2007).

and compared them with the corresponding averages of the latest decade (1998–2007), except for Otsu city, for which the 1960–1969 data set was not available and one for 1978–1987 was used instead (Figure 3). Then, we
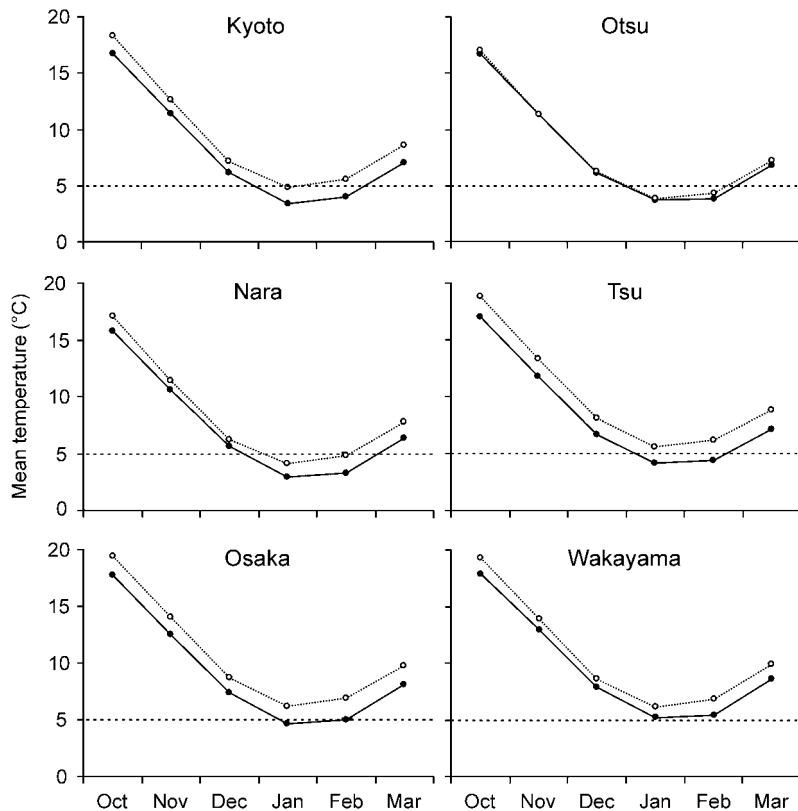
Figure 3 Average monthly mean temperature in 1960–1969 (solid lines) and 1998–2007 (dotted lines) in six capital cities of prefectures in central Japan (except Otsu City, for which averages for 1978–1987 are shown instead of 1960–1969) (data from Japan Meteorological Agency, 2007).

calculated and compared the annual mean numbers of days with the daily mean temperature below +5 °C (further referred to as cold days) during the two coldest months (January and February) and the mean annual lowest temperature in the same capital cities of the six prefectures during the same decades (with the same exception for Otsu City; Figure 4). To reveal whether there was any correlation among these three parameters, a regression analysis was performed using the same sets of data. Finally, to characterize the current climatic conditions in the region, the data on the mean January temperature, mean number of cold days in January and February, and mean annual lowest temperature during 2003–2007 were mapped and analysed (Figure 5). To examine which of the climatic factors play the most significant role in controlling the distribution of *N. viridula*, a general linear model was constructed. For statistical analysis, the JMP release 5.1.2 statistical package (SAS Institute, Cary, NC, USA) was used. All means are followed by ± standard deviation.

Results

Field survey

During the 2006–2007 field survey, 661 individuals of *N. viridula* and 694 individuals of *N. antennata* were

collected. Together with the data from three additional collections, 770 and 705 individuals, respectively, were recorded at 53 locations in the six prefectures. *Nezara viridula* was present at 20 locations and its abundance relative to the total number of *Nezara* spp. individuals ranged from 4.7 to 100% at those locations (Figure 2B).

At the three northernmost locations in Wakayama Prefecture, only *N. antennata* was recorded in the early 1960s (Figure 2A; Kiritani et al., 1963). In contrast, *N. viridula* was not only present but even dominated there in the 2006–2007 field survey (Figure 2B). *Nezara viridula* is also present now at two other nearby locations in the same prefecture situated further from the coast towards the mountains (i.e., in cooler and, thus, more typical habitats of *N. antennata*) (Figure 2B).

Inspections in Osaka Prefecture (north of Wakayama Prefecture) showed a wide distribution of *N. viridula*. It was found in 11 of 14 locations and dominated in 8 of 10 locations where both species were found. In the three more northern and inland prefectures (namely, Nara, Kyoto, and Shiga Prefectures), only *N. antennata* was recorded despite an intensive search. Finally, in the easternmost of all visited prefectures (namely, Mie Prefecture), out of nine locations surveyed, *N. viridula* was present and dominated only at one, situated southernmost and approximately 16 km from the Pacific Ocean.
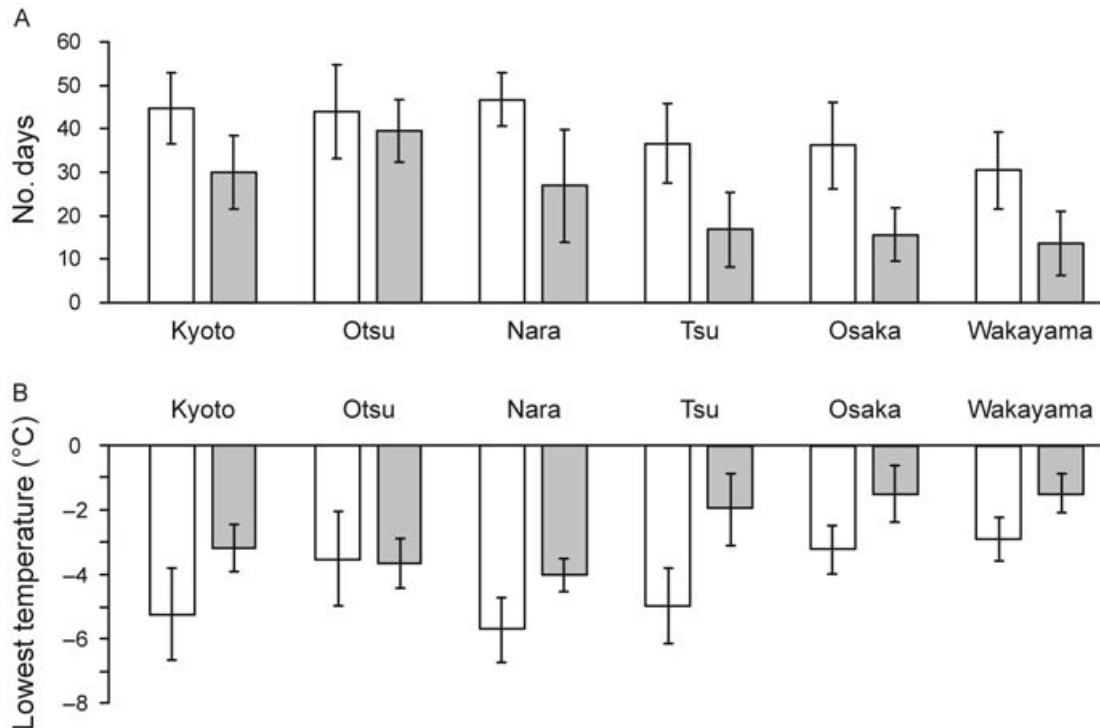
Figure 4 (A) Mean (± standard deviation) number of days in January–February with a daily mean temperature below +5.0 °C (i.e., cold days) and (B) the mean (± standard deviation) annual lowest temperature in 1960–1969 (white bars) and 1998–2007 (grey bars) in six capital cities of prefectures in central Japan (except Otsu City, for which means for 1978–1987 are shown instead of 1960–1969) (data from Japan Meteorological Agency, 2007). In all cases, except Otsu City, the means are significantly different [t-test: t = 2.262–7.620, d.f. = 9, P<0.001; for Otsu City t = 1.104, d.f. = 9, P = 0.3 (A) and t = 0.263, d.f. = 9, P = 0.76 (B)].

Rapid climate warming in central Japan

Data on mean monthly temperature during the over-wintering period (October–March) at six meteorological stations over the range of the field survey show that at five locations mean January and February temperature was 1.03–1.91 °C higher during the last decade (1998–2007) than it was during the decade of the previous field survey (1960–1969, Figure 3). The mean temperature increased much less (0.1 °C in January and 0.4 °C in February) only in Otsu City, although for this location the data set for 1960–1969 was not available, and one for 1978–1987 was used instead, thus shortening the period for comparison to only 20 years. In the 1960s, the coldest month's temperature exceeded the critical +5 °C level only in Wakayama City. Due to warming during the last 45 years, the mean January temperature has exceeded the +5 °C level in Osaka and Tsu, and Kyoto is also very close (4.81 °C; Figure 3).

The mean number of cold days in January–February significantly decreased at five locations from 1960–1969 to 1998–2007 (t-test: t = 2.262–7.620, d.f. = 9, P<0.001 for all locations; Figure 4A). This parameter tended to decrease in

Otsu as well from 43.6 ± 10.76 days in 1978–1987 to 39.1 ± 7.11 days in 1998–2007, although the difference was not statistically significant (t-test: t = 1.104, d.f. = 9, P = 0.3). The mean annual lowest temperature significantly increased at five locations from 1960–1969 to 1998–2007 (t-test: t = 3.522–5.558; d.f. = 9, P<0.001 for all locations; Figure 4B), with the mean temperature increase ranging between 1.4 and 3.0 °C.

Relationships between thermal overwintering parameters

The three characteristics analysed above represent different facets of 'climatic overwintering conditions' and are likely to have varying importance for insect survival and distribution. A pairwise regression analysis including 120 data points (six locations during the two decades) demonstrated that the mean January temperature, the annual lowest temperature, and the number of cold days in January–February are significantly correlated (not shown), with the strongest relationship between the mean January temperature and the mean annual lowest temperature (F = 150.881, d.f. = 119, P = 7.67 × e^{-23}, r^2 = 0.561).
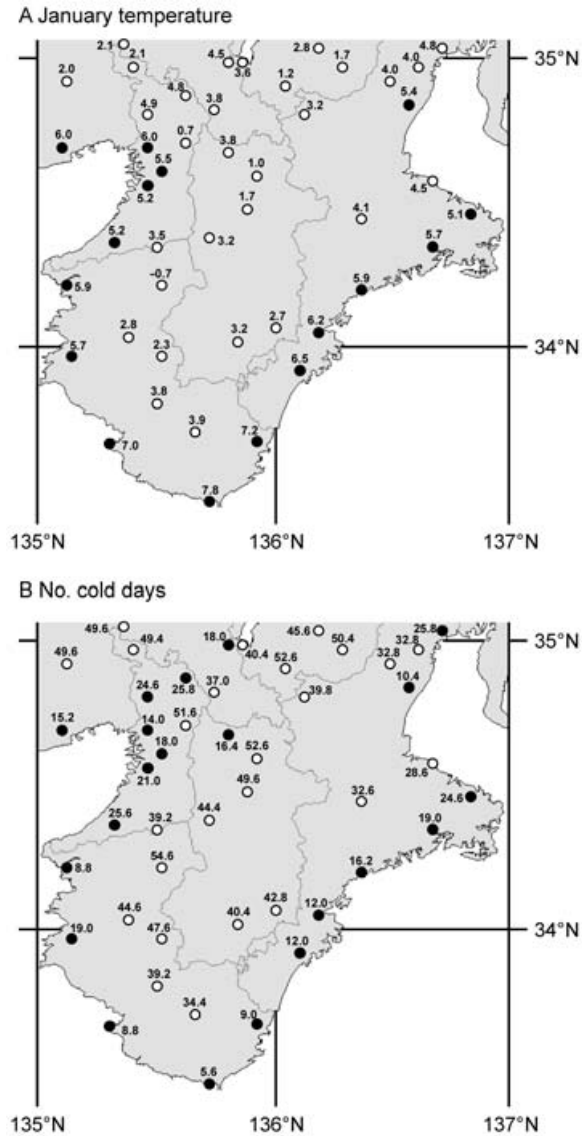
A January temperature

B No. cold days

Figure 5 (A) The average mean January temperature and (B) the average number of days in January–February with daily mean temperature below +5.0 °C (i.e., cold days) during 2003–2007 in central Japan (data from Japan Meteorological Agency, 2007). Black circles, (A) locations with average temperature above +5.0 °C or (B) those with fewer than 26 cold days; white circles, (A) locations with average temperature below +5.0 °C or (B) those with more than 26 cold days.

Climatic conditions determining the current distribution of *Nezara viridula*

Temperature data for 2003–2007 (i.e., just before and during our survey) from 46 local meteorological stations showed that the average monthly mean January temperature exceeded +5 °C at most locations along the

coast (Figure 5A). At the same locations, the number of cold days was low (Figure 5B) and the annual lowest temperature was high (not shown). Going deeper inland results in a rather sharp drop of temperature and greatly prolonged cold period, because a considerable part of the territory is undulating and mountainous, where it is always cooler than in maritime areas (see Figure 2 for data on elevation).

A comparison of the climatic and distribution data revealed that the incidence of *N. viridula* tended to be low or the species was absent north of the latitude 34.6°N, at the locations where the mean January temperature was below +5.0 °C, annual lowest temperature was below −3.0 °C, and the number of cold days exceeded 26. The pairwise regression analysis indicated that each of these parameters was significantly correlated with the incidence of *N. viridula* ($P < 0.02$). The constructed general linear model (incorporating three climatic parameters and their interactions) revealed that the mean January temperature and the number of cold days significantly control the northern limit of distribution of *N. viridula* (Table 1). The effect of the annual lowest temperature is not significant.

Table 1 General linear model showing relationships between the relative abundance of *Nezara viridula* and overwintering thermal conditions[1]

Source	d.f.	F	P
January mean temperature (°C) [a]	1	12.558	0.0009
Annual lowest temperature (°C) [b]	1	0.006	0.9402
Number of cold days [c]	1	5.267	0.0266
a*b	1	3.231	0.0791
b*c	1	0.825	0.3686
a*c	1	3.380	0.0727
a*b*c	1	0.442	0.5099

[1]Dependent variable is the proportion of *N. viridula* (after arcsine transformation) in the total number of *Nezara* spp. individuals collected. Climatic data are means for 2003–2007 at the nearest meteorological stations (see Figure 5 and the text for details).

Discussion

The growing body of information suggests that, as with other insects, many true bug species respond (or are reasonably expected to respond) to current climate warming in varying ways: they change distribution ranges and abundance, shift phenology, alter voltinism, experience physiological and behavioural changes, and modify community structure (Musolin & Fujisaki, 2006; Kiritani, 2007; Musolin, 2007). In many cases, range expansion is recorded when new species invade countries or regions

where they have never been recorded (e.g., Nau, 1997; Aukema, 2003; Reemer et al., 2003; Smith et al., 2007; Rabitsch, 2008). In contrast to some other insect taxa (e.g., Reemer et al., 2003), however, range shifts of true bugs have hardly ever been documented based on wide-scale field surveys repeated in the same regions over years (Eyre et al., 2005; Hickling et al., 2006). Furthermore, ecophysiological mechanisms behind range expansion have never been demonstrated for heteropterans.

Range shift and its rate

The comparison of our data (Figure 2B) with the data of the early 1960s survey (Figure 2A) demonstrates that during the last 45 years, *N. viridula* has considerably shifted the northern limit of its distribution range northwards in central Japan. Northwards, this shift is about 85 km over the study period (i.e., at a mean rate of about 19.0 km per decade). The comparison of range shift rates obtained in different regions and studies can only be an approximation (Parmesan, 2006, 2007). The rate of 19.0 km per decade fits very well in the range of 13.7–24.8 km per decade reported as the mean northward range extension rates for various large data sets for southern vertebrates and invertebrates studied in Great Britain (Hickling et al., 2006), although it exceeds previously reported mean rates for other organisms: 6.1 ± 2.4 km per decade (for 99 species of birds, butterflies, and herbs worldwide; Parmesan & Yohe, 2003) and 9.5 km per decade (for 59 southern British birds; Thomas & Lennon, 1999).

Climatic and ecophysiological backgrounds of the range shift in *Nezara viridula*

The climate is getting warmer in Japan, with the areal mean warming trend of 0.08 °C per decade (0.05–0.11 °C per decade in different parts of the country; based on temperature data for 1920–1992; Kato, 1996). Other studies provide similar estimates (Japan Meteorological Agency, 1993; Park-Ono et al., 1994). This positive trend is most noticeable in winter and spring (the areal mean of 0.1–0.16 °C per decade; Kato, 1996).

As discussed earlier (Musolin, 2007), the distribution of *N. viridula* is not limited by the factors that typically limit insect distribution ranges (namely, seasonal sum of effective temperatures or the availability of food or habitat), because the species is multivoltine even close to its northern range limit and very polyphagous. Instead, winter temperature plays the critical role. Mortality of the overwintering adults greatly depends on ambient temperature: as few as 2.5% of adults survived the very severe winter of 1962/1963 in Wakayama Prefecture when mean January temperature fell to +2.9 °C, whereas survival rate is much higher in warm winters (Kiritani et al., 1966;

Kiritani, 1971, 2007; Musolin & Numata, 2003b). Decrease of 1 °C of mean January temperature results in an approximately 15–16% increase in mean overwintering mortality (Kiritani, 2007; Musolin, 2007). It was suggested that the +5 °C isothermal line of the coldest month (usually January) limits at the north the distribution range of *N. viridula* and, thus, the area of co-existence of two *Nezara* species (Kiritani et al., 1963).

The situation, however, is not so clear in other cases. For instance, the species was recorded in autumn 2005 at two locations [Hinase (34.7°N, 134.2°E) and Ushimado (34.6°N, 134.1°E); Ohno & Nakamura, 2007], where the winters are colder [January mean temperature was $+3.7 \pm 0.7$ °C, mean number of cold days was 39.6 ± 5.5, and average of the annual lowest temperature was -5.1 ± 0.8 °C in 2001–2005 at the nearest meteorological station in Mushiage (34.7°N, 134.2°E); Japan Meteorological Agency, 2007]. Thus, *N. viridula* was recorded in places where overwintering conditions were more severe than our estimates. These insects, however, were collected only during one autumn and, thus, might represent temporal populations that did not survive the subsequent winter. The success of the invasion of *N. viridula* greatly depends not only on climatic conditions, but also on availability of proper overwintering sites and complex relationships with the congeneric *N. antennata* (Kiritani et al., 1962, 1963, 1966).

All temperature data suggest that over the last 45 years, climatic conditions have become more favourable for overwintering of *N. viridula* at many locations in central Japan (Figures 3 and 4). This most probably has promoted the observed northward range expansion of the species in this region. Although the 'heat island' effect is considered local and of negligible influence on a global scale (less than 0.006 °C per decade over the land; Intergovernmental Panel on Climate Change, 2007), it is an important factor on a regional scale. In large Japanese cities with populations exceeding 100 000, the urban-effect temperature increase exceeds the natural temperature increase and can reach 0.1–0.25 °C per decade (Kato, 1996). The 'heat island' phenomenon is especially pronounced in winter and spring (Kato, 1996). This effect has possibly both contributed to local warming and promoted the northward range expansion of *N. viridula* (Kiritani, 2001; Ohno & Nakamura, 2007) as has recently been suggested for a pirate bug, *Orius strigicollis* (Poppius) (Shimizu et al., 2001). The rates of temperature increase are higher in large cities than in rural areas (Kato, 1996). For example, the mean January temperature in Osaka City (35.0°N, 135.8°E) increased from $+4.62 \pm 1.04$ °C in 1960–1969 to $+6.18 \pm 0.84$ °C in 1998–2007 (t-test: t = 3.703, d.f. = 9, P = 0.002), while in the small town of Shionomisaki (33.45°N, 135.76°E), it increased from $+7.22 \pm 1.25$ °C to $+8.13 \pm 0.84$ °C over

the same period (t-test: t = 1.906, d.f. = 9, P = 0.073). Thus, the increase against the corresponding means for the 1960s is 1.56 ± 0.84 °C in Osaka and only 0.91 ± 0.84 °C in Shionomisaki (t-test: t = 1.728, d.f. = 9, P = 0.101). Whereas *N. viridula* was collected over a wide range of different landscapes (suburban as well as rural) in summer, it might suffer lower overwintering mortality in vast urban areas, which are warmer than rural landscapes in winter.

The analysis of distribution and temperature maps suggests that *N. viridula* is most likely to be present at lowland locations where not only the mean January temperature exceeds +5.0 °C (as earlier suggested by Kiritani et al., 1963), but also where the mean number of cold days does not exceed 26 in January–February and where the mean annual lowest temperature does not drop below –3.0 °C (Figures 2 and 5). The annual lowest temperature is less important than the former two parameters in limiting of the distribution range of *N. viridula* (Table 1) and this finding supports those from other locations (Ohno & Nakamura, 2007).

Results of two independent outdoor experiments partly confirm these estimates. *Nezara viridula* was monitored under quasi-natural conditions in Osaka during the winter of 1999/2000 (mean January temperature +7.0 °C, 24 cold days, and annual lowest temperature –0.4 °C) and the mean survival rate ranged from 81 to 97% in different experimental cohorts (Musolin & Numata, 2003b, 2004; Musolin, 2007). In a similar experiment in Kyoto during the colder winter of 2006/2007 (+5.8 °C in January, 10 cold days, annual lowest temperature –2.4 °C), the mean survival rate varied from 38 to 75% (D Musolin, D Tougou & K Fujisaki, unpubl.). In both these cases, conditions were milder than the estimates for the distribution limit indicated above (mean January temperature +5.0 °C, 26 cold days, lowest temperature –3.0 °C) and *N. viridula* survived the winters with varying degree of success.

Response of *Nezara antennata*

The ecology of the congeneric species, *N. antennata*, is less well studied and, thus, it is more difficult to assess the effects of climate warming on this species. It has been shown, however, that the range of favourable temperatures is narrower in *N. antennata* (22.5–27.5 °C) than in *N. viridula* (20.0–30.0 °C; Kariya, 1961). It has been suggested that to escape from the summer heat, *N. antennata* evolved an aestivation (Noda, 1984; Numata & Nakamura, 2002). Increasing summer temperature due to global warming may be unfavourable and, thus, contribute to the retreat of *N. antennata* from the coast into cooler inland hills and mountains, a trend that was observed in our field survey in the northern part of Wakayama Prefecture (cf. Figure 2) and elsewhere (Yukawa et al., 2007).

Effects above the species level

It has been argued that climate change is and will be affecting organisms of all trophic levels as well as interactions among different species (Davis et al., 1998). Under elevated temperature conditions, *N. viridula* will probably be able to produce one additional generation annually, while its egg parasitoids might increase the number of annual generations by two to four, thus increasing the biotic pressure on *N. viridula* (Kiritani, 2006; Yukawa et al., 2007). At the same time, changes in voltinism of *N. antennata* are very unlikely because this species spends part of the summer in aestivation (Noda, 1984; Numata & Nakamura, 2002).

Interspecific mating between *N. viridula* and *N. antennata* is often observed (Kiritani et al., 1963; Yukawa et al., 2007; D Tougou & D Musolin, unpubl.) and is believed to contribute to decreased abundance of *N. antennata* and sometimes even to a total replacement of this species by *N. viridula* (Kiritani et al., 1963). Reproductive interference is believed to be stronger than, for example, resource competition (Kuno, 1992). So far, it is difficult to predict how relationships between all these factors will be influenced under rapidly changing environmental conditions, though the repeated field survey clearly showed the northward expansion of *N. viridula* and retreat of *N. antennata* from the coast into the inland hills and mountains.

Conclusions

Two wide-scale surveys conducted in Wakayama Prefecture in the early 1960s (Kiritani et al., 1963; Kiritani, 1971) and in and around the same region in 2006–2007 (this study) as well as the comprehensive knowledge of the overwintering ecology of *N. viridula* (Kiritani et al., 1962, 1963, 1966; Kiritani & Hokyo, 1970; Musolin & Numata, 2003a,b; Kiritani, 2006, 2007; Musolin, 2007; Musolin et al., 2007) made it possible not only to document the northward shift of the species' northern limit, but also to suggest that the range changed because the overwintering conditions (which are critical for the species' survival) became more favourable in the region.

It has been repeatedly suggested that insects as well as other biota would respond to climate warming both directly and indirectly (e.g., Harrington et al., 1999; Hughes, 2000; Walther et al., 2002; Hickling et al., 2006; Musolin, 2007). *Nezara viridula* is clearly expanding its range northwards and, as this study shows, provides an example of a direct response to increased temperature. It remains unknown whether the overall range of the congeneric species, *N. antennata*, is changing or not, but within its range *N. antennata* retreats from ocean coastal areas towards cooler hills and bottoms of mountains and, thus, might

represent a more complex response including, but probably not limited to, reaction to elevated temperature and interspecific mating with *N. viridula*.

In the near future, as global warming continues, *N. viridula* will most probably continue its northward expansion starting along the coast (where winters are milder) and in the urban areas (due to the 'heat island' effect). Establishing new permanent populations will greatly depend on winter climatic conditions and the ability of the species to adjust its physiological mechanisms of diapause induction (Musolin & Numata, 2003b; Musolin, 2007).

Acknowledgements

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