

## SHORT COMMUNICATION

# Photoperiodic response in the subtropical and warm-temperate zone populations of the southern green stink bug *Nezara viridula*: why does it not fit the common latitudinal trend?

DMITRY L. MUSOLIN<sup>1,2,3</sup>, DAISUKE TOUGOU<sup>1</sup> and KENJI FUJISAKI<sup>1</sup>

<sup>1</sup>Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kyoto, Japan, <sup>2</sup>Department of Entomology, Saint Petersburg State University, Saint Petersburg, Russia and <sup>3</sup>Department of Forest Protection and Game Management, Saint Petersburg State Forest Technical Academy, Saint Petersburg, Russia

**Abstract.** The photoperiodic response of diapause induction is studied in females of five subtropical and warm-temperate zone populations of *Nezara viridula* (L.) (Heteroptera: Pentatomidae) in Japan (26.4–34.7°N; 127.4–135.7°E). Laboratory tests at 25 °C demonstrate that both warm-temperate and subtropical populations have pronounced photoperiodic responses of adult diapause induction. Under short-day conditions (LD 10 : 14 h), 73–100% of females enter diapause, whereas, under long-day conditions (LD 15 : 9 h), 87–100% of females are nondiapause and reproduce. When the critical photoperiod for diapause induction is plotted against the latitude of origin of each population, the data points do not show the expected tendency of increasing critical photoperiod northwards but, instead, vary between 12 h 15 min and 13 h 30 min. It is suggested that adults from different populations of such a highly migratory species move often among subtropical islands (by themselves or being assisted by typhoons), thus constantly destabilizing the photoperiodic responses. Although important for general synchronization of seasonal development in the tropics and subtropics, winter diapause might not be so critical for survival in mild winters in these zones. Such circumstances might make the selective pressure over the photoperiodic response less severe in the tropics and subtropics than in the temperate zone. It is suggested that the current climate warming might contribute to this situation as well by promoting polewards migrations and lessening the selective pressure of overwintering conditions.

**Key words.** Climate warming, diapause induction, geographical difference, Hemiptera (Heteroptera), migration, Pentatomidae, photoperiodism, seasonal adaptations.

## Introduction

Most research on insect diapause focuses on winter diapause induction in the species and populations from the temperate zone where winter is a critical season for survival (Danks, 1987; Saunders, 2002). It is often considered that, in the tropics

and subtropics, diapause is less important, at least for survival in winter. Some insect populations from these regions are known to have no or weakly pronounced photoperiodic responses of diapause induction, whereas this response is the principal overwintering adaptation for the population from the temperate zone (Denlinger, 1986; Shimizu & Kawasaki, 2001; Saunders, 2002). For example, the subtropical populations of the cotton bollworm *Helicoverpa armigera* show a low incidence of diapause, even when photoperiod and temperature decrease, whereas the temperate populations show a high incidence of diapause under the same conditions (Shimizu &

Correspondence: Dr Dmitry L. Musolin, Faculty of Biology and Soil Sciences, Department of Entomology, Saint Petersburg State University, Universitetskaya nab., 7/9, Saint Petersburg 199034, Russia. Tel.: +7 921 3259186; e-mail: musolin@gmail.com

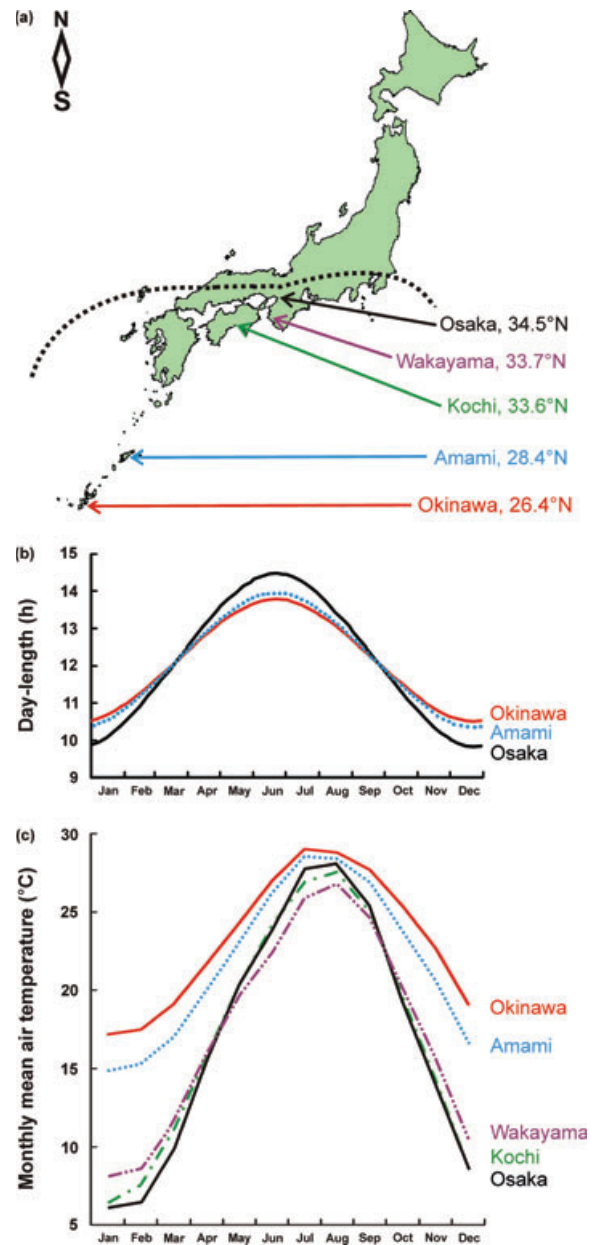
Fujisaki, 2002). However, it is also found that some subtropical insects, such as the ground cricket *Dianemobius fascipes* (Masaki, 1990) and the oriental chinch bug *Cavelerius saccharivorus* (Fujisaki, 1993), show marked egg diapause, although it has a large variation in its intensity within a population. Despite considerable efforts made over several decades, our current understanding of the ecological importance and physiological basis of winter diapause in the tropics and subtropics remains fragmentary.

The present study aims to evaluate geographical differences in the photoperiodic response of winter diapause induction in five subtropical and warm-temperate zone populations of the southern green stink bug *Nezara viridula* (L.) (Heteroptera: Pentatomidae).

*Nezara viridula* is a polyvoltine seed-sucking pentatomid and occurs throughout tropical, subtropical and warm-temperate regions of the world (Panizzi et al., 2000; Musolin, 2007). It is considered to have African (more precisely, Ethiopian) origin (Hokkanen, 1986; Jones, 1988; Kavar et al., 2006). At least in the warm-temperate populations, the adults overwinter in a state of adult diapause (Jones & Sullivan, 1981; Musolin & Numata, 2003; Takeda et al., 2010). In these populations, the induction of winter diapause is controlled by photoperiod and is associated with reversible seasonal polyphenism: adults change body colour from green to russet (= reddish-brown) for overwintering (Ali & Ewies, 1977; Musolin & Numata, 2003; Takeda et al., 2010). In Japan, *N. viridula* has been known from subtropical Kyushu Island since 1874 (Kiritani, 2011). Recently, the species is noted to have expanded its range into the warm-temperate zone and to have reached the central part of the archipelago (Musolin & Numata, 2003; Musolin, 2007; Tougou et al., 2009; Yukawa et al., 2009; Kiritani, 2011). Laboratory experiments reveal a variable photoperiodic response of diapause induction with a comparatively short critical day length in the Osaka population (Musolin & Numata, 2003). Such a photoperiodic response determines relatively late diapause induction in *N. viridula* compared with several other seed-sucking heteropterans native to the Osaka region (Musolin, 2007). Although those studies provide some insight into the photoperiodic control of diapause induction in the warm-temperate zone close to the northern edge of the species' range, there is currently no information available regarding the presence of diapause in the seasonal cycle of *N. viridula* further towards equator, except for studies reporting that low-intensity reproduction is observed in this species during the colder weeks or months in India (23°N) (Singh, 1973) and southern Brazil (23°S) (Panizzi & Hirose, 1995; A. R. Panizzi, personal communication).

## Materials and methods

Approximately 50 female/male pairs of *N. viridula* were collected in summer 2006 at four locations in Japan (Fig. 1a): on Okinawa Island (26.4°N, 127.4°E), on Amami-Oshima Island (referred to as Amami; 28.4°N, 129.3°E), around Kochi City (33.6°N, 133.6°E) and around Wakayama City (33.7°N, 135.7°E). Okinawa and Amami populations represent the



**Fig. 1.** (a) A map of Japan showing the origin of populations used in the present study and the current northern limit of distribution range of *Nezara viridula*. (b) Seasonal changes of natural day-length in Okinawa, Amami and Osaka, without civil twilight; data for Kochi and Wakayama are not shown because the difference is within 2–6 min from those of Osaka (Japan Meteorological Agency, 2011). (c) Seasonal changes of natural monthly mean air temperature in the origin sites of five populations; averages for 1996–2005 (Japan Meteorological Agency, 2011).

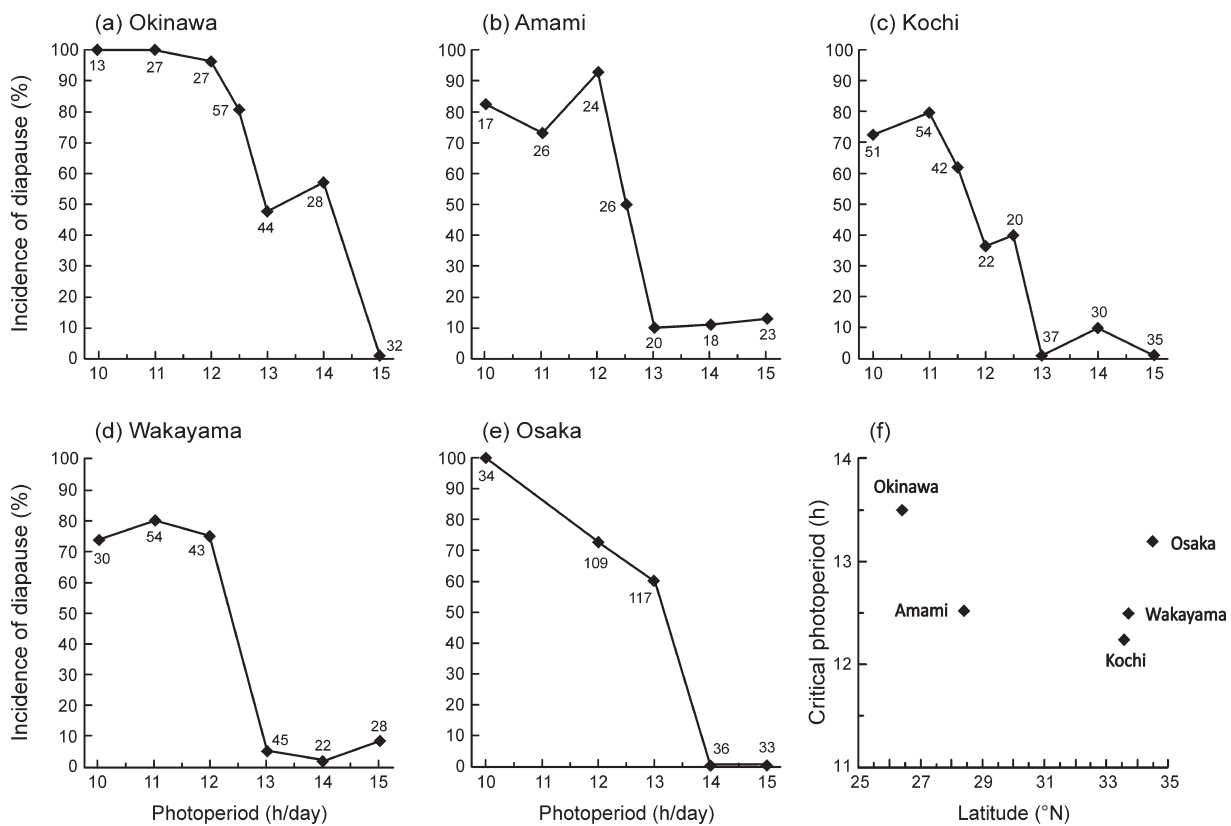
subtropics, whereas those from Kochi and Wakayama represent the warm-temperate zone (Fig. 1b, c). The insects were transferred to Kyoto University to establish a laboratory stock culture. They were reared under an LD 16 : 8 h photocycle at  $25. \pm 1$  °C and supplied with dry soybeans *Glycine max*,

shelled raw peanuts *Arachis hypogaea* and water containing 0.05% sodium L-ascorbate and 0.025% L-cysteine (Musolin & Numata, 2003). The second laboratory generation was used to obtain the photoperiodic response curves for adult diapause induction for each population.

Each egg mass laid in the stock culture was divided into two or three parts, each of which was used in the subsequent experiment in different regimes to provide a higher heterogeneity of the experimental material. The eggs were transferred to transparent plastic containers (diameter 90 mm, depth 45 mm; lids with openings of 45 mm in diameter for aeration covered with mesh) to one of six constant photoperiodic conditions: LD 10 : 14 h, LD 11 : 13 h, LD 12 : 12 h, LD 13 : 11 h, LD 14 : 10 h and LD 15 : 9 h at  $25 \pm 1$  °C. In four cases (Fig. 2a–e), two additional regimes were used: LD 11.5 : 12.5 h and LD 12.5 : 11.5 h at  $25 \pm 1$  °C. Upon hatching, nymphs, and subsequently adults, were provided with the same diet as the stock culture. Food and water were replaced every other day. The density of nymphs was maintained at 40–80 per container for the first and second instars and then gradually reduced to five or six per container by the final (fifth) nymphal instar. After adult emergence, female/male pairs were transferred to a new container and maintained, as described above, for a further 30 days under the same conditions.

Diapause status was judged in females because the response is similar in two sexes (Musolin & Numata, 2003). Start of oviposition was recorded daily and ovipositing females were considered to be nondiapausing. Diapause status of non-ovipositing females was judged on day 30 after emergence by the degree of development of gonads, spermatheca and fat body, as well as by body colour. Non-ovipositing females were dissected and those with clear ovarioles and no oocytes in the germaria, with small empty spermathecae and extended and dense fat bodies, were considered to be in diapause (Musolin & Numata, 2003; Esquivel, 2009; Takeda *et al.*, 2010). Diapause females of *N. viridula* typically had russet (= reddish–brown) body colour (Musolin & Numata, 2003). The critical day-length of diapause induction was determined as the point on the photoperiodic response curve at which diapause is induced in 50% of those individuals that entered diapause in a particular population. This method was applied because the incidence of diapause in three populations did not reach 100% at any tested photoperiod.

For comparison, data from a similar study on the photoperiodic response of diapause induction of the Osaka population were used ( $34.7^{\circ}\text{N}$ ,  $135.5^{\circ}\text{E}$ ) (Musolin & Numata, 2003). In that previous study, the same protocols were used to rear *N. viridula* and to judge the diapause status, although females were dissected on day 60 instead of day 30.



**Fig. 2.** (a–e) Photoperiodic response curves for diapause induction in females of *Nezara viridula* from different populations (at  $25$  °C; sample size is shown under each data point on the curves; data for Osaka (e) are from Musolin & Numata, 2003). (f) Comparison of the critical photoperiods for diapause induction in females among five populations of *N. viridula*.

## Results and Discussion

Both warm-temperate and subtropical populations of *N. viridula* demonstrated a pronounced photoperiodic response of adult diapause induction: under short-day conditions (10–11 h of light per day), 73–100% of females entered diapause, whereas, under long-day conditions (14–15 h of light per day), 43–100% of females were reproductive (Fig. 2a–e). In all cases, photoperiodic response curves had a shape characteristic for the long-day type response of the temperate zone populations of insects.

When critical photoperiod for diapause induction was plotted against the latitude of origin of each population, the data points did not show the expected tendency of increasing critical photoperiod northwards but, instead, varied between 12 h 15 min (Kochi) and 13 h 30 min (Okinawa) (Fig. 2f). The critical photoperiod was approximately 1 h shorter in the Amami population than in the Okinawa population, and even shorter in the Kochi population despite the higher latitudes of Amami and Kochi compared with that of Okinawa. From Kochi and Wakayama to Osaka, the critical photoperiod was increasing (Fig. 2f), as expected.

The results obtained in the present study are somewhat unexpected. Although diapause is still poorly studied in the tropics and subtropics, the known examples often (although not always) show that species and populations in these zones lack winter diapause or show a low or variable diapause incidence (Denlinger, 1986). Such examples are known for heteropterans too. Thus, in the anthocorids *Orius strigicollis* and *Orius sauteri*, the incidence of diapause, even under short-day conditions, decreases towards subtropics and does not exceed 20% in Kochi and Okinawa, whereas it is much higher in other more northern populations (Ito & Nakata, 2000; Shimizu & Kawasaki, 2001; Musolin *et al.*, 2004). The incidence of diapause is also very low under all tested photoperiodic conditions in the Okinawa population of *Orius tanthillus* and the Canary Island population of *Orius albidipennis* (van den Meiracker, 1994; Shimizu & Kawasaki, 2001). Field experiments further show that *O. tanthillus* has no winter diapause on Okinawa (Nakashima & Hirose, 1997). Five tropical lygaeid species of *Oncopeltus* and three tropical populations of *Oncopeltus fasciatus* also demonstrate no symptoms of diapause under short-day conditions (4–19°N) (Dingle *et al.*, 1980). By contrast to these examples, both warm-temperate and subtropical populations of *N. viridula* have a pronounced photoperiodic induction of adult diapause with a high incidence of diapause under short-day conditions, even at a relatively high temperature (25 °C), and this response does not weaken southwards (Fig. 2). This finding suggests that adults in all tested populations spend winter in a diapause state, even though the thermal conditions of these subtropical islands (Fig. 1b, c) (Japan Meteorological Agency, 2011) might allow winter survival in a physiologically active state without entering adult diapause. On the other hand, winter diapause is important for the synchronization of seasonal development, and its adaptive value should prevent diapause from vanishing, even in tropical populations. Among subtropical heteropterans, the presence of winter dormancy is known, for example, in the pyrrhocorid *Dysdercus decussatus*

from Ishigaki-Jima Island (24°N) (Kohno & Bui Thi, 2005). Some other tropical and subtropical heteropterans in addition to (or instead of) winter diapause have summer diapause (aestivation); for example, the pentatomid *Scotinophara lurida* in Sri Lanka (6°N) (Fernando, 1960), the pyrrhocorid *Odontopus sexpunctatus* in Nigeria (7°N) (Entwistle, 1968) and the alydid *Stenocoris elegans* on Ivory Coast (8–9°N) (Rödel & Brändle, 1995). At Barro Colorado Island (8–9°N), the tropical rhopalid *Jadera aeola* enters what is likely to be an aestival–hibernal diapause, although day length does not appear to be involved in induction (Tanaka *et al.*, 1987). Clearly, the nondiapause state of *N. viridula* females under long-day conditions in the present study suggests that adults in these subtropical and warm-temperate populations do not aestivate, even though adult aestivation for survival during hot dry months has been observed in the Indian population of this species (23°N) (Singh, 1973).

It is much more difficult to interpret the absence of the expected northward increasing cline for the critical photoperiod for diapause induction among the five studied populations (Fig. 2f), one similar to those known for a few temperate zone heteropterans (Solbreck & Sillén-Tullberg, 1981; Ito, 1985; Ito & Nakata, 2000) and many nonheteropteran insects (Danks, 1987; Saunders, 2002). An explanation for this discrepancy might be the strong migratory nature of *N. viridula*. This species is a good flier and pre- and post-diapause migrations to and from the overwintering sites comprise parts of the seasonal cycle (Gu & Walter, 1989). It is reported that adults of *N. viridula* are capable of sustained flight for as long as 12 h under laboratory conditions (Kester & Smith, 1984). They can fly over long distances in the wild and have been caught on ships stationed up to 500 km from the nearest coast (Hayashi *et al.*, 1978; Gu & Walter, 1989; Kiritani, 2011). Adults of this species are also known to be carried over long distances by hurricanes (up to 750 km) (Aldrich, 1990). Typhoons often occur in the southwestern islands of Japan and can play a similar role. Thus, it is speculated that individuals from different populations of such a highly migratory species often move among islands (by themselves or being assisted by wind) and, thus, constantly destabilize the photoperiodic response, especially, in its near-critical zone. A variable photoperiodic response of diapause induction is reported for the Osaka population of *N. viridula* (Musolin & Numata, 2003). In general, gene flow initially enhances adaptation to a novel environment, although it ultimately prevents perfect adaptation (Angilletta, 2009). This explanation might be particularly true for the southern subtropical islands where winters are warm (Fig. 1c). The marked cline in photoperiodic response is also not detected in the pupal diapause of another strong flyer, the cotton bollworm *H. armigera* in Japan, including Okinawa Island (Shimizu & Fujisaki, 2002).

Although important for general synchronization of seasonal development in the tropics and subtropics, diapause might be not so critical for survival in mild winters in these regions. Such circumstances might make the selective pressure over the photoperiodic response less severe in the tropics and subtropics than in the temperate zone. The current climate warming might contribute to this situation as well by promoting polewards migrations and lessening the selective pressure of



overwintering conditions. Additional studies into the interpopulation differences in phenology, voltinism and genetic composition are needed to clarify the causes of absence of directional clinal variation in the critical photoperiod for winter diapause induction in this species.

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