ORIGINAL CONTRIBUTION

Geographic variation in thermal and photoperiodic effects on development of zoophytophagous plant bug *Nesidiocoris tenuis*

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Abstract

The zoophytophagous plant bug *Nesidiocoris tenuis* (Reuter) is increasingly used for biological control of various agricultural pests. Its native range includes Southern Europe, North Africa, Southern and South-Eastern Asia, although only the Mediterranean strains have been studied experimentally. We investigated effects of temperature and photoperiod on nymphal survival and development, rate of female maturation and egg load in two strains of *N. tenuis* originating from temperate and subtropical regions of South-Eastern Asia: the 'Temperate strain' (from Suwon, Republic of Korea, yearly average air temperature is 13.3°C) and the 'Subtropical strain' (from Miyazaki, Japan, yearly average air temperature is 18.2°C). Nymphs and adults were reared on tomato leaflets and fed with eggs of the grain moth *Sitotroga cerealella* under four temperatures (15, 20, 25 and 30°C) and three photoperiods (10, 12 and 14 h of light per day). In spite of long-term (40–50 generations) rearing under constant laboratory conditions, the studied strains still show a correlation between thermotolerance indices and climate at origin. In particular, at the low temperature of 15°C, survival of nymphs of the Temperate strain was double that of the Subtropical strain, whereas at the higher tested temperatures, survival of the Subtropical strain was not significantly different or even was higher than that of the Temperate strain. The duration of nymphal development in the Temperate strain was significantly shorter than that in the Subtropical strain at 15–25°C, but not at 30°C. In both strains, nymphal survival, duration of nymphal development and rate of female maturation were not significantly dependent on photoperiod, and diapause was not observed under any conditions tested. We conclude that the Subtropical strain of *N. tenuis* is better adapted to high temperatures, whereas the Temperate strain is more promising for application in greenhouses at medium and low temperatures.

Introduction

True bugs (Heteroptera) comprise the largest suborder of hemimetabolous insects. Various effects of temperature and photoperiod on their development and reproduction have been intensively studied (Ruberson et al. 1998; Musolin and Saulich 1999; Numata 2004; Saulich and Musolin 2007, 2009, 2012). Plant bugs (Miridae) constitute one of the largest and most economically important families of true bugs; the family includes both serious insect pests and efficient biological control agents (Wheeler 2000, 2001). However, parameters of thermolability and patterns of photoperiodic response of plant bugs have not been sufficiently studied. In addition, the performed studies have mostly focused on phytophagous species, partic-

ularly on agricultural pests (e.g. Bloomers et al. 1997; Shintani and Higuchi 2008; Khan et al. 2009). Among predacious bugs, most of the earlier works concerned Anthocoridae and Geocoridae species (Ruberson et al. 1991, 2001; Chyzik et al. 1995; Nakashima and Hirose 1997; Musolin et al. 2004; Musolin and Ito 2008; Saulich and Musolin 2009), although zoophytophagous Miridae have been also studied to some extent (Fauvel et al. 1987; Gillespie et al. 2004; Hughes et al. 2009; Sánchez et al. 2009).

The subject of this study, *Nesidiocoris* (=*Cyrtopeltis*) *tenuis* (Reuter 1895) (Heteroptera: Miridae) is a zoophytophagous bug increasingly used for biological control of whiteflies, thrips, aphids, leafminers, small lepidopterans, spider mites and other pests in fields and greenhouses of the Temperate Zone in Europe and Asia (Wheeler 2000, 2001; Sánchez and Lacasa 2008; Urbaneja et al. 2009; Pazyuk 2010; Mollá et al. 2011; Calvo et al. 2012; Xu et al. 2012). Its native range includes Southern Europe, North Africa and Southern and South-Eastern Asia, although some authors (DAISIE 2009) consider *N. tenuis* a species of unknown origin that cannot be ascribed as being native or alien to Europe (=cryptogenic species). In the Americas and Australia, this species is most likely a recent invader (Wheeler and Henry 1992; Kerzhner and Josifov 1999).

Most of the earlier studies on the life history of *N. tenuis* were field observations conducted in Egypt (El-Dessouki et al. 1976) and Armenia (Manukyan and Terlemezyan 1984). Recently detailed experimental studies were carried out with laboratory strains originating from Morocco (Hughes et al. 2009, 2010) and Spain (Sánchez et al. 2009). Populations from the eastern part of the wide range of *N. tenuis* remain poorly investigated, although parameters of their life history, in particular thermolability and photoperiodic responses, can differ from those of the Mediterranean populations.

We studied effects of temperature and photoperiod, under laboratory conditions, on rates of nymphal development and adult maturation, survival and some other biological parameters of two strains of *N. tenuis* originating from the temperate zone of Korea and from the subtropical zone of Japan. The primary aim of the study was to assess effects of environmental conditions and origin of the population on biological parameters of a laboratory strain derived from this population. Additionally, we intended to obtain information critical for selection of *N. tenuis* strains and improvement of methods of its mass rearing and application as a biological control agent.

Materials and Methods

Insects

The two studied laboratory strains of *N. tenuis* originated from bugs collected in the field in two remote locations: Suwon (Republic of Korea, 37°16′N, 126°59′E, 37 m a.s.l.) and Miyazaki (Japan, 31°55′N, 131°25′E, 6 m a.s.l.) The climate of Suwon is rather temperate: mean temperatures of January and August are −1.1 and 26.1°C, respectively; yearly average is 13.3°C. Miyazaki has a subtropical climate: mean temperatures of January and August are 8.4 and 28.0°C, respectively; yearly average is 18.2°C (Weather Online UK 2013). Thus, the strains originating from Suwon and from Miyazaki will be hereafter referred to as the Temperate strain and the Subtropical strain, respectively. Before the study, both strains had been reared in culture for 40–50 generations under laboratory conditions (temperature of 25–28°C, RH of 70 ± 10% and 24 h of light) on tobacco, *Nicotiana tabacum* L., plants. Nymphs and adults were fed with eggs of the grain moth, *Sitotroga cerealella* (Oliv.) and flower pollen.

Experimental set-up

All experiments were conducted in climate-controlled chambers. In each chamber, temperature varied within a range of 0.2°C. A difference in the mean temperature between chambers with different photoperiods was not larger than 0.1°C. To start the experiment, adults of *N. tenuis* were released on non-infested tobacco plants (15 females and 15 males per plant). The bugs were fed with *S. cerealella* eggs and allowed to oviposit for 24 h at 25°C. Adults were then removed and the deposited eggs were incubated at the same temperature. Every 24 h, the plants were inspected, and freshly emerged nymphs of the first instar were randomly assigned to 12 experimental regimes, that is, combinations of four temperatures (15, 20, 25 and 30°C) and three photoperiods (L: D = 10 : 14, 12 : 12 and 14 : 10 h).

During the experiment, the insects were reared on leaflets of tomato, *Solanum lycopersicum* L. Stems of the leaflets were wrapped in wet cotton covered with a plastic foil (to prevent desiccation) and placed into 250-ml transparent plastic containers. The containers were covered with thin cotton tissue to prevent escape of bugs and provide ventilation. The density was kept at the level of 10–20 insects per container. Nymphs and adults were fed with the grain moth eggs (no less than 100 eggs per insect per day). Fresh food

was provided daily at 30 and 25°C, every other day at 20°C and once every 5 days at 15°C. The adult emergence was recorded daily at 30, 25 and 20°C, and every other day at 15°C. The emerged adults were counted, sexed and placed in groups (several males and females) into the same containers and further reared under the same conditions. At the end of the experiment (11 days after adult emergence at 25 and 30°C, 15 days at 20°C and 20 days after adult emergence at 15°C; the terms derived from the preliminary experiment), all females were dissected and the egg load (the number of mature eggs present in the ovaries of each female) was recorded.

Thus, for each experimental cohort, the proportion of individuals successfully developed to the adult stage, mean duration of nymphal development, proportion of mature females on the day of dissection and egg load were recorded.

Statistics

Development and maturation of two cohorts of nymphs of both strains were studied at each of the 12 above-listed photothermal regimes with a total of 80–328 individuals per 'strain x regime' combination. To avoid pseudoreplication, cohorts (not individuals) were used as units for statistical analysis. For normalization, the data on the mean duration of nymphal development were log-transformed, whereas the percentages (survival, the rate of development and proportion of females that were mature at the moment of dissection) were arcsine square root-transformed before ANOVA. Untransformed results (medians and quartiles or ranges) are given in the text and figures. The effect of temperature on the rate of development (reciprocal of the duration of development) was estimated by the linear regression analysis. The distribution of egg load in mature females was close to normal, and hence, this variable was not transformed before ANOVA; means and SD are given in the corresponding figures.

Results

Nymphal survival

Three-way ANOVA (n = 48, d.d.f. = 24) of the transformed data showed that the proportion of individuals that successfully reached the adult stage was strongly dependent on temperature (d.f. = 3, F = 76.3, P < 0.001), whereas the influence of photoperiod (d.f. = 2, F = 0.6, P = 0.584) and strain (d.f. = 1, F = 0.1, P = 0.721) was not significant. In addition,

strain significantly (d.f. = 3, F = 4.3, P = 0.015) interacted with temperature, whereas all other interactions were not significant (P > 0.3). When the data for all photoperiods were pooled, it became apparent that although the temperature of 15°C markedly reduced survival of nymphs of both strains, the individuals of the Temperate strain were more tolerant to this low temperature (fig. 1). On the contrary, at 20°C, the nymphs of the Subtropical strain survived better than those of the Temperate strain (fig. 1). In addition, the nymphs of the Temperate strain at 25°C survived significantly better than at 30°C, whereas the survival of the nymphs of the Subtropical strain did not significantly change with the temperature increase from 20 to 30°C.

Duration of nymphal development

Four-way ANOVA of the transformed total data set (n = 96, d.d.f. = 48) showed that, as expected, temperature has the strongest effect on the duration of nymphal development (d.f. = 3, F = 19593.9, P < 0.001). Strain was the second important factor (d.f. = 1, F = 139.3, P < 0.001). The sex factor was also highly significant but not as strong (d.f. = 1, F = 12.6, P = 0.001), whereas photoperiod had no significant effect (d.f. = 2, F = 0.8, P = 0.447). Interaction of temperature with strain was rather strong (d.f. = 3, F = 10.8, P < 0.001), whereas all other interactions were not significant (P > 0.1). Thus, the pooled data
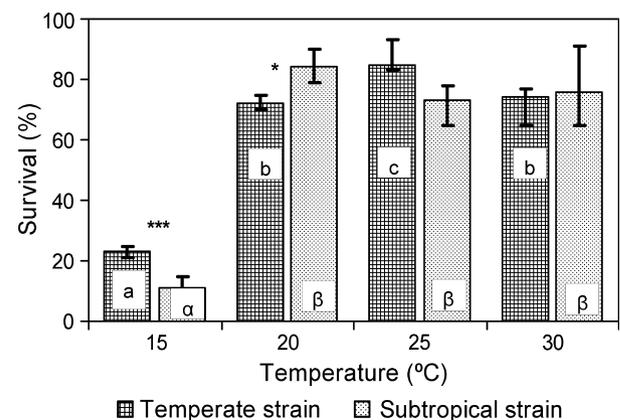
Fig. 1 Survival of *Nesidiocoris tenuis* nymphs from the hatching to adult moulting under different temperatures. Medians and quartiles for six replicates (cohorts) are shown. Different letters indicate significant difference among survival of the Temperate (Latin letters) and Subtropical (Greek letters) strains at different temperatures (P < 0.05 by the Tukey's HSD test of the transformed data). Asterisks above bars indicate significant difference between the two strains reared at the same temperature (*P < 0.05; ***P < 0.001 by ANOVA of the transformed data).

for all photoperiods were used in the further analysis of the effect of temperature on the duration of nymphal development.

When the data for each temperature were analysed separately (strain and sex were considered as factors), two-way ANOVA showed that at 15–25°C the nymphs of the Temperate strain developed significantly faster (P < 0.01) than those of the Subtropical strain. In addition, at 20–30°C, females of each strain tended to develop faster than males, although this effect was only marginally significant (P = 0.05, P = 0.053 and P = 0.02 for 20, 25 and 30°C, correspondingly). Pairwise differences in the durations of the nymphal development between sexes and strains were also not always significant (fig. 2). The interaction of strain and sex was not significant at all temperatures.

Regression analysis showed that within the studied range of temperatures, the thermal influence on the rate of nymphal development of males and females of both strains can be accurately described by a linear model (coefficient of correlation r > 0.99). The lower

developmental thresholds in different sexes and strains estimated with these regressions almost coincided (ranging from 12.8 ± 0.5°C in males of the Temperate strain to 13.0 ± 0.7°C in females of the Subtropical strain). Sums of effective temperatures varied very little: from 174 degree*days (females of the Temperate strain) to 189 degree*days (males of the Subtropical strain).
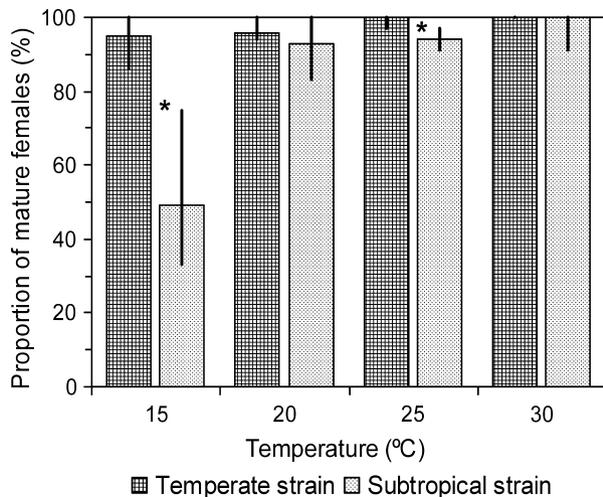
Maturation of females

The three-way ANOVA (n = 48, d.d.f. = 24, temperature, photoperiod and strain as factors) of the transformed data showed that the proportion of females that were mature at the moment of dissection was significantly dependent on strain (d.f. = 1, F = 8.2, P = 0.008), whereas the effect of photoperiod (d.f. = 2, F = 0.7, P = 0.5) was not significant. The percentage of mature females was also significantly dependent on temperature (d.f. = 3, F = 4.3, P = 0.015), but that was most likely conditioned by the fact that female
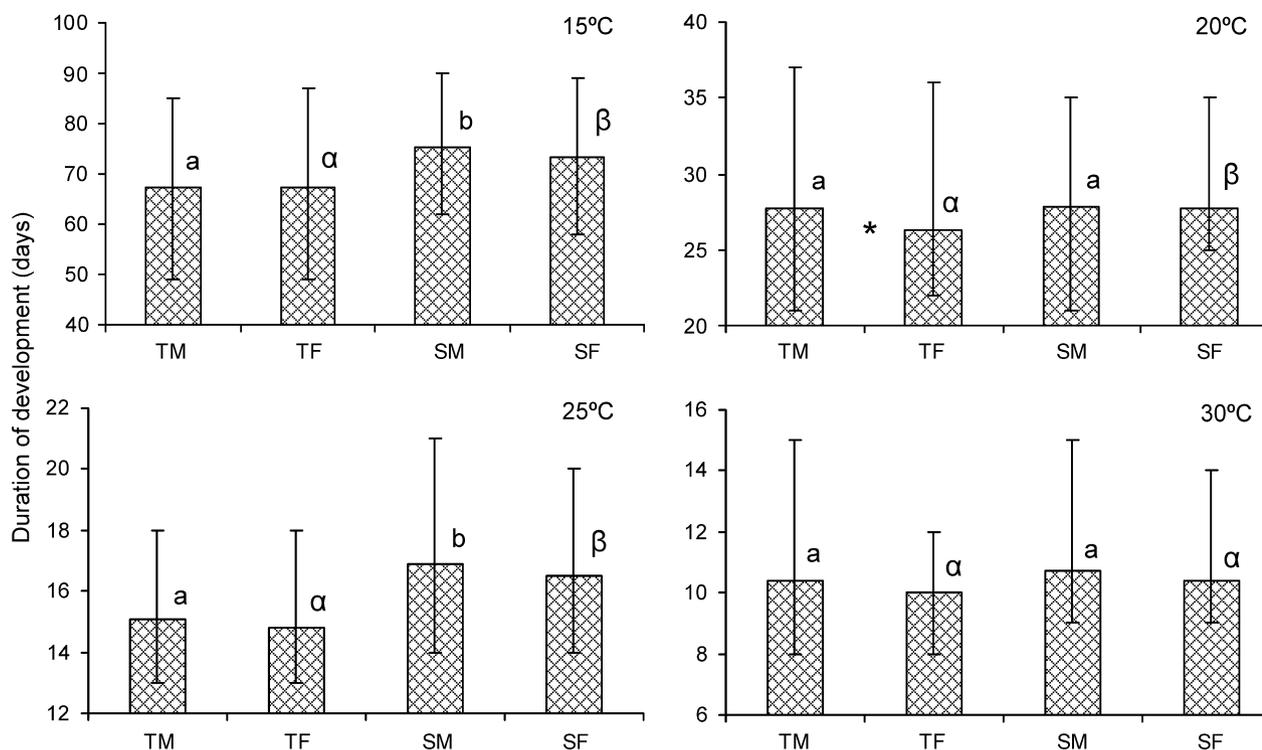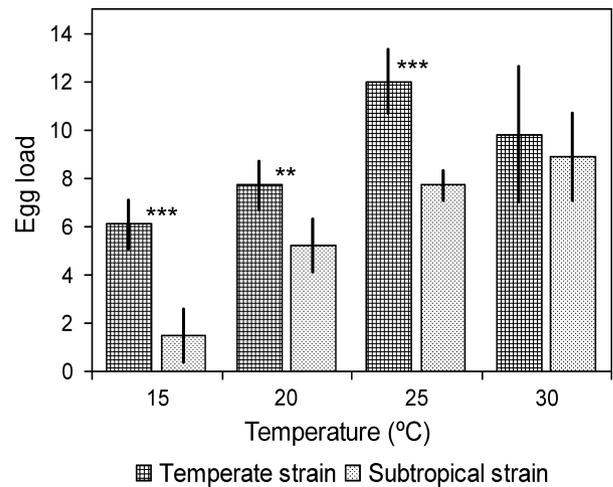

Fig. 2 Duration of *Nesidiocoris tenuis* development from hatching to adult moulting in relation to temperature, origin and sex. Medians for six replicates (each included 5–54 individuals) and the range of individual variation for each combination of factors are shown. TM – males of the Temperate strain, TF – females of the Temperate strain, SM – males of the Subtropical strain, SF – females of the Subtropical strain. Temperature is indicated in the upper-right corner of each graph. Different letters indicate significant difference in the duration of development of individuals of the same sex between the Temperate (Latin letters) and Subtropical (Greek letters) strains (P < 0.05 by ANOVA of the transformed data). An asterisk indicates significant difference between males and females of the same strain (*P < 0.05 by ANOVA of the transformed data).

age at the moment of dissection was different under different temperature regimes (see Materials and Methods). No interactions of the factors were significant. The proportion of mature females in the Temperate strain was always higher than that in the Subtropical strain, although this difference was statistically significant only at 15 and 25°C (fig. 3).

The three-way ANOVA of the data on the mean egg load (n = 48, d.d.f. = 24) demonstrated very similar results: the effect of the strain factor was very strong, (d.f. = 1, F = 45.7, P < 0.001), whereas the photoperiodic effect was not significant (d.f. = 2, F = 1.3, P < 0.287), and the interaction of these factors was also not significant. The difference between the data for different temperatures was significant (d.f. = 3, F = 38.2, P < 0.001) but, as noted above, this might be related to the difference in the age of dissection. At 15, 20 and 25°C, the mean egg load of a mature female of the Temperate strain was higher than that of a female in the Subtropical strain (fig. 4), but when the bugs developed at 30°C, the difference was not significant. In combination, higher proportion of mature females and higher egg load of a mature female suggested that at 15–25°C females of the Temperate strain reach maturity faster than those of the Subtropical strain.

Fig. 4 The mean egg load (number of ovarian eggs per mature female) of *Nesidiocoris tenuis* in relation to origin and temperature. Means and SD are shown. For timing of dissection refer to the legend of Fig. 3. Asterisks above bars indicate significant difference between the two strains reared at the same temperature (**P < 0.01; ***P < 0.001, ANOVA of untransformed data).

Discussion

Nymphal survival

The results of the experiments clearly demonstrated that in spite of the long-term rearing under constant laboratory conditions, the studied strains of *N. tenuis* still demonstrate a correlation between thermotolerance and climate at the origin. In particular, at the low temperature of 15°C, the survival of nymphs of the Temperate strain was twice that of individuals of the Subtropical strain. At the higher temperatures, survival of the Subtropical strain was not significantly different, but was slightly higher than that of the Temperate strain. In addition, the survival of the Temperate strain was the highest at 25°C with a significant decrease towards both lower and higher temperatures, whereas in the individuals of the Subtropical strain the survival at 30°C was even higher, although not significantly, than that at 25°C (fig. 1).

Survival, rates of development, as well as many other important biological parameters of polyphagous insects are well known to depend not only on temperature, but also on diet and other rearing conditions (Fauvel et al. 1987; Urbaneja et al. 2005). Thus, to compare our results with those of earlier studies, we cannot use absolute values but their dependence on temperature. Similar to the current study, the survival of *N. tenuis* originating from subtropical Morocco and Spain was reduced at low temperatures of 15–18°C, but not at high temperatures up to 30°C (Hughes

Fig. 3 Proportion of *Nesidiocoris tenuis* females that were mature at the moment of dissection in relation to temperature and strain. Medians and quartiles for six replicates (each included 2–31 individuals) are shown. Females were dissected on day 20 after emergence at 15°C, on day 15 after emergence at 20°C and on day 11 after emergence at 25 and 30°C. Asterisks above bars indicate significant difference between the two strains reared at the same temperature (P < 0.05, ANOVA of the transformed data).

et al. 2009), although at 35°C, a sharp increase in mortality was observed (Sánchez et al. 2009).

The likely adaptive differences in tolerance to high and low temperatures between strains originating from southern and northern populations of the same species that were observed in our study might seem to be a trivial result. However, for example, in *Dicyphus hesperus* Knight (Miridae), the mortality of the nymphs from California (35°42′N) reared at 35°C was higher than that of the nymphs from British Columbia (49°36′N), whereas at the lower temperatures, the difference was not significant (Gillespie et al. 2004).

Duration of the nymphal period

The data on the duration of the nymphal period obtained in our study agree with those for *N. tenuis* from Morocco (Hughes et al. 2009). Although development of both Temperate and Subtropical strains was a little slower than that of the Moroccan one, this can be explained by the difference in diet and/or rearing methods (Urbaneja et al. 2005). The thermal constant calculated for the strain of *N. tenuis* from Spain (182.3 degree*days) (Sánchez et al. 2009) is also very close to our data (174–189 degree*days), but the lower thermal threshold in *N. tenuis* from Spain (11.7°C) was about 1°C lower than that in the Temperate and Subtropical strains (12.8–13.0°C).

In a zoophytophagous species *D. hesperus,* the average duration of the nymphal period at the corresponding temperatures was close to that observed in our study with *N. tenuis*, but the difference between the northern and southern populations was opposite to our results: the nymphs from California developed faster than those from British Columbia (Gillespie et al. 2004). Shimizu and Kawasaki (2001) also demonstrated that *Orius strigicollis* from Okinawa (26°N) developed slower than those from Kochi (33.5°N).

In general, the comparative analysis of the data for hundreds of insect species of various orders suggests that cold-adapted species develop faster at low temperatures, whereas warm-adapted species develop faster at high temperatures (Trudgill and Perry 1994; Trudgill 1995; Honěk 1996). In our study, this general trend was also observed: the duration of the nymphal period in the Temperate strain was significantly shorter than that in the Subtropical strain at 15–25°C, but not at 30°C. It is noteworthy that this difference was recorded not between, but within a species, whereas it is generally believed that thermal constants do not show significant intraspecific geographic variation (Lamb et al. 1987; Tauber et al. 1987), or this variation is not related to the climatic gradient

(Umeya and Yamada 1973). Possibly, high plasticity and adaptability of *N. tenuis* were among the prerequisites of its very wide distribution.

No difference in the nymphal development time between sexes of *N. tenuis* has been detected in the earlier studies (Urbaneja et al. 2005; Hughes et al. 2009; Sánchez et al. 2009). Our data, however, suggest that females of both studied strains of *N. tenuis* develop slightly faster than males. In general, different species of true bugs demonstrate different intersex distinctions in rates of nymphal development (Musolin and Saulich 1997; Hart et al. 2002; Gillespie et al. 2004; Musolin and Ito 2008; Khan et al. 2009).

For the first time in studies of *N. tenuis*, our experiments focused on the photoperiodic effects on nymphal stage and revealed that day length does not affect the rates of nymphal growth and development. The duration of the nymphal period was independent of day length in a number of other heteropteran species, although in some other true bugs, the rate of development strongly depends on day length, often being an important seasonal adaptation allowing optimization of seasonal development under local conditions (Ruberson et al. 2001; Musolin et al. 2004; Musolin and Ito 2008; Shintani and Higuchi 2008; Saulich and Musolin 2009, 2012 and references therein).

Maturation of females

Females of the Temperate strain matured faster than those of the Subtropical strain and had more mature eggs at the moment of dissection (figs 3 and 4). This is likely due to the earlier onset of oogenesis in females of the Temperate strain. These intraspecific differences, however, were much more pronounced at 15°C than at any other temperature tested, once again suggesting that individuals of the Temperate population are better adapted to live at lower temperatures. Neither the proportion of mature females nor the mean egg load in their ovaries was significantly dependent on day length. This observation agrees well with the absence of the photoperiodic effect on the rate of nymphal development in this species.

Earlier laboratory experiments with Mediterranean populations of *N. tenuis* (Hughes et al. 2009; Sánchez et al. 2009) showed that this species does not have diapause. The same is suggested by field observations in Armenia (Manukyan and Terlemezyan 1984), where this mirid is believed to overwinter in greenhouses, but not under outdoor conditions. In the warmer climates (e.g. in Egypt), adults of *N. tenuis* were found in open fields in all seasons having up to eight generations per year without any indications of

diapause (El-Dessouki et al. 1976). Field observations in India on the congeneric *Nesidiocoris caesar* (Ballard) yielded basically the same results (Chatterjee 1983), although a number of other mirids have a facultative reproductive diapause or demonstrate delayed egg maturation induced by short photoperiod or low temperature (Chyzik et al. 1995; Musolin et al. 2004; Gillespie and Quiring 2005; Hatherly et al. 2008; Musolin and Ito 2008; Saulich and Musolin 2009). In general, an inability to form winter diapause is characteristic of insect populations from tropical and subtropical zones (Tauber et al. 1986; Zaslavski 1988; Shimizu and Kawasaki 2001; Saunders et al. 2002; Danks 2007).

Summarizing the results of our study, we conclude that in spite of the long-term rearing under laboratory conditions, the studied strains of *N. tenuis* show differential thermal adaptations in accordance with the climate of their origin. As to the application for biological control, we conclude that the Subtropical strain of *N. tenuis* seems to be better adapted to high temperatures, whereas the Temperate strain could be more promising for the application in greenhouses at medium and low temperatures.

Acknowledgements

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