Development and thermal requirements of the Nearctic predator *Geocoris punctipes* (Hemiptera: Geocoridae) reared at constant and alternating temperatures and fed on *Anagasta kuehniella* (Lepidoptera: Pyralidae) eggs

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Abstract. Knowledge of the optimal temperatures for development and survival of biological control agents is essential for efficient mass-rearing and introduction of natural enemies in augmentative biological control programs. We studied the effect of constant and alternating temperatures on development and survival of immature stages and the sex ratio at emergence of adults of the Nearctic generalist predator *Geocoris punctipes* (Say). We also determined its thermal requirements. They were reared in climatic chambers at alternating (21/11°C, 24/18°C, 27/21°C and 30/26°C ± 1°C) and constant temperatures (16.8°C, 21.5°C, 24.5°C and 28.3°C ± 1°C), RH 70 ± 10% and a 14 h photophase. Survival and development of *G. punctipes* were the same when reared at constant and alternating temperatures. Five instars were recorded in all temperature regimes. The duration of the egg stage and each instar, as well as that of total larval development were longer, and larval survival lower when reared at 16.8°C, 21/11°C, 21.5°C and 24/18°C than at 24.5°C, 27/21°C, 28.3°C and 30/26°C. The optimal temperature range for development and survival of *G. punctipes* is 24.5°C to 30°C, its lower development threshold temperature is 13.5°C and its thermal constant 295.9 DD. Sex ratios were not significantly different from 1 : 1 male : female ratio in all temperature regimes. There is an excellent match between the temperature regimes at which the prey *Tuta absoluta* (Meyrick) and predator *G. punctipes* are active, which indicates that this predator will function well in crops where this pest is present.

INTRODUCTION

Predators of the genus *Geocoris* are abundant both in nature and agroecosystems (Sweet, 2000). Based on studies carried out in the laboratory, agricultural fields and natural habitats, Schuman et al. (2013) stress the potential of *Geocoris* spp. as biological control agents. However, the potential of *Geocoris* spp. in reducing herbivore populations in crops in the field and greenhouses still remains to be demonstrated. *Geocoris punctipes* (Say) (Hemiptera: Geocoridae) is a predator of aphids, caterpillars and eggs of various Lepidoptera, *Bemisia tabaci* (Gennadius) and *Lygus* spp. on several field crops (Richman et al., 1980; Elvin et al., 1983; Tillman & Mullinix, 2003; Bueno & Zanuncio, 2009; Bueno & van Lenteren, 2012). In addition, *G. punctipes* is frequently recorded on strawberries and vegetables grown in plastic tunnels in the USA (Hagler & Sanches, 2011) and other studies indicate it is an effective predator of various pests of greenhouse crops (Tamaki & Weeks, 1972; Pendleton, 2002). *Geocoris punctipes* was sold on a small scale for controlling Lepidoptera during the 1990s in North America (Bueno & van Lenteren, 2012; van Lenteren, 2012).

In Brazil, information on the occurrence of Geocorid species on crops is restricted to soybean, cotton, corn and tomatoes (Brondani et al., 2008). On tomato *G. punctipes* attacks mainly larvae of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Bueno et al., 2013). Up until now, there has only been biological information on only one Brazilian geocorid species, *Geocoris floridanus* Blatchley (Torres et al., 2004). We initiated work on species of *Geocoris* in order to determine their efficiency as biological control agents, primarily of *T. absoluta*, a very important pest of tomato in Brazil which is now spreading throughout the world (Bueno et al., 2013).

Interest in heteropteran predatory bugs, the number of species commercially available and the areas treated with these insects has increased significantly during the past two decades (Bueno & van Lenteren, 2012; Calvo et al., 2012; van Lenteren, 2012). Screening of heteropteran predators for use in augmentative biological control is currently an important issue and an important step in their evaluation in determining the effect of temperature on their development, survival and reproduction.

It is well known that temperature affects the physiology and biology of invertebrates, such as their metabolic activity, development, growth, survival and body size (e.g., Campbel et al., 1974; Sinclair et al., 2003; Trudgill et al., 2005; Schuldiner-Harpaz & Coll, 2013). Most of these ef-

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fects were determined by rearing them at constant temperatures. However, fluctuating temperatures are typical in natural habitats, and seasonally active species of insect usually exploit intermittent periods of favourable temperatures in order to feed, develop, mate and reproduce, and even repair injuries caused by exposure to low temperature (Colinet et al., 2006, 2007; Lalouette et al., 2007). Bale et al. (2002), among others, stress the importance of measuring survival and development of insects at both constant and fluctuating temperatures. Insect species each have a specific lower developmental temperatures below which they do not develop, and require a certain number of heat units (degree days) in order to complete their development from egg to adult, and quantification of the relationship between insect development and temperature is useful for predicting their seasonal occurrence and population dynamics (Honek et al., 2002). In addition, most of the studies on *Geocoris* spp., including *G. punctipes*, were done at constant temperatures (Champlain & Sholdt, 1966; Dunbar & Bacon, 1972; Crocker et al., 1975; Torres et al., 2004; Schuman et al., 2013). Fluctuating temperatures may affect the development and survival of *G. punctipes* in a different way to constant temperatures, as is reported for other heteropteran predators such as *Orius laevigatus* (Tommasini & Benuzzi, 1996) and *Anthocoris sibiricus* Reuter (Hofsvang, 1976). As there is no published information on the effect of alternating and constant temperature regimes on the generalist predator *G. punctipes*, we determined their effects on the rate of development and survival of the immature stages of this predator fed on the eggs of *Anagasta kuehniella* (Zeller) and determined this predator's lower developmental threshold and thermal constant.

In order to determine whether a certain natural enemy will function efficiently in a particular agroecosystem it is important to have some knowledge of the effect of local temperature regimes on its biology. Further, this knowledge can be used to determine if the development of prey and predator are likely to be synchronized in the field or a greenhouse, and predict the occurrence and duration of the different life stages of the predator during the development of the crop. This information is also valuable for designing an efficient system for the mass rearing and determining the optimum time for releasing predator in augmentative biological control programs. Next, knowledge of the lower developmental temperature and thermal constant of a natural enemy is important when selecting a control agent for release under optimal environmental conditions, and for predicting whether it will be present when the pest is present and active in the field.

MATERIAL AND METHODS

Collection and rearing of *G. punctipes*

Adults of *G. punctipes* were collected on pigweed plants (*Amaranthus viridis* L.) in the field in the municipality of Lavras, Minas Gerais, Brazil, located at 21°14´S, 45°00´W and 918 m a.s.l. Plants in flower were brought to the laboratory and their inflorescences tapped over a white tray, which dislodged any insects and those belonging to the genus *Geocoris* were collected with the aid of a pooter. Individuals were identified under a stereomicroscope using the key to species of *Geocoris* spp. by Mead (2008): we only found *G. punctipes*. Next, samples of *G. punctipes* were sent to a heteropteran specialist (J. Torres, Federal University of Recife, Brazil) who confirmed our identification.

Adults of *G. punctipes* were placed in glass pots (1.7 l) containing shredded paper towels, pigweed inflorescences placed in a glass tube (10 mL) with water (moisture source), and eggs of *Anagasta kuehniella* Zeller (Lepidoptera: Pyralidae) (food source). Both, the paper towels and the pigweed inflorescences were used as oviposition substrates. The number of eggs laid was recorded daily with the aid of a stereomicroscope. Next, the oviposition substrates were transferred to glass Petri dishes (20 cm diameter) containing moistened cotton (maintenance of moisture) and eggs of *A. kuehniella* as food for the larvae. Food was added and the cotton moistened twice per week. Newly-emerged adults were removed from the Petri dishes using a motorized pooter (air compressor model 089/CA, Fanem) and 50 individuals were placed in 1.7 liter glass pots. This procedure provided the stock culture of *G. punctipes*, which was kept in the Biological Control Laboratory of the Federal University of Lavras (UFLA), Minas Gerais, Brazil. This rearing method is based on one previously described by Bueno et al. (2006) and Bueno (2009) for *Orius insidiosus* (Say). The cultures were kept at $25 \pm 2°C$, RH $70 \pm 10\%$ and 14L : 10D photoperiod. Monthly, wild individuals collected from pigweed plants in the field were introduced into the laboratory cultures to avoid genetic drift. Eggs laid by 6th generation individuals in stock cultures were used in the experiments.

Constant and alternating temperature regimes

Temperature regimes used in the experiment were determined from the data of mean, maximum and minimum day and night temperatures recorded in and outside greenhouses in the municipality of Andradas, Minas Gerais state, at 22°04´05˝S and 46°34´09˝W, 920 m a.s.l. This information on temperatures was then grouped into different combinations of day/night temperatures: 21/11°C, 24/18°C, 27/21°C and 30/26°C, all ±1°C. The constant temperatures corresponding to these combinations were 16.8°C, 21.5°C, 24.5°C and 28.3°C, all ±1°C and these temperatures were calculated by determining the weighted average: TM = (Td × Fd) + (Tn × Fn) / ΣF (TM – average temperature, Td – day-time temperature, Tn – nigh-time temperature, Fd – duration of photphase, Fn – duration of scotophase, ΣF – summation of photoperiods). The photoperiod was 14L : 10D in all experiments. These light and temperature regimes were chosen in order to match the regimes in the areas where this predator occurs. The experiment was carried out in climatic chambers in which the RH was $70 \pm 10\%$.

Development and survival of *G. punctipes*

Geocoris punctipes eggs that were at most 24 h old were collected from the stock cultures and placed in glass Petri dishes (20 cm diameter) containing moistened cotton to maintain a sufficiently high humidity. These Petri dishes were kept in climatic chambers kept at one of the different temperature regimes until the larvae hatched. One hundred newly hatched larvae of *G. punctipes* from each temperature regime were put individually in glass Petri dishes (5 cm diameter) containing an ad libitum supply of eggs of *A. kuehniella* (food) and a moistened piece of cotton wool, and reared in the same temperature regime as they were kept in during the egg stage. Water and food were provided every two days. Progress in the development of eggs and larvae was recorded daily.

We calculated development time and survival of the eggs, the number and duration of each instar (by recording the presence of

TABLE 1. Duration of egg development (days) (± SE) and egg survival (%) (± SE) of *Geocoris punctipes* recorded at alternating and constant temperatures, a RH of 70 ± 10% and a 14 h photophase.

Temperature (°C)	n*	Duration of egg development	Egg survival
16.8	30	15.4 ± 0.42 a**	35.3 ± 0.20 a
21/11	28	14.7 ± 0.37 a	41.5 ± 0.27 a
21.5	48	12.4 ± 0.27 a	66.5 ± 0.20 b
24/18	52	12.0 ± 0.18 a	64.3 ± 0.15 b
24.5	170	7.3 ± 0.14 b	89.7 ± 0.16 c
27/21	166	7.1 ± 0.17 b	87.6 ± 0.12 c
28.3	128	8.1 ± 0.12 b	80.7 ± 0.09 c
30/26°C	136	8.2 ± 0.06 b	79.4 ± 0.17 c

*n numbers of egg used to determine their development time and survival. **Means followed by the same letter in a column are not significantly different; non-parametric Kruskal-Wallis test ($p \leq 0.05$).

exuviae), survival of each instar, total larval developmental time, total larval survival and sex ratio of the adults at emergence.

Data analysis

The experiments were carried out using a total random design, with 4 constant and 4 alternating temperatures. Normal distribution of data was checked using the Shapiro-Wilk test ($p \geq 0.05$). As the data on the duration of development of eggs and their survival, duration and survival of instars were not normally distributed, the non-parametric Kruskal-Wallis test was used to compare the means, using the statistical software of the R Development Core Team (2011). Lower developmental threshold (LDT) or base temperature (expressed in degrees Celsius) and thermal constant (K) (expressed in degree-days) were calculated using only constant temperatures and the hyperbolic method (Campbell et al., 1974; Haddad et al., 1999; Bergant & Trdan, 2006). This method is based on the linear regression ($Y = a + bx$), where Y is the reciprocal of the development time and x the temperature. To compare the sex ratio of *G. punctipes* reared in the different temperature regimes, a Chi-square (χ^2) test with 5% significance level was used.

RESULTS

The shortest egg development times (about 8 days) were recorded at 24.5°C, 27/21°C, 28.3°C and 30/26°C,

and the longest (from 12–15 days) at 16.8, 21/11, 21.5 and 24/18°C (Kruskal-Wallis, H = 34.4513, df = 7, p < 0.0001). Egg survival was significantly higher at 24.5°C, 27/21°C, 28.3°C and 30/26°C than at 16.8°C and 21/11°C, 21.5°C and 24/18°C (Table 1: Kruskal-Wallis, H = 27.3608, df = 7, p = 0.0002).

The same number of larval instars was recorded for *G. punctipes* in all the temperature regimes, whether alternating or constant (Table 2). A longer total larval development was recorded at 16.8°C and 21/11°C than in the other temperature regimes (Table 2). No significant difference in the for development times of the different instars was recorded at 24.5°C, 27/21°C, 28.3°C and 30/26°C (Table 2) (Kruskal-Wallis, first instar: H = 16.2145, df = 7, p = 0.1001; second instar: H = 23.0827, df = 7, p = 0.2113; third instar: H = 12.0654, df = 7, p = 0.1101; fourth instar: H = 30.1475, df = 7, p = 0.2021 and fifth instar: H = 26.1749, df = 7, p = 0.103). At 24/18°C the development time of the first instar (8.8 days) (Kruskal-Wallis, H = 24.1532, df = 7, p = 0.0009) was significantly shorter than that of all the other instars reared at the same temperature (Table 2).

TABLE 2. Duration of the different instars (days) (± SE) of *Geocoris punctipes* recorded at constant and alternating temperatures, a RH of 70 ± 10% and a 14 h photophase.

T (°C)	1st instar	2nd instar	3rd instar	4th instar	5th instar
16.8	15.9 ± 0.10 aA* (n = 100**)	17.8 ± 0.13 aA (n = 74)	18.2 ± 0.14 aA (n = 60)	18.5 ± 0.18 aA (n = 44)	19.3 ± 0.81 aA (n = 28)
21/11	15.6 ± 0.07 aA (n = 100)	16.1 ± 0.10 aA (n = 76)	17.3 ± 0.17 aA (n = 58)	16.6 ± 0.19 aA (n = 42)	18.8 ± 0.19 aA (n = 32)
21.5	11.5 ± 0.11 bA (n = 100)	12.6 ± 0.23 bA (n = 81)	10.7 ± 0.12 bA (n = 67)	10.8 ± 0.21 bA (n = 55)	11.2 ± 0.12 bA (n = 39)
24/18	8.8 ± 0.09 bA (n = 100)	10.6 ± 0.12 bB (n = 82)	10.8 ± 0.11 bB (n = 68)	11.0 ± 0.12 bB (n = 54)	11.5 ± 0.24 bB (n = 42)
24.5	3.7 ± 0.13 cA (n = 100)	3.6 ± 0.07 cA (n = 91)	3.4 ± 0.13 cA (n = 79)	4.0 ± 0.14 cA (n = 71)	4.2 ± 0.18 cA (n = 63)
27/21	3.5 ± 0.07 cA (n = 100)	3.6 ± 0.06 cA (n = 92)	3.9 ± 0.15 cA (n = 81)	4.1 ± 0.16 cA (n = 75)	4.3 ± 0.12 cA (n = 66)
28.3	4.4 ± 0.08 cA (n = 100)	5.1 ± 0.08 cA (n = 88)	4.5 ± 0.09 cA (n = 78)	4.1 ± 0.08 cA (n = 70)	5.2 ± 0.10 cA (n = 62)
30/26	3.9 ± 0.06 cA (n = 100)	5.2 ± 0.09 cA (n = 87)	3.8 ± 0.08 cA (n = 79)	3.8 ± 0.09 cA (n = 69)	5.0 ± 0.12 cA (n = 60)

*Means followed by the same capital letter in a line and by the same lower case letter in a column are not significantly different; non-parametric Kruskal-Wallis test ($p \leq 0.05$). **n = number of individuals.
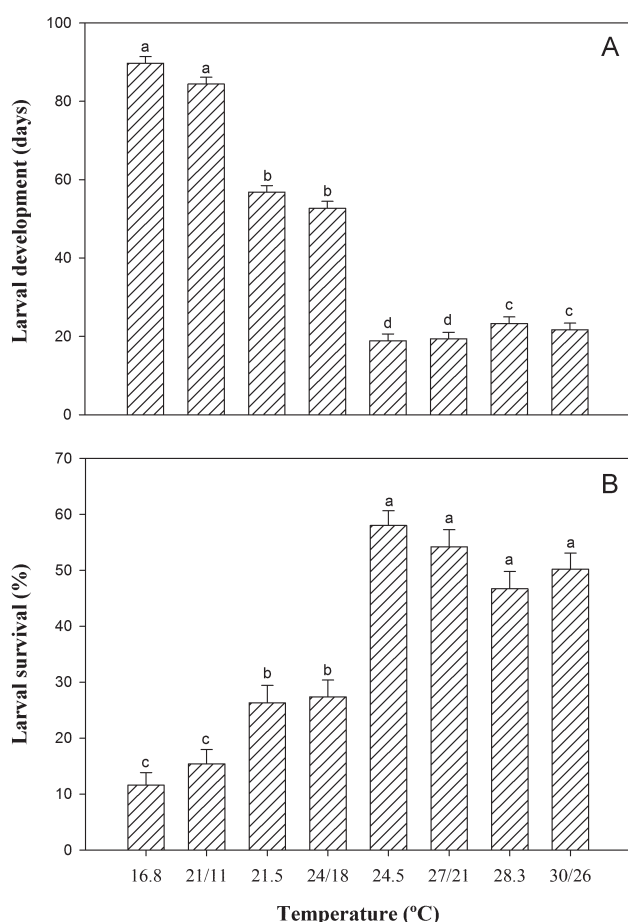
Fig. 1. Larval development times (A) and survival (B) for *Geocoris punctipes* reared at constant and alternating temperatures.
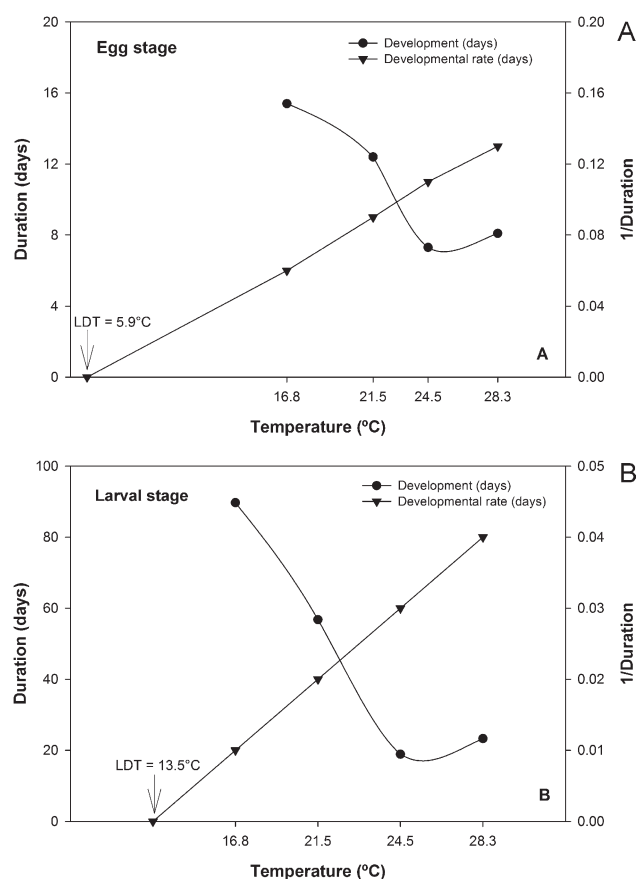

Fig. 2. Relationships between both the duration of development (days) and developmental rate (1/days), and temperature of eggs (A) and larval stages (B) of *Geocoris punctipes*.

Larval development time of *G. punctipes* decreased with increase in temperature (Table 2, Fig. 1A). Larval development was significantly longer (more than 80 days) at 16.8°C and 21/11°C than at the other temperatures (Kruskal-Wallis, H = 26.1749, df = 7, p < 0.0001). At 24.5°C and 27/21°C, the larval development time was about 19 days and significantly shorter than at all the other temperatures. At 28.3°C and 30/26°C the larval development was 23.3 and 21.7 days, respectively (Table 2).

The development rate of *G. punctipes* as a function of temperature is presented in Table 3. The lower developmental temperatures or base temperatures (Tb) and thermal constants (K) differ for the egg (Fig. 2A), each instar and total larval development (Fig. 2B) (Table 3). The lowest development threshold was recorded for the egg stage

(5.9°C) and the highest for the fourth instar (14.3°C). The 4th instar has the smallest thermal constant (52.9 degree-days). The thermal constants of the individual larval instars of *G. punctipes* varied from 52.9 to 67.4 and the thermal constant for the total larval stage was to 295.9 DD (degree-days) (Table 3).

The percentage survival of the different stages was also affected by temperature. At 16.8°C, 21/11°C, 21.5°C and 24/18°C, the percentage survival was significantly lower (Kruskal-Wallis, first instar: H = 32.7789, df = 7, p < 0.0001; second instar: H = 21.1274, df = 7, p = 0.0001; third instar: H = 8.3226, df = 7, p < 0.0001; fourth instar: H = 17.5531, df = 7, p < 0.0001 and fifth instar: H = 6.4523, df = 7, p < 0.0001) for all instars of *G. punctipes* than at the higher temperatures (Table 4). Total percentage larval

TABLE 3. The regression equations and their correlation coefficients (R^2) used to calculate the lower developmental thresholds (LDT) and thermal constants (K) for the different developmental stages of *Geocoris punctipes*.

Stages/Instars	LDT (°C)	K (DD)	Equations (1/D)	R^2 (%)
Egg	5.9	165.6	−0.035987 + 0.006037X	98.0
1st instar	13.4	57.9	−0.231854 + 0.017251X	95.4
2nd instar	13.1	62.9	−0.209605 + 0.015892X	96.2
3rd instar	13.6	55.0	−0.247874 + 0.018180X	94.5
4th instar	14.3	52.9	−0.270034 + 0.018887X	99.0
5th instar	13.1	67.4	−0.194690 + 0.014821X	97.0
Total larval stage	13.5	295.9	−0.045814 + 0.003379X	99.1

TABLE 4. Survival (%) (± SE) of the different instars of *Geocoris punctipes* recorded at different constant and alternating temperatures, a RH of 70 ± 10% and a 14 h photophase. Values for n are the same as in Table 2.

T (°C)	1st instar	2nd instar	3rd instar	4th instar	5th instar
16.8	74.2 ± 0.30 aA*	80.8 ± 0.76 aA	50.7 ± 0.25 aB	53.2 ± 0.22 aB	30.1 ± 0.19 aC
21/11	78.4 ± 0.28 aA	77.8 ± 0.31 aA	55.2 ± 0.26 aB	54.3 ± 0.18 aB	29.4 ± 0.17 aC
21.5	79.3 ± 0.20 aA	70.2 ± 0.21 aA	75.0 ± 0.25 bA	70.0 ± 0.14 bA	60.0 ± 0.20 bA
24/18	84.0 ± 0.19 aA	72.5 ± 0.10 aA	70.0 ± 0.21 bA	72.0 ± 0.10 bA	61.0 ± 0.21 bA
24.5	94.1 ± 0.31 bA	80.7 ± 0.15 aB	83.0 ± 0.24 bB	80.0 ± 0.13 bB	78.0 ± 0.11 bB
27/21	90.6 ± 0.24 bA	91.4 ± 0.09 aA	84.0 ± 0.09 bB	82.0 ± 0.09 bB	76.0 ± 0.13 bB
28.3	90.1 ± 0.23 bA	84.3 ± 0.26 aA	77.1 ± 0.20 bA	68.7 ± 0.28 bB	64.0 ± 0.16 bB
30/26	91.3 ± 0.30 bA	86.2 ± 0.28 aA	80.0 ± 0.24 bA	72.5 ± 0.31 bB	67.5 ± 0.19 bB

*Means followed by the same capital letter in a line and by the same lower case letter in a column are not significantly different; non-parametric Kruskal-Wallis test (p ≤ 0.05).

survival was also significantly lower at the lower temperatures (Kruskal-Wallis, H = 23.1439, df = 7, p = 0.0001). At 16.8°C and 21/11°C the percentage larval survival was 11.6% and 15.4%, respectively (Table 4, Fig. 1B), with that of the fifth instar particularly low. The survival of larvae of the different instars reared at the same temperature differed, particularly at 16.8°C and 21/11°C. At 27/21°C, 24.5°C, 30/26°C and 28.3°C 1st instar survival was highest at about 90%.

Sex ratios did not differ significantly from a 1 : 1 male : female ratio (χ^2 = 5.72, p = 0.0534) in all temperature regimes (Table 5).

DISCUSSION

Temperature affected the rate of development and survival of immature *G. punctipes*, but alternating day and night temperatures resulted in the same survival and development times as their respective constant average temperatures. The latter finding will make mass rearing and predator release programs easier as no corrections for development and survival are needed when working with this predator when temperatures fluctuate approximately between 17 and 30°C. In contrast, there are reports that other heteropteran predators either develop significantly faster (e.g. *A. sibiricus*; Hofsvang, 1976) or slower (e.g. *O. laevigatus*; Tommasini & Benuzzi, 1996) in fluctuating than equivalent constant temperature conditions. However, one needs to consider that the effect of fluctuating temperature on the development time of a pest or natural enemy depends on the optimum temperature and the upper and lower development threshold of the organisms in question (Jakobsen et al., 2006).

Geocoris punctipes eggs and larvae kept at 16.8°C, 21/11°C, 21.5°C and 24/18°C took longer to complete their development than at higher temperatures. Slower development at low temperatures is a general finding in

TABLE 5. Sex ratio of *Geocoris punctipes* recorded at constant and alternating temperatures, a RH of 70 ± 10% and a 14 h photophase.

	Temperatures (°C)							
	16.8	21/11	21.5	24/18	24.5	27/21	28.3	30/26
Sex ratio	0.54*	0.46	0.52	0.50	0.54	0.52	0.48	0.48

* They do not differ significantly from a 1 : 1 (Chi-Square test: χ^2 = 5.72, p = 0.0534).

insects. Roy et al. (2002) stressed that low temperatures lengthen development time because they reduce metabolic rate. These effects may partly explain the high mortality of larvae of *G. punctipes* we recorded at temperatures below 24°C.

The developmental time of the various instars of *G. punctipes* recorded at different temperatures are similar to those reported at constant temperatures for *G. punctipes* reared at 25°C and fed on *Spodoptera frugiperda* (J.E. Smith) (Champlain & Sholdt, 1967a) and at 30°C, fed on *Phtorimaea operculella* (Zeller) (Dunbar & Bacon, 1972). The values are also similar to those for *Geocoris floridanus* Blatchley reared at 26°C [3–7 days and fed on eggs of *Helicoverpa zea* (Boddie)] (Torres et al., 2004), and *Geocoris lubra* Kirkaldy, [3 to 8 days at 27°C and fed on eggs of *Helicoverpa armigera* (Hübner)] (Mansfield et al., 2007). In addition, the total durations of larval development of *G. punctipes* at high temperatures are similar to those reported by Dunbar & Bacon (1972) for *G. punctipes* (21.8 days for females and 22.2 days for males) and by Torres et al. (2004) for *G. floridanus* (21.1 days). Populations of geocorids are likely to develop more rapidly in warm than in cold spring (Tamaki & Weeks 1972, Champlain & Sholdt, 1967a, b). The development rate from egg to adult of *Geocoris* spp. correlates positively with temperatures between 21°C and 37°C, but may differ considerably among species (Schuman et al., 2013) and with the quality of the prey.

Survival of individual larval instars of *G. punctipes* was higher when reared at temperatures above 24°C, but even then survival was not higher than 60%. Mansfield et al. (2007) report survival values of 89% for individual larval stages and 64.8% for the total larval development of *G. lubra* reared at 27°C. These higher values may be due to the use of a different methodology and/or temperature, food or photoperiod. No plant tissue was added to the experimental arenas in our study and this may explain the low survival rates. Plant materials can provide nutritional resources that enhance omnivore survival relative to water alone (e.g. Tamaki & Weeks, 1972), in addition to providing a suitable oviposition substrate for heteropteran predators (Bueno & van Lenteren, 2012). Plant material on its own is insufficient for the full development of larvae of *Geocoris* spp. (Stoner, 1930; York, 1944; Sweet, 1960; Eubanks & Denno, 1999). Therefore, an adequate diet should

contain both plant material and prey (aphids, lepidopteran eggs, etc.). Schuman et al. (2013) mentioned that diet plays a significant role in the development and survival of *Geocoris* spp. Several species of prey are mentioned as suitable food, e.g. *T. absoluta*, *B. tabaci*, aphids (such as *Myzus persicae* (Sulzer) and *Aphis gossypii* Glover), thrips *Frankliniella occidentalis* (Pergande) and mites (Crocker & Whitcomb, 1980; Cohen & Byrne, 1992, Bueno et al., 2013), but our study is the first to use eggs of *A. kuehniella* as prey, which can be easily mass produced. Because of their high nitrogen content, lepidopteran eggs have a high nutritional quality for several heteropteran predatory bugs compared to other insect foods (Cohen, 1989; Bonte & De Clercq, 2010; Calixto et al., 2013). Ferkovich et al. (2007) report that the protein content of the eggs of *A. kuehniella* is higher than that of the eggs of several other species of Lepidoptera.

The lower developmental thresholds of the different stages of development of *G. punctipes* varied between 13.1 to 14.3°C and the thermal constants between 5.5 to 67.4 degree-days. Our results for the lower developmental threshold for the larval development (13.5°C) of *G. punctipes* are similar to those recorded for other important commercial heteropteran predators such as *Nesidiocoris tenuis* Reuter (12.9°C) (Hughes et al., 2009), *Macrolophus pygmaeus* (Rambur) (range 8.80°C–10.06°C) (Perdikis & Lykouressis, 2002), *Orius laevigatus* (Fieber) (11.3°C) (Sanchez & Lacasa, 2002) and *O. insidiosus* (range 12.27°C–13.03°C) (Mendes et al., 2005). The lower developmental threshold is probably similar for all the developmental stages within a population and species (Honek et al., 2002), and probably also for taxonomically related group of species (Dixon et al., 1997). In contrast, the thermal constant is plastic and reflects variation in environmental conditions other than temperature, including for example, food quality, humidity and photoperiod.

The relatively high lower developmental threshold of the larvae of *G. punctipes* (13.5°C) combined with the high mortality below 24°C indicates that this species is adapted to (sub-)tropical climates. We realize that using linear relationships as we did, is an approximation of the real dependence of insect development on temperature, and that other factors can significantly influence development (Bergant & Trdan, 2006), and the thermal constant (Honek et al., 2002).

Two important criteria for evaluating the efficiency of a natural enemy are related to temperature: the natural enemy should be active during the period the pest is present and should be adapted to the local climate (van Lenteren, 2010). Interestingly, *T. absoluta* is active within a temperature range of 19.7°C to 27.1°C (Barrientos et al., 1998). Thus, the pest *T. absoluta* develops over the same temperature range as the immature stages of its predator *G. punctipes*. This climate matching between pest and predator is a positive finding, because it means that predators can establish and develop in crops where prey is present. Knowledge of the temperature requirements of candidate biological control agents, in particular their cold tolerance,

may help predict whether they will become established and their potential for spreading following releases into new areas (Manrique et al., 2008), and whether their appearance will be synchronized with that of its prey, in this case *T. absoluta*. Further improvement of our rearing methodology will optimize the laboratory production of *G. punctipes*. Currently, very limited information is available on the biology, ecology and effectiveness of the biological control agent *Geocoris* spp. native to Brazil and this study is a first step in obtaining such information.

In conclusion egg and larval survival and development time of immature stages of *G. punctipes* are strongly affected by temperature, but that alternating temperatures within a range of 10°C around a certain average temperature results in similar developmental and survival values as the constant average temperature. Further, we conclude that *G. punctipes* is adapted to (sub-)tropical climates. Our results will be used to further develop and improve the mass rearing methods for this predator, estimate where this predator can be successfully established in the field or greenhouses, and synchronize field releases with the development of its prey.

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