

ORIGINAL CONTRIBUTION

Reproduction and population parameters of the Nearctic predator *Geocoris punctipes* at constant and varying temperature regimes

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Abstract

The heteropteran predator *Geocoris punctipes* (Say) has been used in augmentative biological control since 2000 to control Lepidoptera. However, surprisingly, few data are available about the influence of temperature on its population development, which is of key importance to plan the number and moment of releases to obtain sufficient pest reduction. The objective of this study was to evaluate daily and total fecundity, longevity and life table parameters (m_x , l_x , r_m , R , λ , T and TD) of *G. punctipes* at constant (16.8°C, 21.5°C, 24.5°C and 28.3°C) and corresponding varying (day/night) (21/11°C, 24/18°C, 27/21°C and 30/26°C) temperatures. Pairs of adult predators aged 24 h and originating from nymphs exposed to the same temperature regimes were kept at the above-mentioned temperature regimes in Petri dishes containing *Anagasta kuehniella* (Zeller) eggs and an oviposition substrate. Tests were conducted in climatic chambers at the different temperature regimes and a RH 70 ± 10% and a 14L: 10D photoperiod. Reproduction, longevity and life table parameters were significantly affected by temperature, with clear differences between treatments at low (16.8°C, 21/11°C, 21.5°C, 24/18°C) or a high (24.5°C, 27/21°C, 28.3°C, 30/26°C) temperature regimes. Highest reproduction and fastest population growth of *G. punctipes* took place at average temperatures ranging from 24.5°C to 30°C, and neither reproduction nor population growth was negatively influenced by varying temperatures at any of the temperature regimes.

Introduction

Heteropteran predators are important natural enemies of herbivores in natural and agricultural ecosystems, and several species have shown to be efficient biological control agents (Bueno and van Lenteren 2012). Particularly in tropical and subtropical areas, these natural enemies have the ability to reduce the population growth of insect pests (Albajes and Alomar 1999; Lundgren 2011). The heteropteran predators *Macrolophus pygmaeus* (Rambur) and *Nesidiocoris tenuis* (Reuter), for example, play an important role as biological control agents in protected crops and are being

produced and released in great numbers to prevent pest outbreaks of *Bemisia tabaci* (Gennadius) and *Tuta absoluta* (Meyrick) in Europe (Calvo et al. 2012; van Lenteren 2012). Other studies have highlighted that also the heteropteran *Geocoris punctipes* (Say) has potential as a biological control agent (Lingren et al. 1968; Richman et al. 1980; Elvin et al. 1983; Bueno and Zanuncio 2009; Bueno and van Lenteren 2012; Schuman et al. 2013). In North America, this predator has been commercially produced since 2000 for control of lepidopteran and whitefly pests (van Lenteren 2012). The predator can often be found in protected and field crops such as strawberries, vegetables,

soya bean, maize and cotton, and feeds on prey like aphids, whiteflies, beetles, lepidopterans and *Lygus* sp. (Crocker and Whitcomb 1980; Torres et al. 2004; Hagler and Sanchez 2011; Bueno and van Lenteren 2012).

To date, there is little published information on the biology of *G. punctipes*. Brazilian papers reported the occurrence of *Geocoris* spp. in several crops of economic importance (Garcia et al. 2004; Brondani et al. 2008; Torres 2008). We recently published the first data on developmental time, immature survival, sex ratio at constant and varying (day/night) temperature regimes (Calixto et al. 2014), and adult lifespan, fecundity and egg and larval predation of *G. punctipes* with *T. absoluta* as prey on tomato (Bueno et al. 2013).

It is well known that the efficiency of natural enemies is affected by various abiotic factors and that temperature is a major factor influencing development, reproduction and population growth (Medeiros et al. 2004; Tommasini et al. 2004; Baniameri et al. 2005; Kim and Riedl 2005; Bahsi and Tunç 2008; Lu et al. 2009). Parasitoids and predators may terminate or slow down development and reproduction at low and high extremes of temperatures, and this might result in poor performance of natural enemies in certain (micro-) climates. Particularly, in tropical and subtropical regions, the climatic conditions in greenhouses may show large diurnal variations in temperature (Bueno 2005). Such variations may also occur in natural habitats, and seasonally, active species of insects usually exploit intermittent periods of favourable temperatures to feed, develop, mate and reproduce, and even repair injuries caused by exposure to low temperature (Collinet et al. 2007; Lalouette et al. 2007). But also prolonged exposure to a constant temperature may negatively affect the biology of an insect (Horn 1998). In the laboratory and in mass-production facilities, natural enemies are often reared at a constant temperature considered optimal for their development and reproduction. Temperature effects should be taken into account when planning mass production and timing of releases of natural enemies.

The majority of studies performed at variable temperatures have focused on effects on insect developmental time (e.g., Jakobsen et al. 2006; Calixto et al. 2014; Vangansbeke et al. 2015), and only a few on effects on reproduction and population growth (e.g. Siddiqui et al. 1973). Bale et al. (2002), among others, stressed the importance of measuring development and reproduction of insects at both constant and varying temperatures, as varying temperatures can shorten development and increase reproduction (e.g.

Siddiqui et al. 1973), lengthen development and decrease reproduction (e.g. Messenger 1969) or have a neutral effect (e.g. Butler and Lopez 1999; Calixto et al. 2014) when compared with results from experiments performed at constant temperatures. Thus, effects of varying temperature on reproduction and population dynamics of ectothermic organisms should be known to estimate performance of the natural enemy during mass rearing and after releases in the field (Worner 1992). In addition, such knowledge may help to improve biological control by selecting natural enemies that are optimally adapted to certain climate regimes (Jakobsen et al. 2006).

In this study, we report about the reproductive performance and intrinsic rate of population increase of *G. punctipes* at varying day/night temperatures (21/11°C, 24/18°C, 27/21°C and 30/26°C) similar to conditions present in greenhouses and at constant temperatures (16.8°C, 21.5°C, 24.5°C and 28.3°C) equal to those used in the laboratory. With this study, we can determine optimal temperature regimes for timing releases of *G. punctipes* as biological control agent, as well as for mass rearing of *G. punctipes* in the laboratory.

Our working hypotheses are the following: (i) at low temperature regimes, fecundity is lower and lifespan is longer at the varying temperature regime than at a constant temperature with the same average, because during the period of lowest temperatures, reproduction and development ceases in the varying temperature regime; (ii) at high temperature regimes, fecundity is lower and lifespan is shorter at the varying temperature regime than at a constant temperature, because during the period of highest temperatures, reproduction and lifespan are negatively influenced; and (iii) at intermediate temperature regimes, fecundity and lifespan are the same at the varying and constant temperature regimes.

Materials and Methods

Predator rearing

Adults of *G. punctipes* were collected on pigweed plants (*Amaranthus viridis* L.) in the field in the municipality of Lavras, Minas Gerais, Brazil (for details, see Calixto et al. 2014). These adults were placed in glass pots (1.7 l) containing shredded paper towel, pigweed inflorescences placed in a glass tube (10 ml) with water and eggs of *Anagasta kuehniella* Zeller (Lepidoptera: Pyralidae) as food. Both the paper towel and the pigweed inflorescences are used as oviposition substrate by *G. punctipes*. Every 2 days, the oviposition

substrates were transferred to Petri dishes (20 cm diameter) containing moistened cotton (moisture source) and eggs of *A. kuehniella* (food source) for the development of the nymphs. Twice per week, food was added to the Petri dishes, and the cotton was moistened. Emerged adults were removed from Petri dishes by a suction apparatus (air compressor model 089/CA, Fanem) and placed in glass pots (1.7 l) at a density of 50 individuals/pot to restart the reproduction cycle. This maintenance rearing was based on the method developed by Bueno et al. (2006) and Bueno (2009) for *Orius insidiosus* (Say) (Hemiptera: Anthrenidae), and adapted for *G. punctipes* by Calixto et al. (2014). The rearing was kept at $25 \pm 2^\circ\text{C}$, RH $70 \pm 10\%$ and a 14L: 10D photoperiod. Every month, new *G. punctipes* individuals were collected from pigweed plants in the field and were introduced into the laboratory rearing to avoid genetic drift. Newly emerged nymphs from the 6th generation of the maintenance rearing were exposed to the various temperature regimes (Calixto et al. 2014) in order to obtain adults for use in the experiments.

Reproduction, longevity and population growth parameters

Males and females of *G. punctipes* aged up to 24 h, originating from nymphs developed at each of the varying and constant temperature regimes, were used in the experiments. *Geocoris punctipes* couples were kept in Petri dishes (5 cm diameter) containing moistened cotton and *ad libitum* *A. kuehniella* eggs as food. A piece of paper towel (2×2 cm) was used as oviposition substrate. The substrates were observed daily under a stereomicroscope to count the number of eggs. Pre-oviposition and oviposition periods, fecundity (daily and total eggs/female), and longevity (separate for male and female) of *G. punctipes* were

determined at the different temperature regimes, and with these data, fertility life tables were constructed.

The temperature regimes tested were as follows: (i) varying day/night temperature regimes of $21/11^\circ\text{C}$, $24/18^\circ\text{C}$, $27/21^\circ\text{C}$ and $30/26^\circ\text{C}$, all with $\pm 1^\circ\text{C}$, and (ii) constant temperature regimes of 16.8°C , 21.5°C , 24.5°C and 28.3°C , all with $\pm 1^\circ\text{C}$, corresponding to weighted average of the varying temperature regimes [weighted averages: $(TM = (Td \times Fd) + (Tn \times Fn) / \Sigma F)$]; TM: average temperature, Td: daytime temperature, Tn: night-time temperature, Fd: daytime photoperiod, Fn: night-time photoperiod, ΣF : summation of photoperiods). The experiment was carried out in climatic chambers, and independent of the temperature regime, an RH $70 \pm 10\%$ and a 14L: 10D photoperiod was used.

The number of replicates used at the various temperature regimes is given in table 1. The number of replicates was low (5–13) at the lower temperatures due to a high mortality of juveniles at these temperature regimes (Calixto et al. 2014).

Data analysis

Data were checked for normality ($P \geq 0.05$) using a Shapiro–Wilk test. Data (pre-oviposition and oviposition periods, daily and total fecundity and longevity of females and males) were not normally distributed. Therefore, means were compared by the nonparametric Kruskal–Wallis test ($P \leq 0.05$). To compare the longevities of females and males for the same temperature regimes, the nonparametric Mann–Whitney *U*-test ($P \leq 0.05$) was used. The statistical software R Development Core Team (2011) was used for statistical analysis. The fertility life tables for *G. punctipes* were estimated using survival and fecundity data of individual females. Age interval (x), fecundity (m_x ; number of daughters produced) and probability of

Table 1 Pre-oviposition and oviposition periods (days), daily (eggs/female/day) and total fecundity (eggs/female) of *Geocoris punctipes* at varying and constant temperatures, RH $70 \pm 10\%$ and photophase 14 h

T ($^\circ\text{C}$)	Pre-oviposition period	Oviposition period	Daily fecundity	Total fecundity
16.8	9.8 ± 0.37 c ¹ (n = 5) ²	68.6 ± 0.51 b (n = 5)	1.2 ± 0.19 b (n = 5)	31.6 ± 0.49 c (n = 5)
21/11	8.7 ± 0.28 c (n = 7)	74.8 ± 0.73 b (n = 7)	1.3 ± 0.18 b (n = 7)	34.7 ± 0.52 c (n = 7)
21.5	7.4 ± 0.35 b (n = 12)	73.3 ± 0.59 b (n = 12)	1.9 ± 0.15 b (n = 12)	42.0 ± 0.31 c (n = 12)
24/18	7.9 ± 0.25 b (n = 13)	70.8 ± 0.53 b (n = 13)	2.2 ± 0.10 b (n = 13)	45.3 ± 0.64 c (n = 13)
24.5	2.8 ± 0.12 a (n = 28)	61.8 ± 0.38 a (n = 28)	3.6 ± 0.12 a (n = 28)	162.2 ± 0.35 b (n = 28)
27/21	3.0 ± 0.17 a (n = 26)	59.5 ± 0.26 a (n = 26)	3.8 ± 0.16 a (n = 26)	164.5 ± 0.55 b (n = 26)
28.3	3.4 ± 0.30 a (n = 22)	59.7 ± 0.43 a (n = 22)	2.4 ± 0.20 a (n = 22)	134.9 ± 0.39 a (n = 22)
30/26	3.1 ± 0.14 a (n = 24)	58.8 ± 0.48 a (n = 24)	3.0 ± 0.14 a (n = 24)	141.7 ± 0.66 a (n = 24)

¹Means (\pm SE) followed by the same letter in columns do not differ by nonparametric Kruskal–Wallis test.

²n = number of individuals (females) originated from nymphs exposed to the same temperature regimes.

survival (l_x) data were used to calculate the net reproductive rate (R_0), mean generation time (T), intrinsic rate of increase (r_m), finite rate of increase (λ) and population doubling time (TD) by the jackknife method according to Andrewartha and Birch (1954). The age (in days) at which the insects began adulthood, immature survival and sex ratio of offspring of the juveniles exposed to the same temperature regimes (Calixto et al. 2014) were used in the calculation of the population growth parameters. The life table parameters and their standard errors were estimated according to the procedure described by Maia et al. (2000, 2014). Means of the life table parameters were compared in pairs by applying a unilaterally Student's t -test for independent samples ($P \leq 0.05$) using the statistical program SAS (SAS Institute 2000).

Results

Pre-oviposition and oviposition periods at different temperatures

Temperature significantly influenced the pre-oviposition ($H = 45.5749$, d.f. = 7, $P < 0.0001$) and oviposi-

tion periods ($H = 32.3425$, d.f. = 7, $P = 0.001$; table 1). As expected, pre-oviposition and oviposition periods are longer at the lower temperatures. Pre-oviposition and oviposition periods were significantly different between temperature regimes with a day/night temperature $\geq 24.5/21^\circ\text{C}$ and temperature regimes with a day/night temperature $\leq 24/18^\circ\text{C}$ (table 1). The pre-oviposition periods at the temperature regimes 16.8 and $21/11^\circ\text{C}$ were also significantly different from those at the other temperature regimes. Pre-oviposition and oviposition periods did not differ significantly ($H = 62.8726$, d.f. = 7, $P = 0.1001$) when the females were exposed to higher temperatures (24.5°C , $27/21^\circ\text{C}$, 28.3° , $30/26^\circ\text{C}$) (table 1).

Fecundity at different temperatures

The daily fecundity ($H = 53.7124$, d.f. = 7, $P < 0.0001$) and total fecundity ($H = 38.4615$, d.f. = 7, $P < 0.0001$) of *G. punctipes* were significantly affected by temperature regimes. At the varying ($21/11^\circ\text{C}$ and $24/18^\circ\text{C}$) and constant (16.8°C and 21.5°C) temperatures, females had a significantly lower daily

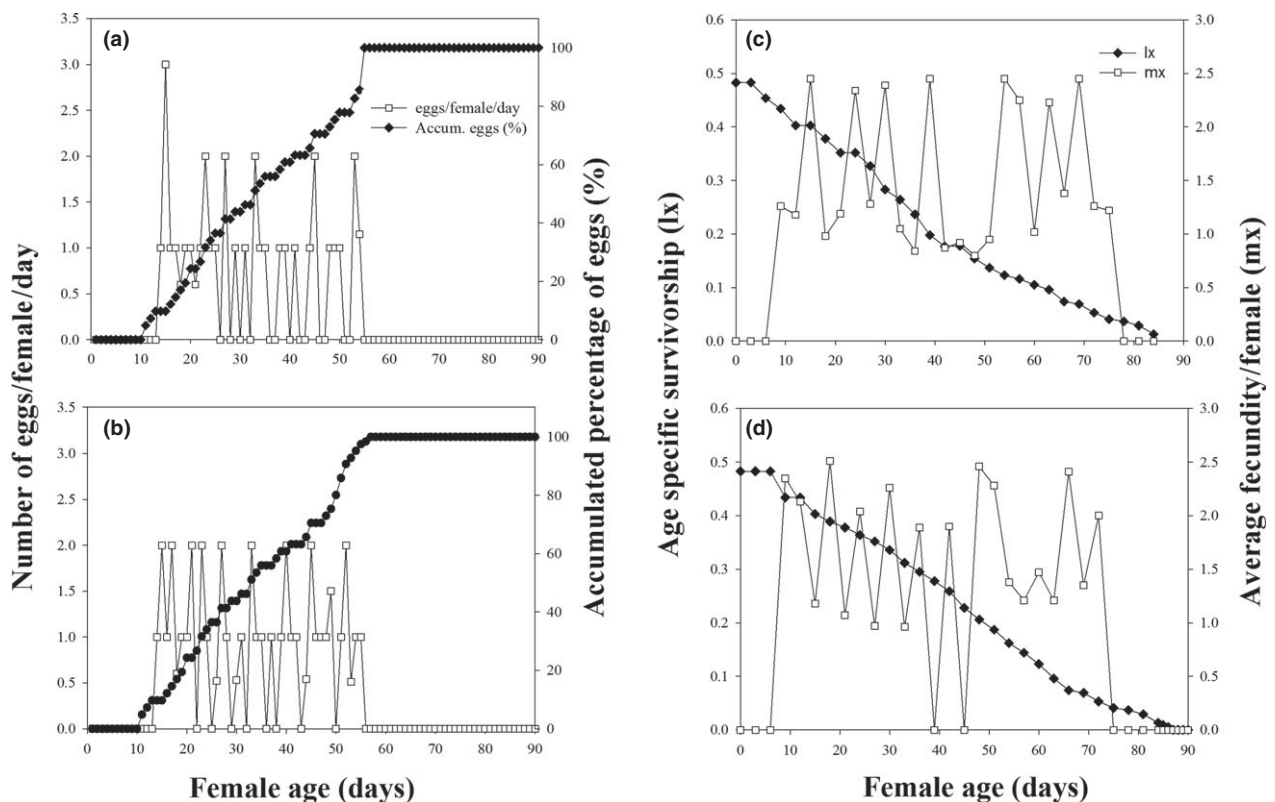


Fig. 1 Number of eggs/female/day and accumulated percentage at 16.8°C (a) and 21/11°C (b), age-specific survivorship (l_x) and average fecundity/female (mx) at 16.8°C (c) and 21/11°C (d) of *Geocoris punctipes*.

and total fecundity than at the highest temperature regimes (table 1). The total fecundity of *G. punctipes* was highest at 24.5°C and 27/11°C (table 1).

The mean number of eggs/female/day and the total number of eggs laid initially increased with increasing temperature, but decreased again at the highest temperatures (figs 1a,b; 2a,b; 3a,b; 4a,b). Average daily fecundity was around 1 egg/female at 16.8°C and 21/11°C, around 2 eggs/female at 21.5°C and 24.8°C, reached a maximum around 3.7 eggs/female at 24.5°C and 27/21°C and then decreased to an average around 2.6 eggs/female at 28.3°C and 30/26°C (figs 1c,d; 2c,d; 3c,d; 4c,d and table 1).

Survival rates (l_x) decreased linearly with female age at most temperature regimes (figs 1c,d; 2c,d; 3c,d; 4c,d) and, as expected, survival is longer at lower than at higher temperatures. As can be seen in these figures, survival rates start around 0.5 at all temperature regimes because we earlier found immature mortalities of about 50% for *G. punctipes* nymphs (Calixto et al. 2014).

Longevity

The longevity of females ($H = 13.1266$, d.f. = 7, $P < 0.0001$) and males ($H = 19.2415$, d.f. = 7, $P < 0.0001$) of *G. punctipes* was significantly influenced by the tested temperature regimes (table 2). The highest values of longevity for both females and males were recorded at 21/11°C, 21.5°C and 24/18°C. At higher temperatures, longevity of both females and males decreased (table 2). When the longevity of females and males was compared per temperature regime, significant differences were found for all pairs, except at the regime of at 24/18°C where longevity was similar (table 2, Mann–Whitney U -test).

Fertility life table

The jackknife method (Andrewartha and Birch 1954) was used to estimate fertility life table parameters for *G. punctipes* females for all the temperature regimes (table 3). Significant differences were observed for all parameters between the temperature regimes with

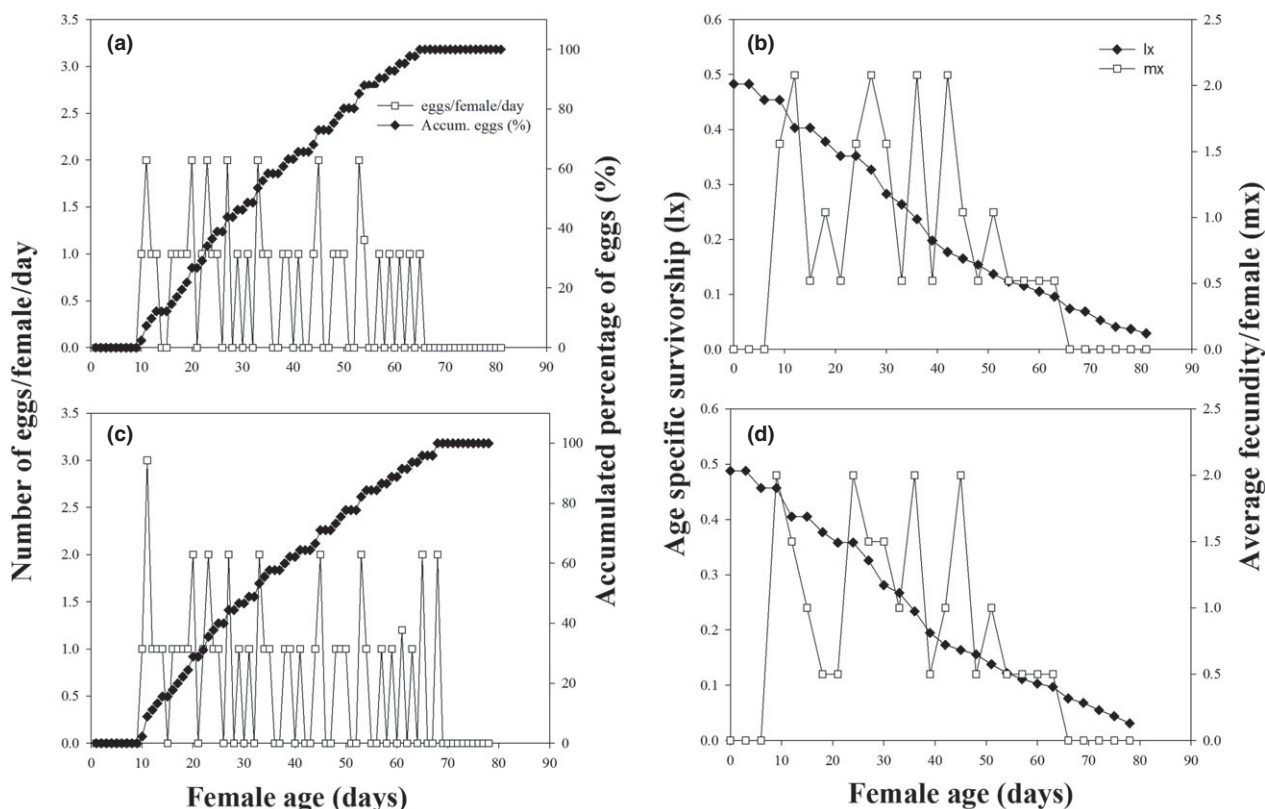


Fig. 2 Number of eggs/female/day and accumulated percentage at 21.5°C (a) and 24/18°C (b), age-specific survivorship (l_x) and average fecundity/female (m_x) at 21.5°C (c) and 24/18°C (d) of *Geocoris punctipes*.

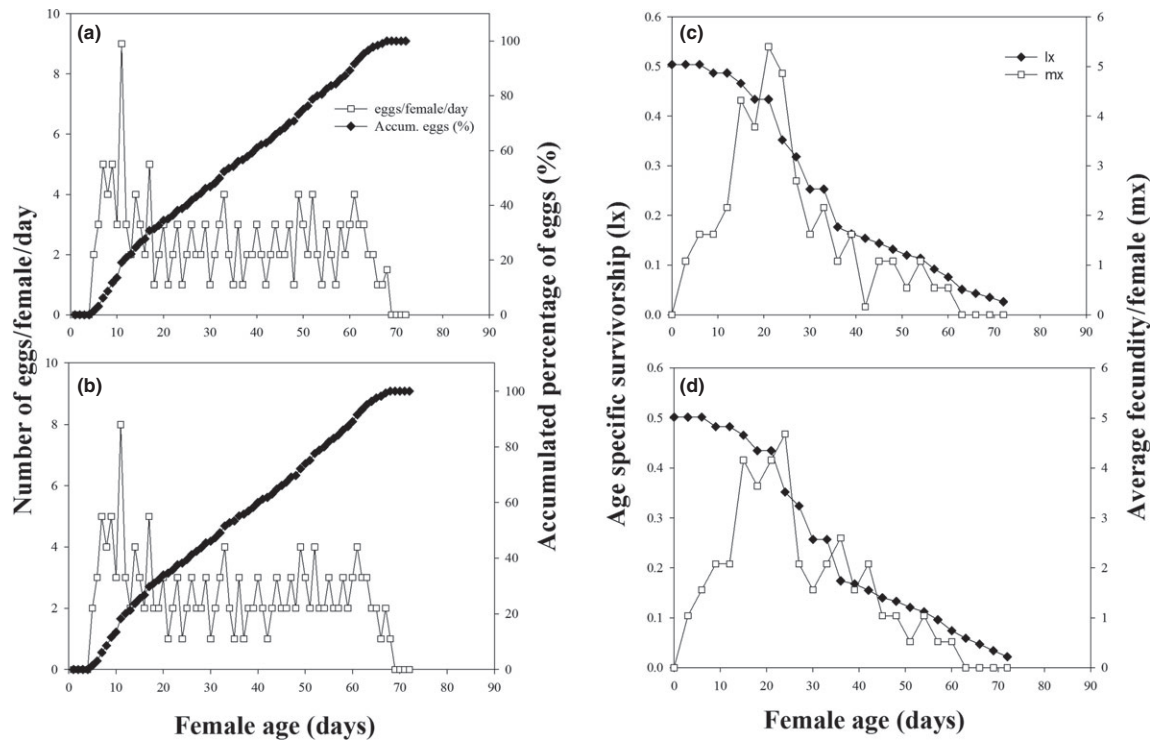


Fig. 3 Number of eggs/female/day and accumulated percentage at 24.5°C (a) and 27/21°C (b), age-specific survivorship (l_x) and average fecundity/female (m_x) at 24.5°C (c) and 27/21°C (d) of *Geocoris punctipes*.

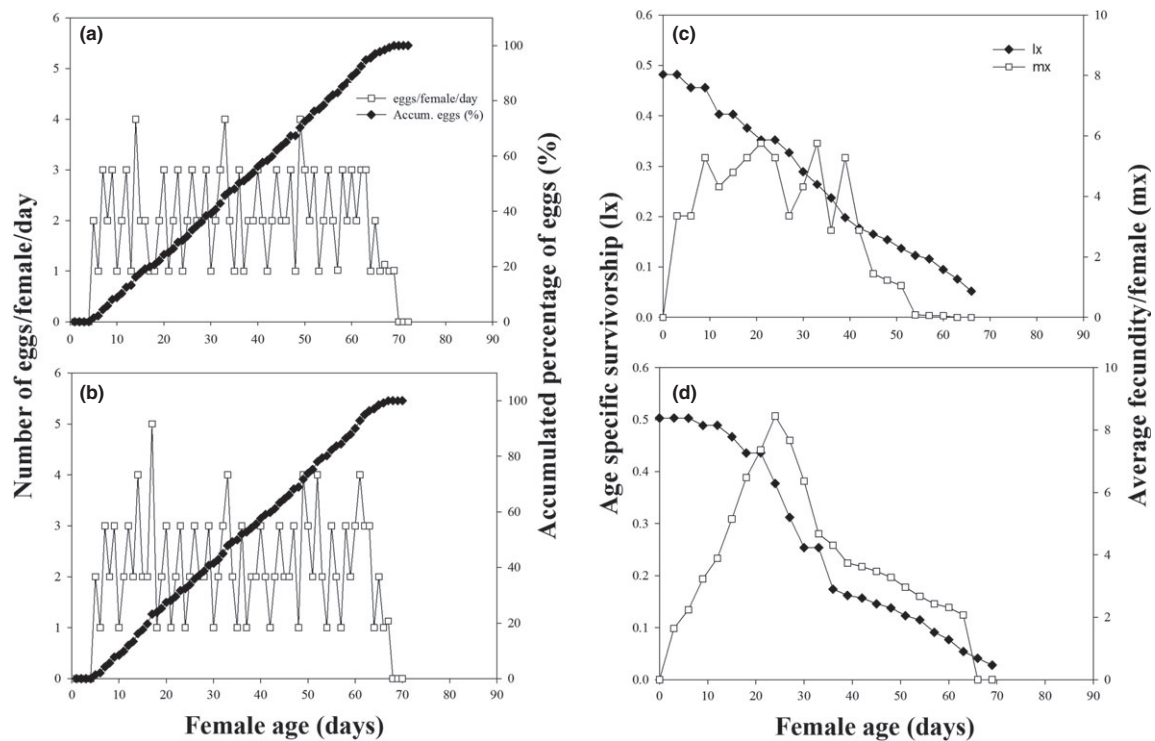


Fig. 4 Number of eggs/female/day and accumulated percentage at 28.3°C (a) and 30/26°C (b), age-specific survivorship (l_x) and average fecundity/female (m_x) at 28.3°C (c) and 30/26°C (d) of *Geocoris punctipes*.

Table 2 Longevity (days) of females and males of *Geocoris punctipes* at varying and constant temperatures, RH 70 \pm 10% and photophase 14 h

Temperature (°C)	Females	Males	U	P values
16.8	77.2 \pm 1.05 a ¹ A ² (n = 5)	65.0 \pm 1.13 aB (n = 5) ³	15	0.045
21/11	84.0 \pm 0.81 aA (n = 7)	73.1 \pm 1.09 aB (n = 7)	28	0.017
21.5	81.4 \pm 0.52 aA (n = 12)	79.6 \pm 0.62 aB (n = 12)	51	0.019
24/18	78.7 \pm 0.74 aA (n = 13)	77.3 \pm 0.51 aA (n = 13)	54	0.066
24.5	64.6 \pm 0.44 bA (n = 28)	61.4 \pm 0.46 bB (n = 28)	375	0.006
27/21	62.5 \pm 0.38 bA (n = 26)	60.1 \pm 0.31 bB (n = 26)	239	<0.001
28.3	63.3 \pm 0.61 bA (n = 22)	55.2 \pm 0.50 bB (n = 22)	253	0.004
30/26	61.4 \pm 0.48 bA (n = 24)	54.6 \pm 0.58 bB (n = 24)	300	0.0168

¹Means (\pm SE) followed by the same lowercase letter in columns do not differ by nonparametric Kruskal–Wallis test.

²Means (\pm SE) followed by the same capital letter in lines do not differ by the nonparametric Mann–Whitney U-test (with U and P values for each temperature).

³n = number of individuals (female and male) originated from nymphs exposed to the same temperature regimes.

low (16.8°C, 21/11°C, 21.5°C, 24/18°C) or high temperatures (24.5°C, 27/21°C, 28.3°C, 30/26°C). For the net reproductive rate (R_0) and the mean generation time (T), an additional significant difference was observed for the treatments with the lowest temperature regime (16.8°C, 21/11°C) and the other temperature regimes (table 3).

Discussion

Temperature regimes significantly influenced all reproduction and population growth parameters of the predator *G. punctipes*. The pre-oviposition periods we found at high temperatures (24.5°C, 27/21°C, 28.3°C and 30/26°C) were shorter than earlier records for this parameter published by Champlain and Sholdt (1966, 1967a,b) (5 days at 27°C) or by Naranjo and Stimac (1987) (5 days at 27°C). The longest oviposition period and daily fecundity of *G. punctipes* recorded in this study (59.7 days at 30/26°C) were similar to those reported by Torres et al. (2004) for the species *G. floridanus* (59.7 days at 26°C).

The total fecundity of *G. punctipes* (141.7 eggs/female) at the varying temperature 30/26°C was lower than the value (178 eggs/female) reported by Champlain and Sholdt (1966, 1967a,b) at a constant temperature of 25°C. Growth of immature stages of *G. punctipes* is influenced by temperature and was found to be slower at low temperatures (Calixto et al. 2014). This may have influenced the size and weight of adults in this study. In females, there is a close relationship between temperature and body mass, and the number of ovarioles and eggs (Ratte 1985). The increase in fecundity of female *G. punctipes* in the temperature range from 16.8 to 24°C may thus well be explained by the effect of temperature on the growth of their immature stages submitted to the same temperature regime (Calixto et al. 2014). Usually, ectothermic organisms tend to have a larger body size when reared at lower temperatures ('temperature-size rule' for ectothermic organisms; Ratte 1985; Atkinson 1994). Surprisingly, we observed that insects reared at low temperatures had a higher frequency of wing and

Table 3 Fertility life table parameters of *Geocoris punctipes* at varying and constant temperatures, RH 70 \pm 10% and photophase 14 h

Temperature (°C)	Parameters of fertility life table				
	R_0 ¹	r_m	T	λ	DT
16.8	8.4 \pm 0.45 c ²	0.038 \pm 0.0065 b	77.8 \pm 0.21 a	1.024 \pm 0.0086 b	107.8 \pm 1.18 a
21/11	11.2 \pm 0.34 c	0.041 \pm 0.0042 b	74.3 \pm 0.35 a	1.021 \pm 0.0042 b	112.0 \pm 1.24 a
21.5	13.6 \pm 0.28 b	0.040 \pm 0.0051 b	55.1 \pm 0.18 b	1.013 \pm 0.0071 b	101.5 \pm 1.05 a
24/18	14.1 \pm 0.57 b	0.050 \pm 0.0074 b	57.4 \pm 0.46 b	1.035 \pm 0.0054 b	98.7 \pm 0.89 a
24.5	25.8 \pm 0.19 a	0.060 \pm 0.0035 a	28.9 \pm 0.39 c	1.107 \pm 0.0033 a	50.1 \pm 0.57 b
27/21	26.2 \pm 0.22 a	0.063 \pm 0.0047 a	29.5 \pm 0.23 c	1.126 \pm 0.0048 a	50.9 \pm 0.44 b
28.3	22.6 \pm 0.31 a	0.071 \pm 0.0023 a	32.4 \pm 0.51 c	1.052 \pm 0.0027 a	65.2 \pm 0.38 b
30/26	24.2 \pm 0.48 a	0.079 \pm 0.0062 a	25.6 \pm 0.19 c	1.078 \pm 0.0063 a	57.0 \pm 0.63 b

¹ R_0 = Net reproductive rate (females); r_m = intrinsic rate of increase (female/female/day); T = mean generation time (days); λ = finite rate of increase (female/day); DT = double time (days).

²Means (\pm SE) followed by the same letter in columns do not differ by test 't' unilateral ($P \leq 0.05$).

ovipositor deformations than insects reared at higher temperatures. This may be the result of exposing the insects to temperatures outside their normally encountered temperature regimes.

Temperature can also considerably influence changes in oviposition rates during adult life and in the total number of eggs (Cammell and Knight 1992). Knowledge of the change in oviposition rate with female age is important for optimizing mass rearing (Coppel and Mertins 1977). The change in oviposition rate of *G. punctipes* during time was different at high and low temperature regimes. At low temperature regimes, there were days without oviposition and the average number of eggs per day was lower than at high temperature regimes.

The longevities of females and males of *G. punctipes* at 28.3°C (63.3 and 55.2 days, respectively) were similar to the values reported by Champlain and Sholdt (1966, 1967a,b) at 25°C (67.7 and 41.5 days, respectively).

When insects are kept at low temperatures, their metabolic activity decreases, reducing the amount of food consumed and their energy expenditure, leading to longer longevity, but lower fecundity (Sinclair et al. 2003). This may explain the increase in longevity and decrease of fecundity of females of *G. punctipes* at the lower temperature regimes in this study. The survival curve (l_x) at the low temperature regimes showed a type II pattern (Towsend et al. 2006), indicating that the mortality rate of the predator was constant from birth until older age. However, at higher temperature regimes (27/21°C and 30/26°C, 24.5°C, 28.3°C), the survival curves (l_x) were higher at the beginning of the reproductive cycle compared to those of the low temperature treatments. The survival curves at 30/26°C and 28.3°C were of type I (Towsend et al. 2006), where high predator mortality is concentrated in individuals of old age.

In a recent paper (Calixto et al. 2014), we published data on development time and survival of the immature stages of *G. punctipes* at the same constant and varying temperatures as used in this paper. The results were in line with what we found for adults: the optimal temperature range for development and survival of *G. punctipes* immatures is 24.5–30°C. The fact that we found this optimum development and survival is not unexpected, as it is in the range of the average annual minimum (11.6°C) and the average annual maximum (28.4°C) temperature, and close to the average annual temperature (23.8°C) found in the region of Minas Gerais where the predators were collected for this study (INMET 2015). *Geocoris punctipes* has a rather wide Nearctic distribution, and we expect

that temperature responses will be different in other regions with a very different climate.

Life tables are of great importance in understanding the population dynamics of an insect, and in particular, the intrinsic rate of population increase (r_m) is a parameter that assists in the evaluation and selection of a natural enemy as a biological control agent (van Lenteren 2010). We recorded r_m values between 0.060 and 0.079 for the average temperatures of 24.5°C and 28.3°C. Torres et al. (2004) reported an r_m of 0.041 female/female/day for *G. floridanus* at 26°C, and Davis (1981) found values of r_m for *Geocoris* species between 0.016 and 0.068 female/female/day at 26.7°C. So, our r_m values are similar or higher than those found by the other authors. The highest value for finite rate of increase (λ) recorded in this study was 1.12. Torres et al. (2004) reported a finite rate of increase of 1.04 female/day at 26°C for *G. floridanus*. The mean generation time (T , the average period between the births of the individual from one generation to the next generation) of *G. punctipes* decreased with increasing temperature. The time it takes for the population to double in number (TD) found in this study at the constant temperature 16.8°C was similar to the value observed by Torres et al. (2004) for *G. floridanus* at a much higher temperature (26°C), so population growth of *G. punctipes* will be faster than that of *G. floridanus*.

Varying temperatures compared to constant ones can have varying effects on biological traits like development and reproduction of pests and natural enemies, and the effects may be similar, neutral or opposite, as demonstrated by Tommasini and Benuzi (1996) for *Orius laevigatus* (Reuter) and by Hofsvang (1976) for *Anthocoris sibiricus* Reuter. The effect of varying temperatures on the development time of a pest or natural enemy depends on the optimum temperature and the upper and lower threshold of the pest or natural enemy in question (Jakobsen et al. 2006). Results also depend on the amplitude of the diurnal temperature ranges. The higher the differences between day and night temperatures, the more likely differences in population growth can be detected. When the temperatures in a varying regime occur within the approximately linear section of the temperature rate relationship, little or no acceleration or retardation of development is observed (Bryant et al. 1999). Although different temperatures affected life table parameters in our experiments, varying or constant temperatures with the same average did not result in significant differences in most of the parameters we determined. This indicates that the lowest and highest

temperatures used in this study within the linear section of the temperature relationship for development and reproduction of *G. punctipes*.

In conclusion, we have to reject our first and second hypothesis stating that at the lowest and the highest temperature, the varying temperature regime is resulting in poorer reproduction and survival performance: none of the data found at constant or varying temperature regimes but with the same average temperature were significantly different. The hypothesis we formulated for the intermediate temperature regimes does, thus, also hold for the lowest and highest temperature regimes: fecundity and lifespan are the same at varying and constant temperature regimes with the same average temperature. The same holds for life table parameters like the net reproductive rate (R_0), the intrinsic rate of increase (r_m) and the mean generation time (T). The best performance of *G. punctipes*, that is the highest rate of population increase, is obtained at high temperatures in the range of 24.5°C and 30°C, and is not negatively influenced by varying temperature.

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