ISRAEL JOURNAL OF ENTOMOLOGY, Vol. 48 (2), pp. 1–22 (27 February 2018)

This contribution is dedicated
to the memory of Prof. Dan Gerling
a scientist, a colleague and a friend

Population growth parameters of three Neotropical mirid predators (Hemiptera: Miridae) at five temperatures on tobacco with *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs as food

V. H. P. Bueno[1], A. M. Calixto[1], F. C. Montes[1] & J. C. van Lenteren[1,2]*
[1]Laboratory of Biological Control, Department of Entomology, Federal University of Lavras,
P. O. Box 3037, 37200-000 Lavras, MG, Brazil. E-mail: vhpbueno@den.ufla.br,
anamaria.calixto@bol.com.br, flaviobiologia2005@hotmail.com
[2]Laboratory of Entomology, Wageningen University, P. O. Box 16, 6700AA,
Wageningen, The Netherlands.
**Corresponding author: joop.vanLenteren@wur.nl*

ABSTRACT

Three Neotropical predators *Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Distant) and *Macrolophus basicornis* (Stål) (Hemiptera: Miridae) are considered in Brazil as potential biological control agents of *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) and other tomato pests. This study evaluated the effect of five constant temperatures (16, 20, 24, 28 and 32°C, all ±1°C) on the reproduction, population growth and longevity of these predatory mirids. Adults freshly emerged from nymphs reared at each temperature, were separated in couples and kept in 1.7 l glass pots with tobacco plant seedlings (*Nicotiana tabacum* L., cv. TNN) as oviposition substrate and *ad libitum Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) eggs as food. The shortest pre-oviposition and the longest oviposition periods were observed at 24°C and 28°C in all three mirid species. At 24°C all three species showed the highest daily and total fecundities. The population growth parameters represented by the intrinsic rate of increase (r_m) and the finite rate of increase (λ) were highest at 24°C and 28°C, and the net reproductive rate (R_0) was highest at 24°C for all three species. Longevities of both males and females were longest at 24°C and 28°C in all three mirids. The size of tibia and adult weight in the three species were greatest at 20°C and 28°C, respectively. Differences in values for all above variables were small and often statistically non-significant for the three mirid species at the same temperature. Also, not a single significant difference was found for any of the growth parameters at each of the temperatures, including r_m. The results indicate that temperatures in the range from 24–28°C are best for reproduction and population growth of *C. infumatus*, *E. varians* and *M. basicornis*. The factitious prey *E. kuehniella* is an excellent food source and tobacco plants provide a good rearing substrate for these mirids. The obtained results may assist in developing a mass rearing method for *C. infumatus*, *E. varians* and *M. basicornis*, in determining optimal timing and frequency of mirid releases in the crop, and in determining whether they are active at the temperature spectrum observed during tomato production in the field or greenhouse.

KEYWORDS: *Campyloneuropsis infumatus*, *Engytatus varians*, *Macrolophus basicornis*, *Tuta absoluta*, agricultural pests, biological control, fecundity, longevity, mass rearing, tomato leafminer.

---

http://www.entomology.org.il/publications; ISSN (online) 2224-6304
urn:lsid:zoobank.org:pub:6541561E-95F9-481A-A153-2EBE455F3833

RESUMO

Três predadores Neotropicais *Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Distant) and *Macrolophus basicornis* (Stål) (Hemiptera: Miridae) são considerados como potenciais agentes de controle biológico de *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) e de outras pragas do tomateiro no Brasil. Neste estudo foram avaliados o efeito de cinco temperaturas constantes (16, 20, 24, 28 e 32°C, todas ±1°C) na reprodução, crescimento populacional e longevidade destes mirideos predadores. Adultos recém-emergidos, originários de ninfas criadas em cada temperatura foram separados em casais e mantidos em potes de vidro de 1.7 l contendo mudas de fumo (*Nicotiana tabacum* L., cv. TNN) como substrato de oviposição e ovos de *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae) *ad libitum* como alimento. Os períodos, mais curto de preoviposição e o mais longo de oviposição, foram observados a 24°C e 28°C em todas as três espécies de mirideos. A 24°C todas as três espécies apresentaram as maiores fecundidades, diária e total. Os parâmetros de crescimento populacional representados pela taxa intrínseca de aumento (r_m) e a taxa finita de aumento (λ) foram maiores a 24°C e 28°C, e a taxa líquida de reprodução (R_0) foi maior a 24°C para todas as três espécies. As longevidades de machos e fêmeas foram mais longas a 24°C e 28°C para os três mirideos. O tamanho da tíbia e o peso do adulto nas três espécies foram maiores a 20°C e 28°C, respectivamente. Diferenças nos valores para todas as variáveis acima foram pequenas e frequentemente não estatisticamente significativas para as três espécies de mirideos na mesma temperatura. Além disso, nenhuma diferença significativa foi encontrada para qualquer um dos parâmetros de crescimento em cada uma das temperaturas, incluindo r_m. Os resultados indicam que temperaturas na faixa de 24–28°C são as melhores para a reprodução e crescimento populacional de *C. infumatus*, *E. varians* e *M. basicornis*. A presa alternativa *E. kuehniella* é uma excelente fonte de alimento e plantas de fumo fornecem um bom substrato para a criação destes mirideos. Os resultados obtidos podem auxiliar no desenvolvimento de um método de criação massal para *C. infumatus*, *E. varians* e *M. basicornis*, na determinação do tempo e frequência ótimos para liberação dos mirídeos no cultivo e na determinação de se eles são ativos no espectro de temperatura observado durante a produção de tomate no campo ou em casas de vegetação.

PALAVRAS-CHAVE: *Campyloneuropsis infumatus*, *Engytatus varians*, *Macrolophus basicornis*, *Tuta absoluta*, pragas agrícolas, controle biológico, fecundidade, longevidade, criação massal, traça do tomateiro.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is the most widely produced fruit vegetable in the world and also plays an important role in the agricultural economy of Brazil, one of the main world tomato producers (Agrianual 2016). In Brazil, tomato crops are being attacked by at least 29 insect pests, including whiteflies, lepidopterans, leaf miners and mites (Pratissoli & Carvalho 2015). The South American tomato borer *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is one of the major pests, causing complete crop losses when no pest control is applied (Guedes & Picanço 2012). *Tuta absoluta* is usually controlled by frequent sprays involving weekly or fortnightly chemical pesticide treatments (Thomazini *et al*. 2001). As a consequence, Brazilian *T. absoluta* populations have acquired resistance to several active ingredients, resulting in a so-named pesticide treadmill, decimation of natural enemies and high residue levels on tomato fruit (van den Bosch 1978; Siqueira *et al.* 2000, 2001; Santos *et al.* 2011; Silva *et al.* 2011). The rapid development of resistance to frequently applied pesticides, together with negative effects on the environment and human health necessitate a search for alternative methods, such as biological control.

One group of natural enemies, predatory mirid bugs (Hemiptera: Miridae) is of special interest for *T. absoluta* management. Mirid predators became popular biological control agents during the past 20 years (van Lenteren *et al.* 2018), which may seem surprising as they are polyphagous as well as zoophytophagous (Silva *et al.* 2016*a*, *b*). However, they are increasingly being reported as promising biocontrol agents of various important pests, mainly in tomato crops (Devi *et al.* 2002; Perdikis & Lykouressis 2002; Blaeser *et al.* 2004; Urbaneja *et al.* 2005; Bueno *et al.* 2013*a*). Two examples of recently successfully commercially used predators are *Nesidiocoris tenuis* (Reuter) and *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) for control of *T. absoluta* and *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) in Europe (Calvo *et al.* 2012; van Lenteren 2012; van Lenteren *et al.* 2018).

In Brazil, natural enemies of *T. absoluta* have been collected and are currently evaluated as biological control agents (Bueno *et al.* 2013*a*, *b*; Silva *et al.* 2016*a*, *b*, 2018). In particular, three mirid species (*Campyloneuropsis infumatus* (Carvalho), *Engytatus varians* (Distant) and *Macrolophus basicornis* (Stål) (Hemiptera: Miridae) seem interesting candidates for control of several tomato pests, as they were found to prey on eggs and larvae of *T. absoluta* (van Lenteren *et al.* 2016, 2017). Also, they prey on eggs and larvae of various other lepidopteran pests of tomato, such as *Neoleucinodes elegantalis* (Guenée) (Lepidoptera: Crambidae), *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) (Bueno 2017). Further, they prey on nymphs of *B. tabaci* (Hemiptera: Aleyrodidae), aphids and mites (Bueno *et al.* 2013*a*, *b*; Bueno 2017). Bueno *et al.* (2012, 2013*a*) and Silva *et al.* (2016*a*) reported that these Neotropical mirids can use tomato plants as oviposition substrate, can complete their development and build up populations on tomato, and, very importantly, can easily walk on stems and leaves of tomato plants despite the presence of sticky and poisonous trichomes. Finally, nymphs and adults of these three Neotropical zoophytophagous mirids appeared to cause little injury to tomato seedlings and fruit, even when present in high densities and in the absence of prey (Silva *et al.* 2016*b*).

Positive characteristics of these mirids and their potential as biological control agents make it critical to obtain basic data about their development and reproduction biology at temperatures, which they are exposed to in tomato crops in the field or greenhouse. Such information would also be relevant for (1) developing a mass rearing method, (2) estimating the timing and frequency of predator releases in the crop, and (3) clarifying if the development of pest and natural enemy populations are synchronized at practical field and greenhouse temperature conditions (van Lenteren 2003, 2010).

This study aimed to evaluate the effect of five constant temperatures (16, 20, 24, 28 and 32°C, all ±1°C) on reproduction, population growth and longevity of the mirid predators *C. infumatus*, *E. varians* and *M. basicornis* feeding on eggs of a factitious host, *Ephestia kuehniella* (Zeller) (Lepidoptera: Pyralidae), and having tobacco as host plant for oviposition and as a source of water. The selected temperature range was based on the optimum temperatures for tomato production in Brazil, during which farmers try to produce tomatoes in the field, with lower and higher values occuring occasionally (Naika *et al*. 2006). Brazilian growers producing tomatoes in greenhouses also attempt to adhere to optimal temperature schedules. We used tobacco instead of tomato in this baseline research for the following reasons: (1) in the field we collected mirids on tobacco, (2) tobacco appeared to be a very good host plant for rearing and maintaining populations of the three mirid species in the laboratory, and (3) on tobacco, mirid eggs can be easily seen on leaves and reliably counted (Bueno *et al.* 2018), which is impossible on tomato (Silva *et al.* 2016*a*).

MATERIALS AND METHODS

Collecting and rearing of mirid predators

Mirid predators *C. infumatus*, *E. varians* and *M. basicornis* were sampled on tobacco crops (*Nicotiana tabacum* L., cv. TNN) located in the Ribeirão Vermelho (21°11'29"S 45°03'45"W, alt. *ca* 790 m) and Lavras (21°14'43"S 44°59'59"W, alt. *ca* 920 m) municipalities, Minas Gerais State, Brazil. Nymphs and adults were identified on basis of visual morphological characters according to the key of mirid species of Ferreira and Henry (2011). Specimens were sent for confirmation of their identity to P.S.F. Ferreira (Dept. of Animal Biology, Federal University of Viçosa, Viçosa, Brazil). Further details about locations, collection and identification are provided by Bueno *et al.* (2012, 2013*a*).

Stock colonies of these mirids were maintained in the laboratory according to the methodology described elsewhere (Bueno *et al*. 2013*a*; Silva *et al.* 2016*a*). Eggs of *E. kuehniella* obtained from Koppert Brasil (http://koppert.com.br) were offered as food and tobacco (cv. TNN) as oviposition substrate. The mirid stock rearings were maintained in a climate room at 25±2°C, relative humidity (RH) 70±10% and 12h photophase. One hundred newly emerged nymphs of each mirid species were isolated and reared at each of the five temperatures (16, 20, 24, 28 and 32°C) until adults emerged to form couples to be used in the experiment described below.

Reproduction, longevity and population growth

Freshly emerged adults of each mirid species that had developed at the same temperature were used in experiments. A couple of each mirid predator of up to 24h old was introduced to a 1.7 l glass containers with a tobacco seedling with up to 3 leaflets planted in a 200 ml plastic cup with soil as oviposition substrate and *ad libitum E. kuehniella* eggs as food. The seedlings were daily replaced by new ones.

Removed seedlings were observed under a stereoscopic microscope Leica EZ4 under 40× magnification, and the number of eggs and, later, hatched nymphs were recorded daily for each mirid species. The experiments were executed in climate chambers at 16°C, 20°C, 24°C, 28°C and 32°C (all ±1°C), RH 70±10% and 12h photophase. The mortality of adults was recorded daily, and the longevity was determined for males and females of each mirid species. The data on daily and total fecundities were based on counting eggs and emerged nymphs (Agustí & Gabarra 2008, 2009; Sanchez *et al*. 2009; Silva *et al*. 2016*a*). Based on these data, the pre-oviposition, oviposition and post-oviposition periods, the fecundity (daily and total) of *C. infumatus*, *E. varians* and *M. basicornis* at the different temperatures were determined. The numbers of replicates (Table 1) varied for different species and temperatures, and depended on the number of nymphs developed into males and females from which the couples were formed.

Weight and size

Weight and size of newly-emerged females and males of each mirid species were determined for the five temperatures. Twenty males and 20 females reared at each temperature were placed individually in a glass tube (2.5×8.0 cm) covered with plastic film and weighed using a precision balance (Shimadzu, model AW-220, 0.0001g of precision). Next, the right hind tibia of each weighed insect was placed on a cover slide with a drop of Hoyer's medium. The length of the tibia was measured using a micrometer ocular under 100× magnification.

Data analysis

The experiment was carried out in a factorial design of 5×3 (five—16°C, 20°C, 24°C, 28°C and 32°C—temperatures and three mirid predator species, viz. *C. infumatus*, *E. varians* and *M. basicornis*). All data were first checked for normality ($P \geq 0.05$) by using a Shapiro-Wilk test. The data from the pre-oviposition, oviposition and post-oviposition periods, daily and total fecundity, and the longevity showed normal distributions and were next exposed to an analysis of variance (two-way ANOVA with the mirid species and temperatures as factors) using the Tukey test ($P \leq 0.05$). To compare weights, sizes of tibia and longevities of females and males for the same temperature, the *t* test was used ($P \leq 0.05$). As data of weights and sizes of female and male tibiae were not normally distributed, they were transformed by square root ($\sqrt{x}$) and exposed to an analysis of variance (two-way ANOVA with the mirid species and temperatures as factors) using the Tukey test ($P \leq 0.05$). All data were analyzed with the R Development Core Team (2014) software.

To determine the life table parameters of the three mirids, the data of survival and fecundity of each female were used. Age interval (x), fecundity (m_x), probability of 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 double time (DT), using the Jackknife method (Maia *et al*. 2000, 2014). The age (in days) at which the insects began adulthood, immature survival and sex ratio of emerged adults when exposed to the same temperature were used in the calculation of the population growth parameters. The life table parameters and their standard errors were estimated by the Life Table Sas Method (Maia *et al.* 2000, 2014). Means of the life table parameters were compared in pairs by applying a unilaterally Student *t* test for independent samples ($P \leq 0.05$) using the statistical program SAS (SAS Institute 2000).

The values of l_x are all lower than 1 (Figs 4–8), because survival was measured based on the development of a cohort of individuals for each species at each temperature, starting with newly emerged eggs. The values presented at day 0 of adult age represent survival data after egg and nymphal mortality (Bueno *et al.* 2018).

RESULTS

Pre-oviposition, oviposition and post-oviposition periods

The pre-oviposition periods were on average 4–5 days at 24°C and 28°C for all three mirid species, and shorter than at the highest (32°C) and lower temperatures (16°C, 20°C) ($F_{4,145}$=4.315, p<0.0001). At 16°C the pre-oviposition periods were longer than those at the other four temperatures ($F_{4,145}$=5.896, p<0.001) for all three mirid species (Fig. 1).

The oviposition periods were longer at 24°C and 28°C ($F_{4,145}$=7.458, p=0.002) than at other temperatures for all three mirids. At 24°C the oviposition periods of *M. basicornis* (26.6 days) and *E. varians* (25.9 days) were longer than in *C. infumatus* (23.9 days) ($F_{4,145}$=2.367, p<0.001). The oviposition period of *M. basicornis* (26.8

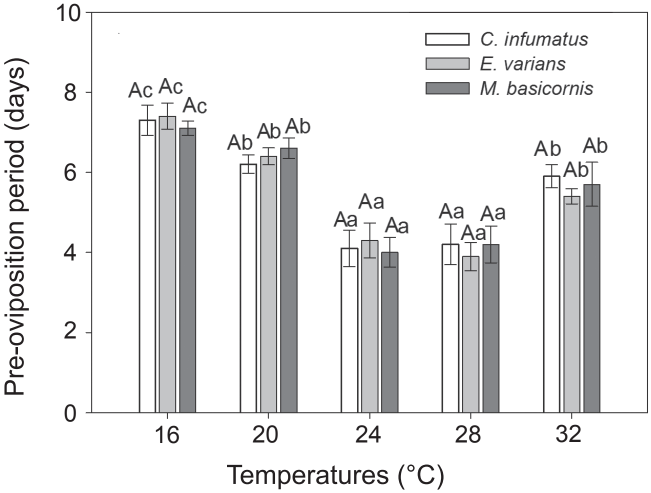

Fig. 1: Pre-oviposition period in days (±SE) of *Campyloneuropsis infumatus*, *Engytatus varians* and *Macrolophus basicornis* at different temperatures, 70±10% RH and 12h photophase. Means (±SE) followed by same capital letter indicate non-significant differences for the species at the same temperature (one-way ANOVA); means followed by the same lower case letter (two-way ANOVA) indicate non-significant differences between the species at different temperatures (Tukey's test, P≤0.05).

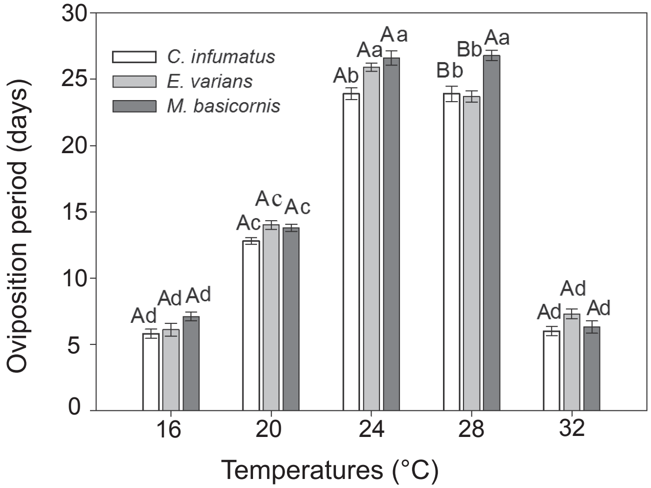

Fig. 2: Oviposition period in days (±SE) of *C. infumatus*, *E. varians* and *M. basicornis* at different temperatures, 70±10 % RH and 12h photophase. Means (±SE) followed by same capital letter indicate non-significant differences for the species at the same temperature (one-way ANOVA), means followed by the same lower case letter (two-way ANOVA) indicate non-significant differences between the species at different temperatures (Tukey's test, P≤0.05).

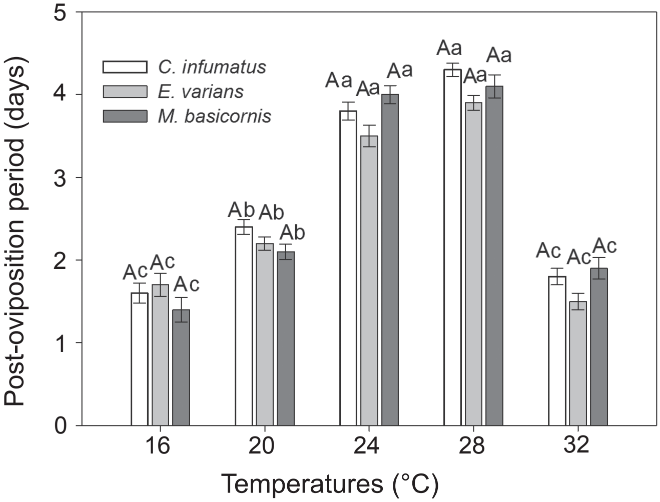

Fig. 3: Post-oviposition period in days (±SE) of *C. infumatus*, *E. varians* and *M. basicornis* at different temperatures, 70±10 % RH and 12h photophase. Means (±SE) followed by same capital letter indicate non-significant differences for the species at the same temperature (one-way ANOVA), means followed by the same lower case letter (two-way ANOVA) indicate non-significant differences between the species at different temperatures (Tukey's test, P≤0.05).

days) was longer than in the other two species at 28°C (*C. infumatus*, 23.8 days and *E. varians*, 23.7 days) ($F_{4,145}$=10.325, p=0.001). There were no differences in oviposition periods for all three species at 16°C and 32°C (Fig. 2).

The post-oviposition periods for all three mirids were longer at 24°C and 28°C, and shorter at 16°C and 32°C ($F_{4,145}$=3.345, p<0.001) (Fig. 3).

Daily and total fecundity

The highest daily fecundities were found at 24°C for all three mirid species (*C. infumatus*, 10.4, *E. varians*, 10.3 and *M. basicornis*, 11.7 nymphs/female/day) ($F_{4,145}$=12.752, p<0.001). *Macrolophus basicornis* showed a higher daily fecundity than in the other two species at 16°C ($F_{2,73}$=4.233, p=0.014), 28°C ($F_{2,99}$=2.684, p<0.001) and 32°C ($F_{2,69}$=5.212, p=0.004) (Table 1). At 28°C the daily fecundities were 6.7 nymphs/female/day (*C. infumatus*), 6.4 nymphs/female/day (*E. varians*) and 8.3 nymphs/female/day (*M. basicornis*).

The highest total fecundities were also found at 24°C (*C. infumatus*, 248.5, *E. varians*, 266.7 and *M. basicornis*, 311.2 nymphs/female) ($F_{4,145}$=6.158, p= 0.003) (Table 1). Fecundities of *M. basicornis* were higher than in the other species at 16°C ($F_{2,73}$=3.664, p<0.001), 24°C ($F_{2,93}$=4.551, p=0.0013) and 28°C ($F_{2,99}$=6.127, p=0.006). Fecundities of *C. infumatus* were lower than in *E. varians* and *M. basicornis* at 20°C ($F_{2,90}$=7.354, p<0.001) and 32°C ($F_{2,69}$=2.443, p<0.001) (Table 1).

Table 1: Daily fecundity (nymphs/female/day) and total fecundity (nymphs/female) of *C. infumatus*, *E. varians* and *M. basicornis* at five constant temperatures (±1°C), 70±10% RH and 12h photophase. Abbreviation: n – number of replicates (females).

T °C	Species	n	Daily fecundity	Total fecundity
16	*C. infumatus*	20	3.0±1.17B*d**	17.4±1.13Bd
	E. varians	25	3.1±0.97Bd	18.9±0.87Bd
	M. basicornis	33	4.6±2.01Ad	32.6±1.21Ad
20	*C. infumatus*	12	5.4±1.23Ac	69.1±1.16Bc
	E. varians	37	5.8±1.12Ac	81.2±1.02Ac
	M. basicornis	44	5.6±0.89Ac	77.2±0.77Ac
24	*C. infumatus*	19	10.4±0.22Aa	248.5±3.23Ba
	E. varians	39	10.3±0.16Aa	266.7±4.16Ba
	M. basicornis	38	11.7±0.31Aa	311.2±4.31Aa
28	*C. infumatus*	15	6.7±0.24Bb	160.1±3.17Bb
	E. varians	45	6.4±0.31Bb	151.6±2.41Bb
	M. basicornis	42	8.3±0.88Ab	222.4±2.68Ab
32	*C. infumatus*	11	3.2±0.13Bd	19.2±1.33Bd
	E. varians	24	3.5±0.21Bd	25.5±0.88Ad
	M. basicornis	36	4.1±0.11Ad	25.8±0.94Ad

Notes: * – Means (±SE) followed by same capital letter in columns indicate non-significant differences for species at same temperature (Tukey's test, P≤0.05); ** – means followed by same lower case letter in columns indicate non-significant differences between species at different temperatures (Tukey's test, P≤0.05).

Average fecundity (m_x), survival (l_x) and growth population parameters

The average fecundity (m_x) reached a maximum of 4 nymphs/female at 16°C and 32°C (Figs 4A, 5A, 6A, 7A, 8A). At 20°C, 24°C and 28°C, the average fecundity (m_x) was 7, 14 and 13 nymphs/female, respectively (Figs 5A, 6A, 7A). The number of nymphs/female/day increased with the mirid female age at 16°C, 20°C, 24°C,

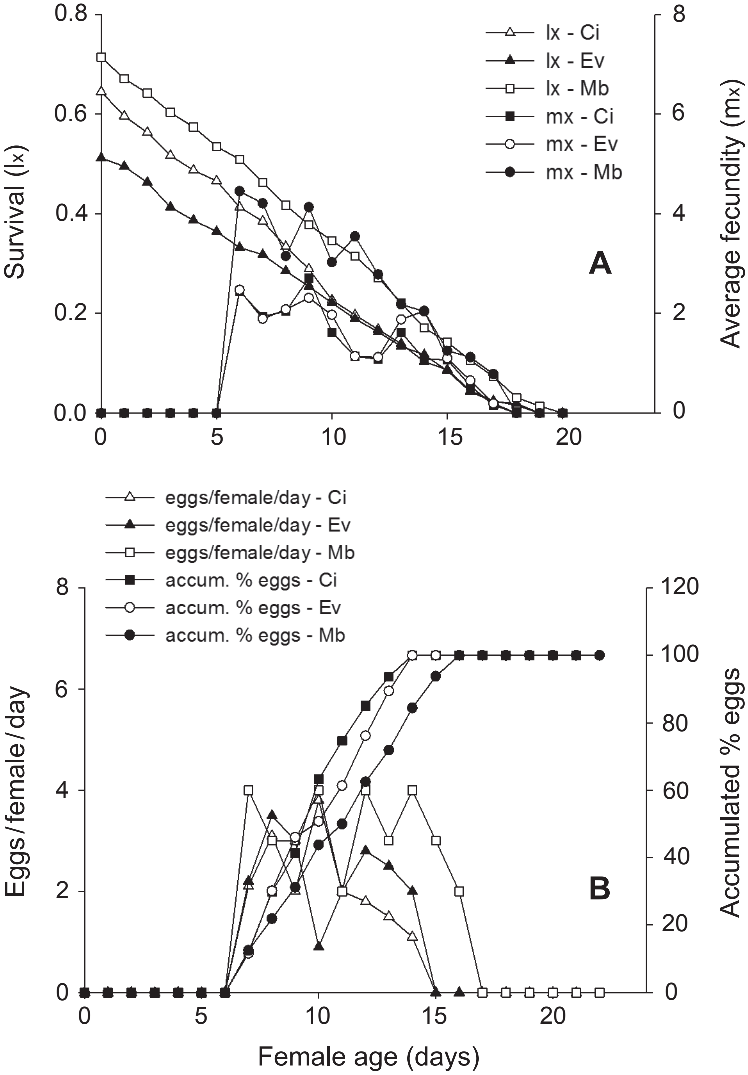

Fig. 4: (A) survival (l_x) and average fecundity (m_x); (B) eggs/female/day and accumulated percentage eggs of *C. infumatus* (Ci), *E. varians* (Ev) and *M. basicornis* (Mb) at 16°C (±1°C), 70±10% RH and 12h photophase.

28°C and 32°C (Figs 4B, 5B, 6B, 7B, 8B). This number started to increase after the 4th day of female adulthood (pre-oviposition period) and decreased after the 25th day at 24°C and 28°C (Figs 6B, 7B). At 24°C and 28°C, *C. infumatus*, *E. varians* and *M. basicornis* females laid more eggs than at other three temperatures (Figs 6A, B & 7A, B). The survival rates (l_x) decreased linearly with the increase of the

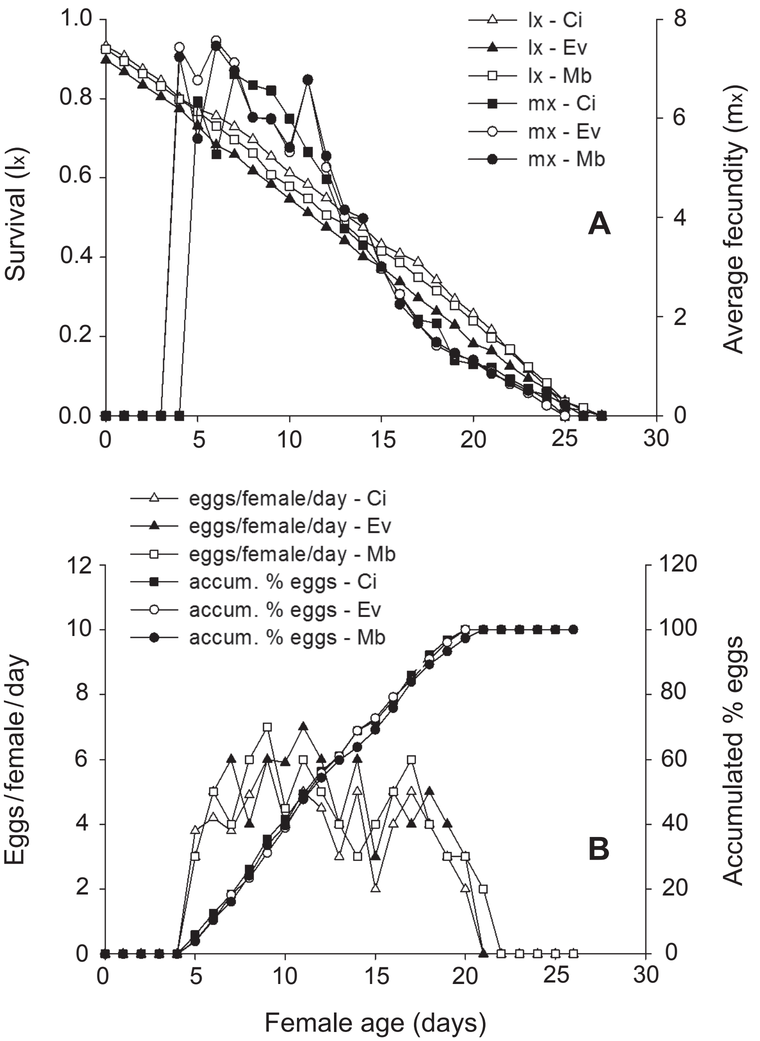

Fig. 5: (A) survival (l_x) and average fecundity (m_x); (B) eggs/female/day and accumulated percentage eggs of *C. infumatus* (Ci), *E. varians* (Ev) and *M. basicornis* (Mb) at 20°C (±1°C), 70±10% RH and 12h photophase.

female age at all temperatures (Figs 4A, 5A, 6A, 7A, 8A). The longest survival (l_x) of females was observed at 24°C and 28°C (Figs 6A, 7A) for all three mirid species.

There were no significant differences among the three mirid species as regards their population growth parameters at each temperature. However, at different

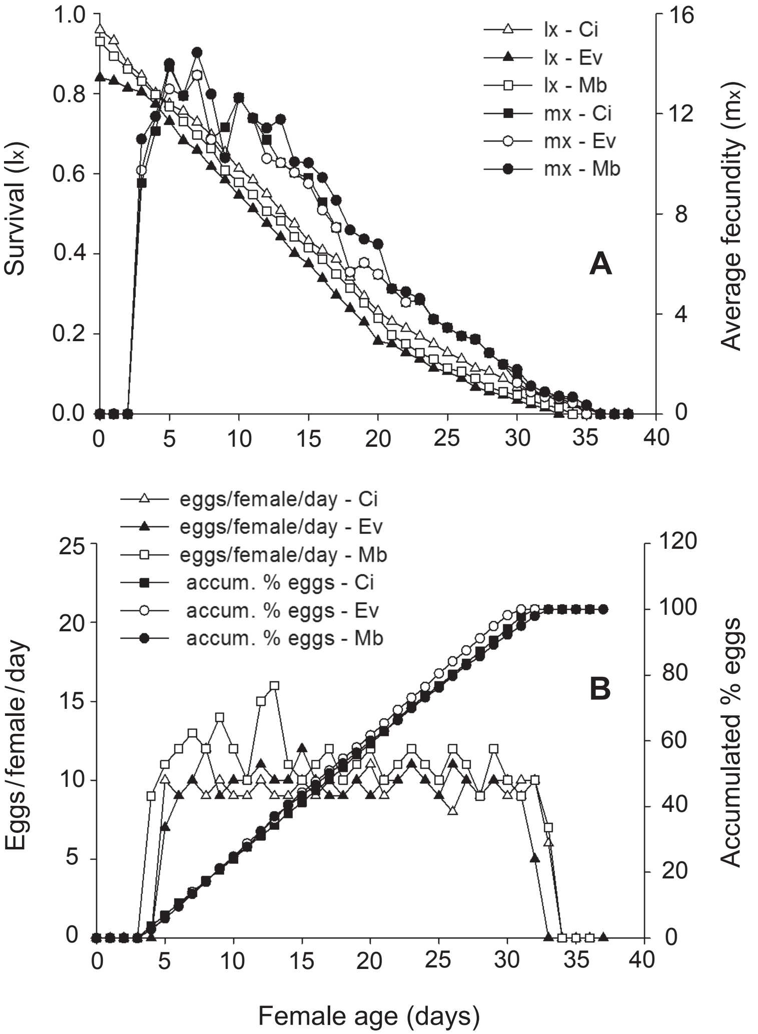

Fig. 6: (A) survival (l_x) and average fecundity (m_x); (B) eggs/female/day and accumulated percentage eggs of *C. infumatus* (Ci), *E. varians* (Ev) and *M. basicornis* (Mb) at 24°C (±1°C), 70±10% RH and 12h photophase.

temperatures, the intrinsic rates of increase (r_m) were significantly higher at 24°C and 28°C for all three mirids (t=2.314, df=4, p<0.001) than at other temperatures. The net reproductive rates (R_0) were higher at 24°C (t=3.987, df=4, P<0.001) for all three species than at other temperatures. The mean generation times (T)

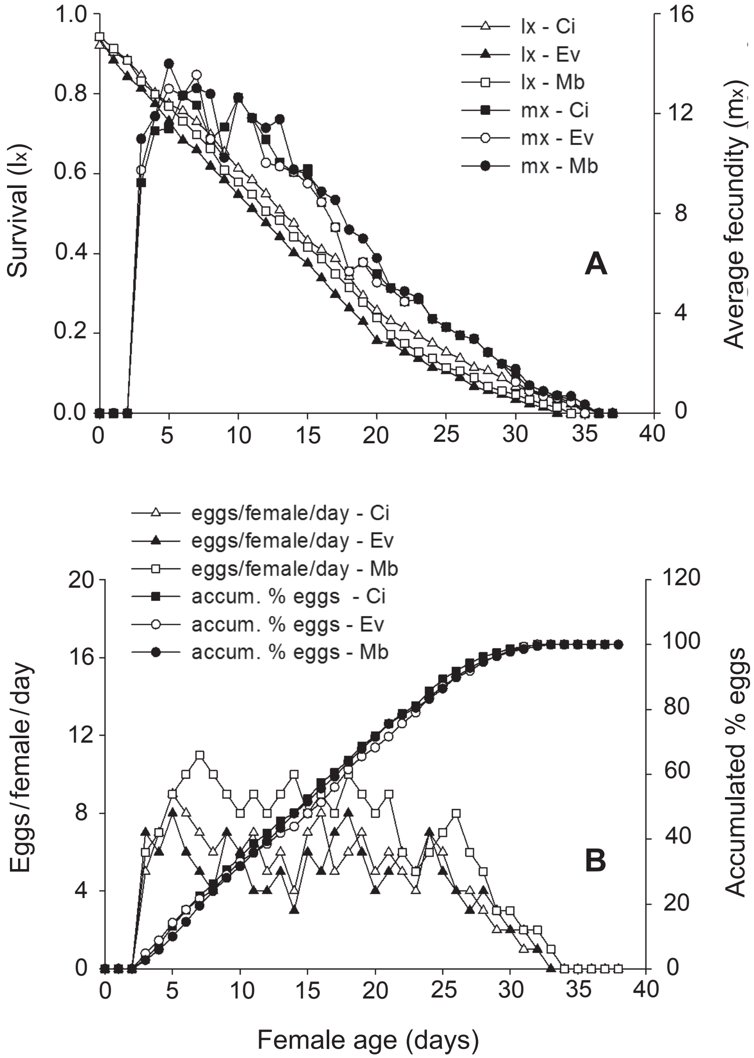

Fig. 7: (A) survival (l_x) and average fecundity (m_x); (B) eggs/female/day and accumulated percentage eggs of *C. infumatus* (Ci), *E. varians* (Ev) and *M. basicornis* (Mb) at 28°C (±1°C), 70±10% RH and 12h photophase.

were higher at 28°C and 32°C (40 days) (t=7.698, df=4, p=0.002) than at other temperatures. The double times (DT) were higher at 24°C, 28°C and 32°C than at other temperatures, and the finite rates of increase (λ) were higher at 24°C and 28°C than at other temperatures (Table 2).

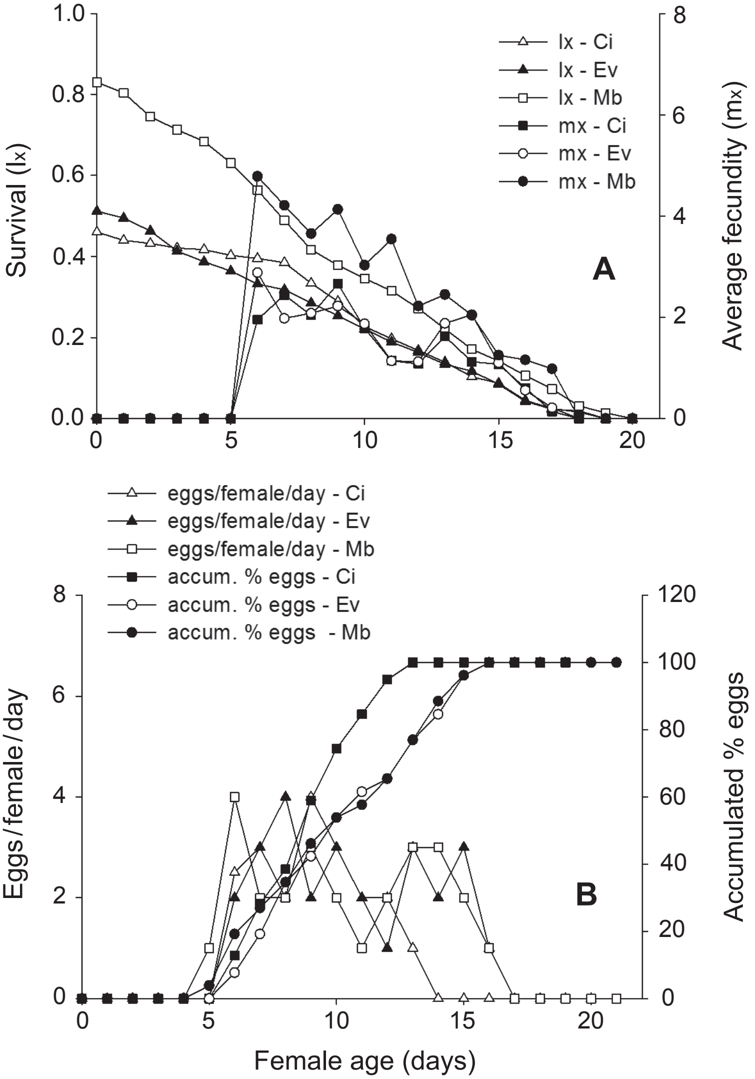

Fig. 8: (A) survival (l_x) and average fecundity (m_x); (B) eggs/female/day and accumulated percentage eggs of *C. infumatus* (Ci), *E. varians* (Ev) and *M. basicornis* (Mb) at 32°C (±1°C), 70±10% RH and 12h photophase.

Table 2: Population growth parameters of *Campyloneuropsis infumatus*, *Engytatus varians* and *Macrolophus basicornis* at five constant temperatures (±1°C), 70±10 % RH and 12 h photophase. Abbreviations: r_m – intrinsic rate of increase, R_0 – net reproductive rate, T – mean generation time, DT – double time, λ – finite rate of increase.

T °C	Species	r_m	R_0	T	DT	λ
16	*C. infumatus*	0.0331±0.004 $A^{*}c^{**}$	33.56±0.21 Ac	81.03±0.22 Ac	19.20±0.12 Ac	1.0388±0.003 Ac
	E. varians	0.0343±0.003 Ac	35.21±0.29 Ac	81.77±0.26 Ac	20.03±0.10 Ac	1.0355±0.004 Ac
	M. basicornis	0.0379±0.005 Ac	38.03±0.28 Ac	80.89±0.34 Ac	19.55±0.09 Ac	1.0374±0.005 Ac
20	*C. infumatus*	0.0651±0.002 Ab	77.04±0.42 Ab	78.03±0.33 Ac	14.08±0.08 Ab	1.0726±0.002 Ab
	E. varians	0.0614±0.006 Ab	78.66±0.44 Ab	80.44±0.34 Ac	14.15±0.09 Ab	1.0831±0.005 Ab
	M. basicornis	0.0678±0.004 Ab	79.13±0.40 Ab	77.22±0.29 Ac	13.99±0.07 Ab	1.0809±0.003 Ab
24	*C. infumatus*	0.0899±0.005 Aa	89.33±0.39 Aa	56.04±0.18 Ab	11.44±0.06 Aa	1.1003±0.010 Aa
	E. varians	0.0972±0.007 Aa	88.45±0.38 Aa	55.86±0.21 Ab	10.89±0.04 Aa	1.1025±0.008 Aa
	M. basicornis	0.0988±0.006 Aa	91.08±0.41 Aa	57.63±0.22 Ab	10.65±0.08 Aa	1.1028±0.009 Aa
28	*C. infumatus*	0.0956±0.008 Aa	80.07±0.55 Ab	41.23±0.11 Aa	10.62±0.11 Aa	1.1053±0.008 Aa
	E. varians	0.0991±0.009 Aa	79.88±0.49 Ab	41.89±0.14 Aa	11.46±0.09 Aa	1.1042±0.009 Aa
	M. basicornis	0.1003±0.010 Aa	81.44±0.51 Ab	42.14±0.18 Aa	10.23±0.12 Aa	1.1098±0.008 Aa
32	*C. infumatus*	0.0645±0.006 Ab	32.34±0.24 Ac	40.02±0.20 Aa	10.45±0.10 Aa	1.0788±0.007 Ab
	E. varians	0.0612±0.007 Ab	31.72±0.19 Ac	39.78±0.23 Aa	11.07±0.08 Aa	1.0767±0.002 Ab
	M. basicornis	0.0701±0.004 Ab	33.57±0.28 Ac	37.04±0.19 Aa	9.18±0.11 Aa	1.0801±0.008 Ab

Notes: *Means (±SE) followed by same capital letter in columns (species at same temperature) and **means followed by same lower case letter (species at different temperatures) in columns do not differ by Unilaterally *T* test at $P \leq 0.05$.

Table 3: Longevity (days) of *Campyloneuropsis infumatus*, *Engytatus varians* and *Macrolophus basicornis* at constant temperatures (±1°C), 70±10 % RH and 12h photophase.

		Longevity					
T °C	**Species**	**Females**	**n**	**Males**	**n**	**t**	***P* value**
	C. infumatus	14.7±1.61A*c**	20	12.3±2.71Bc	20	0.704	0.012
16	*E. varians*	15.2±1.58Ac	25	11.7±1.56Bc	25	1.116	0.003
	M. basicornis	15.6±2.04Ac	33	12.1±1.12Bc	33	0.145	0.024
	C. infumatus	21.4±1.52Ab	12	18.2±1.05Bc	12	1.234	<0.001
20	*E. varians*	22.6±1.13Ab	37	19.1±1.46Bc	37	0.983	0.004
	M. basicornis	22.5±0.99Ab	44	21.7±1.11Ac	44	1.119	0.014
	C. infumatus	31.4±2.15Aa	19	28.4±2.24Ba	19	2.136	0.026
24	*E. varians*	33.7±1.44Aa	39	29.3±1.88Ba	39	0.865	0.035
	M. basicornis	34.6±1.79Aa	38	30.2±1.96Aa	38	1.457	0.123
	C. infumatus	32.4±2.55Aa	15	27.6±1.89Ba	15	2.132	<0.001
28	*E. varians*	31.5±1.77Aa	45	28.9±2.14Ba	45	1.479	0.002
	M. basicornis	35.1±1.19Aa	42	33.7±2.52Aa	42	0.788	0.214
	C. infumatus	13.7±1.86Ac	11	11.9±1.06Bc	11	0.955	0.006
32	*E. varians*	14.2±3.75Ac	24	12.8±0.98Bc	24	1.038	0.041
	M. basicornis	13.9±1.15Ac	36	12.5±1.65Ac	36	0.899	0.075

Notes: *−Means (±SE) followed by same capital letter in columns indicate non-significant differences for species at the same temperature (Tukey's test, P≤0.05); **−means followed by same lower case letter in the columns indicate non-significant differences between the species at different temperatures (Tukey's test, P≤0.05).

Longevity of females and males of *C. infumatus*, *E. varians* and *M. basicornis*

For all three mirid species, longevities for males ($F_{4,145}=6.987$, $p<0.001$) and females ($F_{4,145}=5.324$, $p<0.001$) were longer at 24°C and 28°C than at other temperatures. Longevities of *C. infumatus* and *E. varians* females were greater than in males (Table 3) at all temperatures. At 20°C, 24°C, 28°C and 32°C longevities of females and males of *M. basicornis* did not differ significantly (Table 3).

Weight and tibia length in *C. infumatus*, *E. varians* and *M. basicornis*

The lengths of the right hind tibia of males and females of all three species did not differ significantly at the evaluated temperatures ($t=1.115$, $df=2$, $p=0.233$), with one exception. The lengths of the right hind tibiae in *E. varians* females were greater than in the other two mirid species at 20°C, 24°C and 28°C (Table 4). Females and males of *E. varians* were heavier than those of the other two mirids at all temperatures (Table 5).

DISCUSSION

Temperature affects mirid life histories, as those of most other insects, reflecting genotypic constraints that are modifiable through an individual's interaction with its environment (Wheeler 2001). The three studied Neotropical mirid species appeared to perform best at temperatures between 24–28 °C. The shortest pre-

Table 4: Length of tibia (mm) (±SE) of *Campyloneuropsis infumatus*, *Engytatus varians* and *Macrolophus basicornis* at five constant temperatures (±1 °C), 70±10% RH and 12h photophase. Abbreviation: n – number of replicates (females or males).

T °C	Species	n	Female	Male	t	*P* value
16	*C. infumatus*	20	1.68±0.85A*d**	1.65±0.72Ad	1.115	0.233
	E. varians	20	1.82±1.54Ac	1.80±1.06Ac	0.968	0.314
	M. basicornis	20	1.71±0.47Ad	1.69±0.78Ad	1.010	0.064
20	*C. infumatus*	20	1.83±1.25Ab	1.80±1.24Ab	1.066	0.078
	E. varians	20	1.97±1.06Aa	1.94±0.78Aa	2.013	0.145
	M. basicornis	20	1.88±0.47Ab	1.86±1.15Ab	1.782	0.347
24	*C. infumatus*	20	1.84±1.03Ab	1.82±0.22Ab	0.974	0.081
	E. varians	20	2.29±1.14Aa	2.24±0.98Aa	1.257	0.129
	M. basicornis	20	1.98±0.46Ab	1.93±1.05Ab	2.335	0.206
28	*C. infumatus*	20	1.87±1.37Ab	1.85±0.82Ab	2.153	0.312
	E. varians	20	2.05±1.33Aa	2.03±0.75Aa	1.673	0.211
	M. basicornis	20	1.91±0.87Ab	1.92±1.12Ab	0.931	0.097
32	*C. infumatus*	20	1.65±0.62Ad	1.63±0.34Ad	1.336	0.161
	E. varians	20	1.81±0.98Ac	1.79±0.41Ac	1.099	0.082
	M. basicornis	20	1.72±1.04Ad	1.70±0.58Ad	1.121	0.215

Notes: * – Means (±SE) followed by same capital letter in columns indicate non-significant differences for species at the same temperature (Tukey's test, P≤0.05); ** – means followed by same lower case letter in the columns indicate non-significant differences between the species at different temperatures (Tukey's test, P≤0.05).

Table 5: Weight (mg) of *Campyloneuropsis infumatus*, *Engytatus varians* and *Macrolophus basicornis* at constant temperatures (±1 °C), 70±10% RH and 12h photophase. Abbreviation: n – number of replicates (females or males).

T °C	Species	n	Female	Male	t	*P* value
16	*C. infumatus*	20	1.60±0.75A*d**	1.58±0.22Ad	1.013	0.321
	E. varians	20	1.74±1.31Ac	1.70±1.18Ac	0.987	0.071
	M. basicornis	20	1.64±0.58Ad	1.59±0.83Ad	1.314	0.062
20	*C. infumatus*	20	1.88±1.57Ab	1.86±1.65Ab	0.968	0.115
	E. varians	20	1.98±1.24Aa	1.97±1.18Aa	1.231	0.214
	M. basicornis	20	1.93±1.13Ab	1.90±1.36Ab	0.996	0.147
24	*C. infumatus*	20	1.91±1.21Ab	1.89±0.16Ab	1.321	0.083
	E. varians	20	2.45±1.11Aa	2.39±0.87Aa	2.012	0.106
	M. basicornis	20	2.03±0.24Ab	2.00±1.42Ab	1.459	0.064
28	*C. infumatus*	20	1.92±1.62Ab	1.90±1.44Ab	0.995	0.102
	E. varians	20	2.39±1.26Aa	2.37±0.85Aa	1.132	0.111
	M. basicornis	20	1.92±0.77Ab	1.91±0.89Ab	1.087	0.088
32	*C. infumatus*	20	1.64±0.23Ad	1.61±1.09Ad	0.879	0.109
	E. varians	20	1.79±0.39Ac	1.75±1.04Ac	1.054	0.071
	M. basicornis	20	1.67±1.43Ad	1.66±0.94Ad	2.013	0.061

Notes: * – Means (±SE) followed by same capital letter in columns indicate non-significant differences for species at the same temperature (Tukey's test, P≤0.05); ** – means followed by same lower case letter in the columns indicate non-significant differences between the species at different temperatures (Tukey's test, P≤0.05).

oviposition and longest oviposition periods found at these temperatures were similar to values reported for other mirid species, such as *M. pygmaeus* (Perdikis & Lykouressis 2002) and *Deraeocoris brevis* (Uhler) (Kim & Riedl 2005). Bueno *et al*. (2018) found that development of immatures of the same three Neotropical mirid species on tobacco with *E. kuehniella* as food was optimal at 24°C. Wheeler (2001) mentions that oviposition in heteropteran insects is suppressed at temperatures above and below the optimum. Low temperatures adversely affect fecundity because the female feeding period is extended at the expense of time devoted to oviposition. In this study, the daily and total fecundity of all three mirid species were lower at the lowest (16°C) and highest (32°C) temperatures. The daily fecundities at 24°C of the three mirid species we studied (10.3–11.7 nymphs/female/day on tobacco) were higher than values obtained for the mirid *Deraeocoris brevis* (9.5 eggs/female/day on green beans) (Kim & Riedl 2005), *N. tenuis* (4.3 eggs/female/day on tomato) and *M. pygmaeus* (3.1 eggs/female/day on tomato) (Mollá *et al*. 2014), all having *E. kuehniella* eggs as food, at 25°C. The lower daily fecundities may be characteristic of the three latter species, or be partly explained by the choice of the host plant on which they developed. Silva *et al* (2016*a*) reported lower daily fecundities (4–5 eggs/female/day) for all three Neotropical mirid species when having tomato as substrate for oviposition and a mix of eggs and larvae of *T. absoluta* as prey.

Total average fecundities (249–311 nymphs/female on tobacco) were also highest for the three species at 24°C, while much lower total average fecundities were observed by Sanchez *et al*. (2009) for *N. tenuis* (60 nymphs/female on tomato at 25°C) and by Mollá *et al*. (2014) for *N. tenuis* (83.7 eggs/female on tomato at 25°C) and *M. pygmaeus* (48.1 eggs/female on tomato), all with *E. kuehniella* eggs as food. Here as well the much lower fecundities found for the other species might have been caused by a combination of species characteristics and the quality of the host plant, but not by differences in prey as *E. kuehniella* was used in all experiments. The type of prey does, however, influence development and fecundity of mirids. For example, Mollá *et al.* (2014) concluded that *M. pygmaeus* was not able to reproduce when fed *T. absoluta* eggs on tomato leaf discs in the laboratory, while they did reproduce with *E. kuehniella* as food. Thus, not all lepidopteran eggs have the same nutritional quality as *E. kuehniella* eggs for mirid predators. In general, lepidopteran eggs have a high nitrogen content and consequently high quality protein (Ferkovich *et al*. 2007; Calixto *et al.* 2013; Mollá *et al.* 2014). Particularly, eggs of *E. kuehniella* are considered excellent food for heteropteran predators and they are often used as factitious prey to rear these predators under the laboratory conditions (Bueno *et al*. 2006; Lundgren 2011; Mollá *et al.* 2014).

Temperatures between 24 and 28°C also resulted in the longest adult lifespans (27–35 days) and oviposition periods (24–28 days) for the three studied mirid species. Similar longevities were found for *M. caliginosus* (= *M. pygmaeus*) females (28.7 days at 22°C on tomato and with *Tetranychus urticae* Kock (Acari:

Tetranychidae) as food) (Hansen *et al*. 1999). Molla *et al*. (2014) reported an average female longevity of 29.5 days for *M. pygmaeus* on tomato with *T. absoluta* eggs as food, and 22 days with *E. kuehniella* eggs as food. The longevities we found were lower than those of *M. pygmaeus* females (49.25 days on tomato and with various stages of *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae) as food at 25°C (Perdikis & Lykouressis 2002).

In this study, males and females of *C. infumatus* and *M. basicornis* showed similar weights and sizes, whereas those of *E. varians* were heavier and had longer tibiae compared to the two other mirids. In another experiment, we also found that the nymphs of *E. varians* were heavier and longer than those of *C. infumatus* and *M. basicornis* (Bueno *et al.* 2018). Weight of adults has been also published for *N. tenuis* (Sanchez *et al*. 2009), and it appeared to be lower than in our study.

A general overview of the values of all variables in all three Neotropical mirids shows only small and often non-significant differences (Tables 1, 3–5), and does not warrant a detailed discussion of these dissimilarities. The most important difference is the daily and total fecundity, which is at several temperatures significantly higher in *M. basicornis* than in the other two species (Table 1). However, values for development and reproduction variables are integrated in the aggregate parameter r_m (see below), resulting in a more meaningful basis for comparison of population growth of the three mirids. Temperature also affected the survival rate, average fecundity and population growth parameters of *C. infumatus*, *E. varians* and *M. basicornis*. Nevertheless, not a single significant difference was found for any of the growth parameters at each of the temperatures presented in Table 2. This indicates that, based on the values of r_m alone, it is impossible to select a potentially best mirid for biological control. The survival rate (l_x) showed a type II curve at all temperatures (Townsend *et al.* 2010), indicating that the mortality rate of these mirids were constant along their entire lifespan. The values of the intrinsic rate of increase (r_m) were above zero and the values of net reproductive rate (R_0) were above 1, which indicate that the populations of all three mirid species were increasing at all temperatures tested. The values we found for the intrinsic rates of increase (r_m) and the net reproductive rates (R_0) for the three mirids were similar to those reported by Perdikis and Lykouressis (2002) and Mollá *et al.* (2014) for *M. pygmaeus.* In our study, an increase in temperature by four degrees boosted up the values of the intrinsic rate of increase 1.5 times in the temperature range from 16 to 20 to 24°C in all three mirids. Furthermore, the net reproductive rates (R_0), indicate that *C. infumatus*, *E. varians* and *M. basicornis* have the maximum potential to increase their populations at 24°C 89.33, 88.45 and 91.08 times, respectively. Based on the fact that *T. absoluta* populations develop continuously in the field, with all stages occurring at the same time, synchronization of predator releases is only important in the beginning of the cropping season after the invasion of the pest in order to have predators in place when first eggs and young larvae of the pest appear.

CONCLUSIONS

To sum up, the results of our experiments show that (1) temperatures in the range from 24–28°C result in the best reproductive potential, population growth and longevity of the mirids *C. infumatus*, *E. varians* and *M. basicornis*; (2) the three mirid species can reproduce and are active at the tomato crop production temperatures and the range of temperatures at which *T. absoluta* is present in the crop (Bueno *et al.* 2018)); (3) eggs of the factitious prey *E. kuehniella* are suitable as food for the the three mirid species; (4) tobacco plants are appropriate as oviposition substrate; and (5) the three species show the same rates of population growth on tobacco with *E. kuehniella* as prey. The results are important for developing mass rearing and field release systems for these predators, which is a critical step in augmentative biological control programs.

ACKNOWLEDGEMENTS

We dedicate this article with great respect to the memory of our friend Dan Gerling, with whom we cooperated mainly on biological control of whiteflies, but during recent years also on biocontrol of *Tuta absoluta*. We are grateful for having been able to discuss not only research issues with Dan, but also to talk about topics of general interest, in particular related to international collaboration without political borders, and world peace. The authors thank the National Council for Scientific Research (CNPq), the Coordination for the Improvement of Higher Education Personnel (CAPES) (Program CAPES/NUFFIC – Project 044/12) and the Foundation for Support Research of Minas Gerais (FAPEMIG) for funding this project.

REFERENCES

Agrianual. 2016. *Anuário estatístico da Agricultura Brasileira*. FNP, São Paulo, Brazil. http://www.agrianual.com.br

Agustí, N. & Gabarra, R. 2008. Efecto de la alimentación polífaga sobre la reproducción y otros parâmetros biológicos de *Dicyphus tamaninni* Wagner (Hetroptera: Miridae). *Bolletin Sanidad Vegetal Plagas* **34**: 247–256.

———2009. Effect of adult age and insect density of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on progeny. *Journal of Pest Science* **82**: 241–246.

Blaeser, P., Sengonca, C. & Zegula, T. 2004. The potential use of different predatory bug species in the biological control of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). *Journal of Pest Science* **77**: 211–219.

Bueno, V.H.P. 2017. Specific procedure for finding the best mirid predator of *Tuta absoluta*. *In*: *Livro do 15° Simpósio de Controle Biológico* (SICONBIOL), 4 to 8 June, 2017, Ribeirão Preto, SP, Brazil, p. 83.

Bueno, V.H.P., Mendes, S.M. & Carvalho, L.M. 2006. Evaluation of a rearing-method for the predator *Orius insidiosus*. *Bulletin of Insectology* **59**: 1–6.

Bueno, V.H.P., Montes, F.C., Calixto, A.M., Lins, J.C., Jr. & Van Lenteren, J.C. 2012. Can recently found Brazilian hemipteran predatory bugs control *Tuta absoluta*? *IOBC-WPRS Bulletin* **80**: 63–67.

Bueno, V.H.P., van Lenteren, J.C., Lins, J.C., Jr., Calixto, A.M., Silva, D.B., Santiago, L.D. & Pérez, L.M. 2013*a*. New records of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) predation by Brazilian Hemipteran predatory bugs. *Journal of Applied Entomology* **137** (1–2): 29–34.
https://doi.org/10.1111/jen.12017

Bueno, V.H.P., van Lenteren, J.C., Lins, J.C., Jr., Montes, F.C., Calixto, A.M. & Silva, D.B. 2013*b*. Biological control of *Tuta absoluta*: sampling and evaluation of new hemipteran predators found in Brazil. *In*: Mason, P.G., Gillespie, D.R. & Vicent, C. (Eds), *Proceedings of the 4th*

International Symposium on Biological Control of Arthropods. Agriculture and Agri-Food, Canada, pp. 269–272.

Bueno, V.H.P., Montes, F.C., Sampaio, M.V., Calixto, A.M. & van Lenteren, J.C. 2018. Performance of immatures of three Neotropical Miridae at five temperatures when reared on *Ephestia kuehniella* eggs on tobacco plants. *Bulletin of Insectology* **71** (in press).

Calixto, A.M., Bueno, V.H.P., Montes, F.C., Silva, A.C. & van Lenteren, J.C. 2013. Effect of different diets on reproduction, longevity and predation capacity of *Orius insidiosus* (Say) (Hemiptera: Anthocoridae). *Biocontrol Science and Technology* **23** (11): 1245–1255. https://doi.org/10.1080/09583157.2013.822850

Calvo, F.J., Lorente, M.J., Stansly, P.A. & Belda, J.E. 2012. Preplant release of N*esidiocoris tenuis* and supplementary tactics for control of *Tuta absoluta* and *Bemisia tabaci* in greenhouse tomato. *Entomologia Experimentalis et Applicata* **143** (2): 111–119. https://doi.org/10.1111/j.1570-7458.2012.01238.x

Devi, P.K., Yadav, D.N. & Anand, J. 2002. Role of *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) in natural suppression of tomato fruit borer, *Helicoverpa armigera* (Hubner) (Lepidoptera: Nocuidae). *Pest Management in Horticultural Ecosystems* **8**: 109–113.

Ferkovich, S.M., Venkatesan, T., Shapiro, J.P. & Carpenter, J.E. 2007. Presentation of artificial diet: effects of composition and size of prey and diet domes on egg production by *Orius insidiosus* (Hetroptera: Anthocoridae). *Florida Entomologist* **90** (3): 502–508. https://doi.org/10.1653/0015-4040(2007)90[502:POADEO]2.0.CO;2

Ferreira, P.S.F. & Henry, T.J. 2011. Synopsis and keys to the tribes, genera, and species of Miridae (Hemiptera: Heteroptera) of Minas Gerais, Brazil. Part I: Bryocorinae. *Zootaxa* **2920**: 1–41. http://doi.org/10.5281/zenodo.277915

Guedes, R.N.C. & Picanço, M.C. 2012. The tomato borer *Tuta absoluta* in South America: pest status, management and insecticide resistance. *EPPO Bulletin* **42** (2): 211–216. http://doi.org/10.1111/epp.2557

Hansen, D.L., Brodsgaard, H.F. & Enkegaard, A. 1999. Life table characteristics of *Macrolophus caliginosus* preying upon *Tetranychus urticae*. *Entomologia Experimentalis et Applicata* **93** (3): 267–273. http://doi.org/10.1046/j.1570-7458.1999.00587.x

Kim, D.S. & Riedl, H. 2005. Effect of temperature on development and fecundity of the predaceous plant bug *Deraeocoris brevis* reared on *Ephestia kuehniella* eggs. *BioControl* **50** (6): 881–897. https://doi.org/10.1007/s10526-005-5380-x

Lundgren, J.G. 2011. Reproductive ecology of predaceous Heteroptera. *Biological Control* **59** (1): 37–52. https://doi.org/10.1016/j.biocontrol.2011.02.009

Maia, H.N.M., Luiz, A.J.B. & Campanhola, C. 2000. Statistical inference on associated fertility life table parameters using jackknife technique: computational aspects. *Journal of Economic Entomology* **93** (2): 511–518. https://doi.org/10.1603/0022-0493-93.2.511

Maia, H.N.M., Pazianotto, R.A.A., Luiz, A.J.B., Marinho-Prada, J.S. & Pervez, A. 2014. Influence on arthropod demographic parameters: computational advances using R. *Journal of Economic Entomology* **107** (1): 432–439. https://doi.org/10.1603/EC13222

Mollá, O., Biondi, A., Alonso-Valiente, M. & Urbaneja, A. 2014. A comparative life history study of two mirid bugs preying on *Tuta absoluta* and *Ephestia kuehniella* eggs on tomato crops: implications for biological control. *BioControl* **59** (2): 175–183. https://doi.org/10.1007/s10526-013-9553-8

Naika, S., de Jende, J.H., Goffau, M. de, Hilm, M. & van Dam, B. 2006. *A cultura do tomate: produção, processamento e comercialização*. Agrodok 17, Fundação Agromisa e CTA, Wageningen, The Netherlands, 104 pp.

Perdikis, D.C. & Lykouressis, D.P. 2002. Life table and biological characteristics of *Macrolophus pygmaeus* when feeding on *Myzus persicae* and *Trialeurodes vaporariorum*. *Entomologia Experimentalis et Applicata* **102** (3): 261–272. https://doi.org/10.1046/j.1570-7458.2002.00947.x

Pratissoli, D. & Carvalho, J.R. de. 2015. *Guia de Campo: pragas da cultura do tomateiro. NUDEMAFI* (Série técnica), Centro de Ciências Agrarias – UFES, Alegre, Brazil, 35 pp.

R Development Core Team. 2014. *R: A language and environment for statistical computing*. Reference index version 3.2. R Foundation for Statistical Computing, Vienna. 1 CD-ROM. https://www.r-project.org

Sanchez, J.A., Lacasa, A., Arnó, J., Castané, C. & Alomar, O. 2009. Life history parameters for *Nesidiocoris tenuis* (Reuter) (Het., Miridae) under different temperature regimes. *Journal of Applied Entomology* **133** (2): 125–132. https://doi.org/10.1111/j.1439-0418.2008.01342.x

Santos, A.C., Bueno, R.C.O.F., Vieira, S.S. & Bueno, A.F. 2011. Efficacy of insecticides on *Tuta absoluta* (Meyrick) and other pests in pole tomato. *BioAssay* **6**: Art. 4. https://doi.org/10.14295/BA.v6.0.81

SAS Institute 2000. *JMP version 4.0.2*. SAS Institute, Cary, NC. https://www.jmp.com

Silva, D.B., Bueno, V.H.P., Montes, F.C. & van Lenteren, J.C. 2016*a*. Population growth of three mirid predatory bugs feeding on eggs and larvae of *Tuta absoluta* on tomato. *BioControl* **61** (5): 545–553. http://dx.doi.org/10.1007/s10526-016-9736-1

Silva, D.B., Bueno, V.H.P., Calvo, J.F. & van Lenteren, J.C. 2016*b*. Do nymphs and adults of three Neotropical zoophytophagous mirid damage leaves and fruits of tomato? *Bulletin of Entomological Research* **107** (2): 200–207. https://doi.org/10.1017/S0007485316000778

Silva, D.B., Bueno, V.H.P., van Loon, J.J.A., Penã-Flor, M.F.G.V., Bento, J.M.S. & van Lenteren, J.C. 2018. Attraction of three mirid predators to tomato infested by both the tomato leaf mining moth *Tuta absoluta* and the withefly *Bemisia tabacci*. *Journal of Chemical Ecology* **44** (1): 29–39. https://doi.org/10.1007/s10886-017-0909-x

Silva, G.A., Picanço, M.C., Bacci, L., Crespo, A.L.B., Rosado, J.F. & Guedes, R.N.C. 2011. Control failure likelihood and spatial dependence of insecticide resistance in the tomato pinworm, *Tuta absoluta. Pest Management Science* **67** (8): 913–920. https://doi.org/10.1002/ps.2131

Siqueira, H.A.A., Guedes, R.N.C., Fragoso, D.B. & Magalhães, L.C. 2001. Abamectin resistance and synergism in Brazilian populations of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *International Journal of Pest Management* **47** (4): 247–251. https://doi.org/10.1080/09670870110044634

Siqueira, H.A.A., Guedes, R.N.C. & Picanço, M.C. 2000. Insecticide resistance in populations of *Tuta absoluta* (Lepidoptera: Gelechiidae). *Agricultural and Forest Entomology* **2** (2): 147–153. https://doi.org/10.1046/j.1461-9563.2000.00062.x

Thomazini, A.P.B.W., Vendramim, J.D., Brunherotto, R. & Lopes, M.T.R. 2001. Effect of *Lycopersicom* spp. genotypes on biology and oviposition of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Neotropical Entomology* **30**: 283–288.

Townsend, C.R., Begon, M. & Harper, J.L. 2010. *Fundamentos em ecologia*. 3ª Ediçao. Editora Artmed, Porto Alegre, Brasil, 576 pp.

Urbaneja, A., Tapia, G. & Stansly, P. 2005. Influence of host plant and prey availability on developmental time and survivorship of *Nesidiocoris tenius* (Heteroptera: Miridae). *Biocontrol Science and Technology* **15** (5): 513–518. https://doi.org/10.1080/09583150500088777

van den Bosch, R. 1978. *The pesticide conspiracy*. University of California Press, Berkely, USA.

van Lenteren, J.C. 2003. Need for quality control of mass-produced biological control agents. *In*: van Lenteren, J.C. (Ed.), *Quality control and production of biological control agents: Theory and testing procedures*. CABI International Publishing, London, UK, p. 1–18.

———2010. *Ecology: cool science, but does it help?* Wageningen University, Wageningen, The Netherlands, 44 pp.

———2012. The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. *BioControl* **57** (1): 1–20. https://doi.org/10.1007/s10526-011-9395-1 van Lenteren, J.C., Hemerik, L., Lins, J.C., Jr. & Bueno, V.H.P. 2016. Functional response of three Neotropical mirid predators to egg of *Tuta absoluta* on tomato. *Insects* **7** (3): Art. 34. https://doi.org/10.3390/insects7030034

van Lenteren, J.C., Bueno, V.H.P., Smit, J., Soares, M.A., Calixto, A.M., Montes, F.C. & De Jong, P. 2017. Predation of *Tuta absoluta* eggs during the nymphal stages of three Neotropical mirid predators on tomato. *Bulletin of Insectology* **70** (1): 69–74. http://www.bulletinofinsectology.org/pdfarticles/vol70-2017-069-074vanlenteren.pdf

van Lenteren, J.C., Bolckmans, K., Kohl, J., Ravensberg, W. & Urbaneja, A. 2018. Biological control using invertebrates and microorganisms: plenty of new opportunities. *BioControl* **63** (1): 39–59. http://dx.doi.org/10.1007/s10526-017-9801-4

Wheeler, A.G., Jr. 2001. *Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists*. Cornell University Press, Ithaca, NY, 507 pp.