

Performance of the parasitoid *Praon volucre* in *Aulacorthum solani* at five temperatures

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Abstract

This study aimed to evaluate the effect of temperature on biological parameters of *Praon volucre* (Haliday) (Hymenoptera Braconidae) and to determine its thermal requirements with the aphid *Aulacorthum solani* (Kaltenbach) (Rhynchota Aphididae) as host. Tests were carried out at 18, 20, 22, 24, and 26 ± 1 °C, RH 70 ± 10% and 12h photophase. 24h-old mated *P. volucre* females without previous experience of oviposition were released into a Petri dish containing a leaf disc of lettuce on a water/agar layer (1%) and 20 second- and third-instar nymphs of *A. solani*. Percentages of mummification were highest at 18 °C (64%) and 20 °C (66%). Developmental time decreased as the temperature increased, ranging from 19.8 days at 18 °C to 12.3 days at 26 °C. Emergence rate was not affected by temperature and was between 79.6% and 93.4%. Sex ratios varied between 32% and 51% females, but did not differ significantly at the 5 temperatures. Adult longevity strongly decreased with increasing temperature in the range from 18 °C to 22 °C, but was similar in the range from 22 to 26 °C. *A. solani* had an average tibia length of 0.52 mm when oviposition by *P. volucre* took place, and 1.17 mm at mummification. Even though host size at mummification was not influenced by temperature, parasitoid size was negatively affected by higher temperatures. The threshold temperature for development was 4.5 °C and the thermal constant was 270 DD. Our findings indicate that *P. volucre* performs best at temperatures from 22 °C to 24 °C, and that a mixture of 2nd and 3rd instar nymphs of *A. solani* is adequate for rearing this parasitoid. This information helps optimization of parasitoid mass-rearing, and with timing of parasitoid releases to obtain establishment and synchronization with the host under greenhouse conditions.

Key words: biological control, mass rearing, threshold temperature, thermal constant.

Introduction

Despite the availability of a large number of commercially produced natural enemies for control of aphids (van Lenteren, 2012), management of aphids is still very difficult, especially for species of the tribe Macrosiphini as *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), and *Uroleucon ambrosiae* (Thomas) (De Conti *et al.*, 2010; 2011a; Jandric *et al.*, 2014). These species are pests of open field and greenhouse crops in many countries (Auaad *et al.*, 2002; De Conti *et al.*, 2010; 2011a). Studies have been conducted on the biology and reproduction of the Macrosiphini aphid species (e.g. De Conti *et al.*, 2010; 2011a) as well as on several of their natural enemies (Kavallieratos *et al.*, 2004a; 2010; 2013; Aragón *et al.*, 2007; De Conti *et al.*, 2008, 2011b; Silva *et al.*, 2009; Sidney *et al.*, 2010a; 2010b; Hughes *et al.*, 2011; Dassonville *et al.*, 2012; Lins Jr *et al.*, 2011; 2013). Currently, *Aphidius ervi* (Haliday) and *Praon volucre* (Haliday) are the main agents used for biological control of *A. solani* pests (Starý *et al.*, 2007; Hance and Salin, 2014). Although both parasitoids are natural enemies of *A. solani*, *P. volucre* is superior to *A. ervi* in larval competition, which results in a greater probability of establishment after release when compared with *A. ervi* (Sidney *et al.*, 2010a). In addition, lower levels of parasitism of *A. solani* by *A. ervi* than by *P. volucre* on Solanaceae and Cucurbitaceae crops in agroecosystems of southeastern Europe were reported by Kavallieratos *et al.* (2010).

Several biological and behavioral parameters can be used to evaluate and choose a candidate parasitoid as a biological control agent (van Lenteren, 2010). Many of these parameters, e.g. development, emergence, number of generations and various types of behavior are both host and temperature dependent (Speight *et al.*, 1999).

Temperature is a main factor influencing the life cycle of an insect, and specifically its rate of development (Trudgill *et al.*, 2005). Each species has specific thermal requirements, which are characterized by a threshold temperature and accumulated heat needed for development. Thermal requirements determine the capacity of population growth and can be used to understand the adaptation of insects to different temperature regimes (Sinclair *et al.*, 2003; Honek *et al.*, 2002), and data on thermal requirements are essential in understanding temporal relationships between aphids and their parasitoids (De Conti *et al.*, 2010; 2011).

Temperature also has a strong influence on immature development and on adult size of insects (Chown and Gaston, 2010). The developmental response to temperature is a form of phenotypic plasticity, and one genotype may express different adult body sizes depending on the environmental temperature (Colinet *et al.*, 2007; Souto *et al.*, 2012) and laboratory rearing conditions (Kanegae and Lomanco, 2003). Genotypes that express phenotypic plasticity in response to external conditions are expected to have a selective advantage compared to genotypes without phenotypic plasticity (Colinet *et al.*, 2007; Boivin, 2010; Moreno-Garcia *et al.*, 2010; Wu *et al.*

al., 2011). The parasitoid *P. volucre* was introduced and mass produced in Brazil and then introduced into the South (Parana, Santa Catarina and Rio Grande do Sul), Southeast (Sao Paulo) and Central (Mato Grosso and Goias) regions of Brazil as biological control agent against several aphids in wheat crops. Between 1978 to 1980 a total of 122,822 were released in the above mentioned three regions, where they established (Salles, 1979; Salvadori and Salles, 2000). The origin of the population we collected in Lavras (Minas Gerais) has not been documented.

It is difficult to analyze the effect of temperature on parasitoid size alone, because host size is also affected by temperature. Reduction in the size of parasitoids (Ellers *et al.*, 2001; Li and Mills, 2004) and hyperparasitoids (Souto *et al.*, 2012) at high temperatures is expected to be at least in part a consequence of the reduction in host size. Further, entomophagous insects like *P. volucre* may have different optimum climate conditions than their hosts and may, as a result, be ineffective biological control agents (Horn, 1998). Adaptability to temperature is a key factor influencing the success of beneficial insects in biological control programs (Hance *et al.*, 2007; Gerard *et al.*, 2013). Kavallieratos *et al.* (2004b) reported that *P. volucre* was the dominant parasitoid of *Myzus persicae* (Sulzer) infesting tobacco for two continuous growing seasons in central Greece. However, in another geographical area of Greece, with different climatic conditions, *Aphidius colemani* Viereck and *Diaeretiella rapae* (M'Intosh) were the most abundant parasitoids of *M. persicae* in tobacco crops (Kavallieratos *et al.*, 2005).

An efficient natural enemy is seasonally synchronized with its pest, adapted to the local climate and capable of selecting the best available host (van Lenteren, 2010). Thus, understanding the developmental and reproductive characteristics of *P. volucre* related to temperature in a particular host assists in determining if this parasitoid is able to function under certain climatological conditions.

In order to contribute to the evaluation of aphid parasitoids as natural enemies of Macrosiphini pests, we (1) evaluated the effect of five temperatures on development, parasitism, emergence rate and sex ratio of *P. volucre* having 2nd and 3rd instar nymphs of *A. solani* as hosts, (2) determined its thermal requirements and (3) assessed if the reduction of parasitoid size at high temperatures is an effect of the reduction of *A. solani* body size and/or of temperature.

Materials and methods

Experiments and rearing of aphids and *P. volucre* parasitoids were performed at the Laboratory of Biological Control of the Department of Entomology, Federal University of Lavras, Lavras, Minas Gerais, Brazil.

Origin and rearing of the aphid *A. solani*

Lettuce plants, cultivar Veronica, containing colonies of *A. solani* were collected in a plastic tunnel and transferred to the laboratory. After identification of the aphid

species based on the description by Peña-Martines (1992), *A. solani* individuals were transferred with a paint brush to a Petri dish (15 cm diameter) containing a lettuce leaf disc (cultivar Veronica) (14 cm diameter) on a layer of solidified 1% agar-water solution (Sidney *et al.*, 2010a). Petri dishes were maintained in a climate chamber at 22 ± 1 °C, $70 \pm 10\%$ RH and 12h photophase. To avoid pathogen development, leaf discs were cleaned by immersion in a solution of sodium hypochlorite 1% for about five minutes, rinsed in water and then immersed in distilled water for about ten minutes (Diniz *et al.*, 2006). After 3 days, when the first signals of chlorosis or dehydration of the leaf disc start to appear, the aphid colonies were transferred with a paint brush to another Petri dish containing a new leaf disc. This procedure was followed to avoid variation in host quality as a result of deterioration of the host plant. To obtain 2nd and 3rd instar nymphs for the tests, adult aphid females obtained from the stock colony were isolated individually for six hours in a Petri dish containing a lettuce leaf disc on a layer of 1% water-agar solution. Then, the adult was removed and the nymphs produced during this period were maintained *in situ* at 22 °C and observed daily until they developed to the second or third instar, which can be determined by the presence of exuviae (De Conti *et al.* 2008, 2011a). We used aphids of the 15th generation of the stock colony in our experiments.

Origin and rearing of the parasitoid *P. volucre*

To obtain *P. volucre* individuals, leaves of field-grown lettuce and lilac tassel flower (*Emilia sonchifolia* L.) containing mummies were collected and placed into transparent plastic bags and transported to the laboratory. In the laboratory the mummies were examined and identified on the basis of their distinct characteristics following descriptions by Kavallieratos and Lykouressis (2004) and Helyer *et al.* (2014). *P. volucre* type mummies were pale with silky filaments under the cocoon and pupation occurred outside the host (Sidney *et al.*, 2010a; Helyer *et al.*, 2014). Individual parasitized mummies were placed in labeled glass tubes (100 mm high \times 8 mm diameter) containing a drop each of pure honey and water to provide food for adult parasitoids after emergence, and maintained in an environmental chamber (22 ± 1 °C). Adult *P. volucre* were identified under a stereomicroscope using the key of Kavallieratos *et al.* (2013) and we only found *P. volucre*. Emerged adult parasitoids were kept in glass tubes for mating and later transferred to acrylic cages (60 \times 30 \times 30 cm) containing *A. solani*-infested lettuce plants. Every five days, new greenhouse-grown disease-free lettuce plants were introduced into the cages. The old plants with the mummies were removed after the unparasitized aphids had moved to the new plants. After emergence and mating of adult parasitoids, the *A. solani*-infested lettuce plants were replaced by new ones, thus continuing the parasitoid production in the laboratory at 22 ± 1 °C, $70 \pm 10\%$ RH, and 12 h photophase (De Conti *et al.*, 2011b). Individuals from the 12th laboratory generation of the parasitoid were used in the experiments.

Performance of *P. volucre* in *A. solani* at different temperatures

One 24 h-old *P. volucre* female, previously mated and with no previous oviposition experience, was released into a Petri dish (5 cm diameter) containing a lettuce leaf disc on a 1% agar/water solution and 20 2nd and 3rd instar nymphs of *A. solani*. Aphidiinae parasitoids prefer to parasitize intermediate host instars (Mackauer *et al.*, 1996). Medium size hosts have higher nutritional quality than large or small hosts, which results in highest percentage of mummy being produced in 2–4 days old *A. solani* parasitized by *P. volucre* (Hance and Salin, 2014). Therefore, also in this study 2nd and 3rd instar nymphs of 2-days old with a maximal age difference of 24 hours between nymphs from the *A. solani* stock rearing were used (De Conti *et al.*, 2008; Silva *et al.*, 2008; Lins Jr *et al.*, 2013). At each temperature tested, parasitoid females were allowed to remain in the Petri dish for only 60 minutes, to avoid long superparasitism. The Petri dishes were then sealed with perforated PVC film and turned upside down to avoid death of insects due to water condensation and contact with sticky honeydew. Petri dishes were maintained in a climate chamber at a temperature of 18, 20, 22, 24, or 26 ± 1 °C, 70 ± 10% RH, and 12 h photophase until mummification. Upon mummification, the aphids were put individually in glass vials (100 mm × 8 mm) until adult emergence. Adults were fed honey and distilled water, deposited in the form of small droplets on the vial's inner walls (Sampaio *et al.*, 2007). Emergence and sex of the adult parasitoids were determined daily at the same time. At each temperature 15 replicates were used.

Developmental times were estimated: (1) from oviposition to mummification, (2) from mummification to adult emergence and (3) from oviposition to adult emergence. We also determined percentage parasitism, emergence rate and sex ratio. To assess the longevity of *P. volucre*, 15 males and 15 females, newly-emerged, were maintained individually in glass vials (100 × 8 mm) without hosts and fed daily with honey and water until death. Parasitoid development and survival was checked daily.

Size of parasitoid and host were determined by measuring the length of the right hind tibiae. The tibia length is used as a standard to estimate insect size (Godfray, 1994), as it is strongly correlated with body size (Colinet *et al.*, 2007), dry mass (Chau and Mackauer, 2001) and fertility (Sampaio *et al.*, 2008) of parasitoids. We measured the length of the right hind tibiae of 10 male and 10 female newly-emerged parasitoid adults, of 10 second- and third-instar *A. solani* nymphs at the moment of oviposition (initial host size) by *P. volucre*, and of 10 mummies (final host size). The initial size of the host *A. solani* was measured using the 2nd and 3rd instar individuals reared at 22 °C, and the final host size was measured from mummies developed at all temperatures evaluated. Tibiae were removed and mounted under a coverslip on a slide with a droplet of 70% alcohol and measurements were performed under an optical microscope (Olympus SZ40, USA) with graded ocular at a 100× magnification, according to methodology proposed by Eller *et al.* (2001) and De Conti *et al.* (2008).

Data analysis

Data were analyzed by ANOVA and when significant differences were observed, regression analyses were applied. Five treatments (i.e., rearing temperatures) were used for all evaluated parameters. A total of 15 replicates (i.e. 1 mated parasitoid provided with 20 aphid hosts) per temperature treatment resulting in a total of 75 observations, were used for developmental time, percentage of mummification, percentage of emergence and adult longevity. Ten replicates per temperature treatment, resulting in a total of 50 observations, were used for tibia size of aphids and parasitoids. To determine the difference between a theoretical sex ratio of 1:1 and the observed one, the data were analyzed using a homogeneity χ^2 test with a 0.05 level of significance. To calculate sex ratio percentages data obtained for each *P. volucre* female (n = 15) were pooled. Even when mating is observed, sperm may have not passed into the spermatheca of the female parasitoid, and in that case only male offspring is produced. At least one emerged female occurred in all the Petri dishes, indicating that all females were successfully fertilized. All statistical procedures were performed using software R Development Core Team (2009).

The lower temperature threshold for development (LDT) and the thermal constant (K) were calculated with the hyperbole method. This method makes use of a linear regression $Y = a + bX$, where Y is the reciprocal of the developmental time in days and X is the temperature in degrees Celsius (Campbell *et al.*, 1974; Haddad *et al.*, 1999; Bergant and Trdan, 2006). To estimate the lower temperature threshold with this method, measurements are needed for at least four different temperatures within the optimal range for insect development (Campbell *et al.*, 1974).

Results

The percentage of mummification of *A. solani* parasitized by *P. volucre* was significantly affected by temperature ($F_{4,70} = 3.536$; $P = 0.010$), and it decreased from 64% to 48.6% as temperature increased from 18 to 26 °C (figure 1).

Temperature also significantly affected the developmental time of the parasitoid from oviposition to mummy formation ($F_{4,70} = 73.955$; $P < 0.0001$), from mummy formation to adult emergence ($F_{4,70} = 163.583$; $P < 0.0001$) and from oviposition to adult emergence ($F_{4,70} = 161.151$; $P < 0.0001$). The relationship between temperature and the developmental time from oviposition to mummification and from oviposition to adult emergence could well be described by a linear model, while the developmental time from mummification to adult emergence could be described by a quadratic model (figure 2). The thermal threshold of *P. volucre* represented by the lower development temperature (LTD) was 4.5 °C, and the heat accumulation needed for the complete development from egg to adult was 270 degree days (DD).

Emergence rates ($F = 1.750$; $df = 4$; $P = 0.1519$) and sex ratios ($\chi^2 = 0.80714$; $df = 1$; $P = 0.9375$) of *P. volucre*

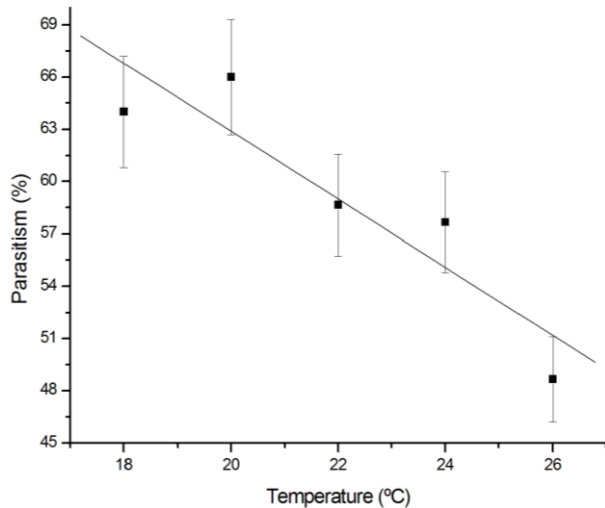


Figure 1. Mean (\pm SE) percentage mummy formation by *P. volucre* in the host *A. solani* at different temperatures ($y = -1.95x + 101.9$; $R^2 = 0.83$).

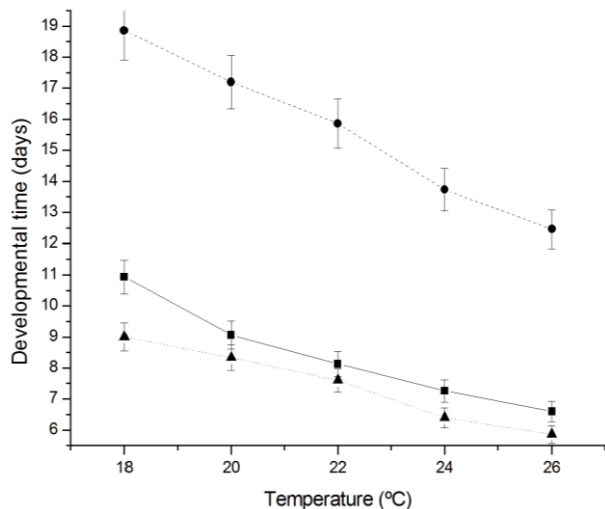


Figure 2. Mean (\pm SE) developmental times of *P. volucre* in *A. solani* at different temperatures. From oviposition to mummy formation (■) ($y = -0.4027x + 16.305$; $R^2 = 0.99$); from mummy formation to adult emergence (▲) ($y = 0.0399x^2 - 2.2998x + 39.317$; $R^2 = 0.99$); and from oviposition to adult emergence (●) ($y = -0.9247x + 36.136$; $R^2 = 0.98$).

were not significantly affected by temperature. At 18, 20, 22, 24 and 26 °C, the emergence rates were 93.4, 87.7, 79.6, 91.0 and 84.7%, respectively. The sex ratios expressed as the percentage of females were 51, 46, 49, 32 and 44% at 18, 20, 22, 24 and 26 °C, respectively.

Longevity was significantly affected by temperature in both males ($F_{4;70} = 49.841$; $P < 0.0001$) and females ($F_{4;70} = 67.789$; $P < 0.0001$). The relation between longevity and temperature could well be described by a quadratic model; longevity decreased with increasing temperature (figure 3). Both females and males of *P. volucre* lived longer when kept at 18 °C than at the higher temperatures.

The length of the right hind tibia of *A. solani* nymphs at the moment of parasitoid oviposition was 0.52 ± 0.086 mm, when reared at 22 °C. The lengths of the right hind tibia of the *A. solani* after mummification were 1.18, 1.31, 1.18, 1.17 and 1.20 mm long at 18, 20, 22, 24 and 26 °C, respectively, and was not significantly affected by temperature ($F_{4;45} = 1.945$; $P = 0.1194$). Tibia size of *P. volucre* adults developed in *A. solani* was significantly smaller at higher temperatures for males ($F_{4;45} = 6.146$; $P = 0.0005$) and females ($F_{4;45} = 3.337$; $P = 0.0178$). Tibia size ranged from 0.50 to 0.69 mm in males and from 0.65 to 0.74 mm in female parasitoids (figure 4).

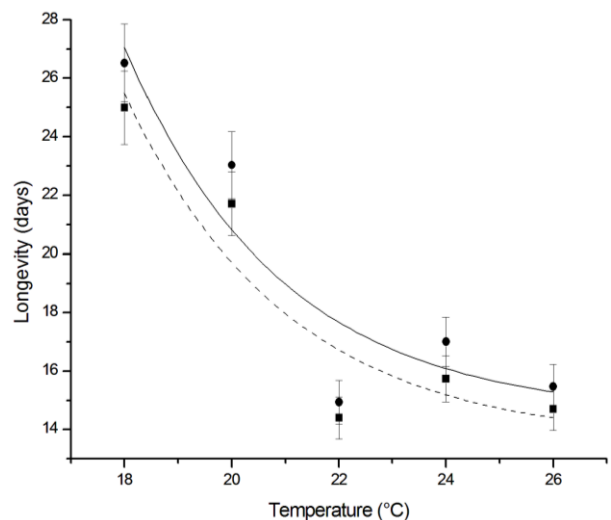


Figure 3. Mean (\pm SE) longevity of females (●) ($y = 0.2512x^2 - 12.478x + 170.22$; $R^2 = 0.89$) and males (■) ($y = 0.2129x^2 - 10.617x + 146$; $R^2 = 0.93$) of *P. volucre* in *A. solani* at different temperatures.

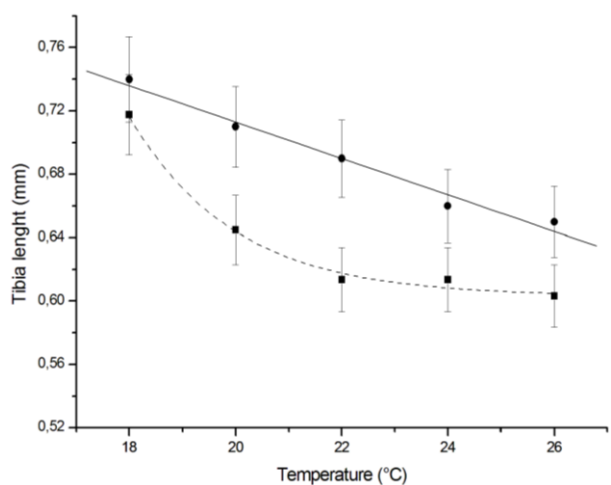


Figure 4. Mean (\pm SE) hind tibia length of females (●) ($y = -0.0116x + 0.9501$; $R^2 = 0.98$) and males (■) ($y = 0.0029x^2 - 0.1398x + 2.2714$; $R^2 = 0.98$) of *P. volucre* in the aphid host *A. solani* at different temperatures.

Discussion

The establishment potential of insects often depends on the capacity of a species to tolerate variation in temperature for the continuation of vital processes such as development and reproduction (Hughes *et al.*, 2011). In parasitoids, the nutritional quality of the host is also important because it determines the acceptance of the host by the female parasitoid and plays an important role in the development of the immature stages of the parasitoid (Nicol and Mackauer, 1999).

In this study, the percentage of mummification is the combined result of host acceptance by adult *P. volucre* and immature parasitoid mortality before mummification. The lowest percentage of mummification was found at the highest temperature (26 °C), suggesting a negative influence of high temperature on host searching and/or on immature survival of *P. volucre*. Previous studies reported low immature survival of this parasitoid at high temperatures, but with a different aphid hosts: *M. euphorbiae* (De Conti *et al.*, 2011b), *M. persicae* (Kavallieratos *et al.*, 2004b; 2005; Sidney *et al.*, 2011) and *Sitobion avenae* (F.) (Langer and Hance, 2004).

The thermal threshold and heat accumulation for development of *P. volucre* are within the rather large range of values estimated for parasitoids of aphids of the subfamily Aphidiinae, 2.2 to 7.5 °C and 116 to 301 DD, respectively (Sampaio *et al.*, 2007; Hughes *et al.*, 2011). The values obtained in this study are in accordance with the values reported for *P. volucre* by De Conti *et al.* (2011). However, the thermal thresholds of the host aphid *A. solani* and *M. euphorbiae* (De Conti *et al.*, 2011) are much lower than the ones reported for *P. volucre*, indicating potential problems in the control of these aphids by *P. volucre* at colder climates.

The parasitoid *P. volucre* is currently used in the control of aphids, primarily *A. solani* and *M. euphorbiae* (van Lenteren, 2012). Comparing our results with previous studies where *P. volucre* was reared on *M. euphorbiae*, we may conclude that *A. solani* is an inferior host for *P. volucre*. The developmental time from oviposition to adult emergence of *P. volucre* in *M. euphorbiae* at 22 °C (14 days) (De Conti *et al.*, 2011) was shorter than in *A. solani* in this study (16 days). Also the longevity of *P. volucre* reared on *M. euphorbiae* (20 days) (De Conti *et al.*, 2011) was longer compared to the ones found in the present study (15 days). The longer longevity might enable *P. volucre* to parasitize more hosts in the field or greenhouse than *A. ervi*. Another parasitoid used to control of *A. solani* is *A. ervi* (van Lenteren, 2012): *P. volucre* shows longer development times (21-23 days) than *A. ervi* (12 and 13 days) (Sidney *et al.*, 2010) when reared on *A. solani*.

In previous studies, emergence of aphid parasitoids was found at temperatures as high as 28 and 30 °C (Rodrigues *et al.*, 2004; Sampaio *et al.*, 2005; 2007; De Conti *et al.*, 2011b), which may explain why the temperature range utilized in the present study (18 to 26 °C) did not significantly influence emergence rates of *P. volucre*.

The sex ratios found by us did not deviate significantly

for 1:1 at the tested temperatures. In previous studies 1:1 sex ratios were also reported for *P. volucre* at 22 °C (De Conti *et al.*, 2011b; Lins *et al.*, 2011; 2013).

The size of *A. solani* mummies, i.e. aphids after being parasitized by *P. volucre*, was not significantly different among temperatures indicating that the parasitoid requires a minimum host size for successful pupation in *A. solani*. However, *P. volucre* males and females had larger tibiae when they developed at low temperatures in *A. solani*. This suggests that morphological phenotypic variability in the parasitoid individuals was mainly due to temperature variation even without differences in host size. In many insect species the adults are larger when their pre-imaginal development takes place at low temperatures (Gilbert and Raworth, 1996). Individuals developing at low temperatures may reach a higher final body weight because they have longer access to food resources and these resources may be better assimilated (Boivin, 2010). In the case of parasitoids, individuals collected in the field during low temperature periods were larger than those collected at high temperatures (Ellers *et al.*, 2001). At lower temperatures developmental time of parasitoids was longer, providing more time for limb formation, which results in larger parasitoids (Gullan and Cranston, 2008).

Although we would have liked to trace the history of the *P. volucre* population we used in this study, we did not succeed. Documentation about introductions of the parasitoid is limited to the early period after import (Salvadori and Salles, 2000), and we do not know when and which population(s) were introduced into Lavras, Minas Gerais.

In conclusion, we showed in this study that size, development, survival and parasitism of *P. volucre* with *A. solani* as host is influenced by temperature. Temperatures ranging from 22 and 24 °C resulted in short developmental time, and percentages of parasitism and emergence above 50%. This temperature range is best for rearing of *P. volucre* in *A. solani* at laboratory conditions and will make establishment and synchronization with the host possible at the timing of release under field conditions. According to De Conti *et al.* (2010; 2011a), *A. solani* are better adapted to moderately high temperatures in the range of 16-25 °C and 22 °C is the optimal temperature for reproduction, development and survival of all nymphal stages of this aphid. This means that the parasitoid *P. volucre* is well adapted to the same range of temperatures as *A. solani*, which is a positive indication for the possibility of using this parasitoid for aphid control. The mixture of 2nd and 3rd instar nymphs of *A. solani* we provided as hosts is adequate to rear the parasitoid.

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