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BIOLOGICAL CONTROL

Temperature-Dependent Parasitism, Survival, and Longevity of Five Species of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae) Associated with *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae)

MR Foerster[1], CA Marchioro[2], LA Foerster[3]

[1]Setor de Educação Profissional, Univ Federal do Paraná, Curitiba, PR, Brasil
[2]Univ Federal de Santa Catarina, Campus Curitibanos, SC, Brasil
[3]Depto de Zoologia, Univ Federal do Paraná, Curitiba, PR, Brasil

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Correspondence
CA Marchioro, Univ Federal de Santa Catarina, 89529-000 Campus Curitibanos, SC, Brasil; cesmarc@gmail.com

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Abstract

Egg parasitoids of the genus *Trichogramma* Westwood play an important role in the control of the velvetbean caterpillar *Anticarisa gemmatalis* Hübner in soybean crops in Southern Brazil. The effectiveness of *Trichogramma* species as biocontrol agents is dependent of several factors, but their adaptation to the climatic conditions of the region where they will be released is one of the most important. In this context, this study evaluated the effects of five constant temperatures ranging from 14 to 30°C on parasitism, age-specific survival, progeny production and longevity of *Trichogramma pretiosum* Riley, *Trichogramma atopovirilia* Oatman & Platner, *Trichogramma acacioi* Brun, Moraes & Soares, *Trichogramma lasallei* Pinto, and *Trichogramma rojasi* Nagaraja & Nagarkatti. We demonstrate that temperature differently affected the species of *Trichogramma* investigated when using eggs of the velvetbean caterpillar. We also demonstrate that *T. pretiosum* and *T. atopovirilia* are better adapted to a wide range of temperatures than the other species evaluated, and are therefore better suited as biocontrol agents for applied biological control programs of *A. gemmatalis*.

Introduction

The velvetbean caterpillar *Anticarsia gemmatalis* Hübner (Lepidoptera: Noctuidae) is one of the most important pests attacking soybean crops in New World agroecosystems. The caterpillar causes significant losses in yield in all areas where soybean is cultivated (Sosa-Gómez 2004, Silva *et al* 2012). Nowadays, control of *A. gemmatalis* is almost exclusively dependent on chemical insecticides. However, in the last years a large number of parasitoids and entomopathogens were found associated with the velvetbean caterpillar (Polaszek & Foerster 1997, Foerster & Avanci 1999, Moscardi 1999), making the implementation of management programs involving the preservation and augmentation of these natural enemies feasible.

Field surveys conducted in southern Brazil recorded seven species of microhymenoptera parasitizing eggs of *A. gemmatalis*, of which five were of the genus *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae): *Trichogramma pretiosum* Riley, *Trichogramma atopovirilia* Oatman & Platner, *Trichogramma acacioi* Brun, Moraes & Soares, *Trichogramma lasallei* Pinto, and *Trichogramma rojasi* Nagaraja & Nagarkatti (Polaszek & Foerster 1997, Foerster & Avanci 1999). In southern Brazil, these egg parasitoids are part of the local ecosystem and play an important role in the natural control of the velvetbean caterpillar, reaching levels of parasitism of up to 29% (Avanci *et al* 2005).

The effectiveness of parasitoids in the control of insect pests in biological control programs is dependent of several factors, but among the most important is their adaptation to the climatic conditions of the region where they will be released (DeBach 1965). Temperature is one of the most important environmental factors influencing various aspects of insect physiology, biology, and behavior (Ratte 1985); and the growth, survival, parasitism rate, and longevity of *Trichogramma* are strongly influenced by temperature (Ratte 1985, Reznik *et al* 2009).

In a previous study, Foerster & Foerster (2009) evaluated the effects of temperature on the development and emergence of five *Trichogramma* species collected in eggs of *A. gemmatalis* on soybean crops in southern Brazil. They estimated the parasitoids' thermal requirements and found that the lower temperature threshold of subtropical populations were lower than those estimated from tropical populations, indicating the adaptation of subtropical species/lineages to cold conditions. These data suggest that other biological parameters may also vary in response to lower temperatures experienced in the subtropics as compared to those recorded in tropical regions.

Apart from the study of Foerster & Foerster (2009), little is known regarding the biology of the complex of *Trichogramma* species associated to the velvetbean caterpillar in southern Brazil. Except for *T. pretiosum*, none of the species had their fitness assessed on eggs of *A. gemmatalis*, and the influence of temperature on parasitism rate, age-specific survival, and longevity remains unclear, especially in the case of the poorly studied species *T. lasallei* and *T. rojasi*. Understanding the effects of temperature on these important life-history traits will facilitate the development of mass rearing procedures for inundative programs of biological control using *Trichogramma* (Prasad *et al* 2002, Maceda *et al* 2003), and contribute to the knowledge on the role of temperature on parasitoid population dynamics. We compared the effects of constant temperatures on the rate of parasitism, age-specific survival, progeny production, and longevity of the five species of *Trichogramma* associated with the velvetbean caterpillar in Brazil.

Material and Methods

Parasitoids origin and maintenance

Stock colonies of *T. pretiosum*, *T. atopovirilia*, *T. acacioi*, *T. lasallei*, and *T. rojasi* were established with parasitized eggs of *A. gemmatalis* collected on soybean crops in the counties of Lapa (25°46′11″S, 49°42′57″W) and Fazenda Rio Grande (25°39′27″S, 49°18′29″W), south-eastern of the state Paraná, Southern Brazil. Parasitoid-rearing procedure followed Foerster & Foerster (2009).

Temperature effects on parasitism of Trichogramma spp

The experiment was conducted under controlled conditions in climatic chambers regulated at 14, 18, 21, 26, and 30±0.5°C; 70±10% RH; and 12L:12D photoperiod. Adult parasitoids used in the experiment were reared since larval eclosion at the evaluated temperatures. For each temperature, ten pairs of each parasitoid species were individually kept in glass tubes (0.5×6 cm) immediately after emergence. Thirty eggs of *A. gemmatalis* were glued onto blue cardboard cards (0.5×4 cm) and offered for parasitization to each pair for 24 h. This procedure was repeated during three consecutive days, which is the period when most of the eggs are laid by the female wasps (Hansen & Jensen 2002). To compensate for the lower parasitism rate at 14 and 18°C, eggs were offered to parasitism every other day at these temperatures. Adult parasitoids were fed with droplets of pure honey deposited on the side of the glass tubes throughout the experiment.

The number of parasitized eggs and parasitoids emerged per host, age-specific survival, progeny production, and longevity were used to assess the effect of temperature on the five *Trichogramma* species selected. The number of parasitoids per host was calculated by dividing the total number of emerged parasitoids in each glass tube by the total number of eggs parasitized. The longevity of each adult parasitoid was recorded, but all data from one replicate was grouped and we used the mean longevity of each replicate (glass tube) when performing the statistical analysis. Therefore, a total of ten replicates were used for longevity and the other parameters evaluated.

Statistical analysis

Differences in life-history parameters were compared using a factorial analysis of variance (ANOVA), considering temperature and parasitoid species as factors. Parasitoid sex was considered as a third factor when longevity in each temperature was compared. When differences were detected by ANOVA, Tukey's HSD test ($p<0.05$) was used for average comparisons. Before proceeding with the analysis, we tested the ANOVA assumptions of normality and homogeneity of variance by using the Shapiro-Wilk's and Levene's tests, respectively. Age-specific survival curves were constructed and statistically compared according to Kaplan & Meier (1958). All statistical procedures were performed using the software Statistica v. 8 (Statsoft Inc 2008).

Results

Total number of parasitized eggs

All five *Trichogramma* species were able to parasitize eggs in a range from 14 to 30°C (Table 1), but the number of parasitized eggs was significantly affected by temperature ($F_{(4,214)}=47.63$; $p<0.001$), parasitoid species ($F_{(4,214)}=57.66$;

Table 1 Mean (±SEM) number of parasitized eggs of *Anticarsia gemmatalis* by females of five *Trichogramma* species during three days (70±10% RH; 12L:12D photoperiod).

Temp. (°C)	*T. pretiosum*	*T. atopovirilia*	*T. lasallei*	*T. acacioi*	*T. rojasi*
14	10.6±1.57 cA	4.6±0.90 cA	2.8±0.51 bA	16.6±2.91 abA	3.3±0.59 bA
18	33.4±2.75 abA	41.1±3.56 abA	13.1±2.02 abB	29.2±1.89 aA	26.8±2.27 aAB
21	24.1±3.62 bcB	50.9±4.98 aA	27.0±3.97 aB	23.2±3.01 abB	12.2±2.28 abC
26	35.1±4.53 abB	55.7±3.00 aA	27.8±2.14 aBC	12.7±3.35 bCD	11.2±1.34 bD
30	41.0±4.55 aA	30.1±5.36 bA	7.7±0.90 bB	8.1±1.32 bB	9.1±0.97 bB

Means followed by the same lower case letter in columns and upper case letters in rows are not significantly different from each other according to ANOVA, Tukey's HSD test ($P \geq 0.05$).

$p<0.001$) and the interaction between these two factors ($F_{(16,214)}=11.83$; $p<0.001$). The number of parasitized eggs was lower at 14°C, but no significant differences were recorded among parasitoid species at this temperature. By contrast, at 18, 21, 26, and 30°C, the number of parasitized eggs varied significantly according to the parasitoid species. In general, *T. pretiosum* and *T. atopovirillia* showed significantly higher rates of parasitism at temperatures above 18°C as compared to the other species. At 21 and 26°C, *T. atopovirilia* showed the highest number of parasitized eggs, whereas at 30°C *T. pretiosum* showed a significant higher number of parasitized eggs compared to *T. lasallei*, *T. acacioi*, and *T. rojasi* (Table 1).

Progeny production

The number of descendents was significantly affected by temperature ($F_{(4,214)}=30.55$; $p<0.001$), parasitoid species ($F_{(4,214)}=10.83$; $p<0.001$) and the interaction between these two factors ($F_{(16,214)}=4.02$; $p<0.001$). In general, progeny production tended to be reduced at 14 and 30°C for all egg parasitoid species. *Trichogramma atopovirilia* produced the highest number of descendents in all temperatures, except at 14°C (Fig 1).

Age-specific survival

According to the Kaplan–Meier's analysis, differences in age-specific survival among *Trichogramma* species were recorded at 14 ($\chi^2_{(4)}=35.17$; $p<0.001$), 18 ($\chi^2_{(4)}=15.00$; $p=0.004$), 21 ($\chi^2_{(4)}=14.15$; $p<0.006$), 26 ($\chi^2_{(4)}=14.15$; $p<0.007$), and 30°C ($\chi^2_{(4)}=35.82$; $p<0.001$). In all temperatures evaluated, *T. pretiosum* was the longest living species compared to the other parasitoids, while *T. lasallei* and *T. rojasi* presented the lowest survival rate (Fig 2).

Longevity

Longevity of the five *Trichogramma* species were affected by temperature ($F_{(4,448)}=244.35$; $p<0.001$), parasitoid species

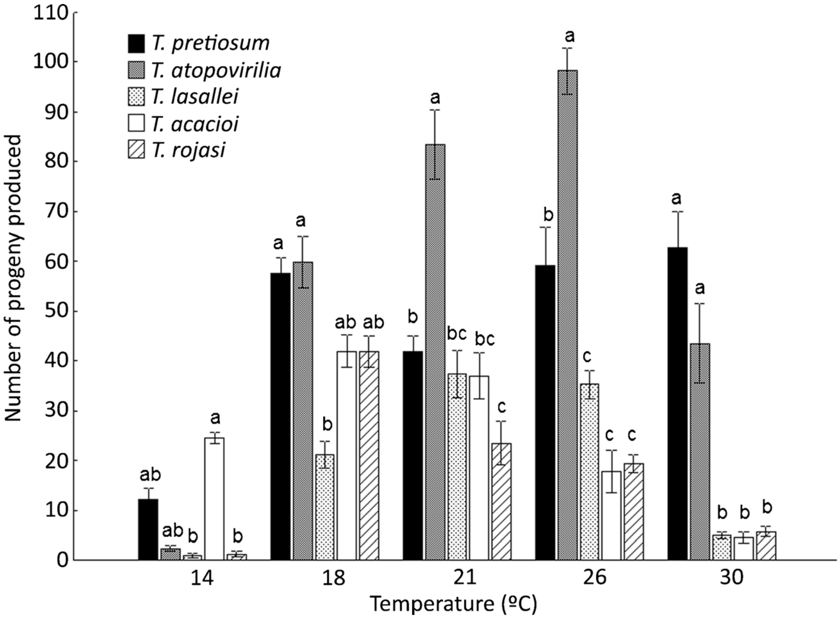

Fig 1 Mean number of adult parasitoids produced after 3 days of parasitism (±SEM) by five *Trichogramma* species reared at different temperature regimes (70±10% RH; 12L:12D photoperiod). The statistic shows differences in progeny production between species within each temperature. Means followed by the same letter in bars are not significantly different from each other according to ANOVA, Tukey's HSD test ($p \geq 0.05$).

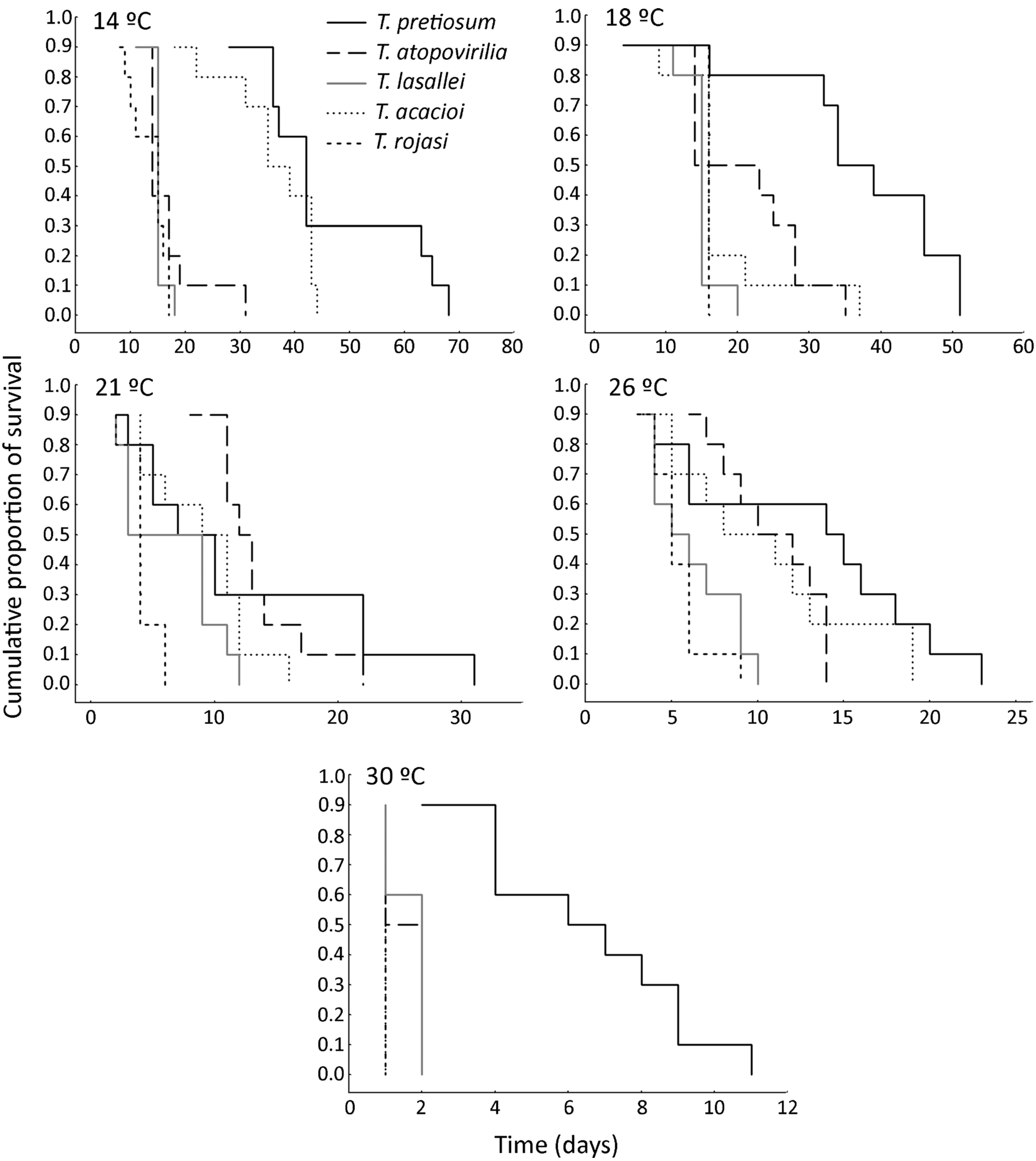

Fig 2 Survival curves of five *Trichogramma* species at different temperature regimes (70±10% RH; 12L:12D photoperiod).

($F_{(4,448)}$=91.77; p<0.001), parasitoid sex ($F_{(1,448)}$=37.95; p<0.001), and by the interactions among these three factors ($F_{(16,448)}$=2.50; p=0.001). For all parasitoid species, longevity decreased as temperature increased. At 14 and 18°C significant differences among species were recorded, with *T. pretiosum* living longer than the other species (Table 2).

Parasitoids emerged per host

The mean number of parasitoids emerged per host was also affected by temperature ($F_{(4,214)}$=73.49; p<0.001), parasitoid species ($F_{(4,214)}$=81.50; p<0.001), and the interaction between these factors ($F_{(16,214)}$=14.71; p<0.001; Table 3).

Table 2 Male and female longevity (days; ±SEM) of five *Trichogramma* species reared at different constant temperatures (70±10% RH; 12L:12D photoperiod).

Temp. (°C)	Sex	*T. pretiosum*	*T. atopovirilia*	*T. lasallei*	*T. acacioi*	*T. rojasi*
14	Female	45.9±4.45 aA	16.8±1.68 abC	14.9±0.53 abC	35.4±2.90 aB	13.3±1.10 abC
	Male	24.9±3.90 cA	11.3±0.80 bB	10.2±1.1 abcB	29.7±2.22 aA	11.6±0.94 abcB
18	Female	35.3±4.83 bA	20.9±2.49 aB	14.7±0.79 abB	16.7±2.70 bB	14.8±1.20 aB
	Male	28.2±1.61 bcA	13.6±0.40 abB	15.1±0.57 aB	17.0±1.46 bB	10.9±1.68 abcB
21	Female	11.7±3.11 dA	13.2±1.23 abA	6.3±1.27 abcA	8.9±1.33 bcA	4.0±0.42 cdA
	Male	11.6±1.63 dA	11.4±1.31 bA	5.8±1.10 bcA	10.0±1.31 bcA	2.9±0.31 cdA
26	Female	12.5±2.27 dA	10.7±0.98 bA	6.1±0.80 abcA	10.2±1.79 bcA	5.3±0.52 bcdA
	Male	13.3±1.16 dA	8.2±0.40 bcAB	4.7±0.80 cAB	8.7±0.30 bcAB	2.8±0.25 cdB
30	Female	6.4±0.91 deA	1.5±0.17 cA	1.0±0.00 cA	1.6±0.16 cA	1.0±0.00 dA
	Male	1.6±0.22 eA	1.0±0.00 cA	1.0±0.00 cA	1.1±0.10 cA	1.0±0.00 dA

Means followed by the same lower case letter in columns and upper case letters in rows are not significantly different from each other according to ANOVA, Tukey's HSD test ($p \geq 0.05$).

Discussion

Temperature significantly affected parasitism, age-specific survival, progeny production, and longevity of all five *Trichogramma* species studied. Although all parasitoids survived and were able to parasitize eggs in the range between 14 and 30°C, the response to the extreme temperatures varied according to the species. For instance, *T. acacioi* showed a higher tolerance to low temperatures compared to *T. pretiosum* and *T. atopovirilia.* A similar adaptation of *T. acacioi* to low temperatures was recorded by Pratissoli *et al* (2009) using factitious hosts.

Our data is in accordance with previous data reported for different species of *Trichogramma* from various regions of the world, demonstrating a large variation in the rate of parasitism at temperatures below 15°C and above 30°C (Pak & van Heiningen 1985, Pizzol *et al* 2010). In general, egg parasitoids of the genus *Trichogramma* tend to reduce their rates of parasitism at temperatures below 25°C. One possible explanation is the loss of turgidity of the host egg at higher temperatures, making difficult the insertion of ovipositor through the host egg chorion (Pereira *et al* 2007). Another possibility is based on the fact that parasitoids need more energy to maintain their activity at high temperatures, and thus feed more frequently causing higher mortality through multiple feeding and stinging instead of parasitism (Shipp & Wang 1998).

Survival rate is also a good indicator of the ability of a species to tolerate a given temperature. Among the parasitoids evaluated in our study, *T. pretiosum* was the one with the highest survival rate at all temperatures, indicating its ability to tolerate a broader range of temperatures compared to the other species evaluated. On the other hand, both *T. lasallei* and *T. rojasi* showed comparatively low survival rates, suggesting they may be effective biocontrol agents of *A. gemmatalis* only under a restricted range of temperatures.

It is expected that the significant differences found in survival and parasitism rates differently affect the parasitoid fitness. These differences in fitness can partially explain the variation recorded in the abundance of *Trichogramma* species in the field. Surveys carried out during summer in soybean crops in south-eastern Brazil, when the average temperature is ca. 23°C, demonstrated that *T. pretiosum* was the dominant parasitoid, being in some seasons responsible for

Table 3 Mean number (±SEM) of parasitoids emerged per host at different constant temperatures.

Temp. (°C)	*T. pretiosum*	*T. atopovirilia*	*T. lasallei*	*T. acacioi*	*T. rojasi*
14	1.1±0.13 bA	0.5±0.13 bB	0.3±0.13 bB	1.5±0.05 aA	0.3±0.09 bB
18	1.8±0.09 aA	1.5±0.05 aA	1.7±0.09 aA	1.4±0.04 aA	1.6±0.03 aA
21	1.8±0.04 aAB	1.7±0.04 aAB	1.5±0.09 aB	1.6±0.09 aAB	2.0±0.13 aA
26	1.7±0.09 aA	1.8±0.05 aA	1.3±0.04 aA	1.5±0.16 aA	1.8±0.12 aA
30	1.5±0.06 abA	1.5±0.08 aA	0.8±0.14 bB	0.5±0.14 bB	0.6±0.12 bB

Only parasitized eggs were used for calculating the number of parasitoids emerged per host (70±10% RH; 12L:12D photoperiod). Means followed by the same lower case letter in columns and upper case letters in rows are not significantly different from each other according to ANOVA, Tukey's HSD test ($p \geq 0.05$).

70% of the parasitized eggs of *A. gemmatalis* (Avanci *et al* 2005). These findings are in accordance with the results obtained in our laboratory study regarding the high rates of parasitism and survival of *T. pretiosum* between 21 and 30°C. Also, *T. lasallei* and *T. rojasi* presented the lowest fecundity and survival rate and were the least abundant parasitoids in the field (Avanci *et al* 2005).

However, data obtained under laboratory conditions should be carefully extrapolated to field conditions due to the occurrence of other factors that might affect the dispersal and ability of parasitoids to locate their hosts, such as plant and habitat-related traits (Romeis *et al* 2005), interespecific competition (Pak & Oatman 1982), and the number of hosts that can be located and parasitized (Godfray 1994, West & Rivero 2000). In our study, *T. atopovirillia* also showed high parasitism rate and progeny production from 21 to 26°C, but was not as abundant in the field as *T. pretiosum* (Avanci *et al* 2005). Similarly, *T. acacioi*, which was the second most abundant parasitoid in the field, showed low survival rates and progeny production if compared to *T. atopovirilia* and *T. pretiosum*. Parasitism rate alone may not be a good predictor of field success, as already demonstrated for *T. carverae* Oatman & Pinto (Thomsom & Hoffmann 2002).

As observed in other studies with several species of *Trichogramma*, the mean longevity decreased as temperature increased (Hansen & Jensen 2002, Maceda *et al* 2003, Bueno *et al* 2010, 2012). This is possibly associated with a decrease in parasitoid activity and, consequently, in their metabolism at low temperatures (Bleicher & Parra 1990). An interesting result, however, is the fact that the longevity we recorded for *T. pretiosum* females was markedly longer than those reported for tropical strains of this species (Alencar *et al* 2000, Bueno *et al* 2010). Differences in the longevity of populations of a species collected in distinct regions suggest their acclimatization to the specific climatic conditions of their area of origin. The acclimatization explains the fact that the subtropical strains we used lived longer than those from the tropics. However, comparisons between studies should be conducted carefully, because differences in life-history parameters can also be attributed to factors related to experimental conditions, such as host quality (Corrigan & Laing 1994), photoperiod (Rounbehler & Ellington 1973). and parasitoid adult access to food sources (Hansen & Jensen 2002).

Other studies came to similar conclusions by comparing the lower temperature threshold (T_0) estimated for populations of *Trichogramma* collected in different regions (Poorjavad *et al* 2011, Pizzol *et al* 2010, Samara *et al* 2011). Foerster & Foerster (2009) compared the lower temperature threshold estimated for subtropical populations of *Trichogramma* with those available in the literature for tropical populations and concluded subtropical strains show a lower T_0. Similarly, Samara *et al* (2011) evaluated the role of temperature on the biology of different strains of *T. aurosum* Sugonjaev & Sorokina, and based on the estimated demographic parameters concluded that some strains showed good adaptability to high temperatures, while others were well adapted to low temperatures.

In conclusion, we demonstrated that temperature differently affect the species complex of the genus *Trichogramma* parasitizing eggs of the velvetbean caterpillar in southern Brazil. These results are useful to understand the differences in parasitoids abundance in the field. Furthermore, considering that success in biological control by *Trichogramma* species depends on the understanding of their ecological requirements (Parra *et al* 1987, van Lenteren *et al* 1997), the data we provided can also aid in the selection of species better adapted to the climatic condition experienced during the critical period of pest attack in soybean crops. Our data indicated *T. pretiosum* and *T. atopovirilia* as the best adapted to a wide range of temperatures among the species we analyzed and the most suitable for use in applied biological control programs of *A. gemmatalis*.

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