BIOLOGICAL CONTROL

Telenomus remus Nixon Egg Parasitization of Three Species of *Spodoptera* Under Different Temperatures

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Abstract

Telenomus remus Nixon is a promising biocontrol agent as an egg parasitoid of *Spodoptera* spp., but the lack of information on the host–parasitoid interactions in this system precludes its applied use in agriculture. Therefore, we studied the parasitism capacity of *T. remus* on eggs of *Spodoptera cosmioides* (Walker), *Spodoptera eridania* (Cramer), and *Spodoptera frugiperda* (Smith) in a range of temperatures (19, 22, 25, 28, 31, and 34±1°C) under controlled conditions (70±10% RH and 12 h photophase). Egg masses of *Spodoptera* spp. were offered to a single-mated *T. remus* female on a daily basis. More than 80% lifetime parasitism on eggs of *S. cosmioides*, *S. frugiperda*, and *S. eridania* was reached from 1 to 5, 1 to 7, and 1 to 9 days, respectively, at temperatures from 19 to 34°C. More than 80% parasitization was obtained at extreme temperatures for all hosts studied. Lifetime parasitization of *S. frugiperda*, *S. cosmioides*, and *S. eridania* was affected by temperature, with the lowest values for *S. frugiperda* (34°C) and *S. cosmioides* (19 and 34°C). Parasitization of *S. eridania* eggs was reduced around 18% at 28 and 31°C, but dropped more severely at 34°C. Parasitoid longevity was reduced as temperature increased. Thus, our data indicated that *T. remus* might be suitable as a biocontrol agent against *S. eridania*, *S. cosmioides*, and *S. frugiperda* in geographical areas that fit the temperature range studied here, even though *T. remus* parasitism was reduced at 34°C.

Introduction

Spodoptera spp. (Lepidoptera: Noctuidae) are widely distributed throughout the world. From the 30 species already described in this genus, about half of them are considered pests of several different and economically important crops (Pogue 2002). In Brasil, 15 species of *Spodoptera* occur as agricultural pests, presenting a high degree of polyphagy, feeding on crops such as cereals and pastures (Pogue 2002), horticultural crops (Silva *et al* 1968), and eucalyptus (Santos *et al* 1980). Furthermore, *Spodoptera frugiperda* (Smith), *Spodoptera eridania* (Cramer), and *Spodoptera cosmioides* (Walker) stand out on the crops such as corn, soybean, and cotton as they cause severe damage (Cruz *et al* 1999, Nagoshi 2009).

Chemical control is the most used strategy for the management of *Spodoptera* (Figueiredo *et al* 1999, Morales *et al* 2000). However, not only has the large utilization of insecticides selected populations that are resistant to several active ingredients (Diez-Rodriguez & Omoto 2001), but also has caused environmental imbalances that favor the increase of secondary pests (Stark & Banks 2003, Desneux *et al* 2007). In this scenario, the implementation of an Integrated Pest Management (IPM) program is necessary

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in order to mitigate problems triggered by the abusive spraying of chemicals (Figueiredo *et al* 1999, Ferrer 2001). IPM aims towards the rational use of insecticides as well as the harmonious integration of different control strategies (Zalucki *et al* 2009). Among the strategies used in IPM programs, a lot of attention has been given to biological control (Ferrer 2001) as it helps to reduce the negative impact of the intensive agriculture on the environment (van Lenteren & Bueno 2003).

Among the natural enemies of *Spodoptera* spp., *Telenomus remus* Nixon (Hymenoptera: Platygastridae) stands out as a highly specialized egg parasitoid (Cave 2000). Its efficiency in controlling the fall armyworm *S. frugiperda* has been proved in countries such as Venezuela and Mexico (Hernández & Díaz 1996, Cave 2000, Figueiredo *et al* 2002, Bueno *et al* 2008). As this parasitoid successfully controls *S. frugiperda*, there is also a chance it may successfully parasitize other species of the same genus, such as *S. eridania* and *S. cosmioides*, whose economic importance has been increased in recent years (Bueno *et al* 2010a, b).

However, complementary studies regarding the successful exploitation of such hosts would be needed before the development of biological control programs using *T. remus*, as well as other studies regarding the biology, climate impact, and parasitization capacity (Figueiredo *et al* 1999, Higley *et al* 1986, Bueno *et al* 2008).

Among several factors affecting the development of natural enemies, thermal adaptation is of major importance since it is known to impair the duration of the developmental period, the sex ratio, the parasitism, and the longevity of adults (Frazer & McGregor 1992). In some cases, parasitoid performance on different hosts may be affected by temperature as well (Bleicher & Parra 1990, Hernández *et al* 1989). Therefore, we aimed to study the parasitism capacity of *T. remus* in different hosts and at different temperatures in order to provide the basic knowledge required for the use of this biological control agent in integrated pest management of the different host species (*S. frugiperda*, *S. eridania*, and *S. cosmioides*). Therefore, this research aimed to evaluate the parasitism capacity of *T. remus* on eggs of those hosts under different temperatures.

Material and Methods

A bioassay was carried out to study the parasitization capacity of *T. remus* on eggs of *S. frugiperda*, *S. cosmioides*, and *S. eridania*. Trials were performed under different temperatures (19, 22, 25, 28, 31, and 34±1°C) at controlled conditions (70±10% RH and a photophase of 12 h). A fully randomized experimental design, with treatments arranged in a 3×6 factorial design (three *Spodoptera* species×six temperatures) with 20 replicates were used. Each replicate consisted of a single-mated *T. remus* female (up to 24-h old) and a fresh egg mass of *Spodoptera* (up to 24-h old) placed in a individual plastic vial (1 cm Ø × 6 cm tall). Egg masses were replaced on a daily basis.

Host and parasitoid rearing

Insects were obtained from colonies kept at Embrapa Soja, located in Londrina, state of Paraná, Brasil. *Spodoptera cosmioides* was originally collected on castor bean plants (*Ricinus communis*) in Pelotas, state of Rio Grande do Sul, and reared for seven generations in the lab before being used in the experiments. *Spodoptera eridania* was originally collected on soybean plants (*Glycine max*) in Mamborê, state of Paraná, and reared for eight generations. *Spodoptera frugiperda* was originally collected on corn plants (*Zea mays*) in Rio Verde, state of Goiás, and reared for 36 generations before use. Since their field collection, all host species were reared under laboratory-controlled conditions (25±2°C, 70±10% RH, and a photophase of 12 h) and fed on an artificial diet based on beans, wheat germ, and soybean (Greene *et al* 1976).

Telenomus remus was originally collected in Ecuador in 1986 and it was multiplied at the parasitoid rearing facilities at the Escola Superior de Agricultura "Luiz de Queiroz"/Universidade de São Paulo, and then tranferred to Embrapa Soja where they have been reared for 5 years before being used in this experiment. *Telenomus remus* has been reared on egg masses of *S. frugiperda* glued onto a cardboard sheet (2×8 cm). Parasitoids were honey-fed and *T. remus* was allowed to parasitize for 24 h.

Parasitism

The egg masses (up to 24-h old) containing nearly 100 eggs of each host were glued on 0.8×5 cm rectangular cards, and individually introduced into a vial where a single, mated, honey-fed female was available. The cards containing the egg masses were replaced on a daily basis until the female's death. Eggs exposed to parasitization were daily transferred to new glass tubes (2 cm Ø × 8 cm tall) and maintained at the same temperatures at which the parasitism occurred until adult eclosion.

The tested temperatures were chosen based on Bueno *et al* (2008), who reported that *T. remus* development was impaired at 15 and 35°C. Therefore, this present study aimed at understanding *T. remus* parasitization capacity at temperatures within the range that could be adequate for this parasitoid (19, 22, 25, 28, 31, and 34°C).

For each temperature, the following biological parameters were observed: number of daily parasitized eggs, lifetime parasitism (percent and percentage of the total number of eggs parasitized during the parasitoid lifetime), total number of eggs parasitized per female, and parental female longevity (days). The total number of parasitized eggs (lifetime parasitization) and parental female longevity were submitted for evaluation of the assumptions of normality residues (Shapiro & Wilk 1965), homogeneity of variance of treatments (Burr & Foster 1972), and additivity of the model to allow for analysis of variance. Means were then compared by Tukey's test at 5% probability (SAS Institute 2001).

Results

The number of parasitized eggs per day varied with temperature and host species, but it was higher on the first 24 h on all studied *Spodoptera* species and temperatures (Figs 1, 2, and 3). Parasitoids decreased the number of eggs daily parasitized on the studied host species as a function of the time of parasitism and of the temperature at which they were subjected (Figs 1, 2, and 3). More than 80% of lifetime parasitization of *T. remus* on eggs of *S. cosmioides* (Fig 1), *S. frugiperda* (Fig 2), and *S. eridania* (Fig 3) was reached, respectively, from 1 to 5, 1 to 7, and 1 to 9 days, depending on the temperature they were exposed to.
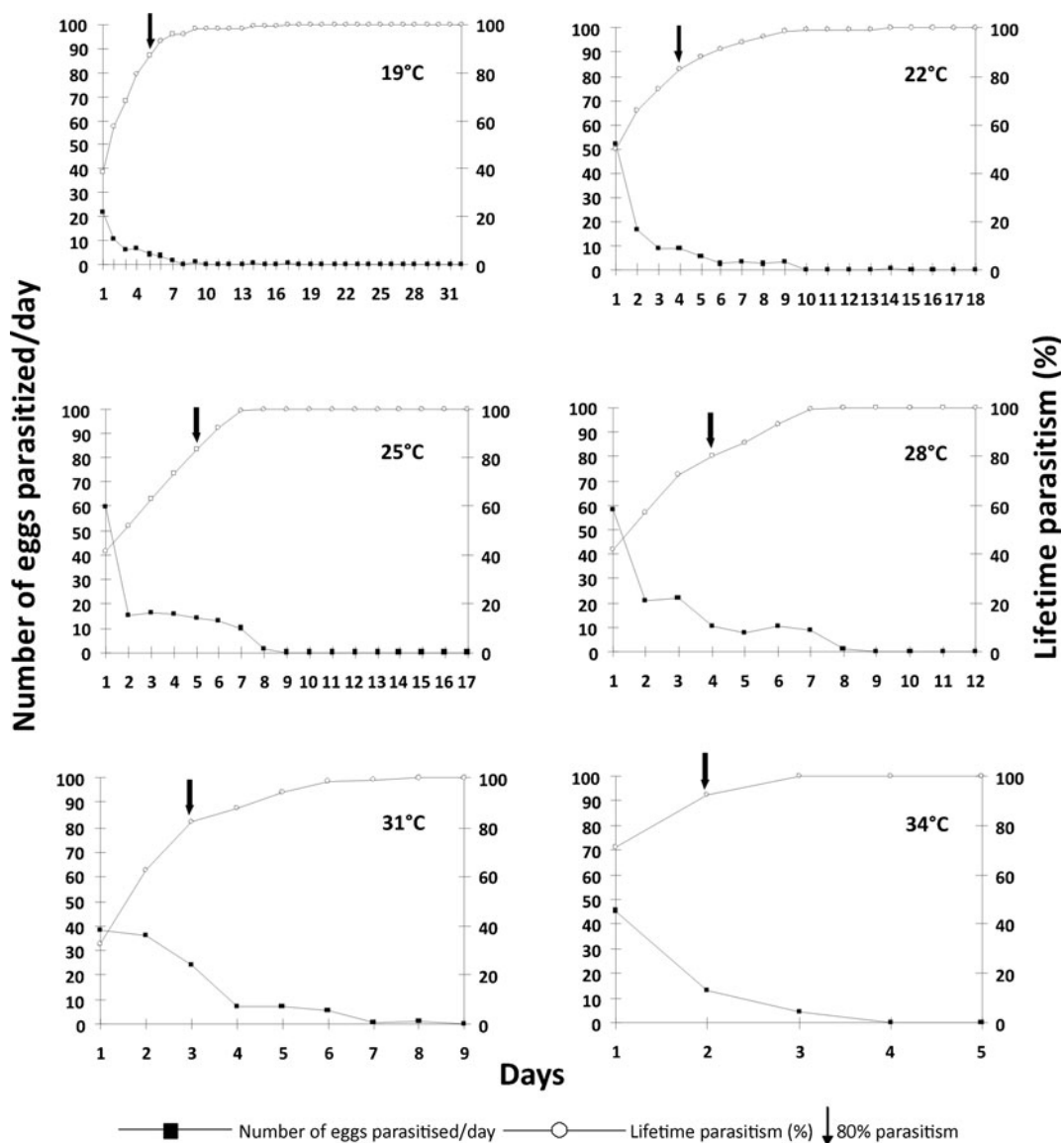

Fig 1 Daily (number) and lifetime parasitism (percentage) of *Spodoptera cosmioides* eggs by *Telenomus remus* at different temperatures.
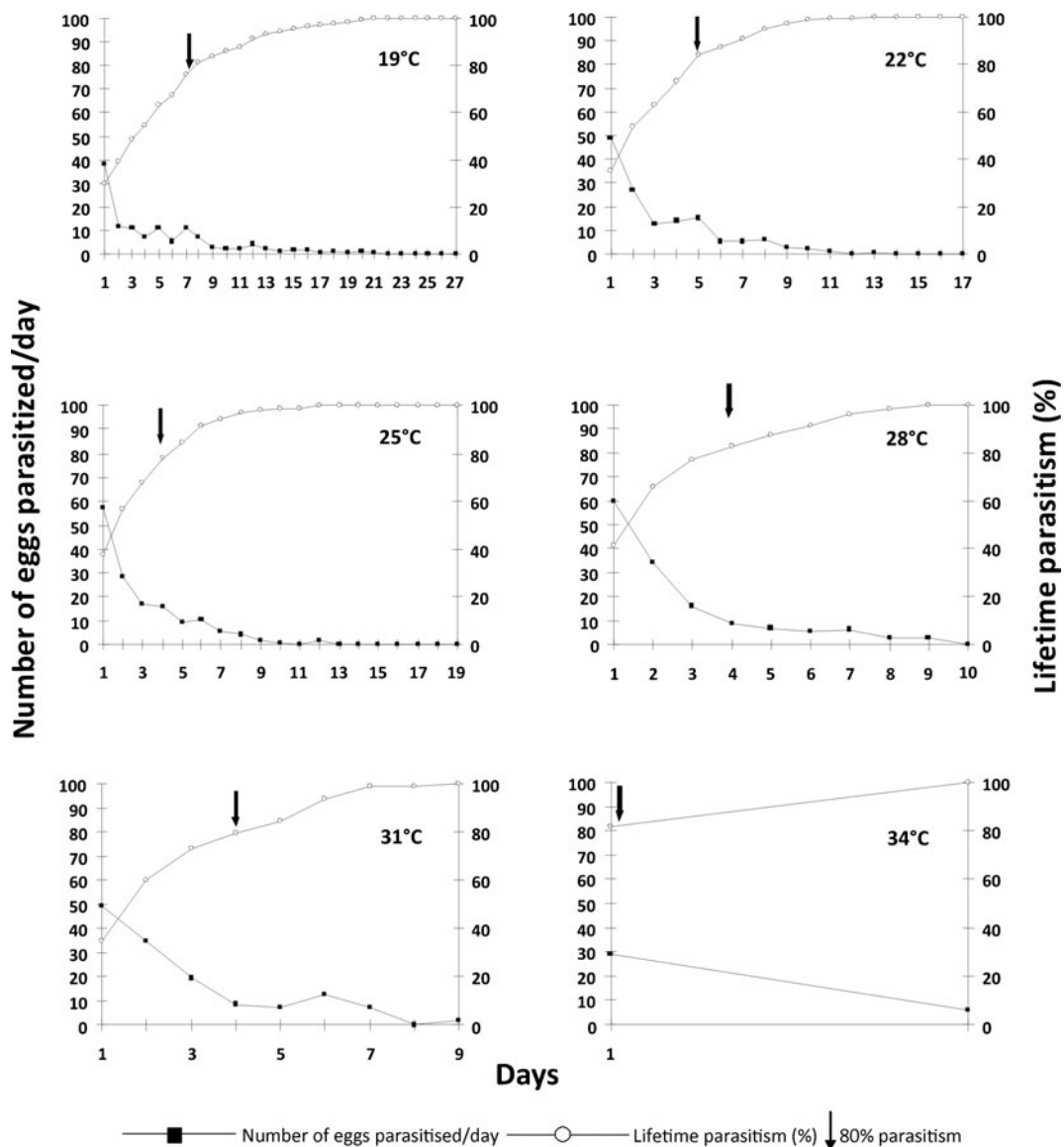
Fig 2 Daily (number) and lifetime parasitism (percentage) of *Spodoptera frugiperda* eggs by *Telenomus remus* at different temperatures.

Parental longevity of *T. remus* females when presented with eggs of *Spodoptera* spp. significantly varied with temperature ($F=323.22$, $df=5$, $p<0.0001$), with host species ($F=43.07$, $df=2$, $p<0.0001$) and with the temperature and host interactions ($F=3.07$, $df=10$, $p=0.0010$). Parental longevity was inversely proportional to temperature for all studied hosts (Table 1). For all tested temperatures and hosts, *T. remus* females presented to *S. cosmioides* eggs had the highest parental longevity, similar to when *T. remus* females was presented to *S. eridania* eggs at 22°C and to both *S. frugiperda* and *S. eridania* eggs at 34°C (Table 1).

As a combination of adult longevity associated with parasitoid egg load and host quality, the lifetime number of parasitized eggs varied among temperatures ($F=40.23$, $df=5$, $p<0.0001$), hosts ($F=7.26$, $df=2$, $p=0.0008$), and the

interaction between temperature and hosts ($F=5.79$, $df=10$, $p<0.0001$; Table 2). Lifetime parasitization of *T. remus* was lower at 34°C and no differences were observed from 19 to 31°C with eggs of *S. frugiperda* as hosts. Lifetime parasitization on eggs of *S. cosmioides* was reduced at 34 and 19°C. Differently, however, *T. remus* lifetime parasitization on *S. eridania* eggs was reduced around 18% at 28°C and 31°C, but much more severely at 34°C (Table 2).

Regarding the hosts, the lowest parasitism by *T. remus* was observed at 34°C on eggs of *S. frugiperda* and *S. eridania* and at 19°C on eggs of *S. cosmioides* (Table 2). There were no significant differences among the studied hosts when they were compared at the temperature range of 25–31°C. At the two lowest temperatures (19 and 22°C), however, *S. eridania* had a higher number of parasitized eggs by *T. remus* than *S.*
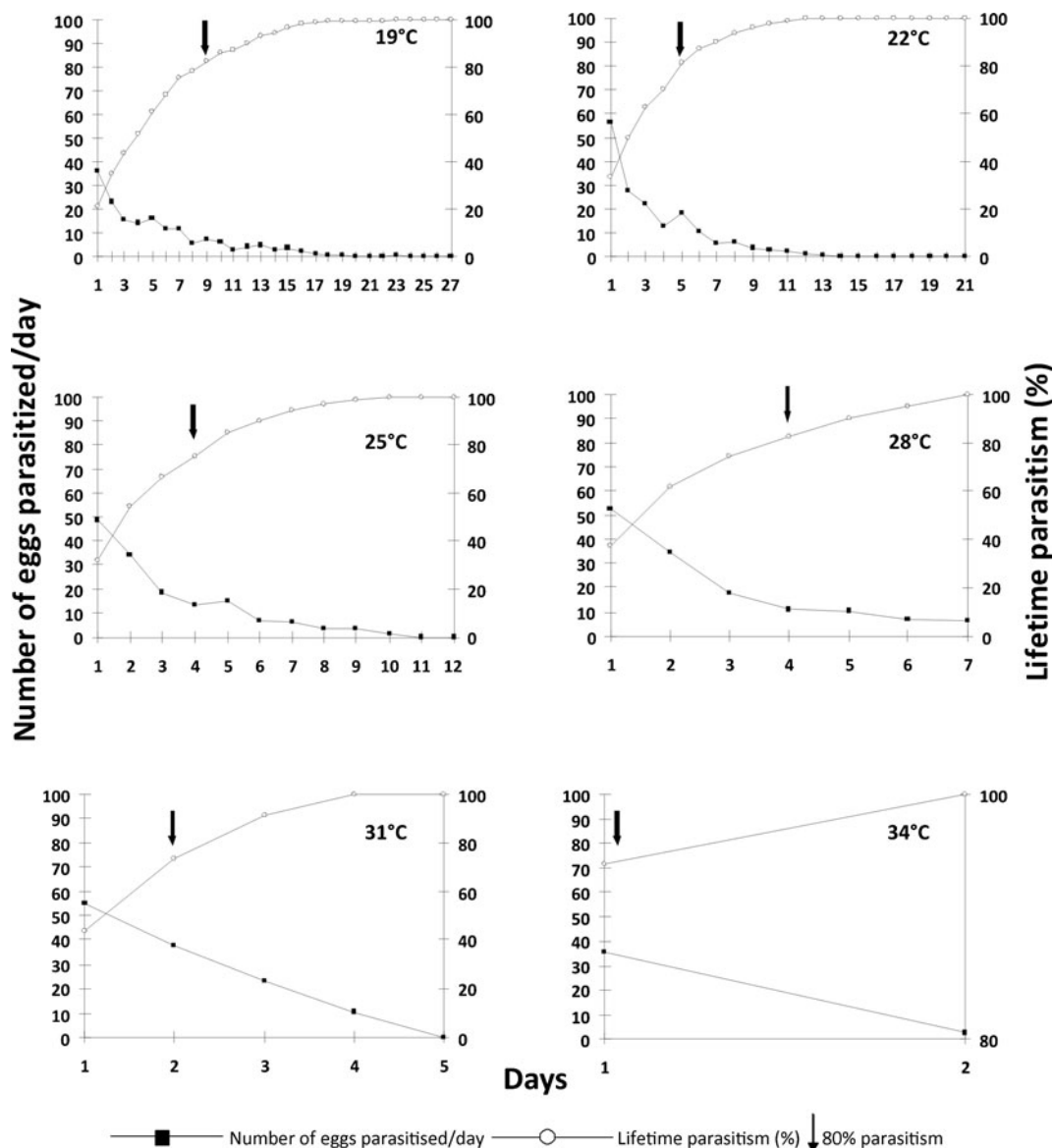
Fig 3 Daily (number) and lifetime parasitism (percentage) of *Spodoptera eridania* eggs by *Telenomus remus* at different temperatures.

frugiperda and *S. cosmioides*. At 34°C, the highest number of parasitized eggs was observed for *S. cosmioides* (Table 2).

Discussion

The parasitization activity of *T. remus* always peaked in the first 24 h of parasitism regardless of the temperature and host species, similar to what has been reported for this species when attacking *S. frugiperda* (Hernández & Diaz 1995, Bueno *et al* 2010a). These results indicate that *T. remus* is a pro-ovigenic species as females eclose with their full or nearly full egg complement (Mills & Kuhlmann 2000), allowing females to parasitize as soon as they emerge.

The concentration of the parasitization activity in the first days of life is not a characteristic only common to *T. remus*, but also to other egg parasitoids, which need to quickly find their hosts and assure the allocation of their progeny. Oviposition peak of different species of egg parasitoids from the genus *Trichogramma*, for example, have been already reported in the literature on the first day after adult emergence (Pak & Oatman 1982, Bai *et al* 1992, Volkoff & Daumal 1994).

Not only oviposition peak can vary as a consequence of pro-ovigenic or synovigenic reproductive strategy, but also due to changes in parasitoid behavior (Denis *et al* 2011). For ectotherm parasitoids, temperature is inversely related to their metabolic rate and lipid consumption (Huey &

Table 1 Parental longevity of *Telenomus remus* females when presented with eggs of *Spodoptera frugiperda*, *Spodoptera cosmioides*, and *Spodoptera eridania* at different temperatures, 70±10% RH, and 12/12 h photoperiod (L/D).

Temperature (°C)	Parental adult longevity (days±SE)[a]		
	Spodoptera frugiperda	*Spodoptera cosmioides*	*Spodoptera eridania*
19	21.17±0.60 aB[a]	26.44±1.44 aA	18.70±0.95 aC
22	10.77±0.45 bC	13.11±0.86 bA	11.40±0.88 bAB
25	8.30±0.62 cB	13.11±0.68 bA	8.00±0.54 cB
28	5.73±0.35 dB	9.11±0.38 cA	4.85±0.30 dB
31	4.67±0.36 dB	7.11±0.56 cA	3.25±0.29 deB
34	2.37±0.25 eA	2.78±0.40 dA	1.50±0.14 eA
CV (%)	29.44		

[a] Means (±standard error) followed by the same small letter in the column and the same capital letter in the line are not statistically different between each other by the Tukey's test at 5% probability.

Berrigan 2001). Thus, lipids accumulated during the larval stage determine adult lifespan and fecundity (Visser & Ellers 2008) and, therefore, its lifetime reproductive success (Huey & Berrigan 2001). Because foraging decisions might be affected by the lipid reserves and the number of mature eggs (Godfray 1994), lipids carried over from the larval stage can be allocated to either egg production or to adult lipid reserves, leading to a trade-off between reproduction and adult survival (Pexton & Mayhew 2002). Therefore, the time for how long parasitoids are active and, most importantly, the time required to reach 80% of their expected lifetime fecundity in the field might vary due to differences in temperature (Reznik & Vaghina 2006),

Table 2 Lifetime number of parasitized eggs of *Spodoptera frugiperda*, *Spodoptera cosmioides*, and *Spodoptera eridania* by *Telenomus remus* at different temperatures, 70±10% RH, and 12/12 h photoperiod (L/D).

Temperature (°C)	Lifetime number of parasitized eggs/female (±SE)[a,b]		
	Spodoptera frugiperda	*Spodoptera cosmioides*	*Spodoptera eridania*
19	124.90±8.23 aB	57.16±4.33 cC	166.99±8.07 aA
22	134.57±8.82 aAB	103.53±13.21 abcB	163.37±8.34 aA
25	140.80±8.46 aA	115.31±6.34 abA	139.48±10.58 abA
28	124.19±6.03 aA	132.06±7.49 aA	115.51±9.21 bA
31	111.40±7.92 aA	115.64±16.76 abA	111.10±10.58 bA
34	35.40±6.45 bB	61.46±2.34 bcA	36.90±4.88 cB
CV (%)	20.28		

[a] Means (±standard error) followed by the same small letter in the column and the same capital letter in the line are not statistically different between each other by the Tukey test at 5% probability.

[b] Original means followed by statistics performed on data transformed by $\sqrt{X + 0.5}$.

hosts (Reznik *et al* 2001), or parasitoid species (Pizzol *et al* 2010) or due to a combination of more than one of these factors. These differences might be directly responsible for their parasitization capacity and consequently to their chances to succeed as a biological control agent. Thus, whether parasitization is more concentrated in the first days of life or evenly distributed throughout adulthood is an important characteristic to be considered when choosing the strategy for parasitoid release (Bueno *et al* 2010a).

In the field, parasitoids are exposed to biotic and abiotic factors that can affect their fitness, such as the contact with chemicals sprayed for the crop management or an abrupt change in temperature (Carmo *et al* 2010, Denis *et al* 2011), that will easily affect the natural enemy but hardly ever kill the pests. Egg parasitoids are usually tiny little wasps more susceptible to the chemicals used in agriculture as herbicides and fungicides than their hosts (Carmo *et al* 2010). This is a crucial parasitoid feature that needs to be taken into consideration in the biological control program strategy.

Telenomus remus reached 80% of its lifetime parasitization capacity from 1 to 9 days in all temperatures and hosts tested, which are much earlier than other egg parasitoids already used in *Spodoptera* control (Bueno *et al* 2008). Therefore, any pesticide spraying needed after *T. remus* release should be performed after that period of time, otherwise *T. remus* performance might be impaired, and this period of time will vary with parasitoid species (Bueno *et al* 2010b, 2012).

Female longevity was inversely proportional to temperature as expected and similar to what has been already published for this parasitoid (Hernández & Diaz 1995, Bueno *et al* 2010a). Thus, it is possible that in warm regions, the mean longevity of the natural enemies may be reduced in field conditions, suggesting that biological control programs using *T. remus* in those regions might demand a higher frequency of releases than in regions with cooler temperatures.

Female longevity can also have a direct impact on lifetime parasitization capacity, a trait directly affected by temperature. The higher lifetime parasitization observed at lower temperatures (19, 22, and 25°C) for *T. remus* parasitizing eggs of *S. eridania* and *S. frugiperda* can be explained by the higher parental longevity of *T. remus* females at those temperatures. According to Gerling (1972), females of *T. remus* live longer at lower temperatures as a consequence of the decreased metabolic rate observed at cold temperatures.

On eggs of *S. cosmioides*, on the other hand, *T. remus* had the lowest lifetime parasitization at both extreme temperatures (19 and 34°C), indicating this particular host is not as suitable to *T. remus* at these temperatures as compared to the others. These results indicate that different hosts offer different degrees of protection against temperature changes. Furthermore, it is important to consider that these extreme temperatures might be close to the lower and

upper thermal limits for the parasitoid development. Bueno *et al* (2008) reported that the lower thermal limit for *T. remus* reared on eggs of *S. frugiperda* is 12.5°C.

Gupta & Pawar (1985) had already reported the influence of temperature on parasitism capacity of *T. remus* on *Spodoptera litura* eggs and reported that the highest parasitization rates were obtained between 20 and 25°C. Bueno *et al* (2010a) also found similar results and emphasized that the highest lifetime parasitism of *T. remus* on eggs of *S. fugiperda* was observed at 20°C.

A relevant aspect that may help to explain the differences observed on the parasitization efficiency is related to the differences among the host species studied and the structure of their egg masses (Pomari *et al* 2012). *Spodoptera eridania* eggs are laid in a single layer, thus facilitating parasitism, while eggs of *S. frugiperda* and *S. cosmioides* are laid in several layers of superposed eggs, thus demanding higher energetic expenditure from the parasitoid to parasitize the inner layers of eggs.

In conclusion, the parasitoid exhibits considerable parasitism capacity even at the extreme tested temperatures (19 and 34°C). It suggest that *T. remus* can be well adapted to environments with such thermal conditions and an alternative to control *S. eridania*, *S. cosmioides*, and *S. frugiperda,* as all of these hosts were successfully parasitized. However, it is important to emphasize that additional field studies are needed in order to propose the implementation of a biological control program using this egg parasitoid. Moreover, there is still the need to investigate several bioecological traits (dispersal capacity, for example) and the best parasitoid release strategy (number of parasitoids to be released/host egg, interval between releases) to allow for the successful use of this biological control agent in the field.

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