Laboratory Population Parameters and Field Impact of the Larval Endoparasitoid *Pseudapanteles dignus* (Hymenoptera: Braconidae) on its Host *Tuta absoluta* (Lepidoptera: Gelechiidae) in Tomato Crops in Argentina

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ABSTRACT The tomato moth, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is a key pest of tomato, *Lycopersicon esculentum* L., crops in Central and South America. At present it is dispersing rapidly in Africa and Eurasian continents as an invasive pest, threatening worldwide tomato production. *Pseudapanteles dignus* (Muesebeck) (Hymenoptera: Braconidae) is an American endoparasitoid reported as the main natural enemy of *T. absoluta* in commercial tomato. To gain knowledge of the potential role of *P. dignus* in the biological control of this pest, we determined its population parameters in laboratory and the parasitoid's impact on *T. absoluta* in the field. In laboratory, lifetime fecundity was 193 eggs per female, and longevity was 24 and 26 d for female and male, respectively. The finite rate of increase (λ) was 1.15 per female per day and the intrinsic rate of natural increase (r_m) was 0.14. The net reproductive rate (R_0) was found to be 51.2, and generation time (T) 28.8 d. The time for doubling the population (DT) was 5 d. Furthermore, field parasitism of *T. absoluta* varied between 33 and 64% in the different years studied. Population parameters estimated in this study can be considered baseline information for a mass-rearing protocol of this parasitoid. Moreover, growth rates of *P. dignus*, particularly r_m, and its impact on field populations of *T. absoluta* indicated that this parasitoid is a valuable candidate for biological control of this pest.

KEY WORDS South American tomato moth, parasitoid, life table, demographic parameter, *Lycopersicon esculentum*

The tomato moth, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is a key pest of tomato, *Lycopersicon esculentum* L. In Central and South America regions, from where it is allegedly native (Vargas 1970, Fernández and Montagne 1990, Ullé and Nakano 1994, Uchoa-Fernandes et al. 1995, Colomo et al. 2002), this pest has been reported to cause up to 70% yield reduction (Torres et al. 2002). After its first record in Spain in 2006, *T. absoluta* rapidly dispersed in Europe and is currently expanding its distribution to Africa and Asia, threatening worldwide tomato production (Desneux et al. 2010, 2011). Although chemical control is currently the primary control tactic against *T. absoluta* in tomato crops, it is quite ineffective due to the concealed (within-leaf) feeding behavior of its larval stage (Lietti et al. 2005).

T. absoluta biological control has recently gained interest in Argentina, and a number of studies came out to select potential biocontrol agents. Among them, introduced Trichogrammatidae species have been evaluated (Riquelme Virgala and Botto 2010) and the native larval ectoparasitoid *Dineulophus phtorimaeae* de Santis (Hymenoptera: Eulophidae), the predator bugs *Tupiocoris cucurbitaceous* (Spinola) (Hemiptera: Miridae), and *Zelus obscuridorsis* (Stal) (Hemiptera: Reduviidae) are currently under assessment (Luna et al. 2010, López et al. 2012, Savino et al. 2012, Speranza et al. 2014).

Other studies have dealt with the interaction between the larval parasitoid *Pseudapanteles dignus* (Muesebeck) (Hymenoptera: Braconidae) and *T. absoluta. P. dignus* is reported as the main natural enemy of this pest in commercial tomato crops (Colomo et al. 2002, Sánchez et al. 2009). It is a solitary endoparasitoid species of American distribution and a narrow host range limited to a few gelechiids (Cardona and Oatman 1971, Oatman and Platner 1989, Bennett 1995). Previous studies indicated that *P. dignus* exhibits some desirable ecological traits as an effective natural enemy of *T. absoluta* in open-field and protected tomato crops (organic and conventional) in Argentina. Among them, a seasonal synchronization with the host, an aggregative response to *T. absoluta* density at tomato leaf scale resulting in a greater risk of parasitism on pest patches of higher densities, and an instantaneous attack rate greater than the *T. absoluta* intrinsic growth rate (r_m; Sánchez et al. 2009).

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In the present study, life history traits and population parameters of *P. dignus* were determined in the laboratory together with the impact on *T. absoluta* populations under natural conditions in tomato fields, to estimate the biological control potential of this parasitoid through augmentative releases.

Materials and Methods

Insect Rearing. Host and parasitoid stock colonies were initiated from tomato leaves damaged by *T. absoluta* collected in organic farms located at the same site where the field study was conducted. They were reared in a walk-in room under constant climatic conditions (25 ± 2°C, 65 ± 5% relative humidity [RH], and a photoperiod of 14:10 [L:D] h), and to avoid inbreeding depression, both colonies were supplemented biweekly with field-collected individuals during the tomato-growing seasons.

T. absoluta larvae were placed in plastic containers (20 cm long by 12 cm wide by 5 cm deep) lined with moistened filter paper, and fed with fresh tomato leaves. Adult females were kept in white voile cages (50 cm long by 50 cm wide by 50 cm deep), fed honey and water, and provided with five to seven expanded leaves of tomato seedlings in pots as substrate for oviposition. Plants were removed every two days and emerged *T. absoluta* larvae were placed in plastic containers to initiate a new cycle, replacing food when necessary.

P. dignus colony was reared on *T. absoluta* host larvae. Once adults emerged, they were paired up (one couple per plastic cup) inside 800-ml capacity plastic cups covered with white voile on top, and fed with honey and water. Every two days, and until the female death, oviposition was allowed by offering tomato seedlings infested with host larvae. Exposed seedlings were transferred to plastic containers (20 cm long by 12 cm wide by 5 cm deep) and checked daily to monitor the formation of parasitoid cocoon and later on the emergence of adults. Newly emerged adults were paired up to initiate a new cycle.

Life Table Construction. We constructed a cohort life table of *P. dignus* by determining: l_x = proportion of initial number of individuals surviving to the beginning of each stage, where x is the stage; d_x = proportion of initial number of individuals dying during the stage interval x to $x + 1$; and q_x = per capita rate of mortality during the stage interval x to $x + 1$. In the adult stage, the variable x represents the age in days, so that all life table data including the female fecundity (female eggs per female; m_x) correspond to a daily basis.

Because *P. dignus* is a larval endoparasitoid that leaves the host at the time of pupation, various complementary stepwise trials were conducted using a destructive method based on dissections of parasitized host larvae to obtain immature survival and fecundity data. All dissections were carried out using a stereoscope microscope (SMZ 645, Nikon, Tokio, Japan).

Survivorship and Developmental Times of Immature Stages of *P. dignus*. Based on knowledge that *P. dignus* females initiate oviposition from the first day after adult emergence (Luna et al. 2007), we determined the initial number and survival (l_x) of eggs and first-instar larvae and egg developmental time, by offering first- and second-instar host larvae ($n = 300$) to 30 newly emerged and mated *P. dignus* females for oviposition, during 1 h. Thereafter, groups of 100 larvae were dissected for counting the numbers of eggs, estimating egg hatching, and egg developmental time at 24 and 48 h, and the number of first-instar larvae at 72 h.

The initial number of pupae and adults, and pupal survival was calculated indirectly. First, we determined the mean number of pupae and adults per female surviving from birth by conducting an additional trial: 10 newly emerged and mated *P. dignus* females were placed individually in plastic containers (1,000 ml) and daily supplemented with 15–20 host larvae until death. Every 24 h, host larvae were transferred individually to Petri dishes and fed fresh tomato leaves until *P. dignus* pupation. Pupae, which are usually protected inside cocoons, were checked daily until adult emergence. From the estimation of the mean fecundity (mean number of eggs per female) described below, and the average number of pupae and adults per female, we calculated the proportion of individuals surviving from birth to the beginning of pupal and adult stages and were then extrapolated to the initial cohort to complete the survival schedule. Larval and pupal developmental times were estimated as the mean time from oviposition to pupal formation subtracting the mean duration of egg stage and the mean number of days from cocoon formation to adult emergence, respectively.

In this experiment, the parasitoid larvae were followed individually until the formation of the cocoon and adult emergence; therefore, we could estimate these life history traits for each sex. Developmental times from egg to pupa, from pupa to adult, and overall from egg to adult were determined. Deviation from 1:1 adult sex ratio was tested by a Chi-square test ($P < 0.05$).

Survivorship and Longevity of Adults of *P. dignus*, and Female Reproductive Traits. To estimate female age-specific survival (l_x), age-specific fecundity (m_x; mean number of female eggs per female per day), and lifetime fecundity (total number of eggs per female), 10 newly emerged wasp females and males were randomly selected from the preceding experiment and allowed to mate for 24 h, removing males afterwards. Then, females were placed individually in plastic containers, fed honey and water, and provided with 15–20 *T. absoluta* larvae per day until death. Every day, the number of surviving females was recorded and exposed host larvae were removed from containers to estimate fecundity through host dissection. This procedure was continued until all parasitoid females died out. To facilitate the visualization of the first-instar larvae during the examination upon dissections, larvae were maintained inside the mines for 72 h to allow parasitoid egg hatching. The total number of eggs per female per day was converted to female eggs per female per day by multiplying with the sex ratio obtained at adult emergence (females / [females + males]).

Reproductive period (period between the first and last oviposition) and longevity were also observed. To estimate male survival and longevity, males ($n = 68$) emerging from cocoons obtained in the previous trial were placed individually in plastic containers, fed honey and water, and monitored daily until death.

Mean daily percentages of parasitism per female were calculated as the host larvae parasitized related to the host larvae offered, with at least one parasitoid egg or larva found in dissections.

Population Parameters. By using immature stage-specific survival (l_x) and adult age-specific survival and fecundity (m_x) schedules of the life table, the following demographic parameters were calculated (Gotelli 2001):

Finite rate of increase:

$$\lambda = e^r$$

Intrinsic rate of natural increase (r_m), calculated by iteration of the Lotka equation:

$$1 = \sum e^{-rx} l_x m_x$$

Net reproductive rate:

$$R_0 = \sum l_x m_x$$

Mean generation time:

$$T = \sum \frac{l_x m_x x}{R_0}$$

Population doubling time:

$$DT = \frac{ln2}{r_m}$$

where x is the stage or age (days), and l_x and m_x as described above.

Means and standard errors of the life table parameters were calculated using the Jacknife technique (Scheiner and Gurevitch 2001).

Field Study. The study site was located in the surroundings of La Plata, northern Buenos Aires province, Argentina (34° 56 S, 57° 59 W). This region currently constitutes the largest horticultural production area in the country. Protected tomato season comprises 10 months a year (August to May), during the warmer seasons. Host and parasitoid population densities were estimated through biweekly samplings of *T. absoluta* larvae along 3 yr in one commercial organic tomato greenhouse. Samplings were conducted from 28 August 2008 to 6 March 2009 and from 4 October 2011 to 27 January 2012 in early season tomatoes. During the second year, samplings were carried out from 13 October 2010 to 1 March 2011 in an early season tomato, and in a second season one from 1 March 2011 to 17 June 2012. The sample unit consisted of one leaflet with evidence of fresh damage. Each sampling date, leaflets of 100 randomly selected plants were taken and brought to the laboratory for further revision. The number of larvae per leaflet was recorded under binocular microscope inspection. Leaflets with *T. absoluta* larvae were placed in Petri dishes and insects were fed, *ad libitum*, with fresh tomato leaves until the formation of host pupae or *P. dignus* cocoons. Dead *T. absoluta* larvae were dissected to determine the presence of immature *P. dignus*. From these data we calculated the percentages of field parasitism as: (number of parasitized larvae / number of collected larvae) × 100.

Field impact of *P. dignus* was considered equivalent to the total losses of *T. absoluta* due to parasitism. Taking into account that percentages of field parasitism are subject to extensive error when measuring host mortality (Hawkins 2005), alternative techniques have been proposed to obtain an effective estimation of total losses due to parasitism for a given host generation derived from parasitoid emergence from field sampling (van Driesche and Taub 1983, van Driesche et al. 1991). Therefore, to determine how much mortality *P. dignus* is capable of inflicting on *T. absoluta*, we proceeded as follows. Density curves were constructed from the mean number of unparasitized and parasitized host larvae per leaflet, for each census date and crop season, and the average number of hosts and parasitoids over an intercensal period was calculated by employing the trapezoidal method (Carey 1993). The average number of individuals per leaflet of two consecutive censuses, divided by the time interval (days) between them represents the surface of a trapezoid. The sum of the trapezoids of all census dates corresponds to the area under the density curve. The areas under the host and parasitoid density curves along the crop cycle depict the population size of each species, also known as the number of insect-day (Carey 1993). Then, the fraction of the parasitoid area with respect to the host area was considered equivalent to the total losses due to parasitism.

Results

Survivorship and Developmental Times of Immature Stages of *P. dignus*. Stage-specific survival (l_x) in the laboratory gradually decreased from egg to adult emergence. Thereafter it remained constant during the next 11 d of female adult life, decreasing abruptly at older ages (Table 1). Survival of eggs and pupae was 94 and 83%, respectively. Mortality rate was higher during larval stage in which 68% of larvae reached the pupal stage. Overall immature mortality of *P. dignus* was 55%, indicating that almost a half of the initial cohort reached the adult stage.

Developmental times of *P. dignus* immature and adult stages are shown in Table 2. Dissections indicated that eggs developed in at most 24 h. Time required to complete the entire development from egg to adult was ≈22–23 d for both sexes. Superparasitism, i.e., >1 parasitoid larvae per host was 37.0% (841 out of 1,930 dissected).

Table 1. Life table of *P. dignus* females on *T. absoluta* larvae at 25 ± 2°C, 65 ± 5% RH, and a photoperiod of 14:10 (L:D) h

x	l_x	d_x	q_x	m_x	l_xm_x
Immature stage					
Egg	1.00	0.06	0.06	–	–
Larva	0.94	0.32	0.34	–	–
Pupa	0.62	0.17	0.27	–	–
Adult stage (d)					
22	0.45	0.00	0.00	8.60	3.87
23	0.45	0.00	0.00	7.25	3.27
24	0.45	0.00	0.00	9.78	4.41
25	0.45	0.00	0.00	10.80	4.86
26	0.45	0.00	0.00	11.13	5.01
27	0.45	0.00	0.00	11.90	5.36
28	0.45	0.00	0.00	10.12	4.56
29	0.45	0.00	0.00	4.68	2.11
30	0.45	0.00	0.00	6.07	2.74
31	0.45	0.00	0.00	9.02	4.06
32	0.45	0.06	0.14	6.75	3.04
33	0.39	0.00	0.00	4.13	1.60
34	0.39	0.19	0.50	3.05	1.18
35	0.19	0.06	0.33	6.89	1.33
36	0.13	0.00	0.00	8.56	1.10
37	0.13	0.00	0.00	6.79	0.87
38	0.13	0.00	0.00	4.73	0.61
39	0.13	0.00	0.00	2.66	0.34
40	0.13	0.06	0.50	6.49	0.84
41	0.06	0.00	0.00	0.00	0.00
42	0.06	0.06	1.00	0.00	0.00

In the adult stage, the variable x represents the age in days.

Table 2. Developmental time (d) of immature stages and adult longevity (d) of *P. dignus* on *T. absoluta* larvae at 25 ± 2°C, 65 ± 5% RH, and a photoperiod of 14:10 (L:D) h

	Female		Male	
	n	Mean ± SE	n	Mean ± SE
Developmental time				
Egg–Pupa	104	13.55 ± 0.20	71	13.06 ± 0.21
Pupa–Adult	98	9.15 ± 0.11	68	9.13 ± 0.15
Egg–Adult	98	22.69 ± 0.22	68	22.15 ± 0.25
Adult longevity	98	26.33 ± 1.47	68	23.65 ± 1.52

Survivorship and Longevity of Adults of *P. dignus*, and Female Reproductive Traits. Adult females had no mortality during the first 10 d of life coinciding with their higher fecundity rates. Females showed no prereproductive period, they started to lay eggs as soon as they emerged, and oviposited until the 19th day of their life span. Duration of reproductive period was 14.3 ± 0.7 d, with a mean daily oviposition rate of 8.5 ± 0.41 female eggs per female, and a lifetime fecundity of 192.4 ± 9.7 eggs per female. Sex ratio of emerging adults was 0.59, with a significant bias toward females ($\chi^2 = 5.42$; df = 1; $P < 0.05$). The age-specific percentage of parasitism curve had a similar trend to the age-specific fecundity schedule, which decreased along the female life span, and peaked at 70% around the fifth day of female life (Fig. 1).

Population Growth. The population parameters values estimated from the life table are shown in Table 3. Results suggest that under optimal laboratory conditions *P. dignus* population can increase 1.15-fold per day (λ) or at an exponential rate of 0.14 per day (r_m), and can duplicate in ≈5 d (DT); each female can multiply by 51.2 every generation (R_o), which requires ≈29 d (T).

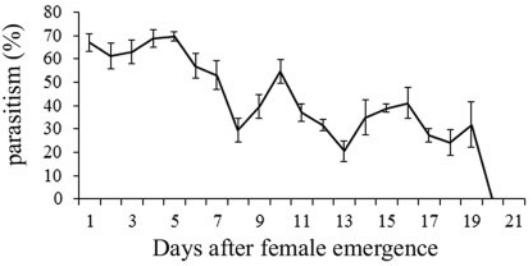

Fig. 1. Percentages of female age-specific parasitism (exposed larvae with at least one parasitoid egg or larva) of *P. dignus* on *T. absoluta* larvae at 25 ± 2°C, 65 ± 5% RH, and a photoperiod of 14:10 (L:D) h. Error bars are SEM.

Table 3. Population parameters of *P. dignus* on *T. absoluta* larvae at 25 ± 2°C, 65 ± 5% RH, and a photoperiod of 14:10 (L:D) h

Population parameters	Mean ± SE
Finite rate of increase (λ)	1.15 ± 0.0005
Intrinsic rate of natural increase(r_m)	0.14 ± 0.0001
Net reproductive rate (R_o)	51.15 ± 0.71
Generation time (T)	28.80 ± 0.12
Population doubling time (DT)	4.87 ± 0.02

Field Study. Parasitism exhibited a similar pattern in the three seasons studied, increasing throughout the cropping season synchronously with the growth of the moth population (Fig. 2a–c). *P. dignus* parasitism reached the highest value in 2010–2011 (Fig. 2b), peaking at 74% at the end of the crop cycle (June). In this season, *T. absoluta* and *P. dignus* attained densities up to 1.5 larvae per leaflet and 0.98 individuals per leaflet in March and May, respectively.

The impact of parasitism varied in the different seasons: 39.0% in 2008–2009 (Fig. 2a), 49.0% and 63.8% in 2010–2011 (early and late tomatoes, respectively; Fig.2b), and 33.2% in 2011–2012 (Fig. 2c).

Discussion

Results of the present study bring new insights into the potential population dynamics of the solitary larval endoparasitoid *P. dignus*, reared on the key pest *T. absoluta* under controlled conditions. Additionally, this research provides, for the first time, information of the seasonal pattern of parasitism on *T. absoluta* populations in tomato crops in the most important horticultural region of Argentina.

Compared with a Mexican population of *Apanteles dignus* (at present *P. dignus*) parasitizing other gelechiid species, the tomato pinworm *Keiferia lycopersicella* (Walshingham) (Cardona and Oatman 1971), our data showed that immature developmental times, adult longevity, and fecundity were higher. Although the precise reasons for these differences were not known, they could be attributed to the disparity of host species and

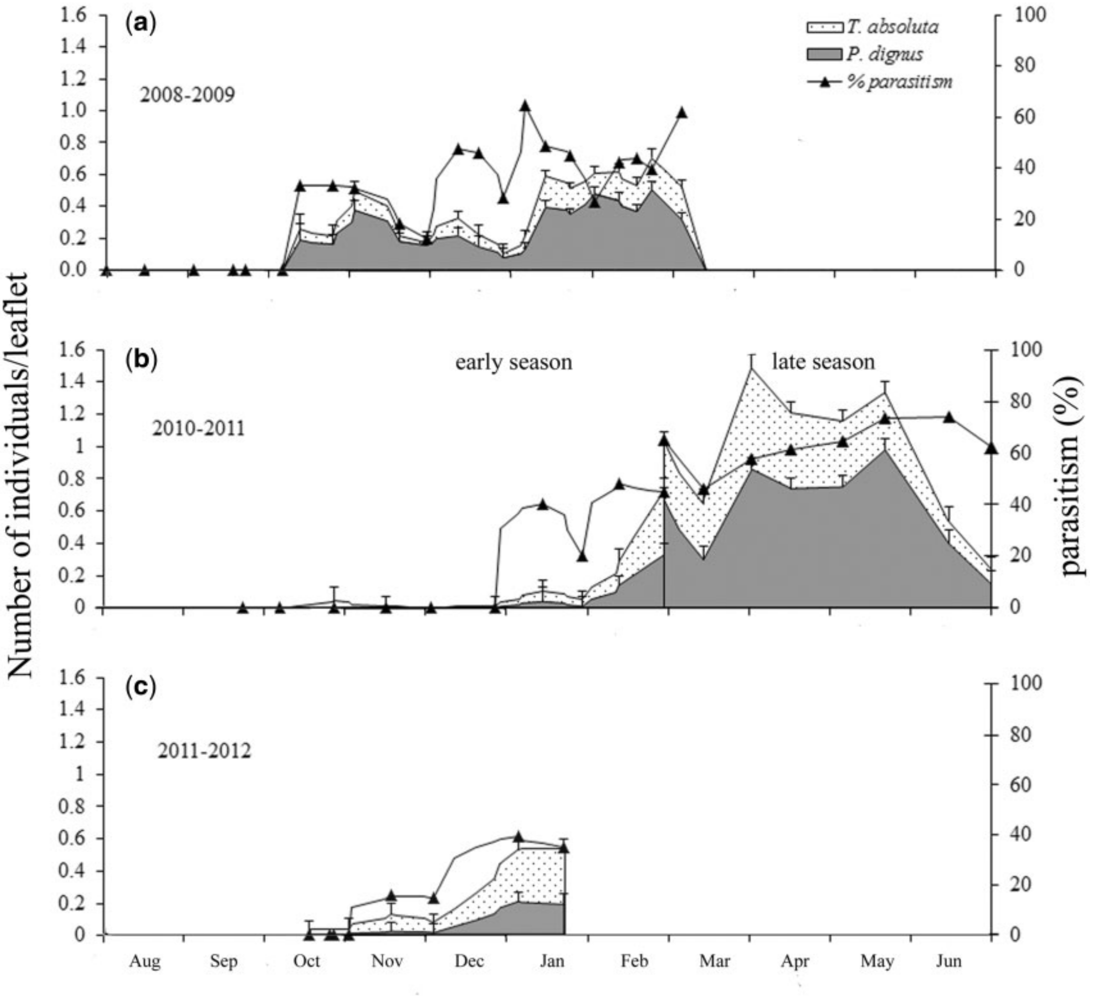

Fig. 2. Mean (± SE) densities of *P. dignus* and *T. absoluta* larvae, and percentages of parasitism in a commercial organic tomato greenhouse in the surroundings of La Plata (Argentina). (a) 2008–2009 early season tomato, (b) 2010–2011 early and late season tomatoes, (c) 2011–2012 early season tomato.

the diverse conditions of photoperiod and temperature at which both studies were conducted.

Some authors have reported that a greater proportion of males in the stock colonies of arrenotokous species of braconids (Green et al. 1982, Dannon et al. 2010) led to mass production failures in applied biological control (Luck et al. 1999). Sex proportion of *P. dignus* found in our study was biased toward females, suggesting an advantageous feature for mass rearing.

The r_m of *P. dignus* estimated in this study was similar to other braconid species. For example, *Agathis unicolor* (Schrottky) and *Agathis gibossa* (Say) showed an r_m of 0.11 and 0.16, and 0.15 and 0.19, respectively, at 24°C and 27°C, when parasitizing the potato leafminer *Phthorimaea opercullela* (Zeller) (Lepidoptera, Gelechiidae) (Odebiyi and Oatman 1977). Moreover, under the same experimental conditions to those of this study, *P. dignus* exhibited an r_m equal to that of *T. absoluta*'s ($r_m = 0.14$; Pereyra and Sánchez 2006) and an instantaneous attack rate (0.22; Luna et al. 2007) larger than the r_m of the host. According to van Lenteren and Manzaroli (1999), a parasitoid will be an effective biological control agent if, in addition to other factors, its r_m and kill rate are equal or greater than the r_m of the targeted pest.

Regarding other *T. absoluta* biological control agents, a laboratory study made by Biondi et al. (2013) on the European larval ectoparasitoid *Bracon nigricans* Szépligeti (Hymenoptera: Braconidae) determined that growth rates values were lower than those estimated in this work for *P. dignus* (r_m: 0.052, R_0: 4.44, and λ: 1.05). *B. nigricans* produces also host mortality due to host feeding (up to 70% of total mortality), a behavior that is absent in *P. dignus*.

Field percentages of parasitism of this research were in accordance with findings from Sánchez et al. (2009) who found up to 46% of parasitism of *P. dignus* on *T.*

absoluta in tomato crops without chemical control, and 17 to 26% in crops with frequent applications of pesticides. In turn, Polack (2008) reported an increase of parasitism from 25 up to 90% in the late season for greenhouse tomato in northern Buenos Aires province, Argentina.

Impact of parasitism throughout this study ranged from 33 to 49% of total mortality in the early season, and was 64% at the end of the season. These results suggest that when the tomato was cultivated over a long period, parasitism increased toward the end of the season. This could be explained by the short generation time and relatively high population growth rate of the parasitoid that would allow a numerical increase following the population growth of *T. absoluta* throughout the season.

Because parasitoid species attacking *T. absoluta*, both in its original and in the invaded distribution regions, conform a diverse group of natural enemies (Desneux et al. 2011, Luna et al. 2012, Zappalà et al. 2012), we emphasize continuing studies on these entomophages to find alternatives to chemical control to better managing this tomato pest.

In conclusion, *P. dignus* may significantly contribute toward a successful control of *T. absoluta* populations in greenhouse tomato production. Natural populations of this parasitoid should be promoted through the reduction and elimination of nonselective pesticides, along with the implementation of other management alternatives, such as conservation of habitat diversity, to promote their persistence. Furthermore, knowledge of life history traits obtained in this study will be useful to optimize *P. dignus* mass rearing for augmentative biological control against *T. absoluta*.

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