Biology of *Dineulophus phtorimaeae* (Hymenoptera: Eulophidae) and Field Interaction With *Pseudapanteles dignus* (Hymenoptera: Braconidae), Larval Parasitoids of *Tuta absoluta* (Lepidoptera: Gelechiidae) in Tomato

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ABSTRACT   Some biological characteristics of the ectoparasitoid *Dineulophus phtorimaeae* (de Santis) (Hymenoptera: Eulophidae) and field interaction with the endoparasitoid *Pseudapanteles dignus* (Muesebeck), both larval parasitoids of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), were examined. In addition, we completed the original description of *D. phtorimaeae*. Preimaginal developmental time of the ectoparasitoid was 11.17 ± 0.60 d for both sexes, and adult life span was 11.73 ± 0.92 d for females and 8.78 ± 0.93 d for males. The proportion of males to females was equal. In the field, hosts were parasitized at the third larval instar. On average, a female attacked ca. four hosts throughout her lifetime and deposited eggs in $\approx$50% of cases. The most successful female attacked six hosts, yielding a potential fecundity of $\approx$10 eggs. Host paralysis without parasitism was observed, suggesting stinging for host feeding. The daily oviposition curve is compatible with a synovigenic-type parasitoid. Our prediction stating that *D. phtorimaeae* would succeed when competing for hosts with *P. dignus* was correct, because the former species had greater parasitism rates. In the field, both *T. absoluta* parasitoids were able to coexist at leaf scale. The negative aspects of differences in feeding behavior, narrower host range (third instar), and lower fecundity of *D. phtorimaeae* would be compensated by its better attributes as natural enemy, in comparison with *P. dignus*, enabling coexistence.

KEY WORDS   *Dineulophus phtorimaeae*, *Pseudapanteles dignus*, parasitoid, coexistence, *Tuta absoluta*

Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae) is a major pest of greenhouse and open-field tomato, *Solanum lycopersicum* L., crops in South America (Fernández and Montagne 1990; Botto 1999; Ecole et al. 2000; Siqueira et al. 2000, and references therein). It has recently been introduced to Europe (Urbaneja et al. 2009, Netherlands Plant Protection Service 2009, Speranza et al. 2009). Larvae cause plant damage by mining leaves and fruit; therefore, the use of chemical pesticides is a widespread practice to control this pest. Considering the adverse effects of pesticides to human health and environment quality, it is important that alternative methods, such as biological control, are developed for incorporation into a tomato integrated pest management (IPM) program (Lewis et al. 1997, Sánchez et al. 2009).

Successful biological control programs in horticultural crops have been obtained by seasonal augmentative releases of parasitoids (Bale et al. 2008). In Argentina, *T. absoluta* has two main native larval parasitoids in tomato crops. They belong to different parasitoid guilds: the endoparasitoid *Pseudapanteles dignus* (Muesebeck) (Hymenoptera: Braconidae), which is currently under study as a moth control agent (Luna et al. 2007, Sánchez et al. 2009); and the ectoparasitoid *Dineulophus phtorimaeae* (de Santis) (Hymenoptera: Eulophidae) (de Santis 1983, Colomo et al. 2002). *P. dignus* shows some positive biological traits that make it a promising candidate for conservation biological control, seasonal augmentative releases, or both (Luna et al. 2007, Sánchez et al. 2009). *D. phtorimaeae* is less well known, with only partial morphological description (de Santis 1983) and historical reports of its presence in tomato crops from Argentina and Chile (Vargas 1970, Larraín 1986, Colomo et al. 2002).

Parasitoids are classified as koinobionts or idiobionts (Haeselbarth 1979, Askew and Shaw 1986). Koinobionts allow the host to develop beyond the stage attacked, whereas idiobionts permanently paralyze or kill the host in the stage attacked. In addition, idiobionts are relatively more generalist (i.e., have broader specific host range), have larger eggs, faster larval development, and longer adult life span, and they live in more protected sites (the majority attack

concealed hosts) than koinobionts. Furthermore, they do not elicit physiological defense mechanisms of the host, e.g., encapsulation. The majority of successful cultures, including in vitro rearings, have involved idiobionts, and, in particular, ectoparasitoids (Quicke 1997).

Multiparasitism, i.e., the use of a single host individual by two or more parasitoid species, is very common in nature (Lane et al. 2006). As a result, parasitoids can experience intra- and interspecific competition. Categorization of parasitoids in koino- and idiobionts is a practical indication useful to analyze their potential as a biological control agent as well as their ability to compete within a particular parasitoid assemblage (Mills 2006). Life history traits such as host immobilization, shorter developmental times, and higher searching abilities allow predicting that ectoparasitoid idiobionts are competitively superior to koinobionts (Hawkins 2000, Strand 2000). The study of potential coexistence of two parasitoid species on the same host and their impact on to top-down limitation of a pest population is a relevant topic in biological control.

The goals of this research were two-fold: 1) to study some general biological aspects of *D. phtorimaeae* and 2) to assess its interaction with *P. dignus* in tomato fields. Based on the hypothesis that the idiobiont *D. phtorimaeae* would be a better competitor than the koinobiont *P. dignus*, we predicted that in the field *D. phtorimaeae* would produce higher parasitism rates than the endoparasitoid *P. dignus.*

Materials and Methods

Biology of *D. phtorimaeae*. Field collections of tomato leaves with *T. absoluta* damage were made in commercial crops located in the vicinity of La Plata, a major horticultural region of Buenos Aires province, Argentina (34° 58′ S, 57° 59′ W) (Sánchez et al. 2009). Host stage attacked, preimaginal developmental time of the parasitoid, and sex ratio were determined and recorded.

Mines were dissected under a stereomicroscope to search for presence of miners and parasitoids and to observe the instar attacked. All hosts with the presence of *D. phtorimaeae* larvae were individually reared in 5-ml glass vials. To allow proper pupal formation and prevent degradation of plant material, vials were provided with one by 0.5-cm filter paper card wetted with distilled water and kept sealed. They were checked daily to correct water saturation or dryness inside. Sexes were identified at pupal stage based on dimorphic differences, such as shorter body length and a translucent area on the gaster in males, visible ≈24 h before adult emergence (de Santis 1983). Insects were kept in a walk-in-chamber at 25 ± 3°C, 70 ± 10% RH, and a photoperiod of 14:10 (L:D) h.

The specimens obtained through these collections were observed under a stereomicroscope (model SMZ 800, Nikon, Melville, NY) to describe pupal and imaginal morphology. Ten wasps of each sex were dissected in distilled water and transferred into glycerin to mea-

sure pupal and adult body sizes (length). Means and SEs were calculated as descriptive statistics. In addition, illustrations of adults of both sexes were made, because only partial visual descriptions made by de Santis (1983) were available thus far. The parasitoid preimaginal developmental time for both sexes was calculated as the mean number of days from larvae at early instars (L1 to L2) to adult emergence. The sex ratio was calculated as the total number of males/ (number of males + number of females).

For the adult stage, the following biological characteristics were recorded in the laboratory: longevity (both sexes), oviposition behavior (host feeding and egg laying), daily oviposition rate, total fecundity, and mean brood size. Newly emerged adults were paired and placed in 5-ml glass vials containing a 1- by 0.5-cm filter paper card with honey solution (50%). Couples were allowed to mate for 24 h, and then mated females were relocated to 60-ml vials and provided with five third-instar host larvae from a laboratory colony (see below). Vials were monitored daily and batches of five hosts were replaced when signs of parasitoid attack were detected, until each female died. Males were kept apart, provided with honey solution until death.

Hosts were produced by rearing a *T. absoluta* colony as reported previously (Luna et al. 2007). All hosts used during the experiment were already installed in mines.

To determine host parasitoid attack (host paralysis or presence of *D. phtorimaeae* eggs or larvae) individuals were checked under a stereomicroscope. All parasitized hosts were transferred to 5-ml vials until parasitoid pupa formation. Mean adult longevity of both sexes was measured as the mean number of days wasps lived, from adult emergence to death.

Fecundity was measured by two means: 1) lifetime fecundity, as the mean number of eggs per female wasp; and 2) potential fecundity (as in Zaviezo and Mills 1999), by multiplying the average number of eggs laid per host by each female by the number of hosts parasitized by the most successful female.

Life history data are presented as mean ± SE. Differences in preimaginal developmental time and adult longevity between sexes of *D. phtorimaeae* were analyzed by one-way analysis of variance (ANOVA). Before analysis, data were checked for normality and homogeneity of variances. When ANOVA assumptions were violated, a Kruskal–Wallis test was used. Differences were considered significant at $P \leq 0.05$. Analyses were performed with Statistica 7.0 (StatSoft 2007).

Field Interaction With *P. dignus*. To assess interaction between *D. phtorimaeae* and *P. dignus* in the field, we carried out a sampling of both parasitoid species in an organic open-field tomato crop in the study area. The influence of the spatial scale of analysis on patterns of parasitism has been widely discussed previously (Heads and Lawton 1983, Lill 1998). A previous study indicated that *P. dignus* concentrates on tomato crops with greater host density but displays a density-independent rate of parasitism in relation to *T. absoluta* larval density, at the leaf spatial scale

(Sánchez et al. 2009). Thus, we analyzed the interaction between both parasitoids at that spatial scale, and established groups according to host density recorded (from one to the maximum number of larvae found) per leaf.

The sampling took place in late March 2004, when host and parasitoid populations were conspicuously settled in crops. Samples consisted of the third apical part (containing approximately eight expanded leaves) of 20 plants, randomly selected. In the laboratory, plants were sorted in all component leaves and then viewed under a stereomicroscope to search for *T. absoluta* larvae and for the ectoparasitoid (egg, larva, or pupa). To find the endoparasitoid, living host larvae were placed individually in petri dishes, provided with fresh tomato leaves as food, and maintained in a walk-in rearing chamber at $25 \pm 2°C$ temperature, 70% RH, and a photoperiod of 14:10 (L:D) h until *P. dignus* cocoon formation. Dead hosts were dissected to check whether they were parasitized by the endoparasitoid (egg and larva).

The number of *T. absoluta* larvae and the number of ecto- and endoparasitoids per leaf were recorded. The proportions of parasitized *T. absoluta* for each parasitoid species, and for both species in the same leaf, were estimated as the number of parasitized larvae/ total number of hosts collected. Proportions were averaged by each host density group and arcsine transformed for further analyses.

The differences in mean proportions of parasitism (response variable) by each parasitoid species, occurring alone or together in the same leaf (categorical independent variable with three categories: *P. dignus* only, *D. phtorimaeae* only, or both), at each host density category (continuous independent variable) could not be analyzed by a two-way ANOVA due to non-normality of data. One-way analysis of covariance for the same response variable and using the number of parasitoids found per leaf (*P. dignus*, *D. phtorimaeae*, or both) as a categorical independent variable and the host density as a covariate (more than one larva per leaf) could not be used either because the categorical variable slopes were heterogeneous (Gotelli and Ellison 2004). Thus, we evaluated the response variable for each host density group separately, using one-way ANOVA (or Kruskal–Wallis when ANOVA assumptions could not be corrected with transformations). Additionally, we examined the relationship between mean total proportions of parasitism by each single species (occurring alone or together with the other parasitoid in the same leaf) by linear regressions. The null hypothesis was that the proportion of parasitism by each species does not vary with host density. Analyses were performed with Statistica 7.0 (StatSoft 2007), and a significance level of $P \leq 0.05$ was chosen for all statistical analyses.

Results

Biology of *D. phtorimaeae*. Body size (length) was 2.28 ± 0.09 mm ($n = 47$) for the pupal stage, 1.69 ± 0.14 mm ($n = 10$) for the adult male, and 2.17 ± 0.13
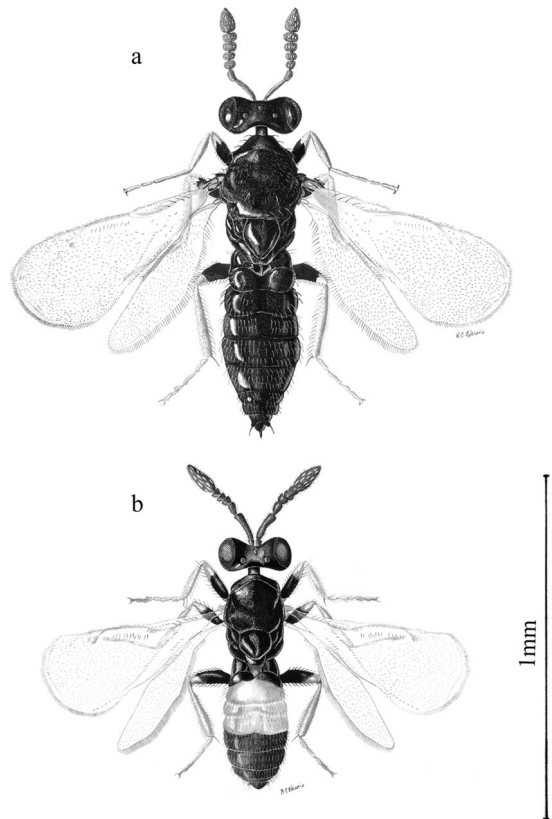

Fig. 1. *D. phtorimaeae* adult female (a) and male (b).

mm ($n = 10$) for females (Fig. 1). The latter value is larger than that described previously (de Santis 1983). Sexual dimorphism was noted at pupal stage: males can be distinguished 24 h before adult emergence by the translucent area on the gaster, a characteristic described for the imago (de Santis 1983).

Preimaginal developmental time was 11 d for both sexes ($H = 0.31$, df = 1, $P = 0.57$; $n = 47$) (Table 1). Adult longevity differed significantly between sexes, being longer for females ($F = 4.45$; df = 1, 34; $P = 0.04$).

Table 1. Life history traits of *D. phtorimaeae*, a larval ecto-parasitoid of *T. absoluta*

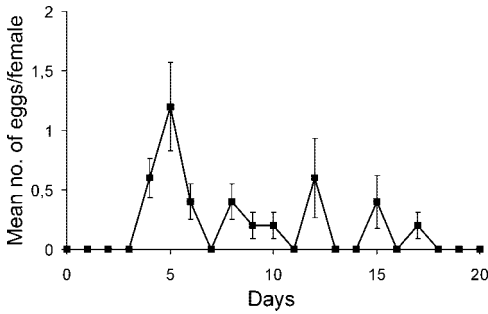| Trait	Value
Preimaginal developmental time (mean ± SE, d)	
Female	11.06 ± 0.38
Male	11.29 ± 0.81
Total	11.17 ± 0.60
Adult longevity (mean ± SE, d)	
Female	11.73 ± 0.92
Male	8.78 ± 0.93
Sex ratio (no. males/no. males + no. females) = 0.51 ($n = 48$)	
Reproductive behavior (mean ± SE no.)	
Paralyzed hosts/female ($n = 13$)	2.00 ± 0.60
Parasitized hosts/female ($n = 9$)	1.61 ± 0.60
Potential fecundity (eggs/female) ($n = 9$)	9.69 ± 3.61

Fig. 2. Daily number of eggs (mean ± SE) oviposited over the lifetime of *D. phtorimaeae* females with a *T. absoluta* larval density of five per day.

The proportion of sexes was equal under field conditions (*n* = 48).

D. phtorimaeae larval morphology was hymenopteriform. All parasitized host larvae collected in the field and brought to the laboratory were late larvae (mainly third instar), and all had only a single parasitoid larva (*n* = 122).

Thirteen of 24 coupled *D. phtorimaeae* attacked hosts, and nine of those 13 *D. phtorimaeae* effectively parasitized *T. absoluta* larvae. All of them showed symptoms of permanent paralysis and could be distinguished from active larvae by their yellowish coloration and lack of mobility. The host larvae died within 24 h after the parasitoids began to feed. Some paralyzed hosts lacked a *D. phtorimaeae* egg, an indication of nonconcurrent host feeding. On average, a female attacked four hosts throughout her lifetime and deposited eggs in ≈50% of the cases. The number of hosts attacked by the most successful female was six, yielding a potential fecundity of ≈10 eggs (Table 1). Only one individual parasitoid per host developed effectively, although up to two *D. phtorimaeae* eggs were observed on some hosts. Females frequently entered the mines to attack *T. absoluta* larvae and failed to parasitize moth larvae outside tomato leaves. Pleiotropism of hatched larvae on paralyzed hosts was observed.

The first oviposition event took place 4 d after the first batch of hosts was offered and the maximal daily mean of oviposition rate was 1.2 hosts, at the fifth day of female life. The shape of the oviposition curve showed a synovigenic-type parasitoid behavior (Fig. 2).

Evidence for Parasitoid Guild Interaction. In total, 160 leaves were observed, yielding 324 *T. absoluta* larvae in 97 leaves. In total, both parasitoid species attacked ≈45% of *T. absoluta* larvae; 20% were affected by the ectoparasitoid and 23.34% by the endoparasitoid. We recorded six groups of parasitized host densities at leaf spatial scale (1, 2, 3, 4–6, 7–10, and 12–16 larvae per leaf). The range of host densities agreed with those reported for organic tomato crops in the region (Sánchez et al. 2009).

Differences in percentages of parasitism among categories were found at a density of one host per leaf

(*H* = 7.70, df = 1, *P* = 0.005; *n* = 64), with *P. dignus* parasitism higher than that of *D. phtorimaeae* (Fig. 3a). We also found that parasitism due to both species in the same leaf, at a density of four to six larvae per leaf, was significantly greater than those caused by each parasitoid alone (*F* = 9.04, df = 2, *P* = 0.002) (Fig. 3d). However, at most host densities there were no differences in percentages of parasitism among categories (two hosts per leaf: *H* = 5.65, df = 2, *P* = 0.06 [*n* = 12]; three hosts per leaf: *H* = 3.01, df = 2, *P* = 0.22 [*n* = 11]; and 7–10 hosts per leaf: *H* = 1.97, df = 2, *P* = 0.37 [*n* = 8]) (Fig. 3b, c, and e). It also was observed that at the host density category >10 hosts per leaf, parasitism always involved both species (Fig. 3f). When the proportion of parasitism by each single species was discriminated in the both species in the same leaf category across the host densities (Fig. 3b–f), we observed that the ectoparasitoid increased its percentage of parasitism of *T. absoluta* with respect to *P. dignus*, as the host density increased, attaining values as high as 85–95%.

Regression analyses revealed that total mean proportion of parasitism by *D. phtorimaeae* increased significantly with host density, whereas that caused by *P. dignus* showed a decreasing pattern, although the slope was not significant in the latter case (Table 2).

Discussion

The preimaginal and imaginal morphological traits of *D. phtorimaeae* reported in this article expand the original descriptions made by Blanchard (1939) and de Santis (1983).

D. phtorimaeae exhibits promising traits to be a successful biocontrol agent. This study provides evidence that it can immobilize hosts permanently, in the presence or absence of oviposition. A relatively faster preimaginal developmental time for both sexes and a slightly longer adult life span confer a moderate short-lived generation of ≈23 d, compared with *P. dignus* (≈36 d; Luna et al. 2007).

In the field, *D. phtorimaeae* can be responsible for ≈30% parasitism of its host, as demonstrated in this study and reported previously (Larraín 1986, Colomo et al. 2002), and its attack rates can increase with host density increment. An extra benefit can be obtained by host feeding, which causes additional host mortality and prevents consumption of foliage (Briggs 1993, Jervis and Kidd 1999). However, the amount of *T. absoluta* mortality by host feeding in the field was not estimated in this study.

Relatively low *D. phtorimaeae* fecundity can be related to synovigeny, a predominant egg maturation pattern among parasitoid wasps (Jervis et al. 2001), because this results in energetically expensive production of eggs with large quantities of yolk. Host feeding can provide those nutrients but is another costly and time-consuming process that can also limit the number of progeny (Rivero and West 2005). Although high fecundity is an expected positive life trait for an efficient biological control agent, there are
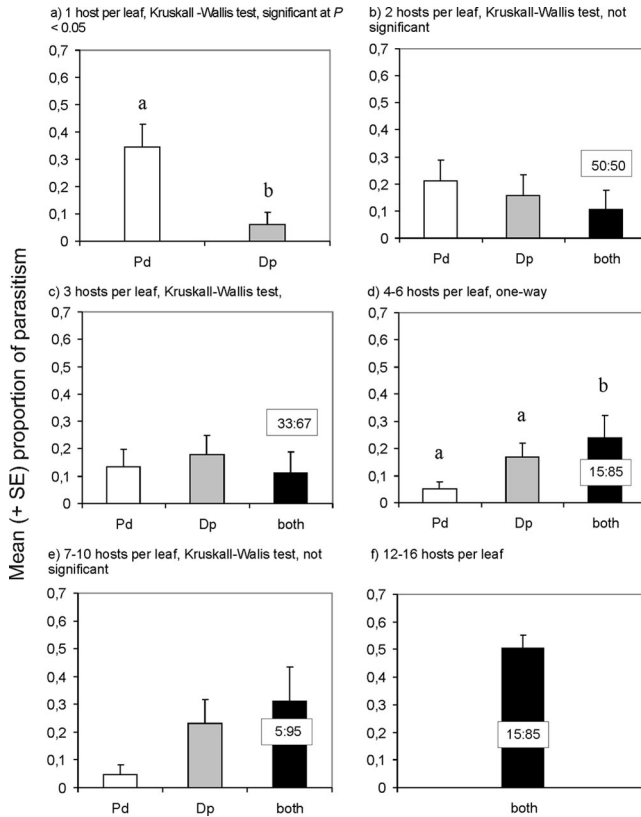
Fig. 3. Mean (+SE) proportions of field-parasitized *T. absoluta* larvae by two parasitoid species at six different host densities (La Plata, Buenos Aires, Argentina). Pd, *P. dignus* alone in a leaf; Dp, *D. phtorimaeae* alone in a leaf; and Both, two species in the same leaf. Significant differences are given by different letters. Parasitism ratios of *P. dignus* versus *D. phtorimaeae* are indicated in the box.

reports of successful agents with similar oviposition rates to *D. phtorimaeae,* such as the bethylid *Prorops nasuta* Waterston (Infante et al. 2005), with 4.3 progeny per female; the eulophids *Eulophus pennicornis* (Nees), *Hyssopus pallidus* (Askew), and *Euplectrus maternus* Bhatnagar, with 1.5 and 14 hosts per female and 22.2 eggs per female, respectively (Marris and Edwards 1995, Zaviezo and Mills 1999, Muniappan et al. 2004); and for the ichneumonid *Mastrus ridibundus* Gravenhorst, with 0.4–0.9 hosts per day (Bezemer and Mills 2001).

Our prediction stating that *D. phtorimaeae* would succeed when competing for hosts with *P. dignus* was correct; indeed, we registered higher *D. phtorimaeae* parasitism. Both parasitoids can coexist at the host

densities recorded in the field and also produce higher parasitism rates than those reported for *P. dignus* when it occurred alone (Sánchez et al. 2009).

Modeling results of host-parasitoid interactions (Lane et al. 2006) indicated that a limited fecundity of one species does not inevitably reduce the potential for coexistence, provided one is more efficient and the other more fecund. Also, different host density levels and host niche differentiation contribute to multiple parasitoid species coexistence (Briggs 1993, Mills 2006). All these factors seem to occur in the *P. dignus–D. phtorimaeae–T. absoluta* system.

Interspecific competition in primary parasitoids has been explained by competitive exclusion and coexistence (Briggs 1993, Ueno 1999, Collier and Hunter 2001, Collier et al. 2007, Mills 2006). Mechanisms involved in competitive interaction of dual parasitoid species at immature stages are as follows: 1) interference, with both larvae in the same host, including multiparasitism and intraguild predation via killing competitors, ovicide, and host feeding; and 2) exploitation, when earlier-attacking parasitoids reduce host density for the second species. There is also the potential for adult competition via mutual interference by females searching for hosts and mechanisms deal-

Table 2. Regression analyses of total proportion of *T. absoluta* parasitized by *P. dignus* and *D. phtorimaeae*, occurring alone or both in the same leaf, on six host densities per leaf (1, 2, 3, 4–6, 7–10, and 12–16)

Species	Slope ± SE	R^2	F	df	P
D. phtorimaeae	0.32 ± 0.10	0.10	10.74	1, 95	0.02*
P. dignus	−0.13 ± 0.10	0.02	1.67	1, 95	0.20

* Significant differences at $P < 0.05$.

ing with spatial and temporal heterogeneity on host resources (Hawkins 2000).

The mechanisms involved in the competence between *P. dignus* and *D. phtorimaeae* are thought to be mainly via interference, although exploitation deserves to be further explored, because *P. dignus* needs healthy hosts in which to oviposit (Larraín 1986, Luna et al., 2007, Sánchez et al. 2009). According to Mills (2006), despite theoretical predictions of competitive exclusion, field data indicate that multiple natural enemy coexist on shared hosts, at least on a seasonal basis.

In the current study, two effective natural enemies of *T. absoluta*, a key pest in South America, have been identified. This research documents the potential importance of two native parasitoids for the development of biological control programs for *T. absoluta*, and demonstrates how two competing species with complementary combinations of life history traits can be compatible. This type of information is also critically important if these wasps are to be considered for importation into Europe, where *T. absoluta* has recently been introduced, or elsewhere.

Acknowledgments

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