

Possible effects of inter-specific competition on the coexistence of two parasitoid species: *Trichogramma brassicae* Bezdenko and *Chelonus oculator* (F.) (Hymenoptera: Trichogrammatidae, Braconidae)

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Abstract. Insect parasitoids have been widely studied, particularly due to their ecological implications through the study of the special relationships observed among this kind of species, as well as to their expression in mathematical models. However, there are still scarce studies on parasitoid relationships and their expression in more realistic mathematical models. The present work is aimed at deepening into competition relationships among parasitoids. Bearing this purpose in mind, the system shaped by two parasitoids was chosen: *Trichogramma brassicae* (idiobiont egg parasitoid) and *Chelonus oculator* (koinobiont egg-larval parasitoid). Both species compete against each other for the same host species (Lepidoptera). The results obtained in the laboratory point out that *T. brassicae* may be considered a better competitor than *Ch. oculator*. This is the result of the extrinsic competition due to the substances injected by the female during parasitization. However, our results show this classification into better and worse competitors inaccurate. Thus, these interspecific competition influences are detrimental to both parasitoid species. This is the first time that the effect of this competition is mentioned regarding parasitoid functional response. Our results and their ecological implications are reported and discussed.

1. Introduction

The natural enemies of terrestrial arthropods include entomophages (predators and parasitoids) and entomopathogens (van Driesche et al. 2007). These play an essential role in the regulation of the populations of arthropods in non-natural ecosystems such as agrosystems (Hawkins and Cornell 1994, van Driesche et al. 2007) and, particularly, in their application in biological control methods (van Driesche et al. 2007). It has been attempted to extend the foregoing to the regulation of natural ecosystems or to some applications within them (Berryman et al. 1987, Headrick and Goeden 2001, Hoddle 2004). However, the main role of natural enemies in these ecosystems does not seem so clear, perhaps due to the complexity of the ecological community, as well as to other factors (Hunter and Prince 1992, Rosenheim 1998, Nehler 1999), when compared to the simplicity of agricultural systems (Hawkins et al. 1999).

Of parasitoid groups, the Parasitica section of Hymenoptera is enormously successful evolutionarily. More than 100,000 species of these wasps have been named and the total number of species has been estimated at over a million, although not all of the Parasitica are parasitoids. Furthermore, there has been a great deal of research on these species over the last 100 years (Quicke 1997, Gordh et al. 1999, Wajnberg et al. 2008).

Two life-history strategies exist among parasitoid wasps; idiobionts, where the host does not grow during the development of the parasitoid larvae and koinobionts where the host continues to grow during parasitoid development (Askev and Shaw 1986). In idiobionts the female wasp uses its ovipositor to sting and kill or immobilize the host. The female's progeny thus have to develop on a fixed amount of food. Idiobionts seem to be the evolutionarily older and less specialized. Most idiobiont species are ectoparasitoids of protected hosts inside the host plant or endoparasitoids. In koinobionts, the host is not killed or immobilized and continues to grow after the female wasp oviposits. The progeny are thus not restricted to the original amount of food. These species tend to attack unprotected or scarcely-protected hosts and most are endoparasitoids. They appear to be an evolutionarily more recent group. However, there is no general agreement regarding their origin (Laurenne 2008). These two strategies have received considerable attention (Gauld and Bolton 1996, Vinson 1998, Pennacchio and Strand 2006).

The species in the genus *Chelonus* (Cheloninae subfamily) constitute a wide group within the Braconidae family (Ichemonoidea superfamily). Over 700 species have been described worldwide (Shaw and Huddleston 1991), including 180 Palaearctic species (Tobias 1975). All Cheloninae species are egg-larval Lepidoptera solitary koinobiont en-

doparasitoids. Females oviposit inside the host egg and subsequently, at the beginning of the third larval instar, the parasitoid leaves it to become a pupa (Gauld and Bolton 1996, Garcia-Martín et al. 2005).

The behaviour in host selection for the species in the *Chelonus* genus shows that the scales left by host females during oviposition contain substances acting as kairomones (Vinson 1976, Chiri and Legner 1982). It must be pointed out that the kairomones in the scales play a very important role in the search of hosts by species (egg parasitoids) in the genus *Trichogramma* (Vinson 1976, Cabello 1985). However, *Chelonus* species are not specific regarding the response to the kairomones in scales. On one hand, this represents an adaptive advantage, as it allows them to exploit more abundant hosts satisfactorily in a given location. However, this behaviour also entails a disadvantage, as it reduces its effectiveness due to increased search time, which can be reduced with an adaptation process (i.e., learning) (Chiri and Legner 1986). When the *Chelonus* female contacts a new host, the chemical stimuli it perceives from the host by means of antennae are very important (Vinson 1976). Subsequently, when it inserts its ovipositor, the chemoreceptors in the ovipositor may also play an important role in host acceptance, as found in *Chelonus* sp. nr. *curvamaculatus* (Kainoh and Brown 1994). The last process in the host-parasitoid relationship is the host suitability for development of parasitoid progeny, which involves—in koinobionts but not in idiobionts—synchronizing and adapting the development of both elements. This was reviewed for the Cheloninae subfamily by Jones (1996).

The family Trichogrammatidae comprises 63 genera within the superfamily Chalcidoidea (Nagarkatti and Nagaraja 1977). All the *Trichogramma* species, very little insects (0.2–1.5 mm), are either solitary or gregarious idiobiont endoparasitoids, mainly Lepidopteran but also Dipteran, Coleopteran, Neuropteran and Hymenopteran eggs; their development takes place inside the host egg (Quicke 1997, Pennacchio and Strand 2006).

Unlike *Chelonus*, greater knowledge is available on the behaviour of the *Trichogramma* species in host selection and acceptance due to the higher number of works. Thus, the classical sequential behaviour for host-habitat and host location, host acceptance, and host suitability—typical of entomophagous insects (Doutt 1984)—was observed in *T. pretiosum* by Morrison and Lewis (1981). In the location of the host's habitat the plant was found to influence the activity and parasitization of several *Trichogramma* species due to the volatile substances of the plant (Cabello and Vargas 1985, Colazza et al. 2010). At the same time, for the location of the host in its habitat, the scales left by Lepidoptera females upon oviposition stimulate this searching activity (Lewis et al., 1972, Cabello and Vargas, 1985, Colazza et al. 2010), as already mentioned for the *Chelonus* species. However, adults in some *Trichogramma* species have been reported to be attracted or retained by the sexual pheromones of their hosts (Lewis et al. 1982, Noldus et al. 1991, Fatouros

et al. 2008), anti-sexual pheromones (Fatouros et al. 2005) in some cases after a learning process (McGregor and Henderson 1998). This may be related to phoretic dispersion (Fatouros et al. 2005), as observed in other groups of parasitoid species (Clausen 1976). This involves a reduction of the searching mechanism of the host egg, as well as the time employed by *Trichogramma* adult females, thus assuring greater offspring success through their dispersion.

After host-egg location by *Trichogramma* females, their behaviour can be divided into several stages: a) movements over the substrate and visual attraction by the small objects on the surface; b) inspection of the egg by means of their antennae; c) ovipositor insertion; and d) egg oviposition (Klomp and Teerink 1962, Voegele et al. 1974, Hohmann et al. 1988). The parasitization of the host egg depends on its acceptance, which in turn depends on its species and age, as well as on the existence of previous parasitization (Benoit and Voegele 1979, Houseweart et al. 1982, Pak and Oatman 1982). In turn, host-egg fertilization seems to have no influence on parasitoid development and emergence (Makeeva 2006).

According to that previously reported for the features of idiobionts and koinobionts of parasitoids which compete for Lepidopteran eggs in natural conditions, the present work is aimed at giving an insight into the relevance of idio/koinobiont difference. With this purpose, an egg idiobiont parasitoid (*T. brassicae*) and an egg-larval koinobiont parasitoid (*Ch. oculator*) were used.

2. Materials and methods

The insects used in the different bioassays (*Ephestيا kuehniella*, *Trichogramma brassicae* and *Chelonus oculator*) come from populations kept in the Applied Entomology Laboratory at the University of Almeria, according to the methodology proposed by Rodriguez et al. (1988a,b) Cabello (1985) and Cabello et al. (2005). Both species of parasitoids were reared in *E. kuehniella*.

2.1 *T. brassicae* and *Ch. oculator* competition

Test design was completely random, with 5 treatments: parasitization by each of the used species (*Ch. oculator* and *T. brassicae*) separately, parasitization by one of them and subsequently the other, apart from the control group (no parasitization). Four repetitions were performed in each treatment, each of them consisting on a batch of 50 new hosts.

48-hour-old adult females of each parasitoid were used for testing. They had previous experience in the parasitization of the eggs of the selected host. The parasitization containers used were glass vials (7.0 cm × 0.9 cm) The wasps were kept in a glass vial and an egg card (5.0 cm × 0.9 cm) was added that contained 50 host eggs and some honey:water (1:1) as a food source for the wasps. One hour was used for parasitization for each species, using one female of *Ch. oculator* or 25–30 females of *T. brassicae* per each cardboard

containing 50 host eggs. In case of sequential parasitization by each of the assayed species, the eggs were exposed the afore-reported time (1 h). The females were subsequently removed and the host eggs were immediately exposed to another kind of parasitoid also for 1 hour. The test was performed at $25\pm 2^\circ\text{C}$ and 60-80% R.H. Along these periods of exposure to parasitization, the containers were observed under a stereoscopic microscope so as to assure that eggs were accepted and parasitized by the females, both in treatments with one only species and in sequential parasitization. After that, the cardboards containing the host eggs were evolved under the afore-reported conditions. The percentages of dead and parasitized host eggs —as well as the percentage of adults of the 3 species which eventually emerged— were subjected to GLM analysis and the average values were compared by Tukey's test ($P = 0.05$) by means of the statistical software PASW version 18 (SPSS 2009).

2.2 Functional response of *T. brassicae*

Two bioassays were carried out. The first determined the functional response of *T. brassicae* at 20°C , and the second at 30°C . Egg hosts were used in both testing groups: *E. kuehniella*, less than 24-hours-old, obtained from populations maintained in laboratory and adults of *T. brassicae*, less than 48-hours-old since the emergence of the egg host, but with no previous parasitization experience, also obtained from laboratory cultures. The reported methodology was followed in all cases.

The adults of *T. brassicae* were obtained by isolating parasitized eggs of *E. kuehniella* from the laboratory cultures. This was performed by removing them with a wet fine brush (no. 0). These eggs were individually placed in glass vials covered with cotton and a water-honey (1:1) drop, and subsequently evolved up to the emergence of adults. Upon emergence, their sex was determined and couples were formed (1male + 1 female) and the females were used for testing.

For each test (20 and 30°C), the experimental design was completely randomized with only one factor: density of host egg at eight levels: 10, 20, 30, 40, 50, 60, 70 and 90. These eggs were adhered by means of a wet brush to $5.0\text{ cm} \times 0.9\text{ cm}$ cardboards, in rows and columns separated 2 mm. The number of repetitions was variable for each level of treatment. The minimum value was 10. Each of the repetitions consisted in an adult and mated female of *T. brassicae*.

Every test was performed at either 20 or $30\pm 2^\circ\text{C}$, 60-80% RH and 18:6 hours of light:dark. The exposure time of hosts to parasitoids was 24 hours. The adults were subsequently removed and the cardboards were evolved up to offspring emergence. The reported data were parasitized eggs, emerged host larvae and collapsed eggs.

After adjustments of the functional response, data were subjected to two kinds of statistical analysis. Firstly, the significance of the density factor was determined by GLM analysis and the average values were compared by Tukey's

test ($P = 0.05$) by means of the statistical software PASW version 18 (SPSS 2009).

Second, the three equations of functional response (types I, II and III) were subsequently adjusted for *T. brassicae*, according to the following expressions (Cabello et al. 2007, Garcia-Martin et al. 2008):

$$\text{Type I} \quad N_a = N_t [1 - \exp(-a'TP_t)]$$

$$\text{Type II} \quad N_a = N_t \left[1 - \exp\left(-\frac{a'TP_t}{1 + a'T_h N_t}\right) \right]$$

$$\text{Type III} \quad N_a = N_t \left[1 - \exp\left(-\frac{\alpha TN_t P_t}{1 + \alpha T_h N_t + \alpha T_h N_t^2}\right) \right]$$

where N_a is the number of parasitized hosts; N_t is the density of the host or prey; a' is the instantaneous search rate (equivalent to Nicholson-Bailey's "area of discovery": $a = a'T$, days⁻¹); T is the total available search time (days); P_t is the number of parasitoids; T_h is the host-manipulation time; and α is parasitoid mortality potential.

The adjustments mentioned so far were performed by means of the software Tablecurve 2D, version 5.0 (Jandel Scientific 1994). The corrected Akaike information criterion (AIC_c) was used to choose the best adjustment model, as it provides better statistical accuracy for comparisons between models than the regression coefficient (r^2) (Motulsky and Christopoulos 2003). However, the latter was calculated to determine the goodness of each performed adjustment.

2.3 Effect of competition on the functional response of *T. brassicae*

Two trials were completed at 20 and 30°C . A split-plot design was used in each one, with a principal factor: density of host eggs, at eight levels: 10 (5+5), 20 (10+10), 30 (15+15), 40 (20+20), 50 (25+25), 60 (30+30), 70 (35+35) and 90 (45+45) and a secondary factor: interspecific competition, at two levels: parasitisation or not by the other parasitoid species, *Ch. oculator*.

The material used includes eggs of *E. kuehniella* (less than 24-hours-old). The adults of both *Ch. oculator* and *T. brassicae* were obtained from laboratory populations, as indicated.

For previous parasitization, half of the eggs in each density (5, 10, 15, 20, 25, 30, 35 and 45 eggs) were adhered by means of a wet brush to cardboards and they were offering an experienced, previously-copulated female of *Ch. oculator*. After five hours, the cardboards were removed and the corresponding densities were completed by adhering new host eggs by means of a wet brush. These eggs were placed in rows paired with the previous ones. The cardboards were finally used in the test, as indicated above.

Likewise, the remaining conditions were 60-80% RH and 16:8 hours of light:dark. The registered data were the same as those registered in previous tests, in the functional response of *T. brassicae*. However, there was one only ex-

Table 1. Average percentage of adults emergency from host eggs (*Ephestia kuehniella*) in parasitoid competition: *Chelonus oculator* and *Trichogramma brassicae*, in laboratory conditions ($25\pm 2^{\circ}\text{C}$; 60-80% H.R. and 16:8 hours L:D) (Values in columns, followed by the same letter, does not present significant differences at $P = 0.05$).

Treatment	Mortality (%)	Parasitism (%)	percentage of adults' emergency		
			<i>E. kuehniella</i>	<i>T. brassicae</i>	<i>Ch. oculator</i>
Control	7.02a	-	92.98a	-	-
<i>C. oculator</i>	94.66b	84.40c	5.34b	-	84.40b
<i>T. brassicae</i>	91.39b	82.28bc	8.61b	82.28c	-
<i>Ch. oculator</i> + <i>T. brassicae</i>	97.83b	66.22b	2.17b	58.61b	7.61a
<i>T. brassicae</i> + <i>Ch. oculator</i>	91.64b	35.58a	8.36b	26.85a	8.73a

Table 2. Percentage of parasitized *Ephestia kuehniella* eggs by *Trichogramma brassicae* females according to host density, temperature and interspecific competition, under laboratory condition ($25\pm 2^{\circ}\text{C}$; 60-80% R.H. and 16:8 hours L:D) (Between parentheses host eggs that were exposed or not previously to parasitism by *Ch. oculator*) (Values, in columns, followed by the same letter do not differ significantly at $P = 0.05$).

Egg density	Without previous parasitization		Egg density	With previous parasitization	
	20 °C	30 °C		20 °C	30 °C
10	68.00b	92.00d	10 (5+5)	78.00c	91.00f
20	67.00b	82.50cd	20 (10+10)	68.00bc	74.00de
30	64.67b	74.33bc	30 (15+15)	68.33bc	80.00e
40	55.75ab	78.75cd	40 (20+20)	71.00bc	67.25cd
50	55.80ab	74.60bc	50 (25+25)	59.4abc	68.20cd
60	55.33ab	71.17bc	60 (30+30)	56.5abc	61.17bc
70	65.14b	60.14ab	70 (35+35)	51.86ab	56.57ab
90	45.22a	52.44a	90 (45+45)	40.33a	49.89a

ception: the emerged larvae of *E. kuehniella* were transferred into a developmental container (100 ml) fed on a flour-yeast-germ diet and evolved up to adult emergence. This was aimed at confirming *Ch. oculator* parasitization.

The values of the total number of host eggs parasitized by *T. brassicae*, in each test (20 and 30°C) were subjected to the general linear model (GLM) procedure, followed by Tukey's test ($P = 0.05$) using statistical software PASW v. 18 (SPSS 2009). Finally, the values of the number of parasitized eggs were adjusted to the equations type I, II and III according to the previously-described methodology by means of the software Tablecurve 2D, version 5.0 (Jandel Scientific, 1994). Likewise, the best adjustment model was established by the lowest value in the AIC_c parameter.

3. Results

3.1 Competition between *T. brassicae* and *Ch. oculator*

The mortality, parasitism and adult emergence obtained in the competition trial between *C. oculator* and *T. brassicae* under laboratory conditions are shown in Table 1. The treatments showed highly significant effects in the analyses of variance on the total percentage of mortality ($F=274.99$, $df=4$, $P<0.01$), percentage of parasitism ($F=34.32$, $df=3$, $P<0.01$), emerged *T. brassicae* adults ($F=16.50$, $df=2$, $P<0.01$), emerged *Ch. oculator* adults ($F=92.73$, $df=2$, $P<0.01$) and emerged *E. kuehniella* adults ($F=274.99$, $df=4$, $P<0.01$). Without taking the control group into account, no significant differences were observed in the total mortality in

the treatments corresponding to each parasitoid species either separately or sequentially. This seems to indicate that, under test conditions, none of the assayed parasitoids rejected to oviposit in host eggs both separately and sequentially. On the contrary, the percentage of apparent parasitism—in cases involving complete parasitoid development and emergence from host (egg or egg-larva for *T. brassicae* and *Ch. oculator*, respectively) did show significant differences in average values. Thus, the values for *Ch. oculator* were significantly reduced by competition with the other species. In turn, this effect was observed in *T. brassicae*, although slightly less markedly. This may indicate the role played by the substances injected by *Trichogramma* females during oviposition, as we shall discuss later on.

3.2 Functional response of *T. brassicae*

Table 2 shows the average values of the number of parasitized eggs in the functional response test of *T. brassicae* at both assayed temperatures: 20 and 30°C , using *E. kuehniella* host and under laboratory conditions. The analysis of variance showed a highly significant effect ($P<0.01$) of the density of host eggs over parasitism for every tested temperature ($F=3.35$, $df=7$, $P<0.01$ at 20°C and $F=13.56$, $df=7$, $P<0.01$ at 30°C). The highest temperature (30°C) can be observed to lead to higher amounts of parasitized eggs (average 73.24%) than the other temperature (20°C , average 59.61%). A type-I functional response corresponded in the values of the number parasitized eggs (according to density), as shown in Figure 1 both at 20 and 30°C , whose adjustments showed lower values in the corrected Akaike indices (AIC_c) (see Table 3).

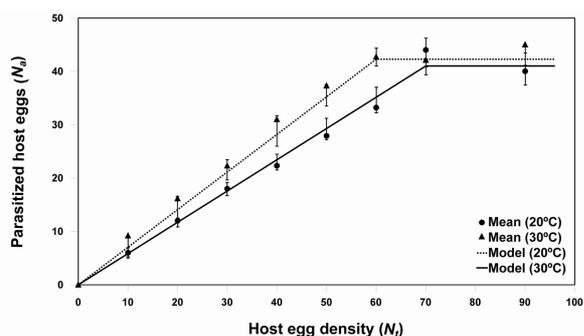


Figure 1. Functional response of *Trichogramma brassicae* female parasitizing *Ephestia kuehniella* egg, at two different temperature levels and under laboratory conditions (60-80% R.H. and 16:8 hours L:D) (Vertical lines represent standard errors of models, $P = 0.05$).

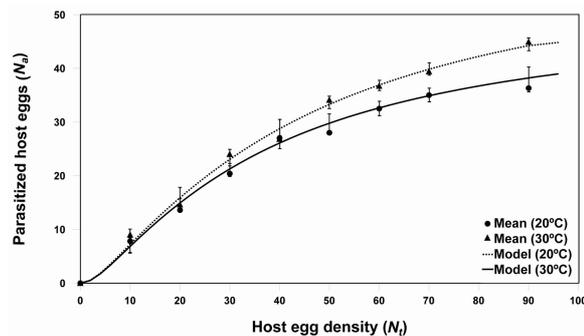


Figure 2. Percentage of parasitized *Ephestia kuehniella* eggs by *Trichogramma brassicae* females according to host density and interspecific competition at $20\pm 2^\circ\text{C}$, under laboratory condition 60-80% H.R. and 16:8 hours L:D) (Vertical lines represent standard errors of models, $P = 0.05$).

3.3 Effect of competition on the functional response

The percentage of host eggs parasitized by *T. brassicae*, according to density and temperature, when half of them were previously exposed or not to *Ch. oculator* parasitization, is also shown in Table 2. Highly significant effects of density were found for these values both at 20°C ($F=5.72$, $df=7$, $P<0.01$) and 30°C ($F=31.13$, $df=7$, $P<0.01$). In this case, it can be observed that the values for each density of host eggs involved little differences between both temperatures, as average values were 62.39 and 68.51% for 20 and 30°C , respectively.

In turn, the average values of parasitism for each parasitoid species and each half of host eggs (previously exposed to parasitization or not by the other species) are shown in Figures 2 and 3 for 20 and 30°C , respectively. In this case, the analysis of variance rendered highly significant effects of density and previous *Ch. oculator* parasitization ($F=7.17$, $df=7$, $P<0.01$ and $F=22.56$, $df=1$, $P<0.01$, respectively). The data in these figures show, on the one hand, that the percentage of *Ch. oculator* parasitism was rather low and only appeared in the highest densities of host eggs, while —on the other hand— in most cases and both temperatures, the percentage of eggs parasitized by *T. brassicae* in the non-exposed half of the host eggs was significantly higher than in the exposed half. Nevertheless, no marked differences were observed except for the lowest temperatures and densities of host eggs (Figures 2 and 3).

The adjustment parameters and their significance for the three types of functional response equations, at both temperatures are shown in Table 4. Unlike previously reported in section 3.2, in this case the equation which represents best the data found in competition is type-III (Figure 4), which showed a lower AIC_c value in each temperature.

4. Discussion

The results obtained in the first test (Table 1) indicate that the females of both parasitoid species seem to accept previously-parasitized host eggs for parasitization. This agrees

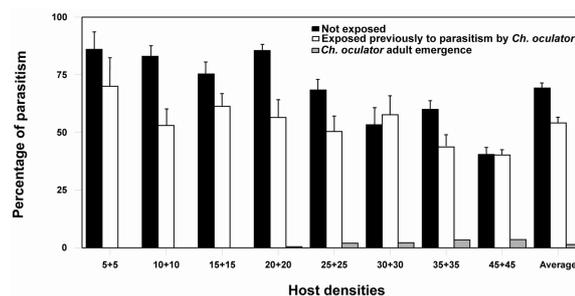


Figure 3. Percentage of parasitized *Ephestia kuehniella* eggs by *Trichogramma brassicae* females according to host density and interspecific competition at $30\pm 2^\circ\text{C}$, under laboratory condition 60-80% H.R. and 16:8 hours L:D) (Vertical lines represent standard errors of models, $P = 0.05$).

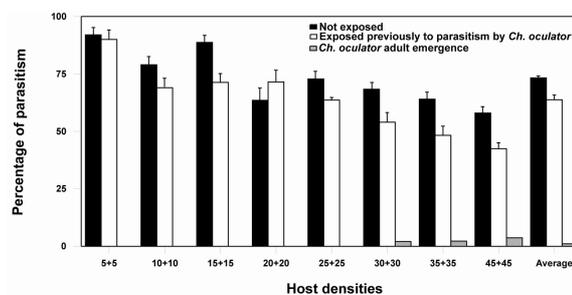


Figure 4. Functional response of *Trichogramma brassicae* female parasitizing *Ephestia kuehniella* egg, in interspecific competition with *Chelonus oculator* and at two different temperature levels and under laboratory conditions (60-80% R.H. and 16:8 hours de L:D) (Vertical lines represent standard errors of models, $P = 0.05$).

with previous studies on close species such as *T. pretiosum*, *Ch. insularis* and *Telenomus heliothidis*, whose females oviposit inside eggs previously parasitized by the other species (Ables et al. 1981). The same behaviour was observed in *Chelonus insularis* and *Telenomus remus* (Earl and Graham

Table 3. Parameters and statistical significance for functional response equations for numbers of *Ephestia kuehniella* eggs parasitized by *Trichogramma brassicae*, at two temperatures (20 and 30±2°C) and under laboratory condition (60-80 % R.H. and 16:8 hours L:D).

Type	Parameters			Statistical parameters		
	T_h	a'	α	A/Cc	df	r^2
20 °C						
I	-	0.88137		10.40408	7	0.98236
II	0.00907	1.42166		22.13321	7	0.96340
III	0.01528		0.06545	24.22528	7	0.91803
30 °C						
I	-	1.21911		17.75842	6	0.93274
II	0.01179	3.58638		22.00580	7	0.95956
III	0.01449		0.19825	22.09052	7	0.95917

Table 4. Parameters and statistical significance for functional response equations for numbers of *Ephestia kuehniella* eggs parasitized by *Trichogramma brassicae*, at two temperatures (20 and 30±2°C), in interspecific competition with *Chelonus oculator*, and under laboratory condition (60-80 % R.H. and 16:8 hours L:D).

Type	Parameters			Statistical parameters		
	T_h	a'	α	A/Cc	df	r^2
20 °C						
I	-	0.87364	-	16.04060	7	0.94584
II	0.01648	3.4076	-	13.44166	6	0.97715
III	0.01907	-	0.15673	9.68275	6	0.98495
30 °C						
I	-	0.87423	-	24.34078	7	0.89906
II	0.01212	2.91749	-	6.43423	7	0.99161
III	0.01551	-	0.16496	5.53092	7	0.99241

1984), as well as in *Trissolcus nigripedius* and *Telenomus gi-fuensis* (Mahmoud and Lim 2008). The capacity of endoparasitoids to discriminate between parasitized and non-parasitized eggs generally seems to vary (Mackauer 1990, Scholz and Höller 1992), although it is often reported as a rare phenomenon (Baaren et al. 1994, Royer et al. 1999, Boivin and Brodeur 2006).

Mackauer (1990) points out that female parasitoid may either accept or not a previously-parasitized host by a different species depending on the survival probability of their offspring. Thus, this parasitization —particularly at low host density —takes place when the progeny can be sure of reaching adult stage. Otherwise, adult female parasitoids avoid parasitisation. According to our results, this hypothesis must be discarded, as both parasitoid species parasitized eggs. However, as results show and shall be discussed later on, only one of them seems to have guaranteed offspring success. It must be borne in mind that females in the tests had no oviposition pressure (less than 48 hours since emergence) and there were enough available hosts. The environmental importance of the acceptance of previously-parasitized hosts was emphasized by Turlings et al. (1985), who demonstrated —by means of mathematical models —that no parasitoid

species can gain fitness by rejecting previously-parasitized hosts.

Mackauer (1990) points out that interspecific competition at host level may be due to the interactions among immature stages or to the mother's action. The former seems to agree with the available data (Table 1), in case of sequential parasitisation by both species. In both cases, the emergence of *Ch. oculator* was rather low (7.61 and 8.73%) and showed no significant differences. In this sense, solitary endoparasitoids present different mechanisms to eliminate the eggs or larvae of potential competitors: Direct fight (especially first instars, which are particularly prepared for this) or physiological suppression (Mackauer 1990, Boivin and Brodeur 2006, Uka et al. 2006). However, also in agreement with the obtained results (Table 1), there seems to be more than one effect due to the mother's action, since otherwise the emergence of *Trichogramma* from eggs parasitized only by this species —relative to when they were previously or subsequently parasitized by the other species —should involve no significant difference; however, this does not occur. On the contrary, a reduction in the emergence of the offspring of *T. brassicae* is observed, particularly when *Ch. oculator* is the last to parasitize.

This fact seems to be due to the injected substances by each species during oviposition. Thus, *Chelonus* females lay their egg in the yolk of the egg host and take certain time (16 hour) to hatch; immediately later, this one penetrates in the host's embryo (Rechav and Orion 1975, Kaeslin et al. 2005). In turn, *Trichogramma* females also lay their eggs in the yolk of the host egg and take 19-27 hours to hatch (Volkoff et al. 1995, Jarjees et al. 1998). Thus, the eggs of both competing parasitoid species and the newborn *Chelonus* larva remain exposed to the substances injected by the females of the other parasitoid species. *Trichogramma* species inject protease and phosphatase with the egg (Strand 1986) to disaggregate all the tissues in their host, so as to make them easily and quickly absorbed by the parasitoid larva (Benoit and Voegelé 1979, Hawlitzky and Boulay 1982, Jarjees and Merritt 2002). This would provide a better explanation of the obtained data (Table 1) in competing parasitization and the greater success of the offspring of *T. brassicae*. However, this success is not complete, because when *Ch. oculator* parasitizes last, the emergence of *Trichogramma* adults is severely reduced, probably due to the toxins and polydnarivuses injected by *Chelonus* female (Grossniklaus-Bürgin et al. 1998), on which the proteases and phosphatases –previously injected by the *Trichogramma* female –cannot act. This loss of efficiency of these substances were related to the increase in age of the host egg (Hawlitzky and Boulay 1982, Voegelé et al. 1974).

Apart from the previously-reported effects, influence on functional response was another effect by the obtained results. Thus, *T. brassicae* presents a type-I functional response both at 20 and 30°C, when it parasitized previously-non-exposed eggs (Figure 1). These results agree with that observed for other studied *Trichogramma* and *Trichogrammatoidea* species, in which most cases present type-I functional responses (Cabello and Vargas 1988, Faria et al. 2000, Mills and Lacan 2004, Kalyebia et al. 2005). On the contrary, functional responses change to type III when females must parasitize previously-parasitized eggs, which is a highly frequent phenomenon under natural conditions. However, changes in the functional response of *Trichogramma* have been reported due to the effect of temperature (Wang and Ferro 1998) or the host typology (Reay-Jones et al. 2006). Besides, similar changes have also been reported in other parasitoid species (García-Martin et al. 2008).

In the case of *T. brassicae* females, the presence of eggs previously parasitized by *Ch. oculator* —yet not the whole patch —hinders high-density parasitism, which must be the result of higher handling time (T_h), which in turns depends on density. It must be pointed out that competition among different parasitoid species can modify the distribution of their eggs in the hosts in the patch (Alphen and Jarvis 1996). Increase in handling time may be due to several reasons: 1) increase in the time devoted to host acceptance, in view of the need to be able to discriminate between previously-parasitized eggs; however, this seems a rather unlikely reason; and 2) increase in the time devoted to examine host eggs, given the physiological change originated by *Ch. oculator*

parasitization. In this sense, it must be pointed out that *Trichogramma*'s discrimination is based on the physiological state of the host: presence or absence of embryo and its developmental stage (Benoit and Voegelé 1979, Juliano 1982).

Results show that *Ch. oculator* competes badly with *T. brassicae*. Thus, in principle the former may be included in the group of the so-called 'inferior competitors'. This has also been reported for other species (Zwölfer 1971, Miller 1977, Cave 2000). In these cases, the competitively inferior species is found to present greater fecundity than the competitively superior species (Hassell 1978). In the present case, the foregoing also applies for the pair *T. brassicae*-*Ch. oculator*. Thus, the fecundity of the latter oscillates between 234 and 481 parasitized eggs per female, depending on temperature (García-Martin et al. 2005). On the other hand, the fertility of *T. brassicae* ranges between 58 and 81 (Ozder and Saglam 2005). These values were taken for the same host-egg species (*E. kuehniella*) under laboratory conditions.

The foregoing leads us to the coexistence of both species in Nature. Thus, although it is difficult to determine the range of hosts of a given parasitoids (Shaw 1994) and there are multiple errors in the currently available literature (Shaw 2006), *Ch. oculator* has been mentioned as parasitoid of 10 Lepidoptera species belonging to four families (Tobias 1975 1997). At the same time, *T. brassicae* presents a much wider range of hosts which includes 64 species belonging to 15 families, plus a Diptera species (Polaszek 2010). Out of all known host species, both parasitoids share common hosts belonging to three important Lepidoptera families: Noctuidae, Pyralidae and Tortricidae. The same overlap is observed in close species to both parasitoid genera (Cabello 1989). All this highlights this coexistence. The foregoing corroborates that the general experience in a field is that multiple enemies coexist in shared hosts, at least seasonally. There are multiple examples of this among parasitoid species and other natural enemies, at least within a short term and local scale (Mills 2006).

To explain this coexistence, the following hypotheses can be formulated, among others (see Godfray and Müller 1998, Bonsall et al. 2002, Mills 2006, Shaw 2006). First, the greater search capacity of the competitive inferior species, in spite of its greater fecundity, relative to the competitive superior species (Hassell 1978, Amarasekare 2000). In the present case, according to the obtained results, the search rate measured by host's survival or parasitism potential which allows us to compare the different types of functional response (Cabello et al. 2007); *T. brassicae* values —in absence of competition— were rather higher (1.819-0.881) than those presented by *Ch. oculator* (0.009-0.341). It should also be borne in mind that it presented a type-II functional response which involves the handling time as a brake (0.00028-0.00306 day⁻¹) (García-Martin et al. 2008). Nevertheless, it must be pointed out that there may be differences between the amounts of devoted time among the patches (data not available for these species). In this sense, it must be pointed

out that *Trichogramma* species present proper and quick—and even higher—direct dispersion (Chapman et al. 2009) particularly if performed through phoresy (Fatouros et al. 2005). Likewise, *Ch. oculator*—due to its greater size—has full capacity to fly (García-Martin et al. 2005). For this reason, the afore-raised hypothesis is considered unlikely to be true. Besides, the coexistence of two parasitoid species has been to demand the competitive inferior species no dispersion advantage over the competitive superior species (Amarasekare 2000).

A second hypothesis posed to explain coexistence, under meta-population conditions, is the existence of different patch states. Some of them show the host and both parasitoid species, while some others contain the host and one of the species (van Nouhys and Hanski 2002). This conclusion was drawn from the field data (Amarasekare 2000). Obviously, in the light of the data rendered by the completed tests, this hypothesis cannot be confirmed. Nevertheless, according to previously-obtained data (Cabello 1989), this hypothesis is likely to be fulfilled in case of competition between *Trichogramma* and *Chelonus*.

A third hypothesis may also be posed in view of the results obtained for predators remunerated opportunistically and their advantages (Garay and Móri 2010). Thus, some Lepidoptera Noctuidae species (e.g., *Spodoptera*) protect their eggs with scales upon oviposition (Belda et al. 1994). These eggs can be parasitized by *Chelonus* species (García-Martin et al. 2005) but not by *Trichogramma*. However, insofar as the age of adult females rises, they oviposit less compactly and with scarce scale-protection (Belda et al. 1994, Consoli et al. 1999), thus, this makes them accessible to *Trichogramma* parasitisation (Beserra and Parra 2005).

The afore detailed results might suggest but do not prove at all that the coexistence would be implied by the idio-biont/koinobiont difference. Such a hypothesis could be tested only involving several other species as well.

Finally, it should be pointed out that—according to the available bibliography—this is the first time that the negative effect of extrinsic competition on the functional response of a parasitoid is mentioned. Thus, the previously-presented classification into competitive superior and inferior species is not real, as it must also take into account that the harmful effect of competition does not only affect the competitive inferior species, but also has a marked effect on the competitive superior species. This is particularly important in host-parasitoid models, under competition conditions, in order to set up more realistic mathematical models.

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