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Larval competition between *Aphidius colemani* and *Lysiphlebus testaceipes* after multiparasitism of the host *Aphis gossypii*

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Abstract

The parasitoids *Aphidius colemani* Viereck and *Lysiphlebus testaceipes* (Cresson) (Hymenoptera Braconidae and Aphidiinae) play an important role in both natural and applied biological control of *Aphis gossypii* Glover (Rhynchota Aphididae). The use of both parasitoid species in biological control of *A. gossypii* may expose them to interspecific competition. Larval competition was evaluated to determine the existence of intrinsic superiority of either *A. colemani* or *L. testaceipes* after multiparasitism of *A. gossypii*. Nymphs of the 2nd instar of *A. gossypii* parasitized by both parasitoid species were used to test the outcome of interspecific larval competition. Thirty nine adults of *A. colemani* and 72 adults of *L. testaceipes* emerged from multiparasitized aphids. It appears that the parasitoid *L. testaceipes* was superior in larval competition ($\chi^2_{IGL} = 15.46$, $P \leq 0.01$) to *A. colemani* in *A. gossypii*. The intrinsic superiority of *L. testaceipes* may cause the displacement of *A. colemani* and, therefore, the simultaneous use of both parasitoids in biological control of *A. gossypii* should be carefully analyzed.

Key words: Intrinsic competition, parasitoid, Braconidae, Aphidiinae, Aphididae.

Introduction

Competition among parasitoids can occur extrinsically or intrinsically. Extrinsic competition involves host population exploration by a female parasitoid through effective host localisation and parasitism. Intrinsic competition occurs among larvae after multiparasitism within the host (Zwolfer, 1971). In solitary parasitoids only one adult emerges per host. All other parasitoids are eliminated by competition and usually this occurs during the parasitoid's larval stages (Vinson and Iwantsch, 1980). According to the counter-balance competition model, one of the parasitoid species in competition will be the winner in intrinsic competition and may exclude the other parasitoid species (Zwolfer, 1971; Force, 1972; Briggs, 1993).

Using one or several species of natural enemies for biological control of a given pest is a controversial issue among biological control scientists. According to Briggs (1993), the use of the most effective parasitoid species only gives better control of the host population compared to releasing several parasitoid species. However, it is extremely difficult to determine the best candidate from a parasitoid assemblage (Ehler, 1990). Thus, the advantages of finding the most effective parasitoid species and using it alone, or to use multiple species introductions should be investigated (Hagvar, 1989; Briggs, 1993; Heinz and Nelson, 1996; Collier *et al*., 2002).

The subfamily Aphidiinae is composed of solitary parasitoids of aphids (Hagen and Bosh, 1968). *Aphidius colemani* Viereck and *Lysiphlebus testaceipes* (Cresson) are the dominant species occurring in South America; both have a broad host range and parasitize various aphid species (Starý and Cermeli, 1989; Sampaio *et al*. 2005a). Völkl and Stadler (1991) did not find intrinsic superiority with larval competition between *A. colemani* and *L. testaceipes* and recommended the simultaneous use of these parasitoids in biological control programs. Van Steenis (1993) pointed out that the use of *A. colemani* should be preferred over *L. testaceipes* for biological control of *Aphis gossypii* Glover in protected crops, since *Myzus persicae* (Sulzer) could also be attacked by that parasitoid.

We evaluated larval competition between *A. colemani* and *L. testaceipes* after multiparasitism of the host *A. gossypii*, (1) to determine the occurrence of possible intrinsic superiority between these two aphid parasitoids and (2) to evaluate the best release programme for aphid biological control in protected cultivation, i.e. the release of one or two parasitoid species.

Materials and methods

Aphid rearing

Cotton aphids, *A. gossypii* were collected on cucumber plants (*Cucumis sativus* L.), and reared on cucumber cv. 'Caipira' plants in the laboratory. About 30 to 50 adult female *A. gossypii* were removed from the rearing and placed into a Petri dish (15 cm diameter) containing a cucumber leaf disc on a layer of 1% water-agar, and kept in a climatic chamber at 25 ± 1 °C and 70 ± 10% RH. Twenty four hours later the adult females were removed, and nymphs of 48 hours old were used in the experiments.

A. colemani and *L. testaceipes* rearing

The parasitoid *A. colemani* was obtained from mummified *Aphis spiraecola* Patch collected on *Citrus sinensis* (L.) on August 21, 2002. *L. testaceipes* was obtained from *A. gossypii* on cotton (*Gossypium hirsutum* L.) plants in the field on August 23, 2002. Both parasitoid species were collected at the campus of the Federal University of Lavras, in Lavras (21°14'43" south latitude and 44°59'59" west longitude), Minas Gerais State, Brazil. The parasitoids were reared for 16 generations on *Schizaphis graminum* (Rondani) on sorghum (*Sorghum bicolor* L.) at 19-25 ºC, 12h photophase and 75 ± 15% RH under laboratory conditions.

Six mated females of each parasitoid species from the stock rearing were released in a Petri dish with about 100 2nd instar *A. gossypii* nymphs placed on a cucumber leaf disc on a layer of 1% water-agar. The parasitoids were allowed to parasitize the aphids for a period of 2h. Thereafter, the aphids were kept in a climatic chamber at 22 ± 1 °C, 70 ± 10% RH and 12h photophase, until emergence of adult parasitoids.

Competition between *A. colemani* and *L. testaceipes* larvae

To obtain parasitized aphids, 24-48h old mated females of *A. colemani* and *L. testaceipes* and 2nd instar *A. gossypii* nymphs were used. The parasitized aphids, both after single or multiple parasitism, were kept in Petri dishes (5-cm) containing a cucumber leaf disc (4-cm) on a layer of 1% water-agar.

After multiparasitism, the aphids were kept in groups of 7-11 individuals until mummy formation. Four days after oviposition by the parasitoids, the aphids were transferred to a new Petri dish (5-cm) with a new leaf disc. The formed mummies were individually put into glass tubes (100 x 8mm) and observed daily until emergence of the parasitoids. The parasitoids were identified to evaluate the number of adult of each species that emerged from multiparasitized hosts.

Single parasitism of the host

One *A. colemani* or *L. testaceipes* female was released in a Petri dish with a cucumber leaf disc and six 2nd instar *A. gossypii* nymphs. Parasitism was observed under a stereo microscope and each host was allowed to be attacked only once by the parasitoid female. Nymphs that had been attacked by parasitoids on the thorax or abdomen were used in the experiments. Hosts were discarded when oviposition occurred in other body parts or when they were only probed with the ovipositor and refused for oviposition by the parasitoid, according to the methodology proposed by Giri *et al.* (1982). After all nymphs were attacked by the parasitoid, six other nymphs were added in the arena until each female had parasitized 14-18 aphids. Six *L. testaceipes* and seven *A. colemani* females were used to obtain a total of 108 single parasitized aphids per parasitoid species. About 4-5 attacked aphids per parasitoid female were allowed to develop in order to evaluate the presence of the parasitoid larvae in its interior (see section "Percentage effective single and multiparasitism").

Multiple parasitism of the host

About 70% of the aphids attacked by one parasitoid female (11-14 individuals) were offered in groups of six hosts to one female of the other parasitoid species. The following oviposition sequences were used to obtain multiparasitized hosts: one oviposition by *A. colemani* with a subsequent one by *L. testaceipes*; or one oviposition by *L. testaceipes* with a subsequent one by *A. colemani*. Seven *L. testaceipes* and six *A. colemani* females were used to obtain 83 multiparasitized hosts for each oviposition sequence. The interval between interspecific ovipositions in the same host did not exceed three hours. Twenty five hosts from each oviposition sequence were dissected to determine the presence of larvae of both parasitoid species in the same host. All other multiparasitized hosts (58 individuals per oviposition sequence) were allowed to develop until adult parasitoid emergence.

Percentage effective single and multiparasitism

To evaluate the percentage of parasitoid attacks resulting in oviposition, 25 aphids that were attacked only once were dissected under a stereo microscope three days after attack. The percentage of hosts with a parasitoid larva was determined for the two parasitoid species, which we consider as the percentage effective ovipositions. According to the methodology proposed by Völkl and Stadler (1991), this percentage effective ovipositions was used to estimate the number of emerging parasitoid adults for the two species after multiparasitism. The calculation of the estimate was base on the assumption that neither of the two parasitoid species was superior in elimination and, thus, that elimination would be at random.

The number of emerging parasitoids emerging from a multiparasitized host can be estimated as follows: (1) The number of *L. testaceipes* is $CN_{Lt} = N_{Lt}*(EO_{Ac}/100)$, where CN_{Lt} is the corrected number of *L. testaceipes* individuals that developed after multiple parasitism of the host; N_{Lt} is the number of emerged *L. testaceipes*; and EO_{Ac} is the percentage effective ovipositions by *A. colemani*. (2) The number of *A. colemani* is $CN_{Ac} = N_{Ac} *(EO_{Lt}/100)$.

The estimated number of parasitoids that should be found for one parasitoid species after single parasitism of the host, if no selective elimination occurs, can be obtained by multiplying the number of all the emerged parasitoid adults of both species by the percentage effective oviposition of that species. Thus, the expected number of *L. testaceipes* individuals (EN_{Lt}) after single parasitism is $[EN_{Lt} = (N_{Lt} + N_{Ac})*(EO_{Lt}/100)]$, where is N_{Lt} is the number of emerged *L. testaceipes,* N_{Ac} is the number of emerged *A. colemani*, and EO_{Lt} is the percentage effective ovipositions by *L. testaceipes*. The expected number (EN_{Ac}) of *A. colemani* individuals after single parasitism is $[EN_{Ac} = (N_{Lt} + N_{Ac})*(EO_{Ac}/100)]$.

Statistical analyses

The influence of the oviposition sequence on the number of emerged parasitoids of each species after multiparasitism of the host was evaluated by the G Test of Independence with William's correction (Sokal and Rohlf, 1995). The comparison of the number of emerged adults of each parasitoid species after multiparasitism of

Table 1. Percentage of *A. gossypii* with parasitoid larvae of *A. colemani* and *L. testaceipes* after one or two ovipositions per aphid and percentage effective ovipositions (EO).

Oviposition number and sequence	*A. gossypii* with parasitoid larvae (%)*			% Effective Ovipositions
	No larva	1 larva	2 larvae	(EO)
One *A. colemani* oviposition	8	92	-	EO_{Ac} = 92%
One *L. testaceipes* oviposition	28	72	-	EO_{Lt} = 72%
One *A. colemani* + one *L. testaceipes* oviposition	4	20	76	EO_{Ac+Lt} = 76%
One *L. testaceipes* + one *A. colemani* oviposition	0	24	76	EO_{Lt+Ac} = 76%

* Number of aphids per treatment = 25.

the host was analyzed by the Contingency Tables Association test (Rosner, 1994), considering as the null hypothesis that both parasitoid species emerged in the same proportion, independently of the oviposition sequence. The statistical analyses of these parameters were done considering the corrected number of parasitoids (CN_{Ac} and CN_{Lt}).

The impact of the presence of one parasitoid species on the other species due multiparasitism of the host, was evaluated by comparing the number of parasitoids of each species after multiparasitization of the host (N_{Ac} and N_{Lt}) with the estimated number of parasitoids of each species after single parasitism of the host (EN_{Ac} and EN_{Lt}). This analysis was done by the Contingency Tables Association test (Rosner, 1994).

Results

The percentages effective ovipositions in *A. gossypii* by the parasitoid *A. colemani* and by *L. testaceipes* were 92% and 72%, respectively. After multiparasitism of *A. gossypii* two parasitoid larvae were found in 76% of the dissected aphids, independently of the attack order (table 1).

The number of adult individuals that emerged from each parasitoid species after multiparasitism of the host was 18 for *A. colemani* when this species was ovipositing first, and 21 *A. colemani* individuals when *L. testaceipes* oviposited first. In *L. testaceipes* 36 adult individuals were found after both oviposition sequences (table 2).

The corrected number of adult individuals from each parasitoid that was estimated to emerge after multiparasitization of *A. gossypii,* was 13 and 15 individuals for *A. colemani,* and 33 individuals for *L. testaceipes* (table 2). The number of adult individuals of the two parasitoid species that emerged did not differ significantly for the two oviposition sequences (G_{adj} = 0.023, P > 0.05). However, the number of emerged *L. testaceipes* after multiparasitism of the host was significantly higher than that of *A. colemani* (χ^2_{1GL}= 15.46, P ≤ 0.01) (table 2).

The number of *L. testaceipes* parasitoids expected after single parasitism of *A. gossypii* (80 individuals) was similar to the number that emerged after multiparasitism (72 individuals). Thus, there were no significant differences between the estimated number of parasitoids after single or multiparasitism for *L. testaceipes* (χ^2_{1GL}= 0.80, P ≥ 0.05). However, the number of *A. colemani* after multiparasitism (39 individuals) was 2.6 times smaller than the estimated number after single parasitism (102 individuals). So, for *A. colemani* (χ^2_{1GL}= 38.91, P ≤ 0.01), the number of emerged parasitoids after multiparasitism was much lower compared to the estimated number after single parasitism (table 3).

Discussion

The percentages effective ovipositions of *A. gossypii* from *A. colemani* (92%) and *L. testaceipes* (72%) were higher than those observed by Sampaio *et al*. (2001) for *A. colemani* (86%) and Bueno *et al*. (2003) for *L. testaceipes* (48%). This high number of effective ovipositions was possibly due the fact that we only used hosts that were attacked by the parasitoid in the thorax and abdomen (Giri *et al*. 1982).

Table 2. Number (N) and corrected number (CN) of emerged adult parasitoids of *A. colemani* (N_{Ac} and CN_{Ac}) and of *L. testaceipes* (N_{Lt} and CN_{Lt}) after multiparasitism of *A. gossypii*. Averages followed by the same small letter in the row do not differ by the G Independence test with Williams correction at 5% (G_{adj} = 0.023). Averages followed by the same capital letter in the column do not differ by the Contingency Table Association test at 1% (χ^2_{1GL}= 15,46).

Adult parasitoid obtained	First parasitoid ovipositing		
	A. colemani (n= 58)	*L. testaceipes* (n= 58)	Total
N_{Ac}	18	21	39
N_{Lt}	36	36	72
Total	54	57	
CN_{Ac}	13 a	15 a	28 B
CN_{Lt}	33 a	33 a	66 A

Table 3. Number (N) of emerged parasitoid adults after multiparasitism of *A. gossypii* and estimated number (EN) after single parasitization by *A. colemani* and by *L. testaceipes*. Averages followed by the same capital letter in the column do not differ by the Contingency Table Association test (χ^2_{1GL}= 38.91 for *A. colemani* - significant at 1%; χ^2_{1GL}= 0.80 for *L. testaceipes* - non significant at 5%).

Parasitism type	Parasitoid species	
	A. colemani (n= 111)	*L. testaceipes* (n= 111)
N (multiparasitism)	39 B	72 A
EN (single parasitism)	102 A	80 A

The use of an interval of maximally 3 hours between successive ovipositions led to 76% multiparasitized aphids, showing that during this period interspecific discrimination between *A. colemani* and *L. testaceipes* did not occur. Völkl and Stadler (1991) found evidence for interspecific discrimination after larval development in *A. colemani* and *L. testaceipes*. According to these authors, there was no host discrimination with oviposition intervals of zero to six hours. However, when a longer interval between ovipositions (16 hours) was used, both parasitoid species rejected the aphids previously parasitized by the other species.

According to Chow and Mackauer (1986), discrimination of parasitized hosts in afidiines occurs among conspecific insects in a short period after their oviposition, through external chemical marking of the host. After oviposition there are physiological and biochemical changes over time in the host due to the development of the parasitoid larva, and this again allows discrimination of parasitized hosts in many species of parasitoids.

Host physiological and biochemical changes may function as internal markers and can sometimes be detected by other parasitoid species, in contrast to external markers, which are species specific (Mackauer, 1990).

In our study, the oviposition sequence did not affect the competition between *A. colemani* and *L. testaceipes* larvae, showing that the three hour interval between ovipositions did not benefit either the species ovipositing first, or the species ovipositing last. Völkl and Stadler (1991) found similar results with oviposition intervals from zero to six hours.

The number of emerged adult parasitoids after multiparasitism of *A. gossypii* was higher for *L. testaceipes* than for *A. colemani*. Therefore, we conclude that *L. testaceipes* was intrinsically superior to *A. colemani*, which is in disagreement with the results found by Völkl and Stadler (1991), who stated that there is no intrinsic superiority for any of these two parasitoid species. However our results are in agreement with most studies on afidiines parasitoid larval competition, where one of the parasitoid species shows intrinsic superiority over the other (Chow and Mackauer, 1984; Chow and Mackauer, 1986; Hofsvang, 1988; Mackauer, 1990; Mcbrien and Mackauer, 1990; Mackauer *et al.*, 1992).

In our study, it was not possible to determine what kind of elimination mechanism had been used by the competing parasitoids after multiparasitism. The use of physical attack by use of mandibles is common in first instar solitary parasitoids (Mackauer, 1990). According to Völkl and Stadler (1991), mandible use was the only mechanism detected in larval competition between *A. colemani* and *L. testaceipes*. The parasitoid that has the shortest egg incubation period and emerges first is supposed to have the greatest chance of eliminating the other species (Collier *et al.* 2002). The egg incubation period of *L. testaceipes* and *A. colemani* is not know, but this information could elucidate the mechanisms used in the combat between *L. testaceipes* and *A. colemani*.

The number of parasitoids expected after single parasitism of *A. gossypii* and the number of parasitoids obtained after multiparasitism indicates that *L. testaceipes*, the superior species in intrinsic competition, has great potential in reducing the population of *A. colemani*.

According to Sampaio *et al.* (2005a) there is an inverse correlation between the co-occurrence of *A. colemani* and *L. testaceipes*. Those authors found that in periods of high aphid densities both parasitoid species co-exist in aphids of the genera *Aphis*, *Rhopalosiphum* and *Schizaphis*. However, in times of scarcity of hosts, *L. testaceipes* was found in *A. gossypii* while *A. colemani* was not found. The authors pointed at the possibility of competition with *L. testaceipes* as probable causes for the non-occurrence of *A. colemani*, but also stated that it might be the effect of high temperatures. In fact, constant temperatures of 28 and 30°C are detrimental to both parasitoid species by reducing adult emergence (Toussidou *et al.*, 1999; Rodrigues *et al.*, 2004; Sampaio, 2004). However, there are *A. colemani* biotypes in Brazil that tolerate constant temperatures up to 28°C without reducing emergence (Sampaio *et al.*, 2005b) So, in this case the effect of high temperatures as a cause for the lack of *A. colemani* at times of low host density can be discarded.

Conclusions

The results reported here, together with those of Sampaio *et al.* (2005a), that competition with *L. testaceipes* is the cause for the change in *A. colemani* occurrence, support the counter-balance competition model (Zwolfer, 1971; Force, 1972; Briggs, 1993), in which the parasitoid *L. testaceipes* is winning the intrinsic competition, and thus potentially interferes negatively with the parasitoid *A. colemani* that is intrinsically inferior.

The combined use of *L. testaceipes* and *A. colemani* for *A. gossypii* control in greenhouses may cause the exclusion of *A. colemani*. In a situation with a low aphid density, it is expected that superior competitor will remain in the crop and will exclude the poorer competitor. However, the superior competitor may be not the most effective parasitoid for aphid control (Zwolfer, 1971; Force, 1972; Briggs, 1993).

The parasitoid *A. colemani* presents great potential for control of *A. gossypii* and *M. persicae* (van Steenis, 1993; Sampaio *et al.*, 2001), while *L. testaceipes* presents potential for the control of *A. gossypii*. *L. testaceipes* is not suitable for the control of *M. persicae* (van Steenis, 1993; Bueno *et al.* 2003; Carnevale *et al.*, 2003; Rodrigues *et al.* 2004). Thus, the best way of using these parasitoid species for biological control of *A. gossypii* in crops where *M. persicae* also is a pest, should be carefully analyzed.

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