Acceptance and suitability of *Acyrthosiphon pisum* and *Sitobion avenae* as hosts of the aphid parasitoid *Aphidius ervi* (Hymenoptera: Braconidae)

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Abstract. *Aphidius ervi* Haliday is a parasitoid of natural populations of both *Acyrthosiphon pisum* (Harris) on alfalfa and *Sitobion avenae* (Fabricius) on wheat in Chile. In this study the performance of the aphid parasitoid on both host species was evaluated. Regardless of origin, both females and males of *A. ervi* were significantly smaller when reared on *S. avenae* than on *A. pisum*. Males and females of *A. ervi* reared on *S. avenae* on wheat also took significantly longer to develop than when reared on *A. pisum*. There was no significant difference in the sex ratio of the parasitoid when reared on these two host aphids. Survival of parasitoids from the *A. pisum* - alfalfa system was significantly lower when reared on *S. avenae* relative to those reared on *A. pisum*, but no significant difference in survival on both hosts was detected in parasitoids from the *S. avenae* - wheat system. Behaviour of parasitoid females during oviposition, such as frequency of encounters, number of attacks and stabbings of host aphids, were significantly higher in the *A. pisum – A. ervi* interaction than in the *S. avenae – A. ervi* interaction, regardless of the origin of the parasitoid. Aphid defensive reactions such as kicking or production of cornicle secretion, were significantly higher in the *A. pisum – A. ervi* than the *S. avenae – A. ervi* interaction. The results are discussed in relation to the effect of host quality and host aphid body size on parasitoid development.

INTRODUCTION

Aphidiinae wasps (Hymenoptera: Braconidae) are solitary, koinobiont endoparasitoids, which only parasitize aphids (Hemiptera: Aphididae). They range from specialist to generalist species, which differ in host recognition and acceptance (Mackauer et al., 1996). *Aphidius ervi* Haliday is an oligophagous aphid parasitoid, variable in its preferences and performance on different aphid host species (Cameron et al., 1984; Pungerl, 1984; Starý et al., 1985; Powell & Wright, 1988; 1991; Christiansen-Weniger & Hardie, 1997; Takada & Tada, 2000). Such differences are frequently interpreted as evidence of the existence of strains or biotypes adapted to particular aphid host species, which may result in genetic divergence between these strains both in the field (Starý et al., 1985; Powell, 1994; Takada & Tada, 2000) and under laboratory conditions (Powell & Wright, 1988).

Aphidius ervi is widely distributed in Eurasia, parasitizing mainly Macrosiphinae aphids such as *Acyrthosiphon pisum* (Harris) on legumes and, to a lesser degree, *Macrosiphum euphorbiae* (Thomas) and *Aulacorthum solani* (Kaltenbach) on other host-plants (Takada & Tada, 2000). In Japan, its distribution is restricted to *A. pisum* and *Acyrthosiphon kondoi* Shinji (Takada & Tada, 2000). *Aphidius ervi* has become one of the most widely used agents for the control of *A. pisum*, and also of *A. kondoi* on lucerne in several countries around the world (Powell & Wright, 1988). Although *Sitobion avenae* (Fabricius) on cereals is a suitable host of *A. ervi*, this parasitoid is of

only minor importance as an aphid biocontrol agent of aphids on cereals in Europe (Cameron et al., 1984). This situation is expected to improve if cereals are grown near perennial legume fields (Starý, 1978). In Chile, the introduction of this parasitoid from cereal hosts in France occurred nearly 25 years ago (Zúñiga, 1990), and it now parasitizes here both *A. pisum* on alfalfa and *S. avenae* on wheat (Starý et al., 1993; Starý, 1993).

In Chile, where *A. ervi* parasitizes both aphid species, this parasitoid shows behavioural differences in its response to aphid host-plant volatiles, which seem to result from conditioning and adult experience, and not from genetic differentiation of *A. ervi* subpopulations on alfalfa and wheat (Daza-Bustamante et al., 2002; Rodríguez et al., 2002). Thus, *A. ervi* responds more strongly to the volatile olfactory cues emanating from the aphid-host-plant complex in which they were reared, regardless of the origin of the parasitoid (wheat or alfalfa) (Daza-Bustamante et al., 2002). We hypothesise that there will be differences in host acceptance and suitability of the aphid hosts from alfalfa and wheat, in particular that *A. ervi* from *A. pisum* on alfalfa and *S. avenae* on wheat reared on *A. pisum* and *S. avenae*, will differ in their acceptance and subsequent performance on these host aphids. The present work evaluates parasitoid host acceptance, aphid defensive behaviour, and parasitoid performance on *A. pisum* on alfalfa and *S. avenae* on wheat.

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MATERIALS AND METHODS

Stock cultures

Aphidius ervi was obtained from parasitised aphids (mummies) collected on alfalfa, *Medicago sativa* L., or wheat, *Triticum aestivum* L., at INIA-La Platina fields in Santiago, Chile. The parasitoids that emerged were reared on the same aphid host - plant combination as they were collected from. The colonies were maintained at 20 ± 1°C and 14L : 10D photoperiod, and were supplemented twice (at two-monthly intervals) with specimens brought from the same aphid host - plant combination in the field. They were allowed to intercross *ad libitum* with individuals in the existing colony. Individuals used in this study were raised in the laboratory for at least 6 generations.

Host acceptance by parasitoids and aphid defensive behaviour

Batches of 50–80 parasitoids were collected as mummies from stock cultures and placed singly in small glass vials. Newly-emerged parasitoids were sexed, fed diluted honey and allowed to mate overnight. Pilot experiments indicated that this time period was sufficient to insure mating. Nymphs of both host aphid species from the stock cultures were synchronised by allowing adults to reproduce and using those nymphs produced within a 6-h period. Synchronised second-instar nymphs were placed singly in Petri dishes (3.5 cm diameter, 1 cm height) containing a leaf of the aphid's food plant. Aphids were allowed to settle for 10 min, after which a single naïve mated female parasitoid was introduced into each dish. All experiments were performed between 11:00 and 17:00 h. Aphids and parasitoids were used only once. The behaviour of parasitoids and aphids was observed under a stereoscopic microscope and data recorded using the software "The Observer". The observation period lasted for 5 minutes. The following parasitoid and aphid behavioural events were recorded: (i) Encounter – a female parasitoid approaches an aphid and taps the aphid's body with its antennae, (ii) Attack – a female parasitoid bends its abdomen forward, and either reaches the aphid body or doesn't, (iii) Stab – a female parasitoid reaches an aphid's body with its ovipositor, and (iv) Kick – an aphid kicks backwards with its hind legs after being contacted by a foraging parasitoid. Experiments were repeated until a set of 20 replicates of each treatment was completed in which parasitoids or aphids showed at least one of the behavioral events described above. Shortly after the experiments the aphids and parasitoids were transferred to an oven, dried for 2 days at 50°C, and individually weighted on an electronic microbalance (sensitivity 0.0001 mg).

Parasitoid performance

Synchronised second-instar nymphs of either *A. pisum* or *S. avenae* were placed singly in Petri dishes (3.5 cm diameter, 1 cm height). After a 10-min settling period, a mated naïve female parasitoid, which had been treated in the same way as in the above experiment, was introduced into the Petri dish. To avoid superparasitism, wasps were allowed to stab a host only once with its ovipositor. Potentially parasitised aphids were clip-caged on alfalfa or wheat plants in a controlled environment chamber at 22 ± 1°C, 70 ± 10% r.h. and a 14L : 10D photoperiod. Parasitised aphids were observed daily (between 10:00 and 10:30 h) until adult parasitoid emergence, and total developmental time, pupal survival, secondary sex ratio and adult body size (measured as adult dry mass) were recorded. A mummy was considered to be formed when an aphid developed a brownish and opaque colour. After emergence, parasitoids were killed and their dry mass determined as described above. All aphids were parasitised since they all reached the mummy stage. Twenty replicates were performed of each treatment for the evaluation of survival and secondary sex ratio. For the evaluation of development time and adult body size, experiments were repeated until twelve females and twelve males developed. All parasitoids and aphids were used only once in the experiments.

Statistical analyses

Since the assumption of homogeneity of variances was not valid for the data obtained when recording aphid acceptance by the parasitoid, it was analysed using the non-parametric Kruskal–Wallis test (Siegel & Castellan, 1988). Data on the developmental time of the parasitoid on different host aphids once $\sqrt{(x+0.5)}$ transformed did not invalidate the assumption of homogeneity of variances; hence, a three-way ANOVA was used with parasitoid origin, aphid host and parasitoid sex as the main effects. No transformation of the data on the dry weight of parasitoid adults resulted in homogeneity of variances. Thus, the non-parametric Scheirer-Ray-Hare extension of the Kruskal-Wallis test for factorial ANOVA was used in this case (Sokal & Rohlf, 1998). Finally, the *G*-test was used to compare survival and secondary sex ratio of the parasitoids (Sokal & Rohlf, 1998).

RESULTS

Aphid - parasitoid interaction

Female parasitoids from the *S. avenae* - wheat system were smaller than females from the *A. pisum* - alfalfa system (Table 1). Frequency of encounters, attacks and stabs by the parasitoid were higher on *A. pisum* than on *S. avenae,* when the origin of the parasitoid was the *A. pisum* - alfalfa system, but not when it was the *S. avenae* - wheat system (Table 1). Body size of *A. ervi* from *S. avenae* on wheat was smaller than from *A. pisum* on alfalfa (Table 1). Incidence of aphid defense against parasitoid attack, i.e. kicking, was significantly higher in *A. pisum* than in *S. avenae,* regardless of parasitoid origin (Table 1). Body size of *A. pisum* was larger than that of *S. avenae* (Table 1).

Parasitoid performance

Regardless of sex, total parasitoid development time was significantly higher on *S. avenae* than on *A. pisum* when parasitoid origin was the *S. avenae* - wheat system, but not when it was the *A. pisum* - alfalfa system (Table 2, MS origin = 0.055, $F_{1,88}$ = 3.769, p = 0.055; MS host = 0.460, $F_{1,88}$ = 31.847, p < 0.001; MS sex = 0.012, $F_{1,88}$ = 0.837, p = 0.363; MS origin × host = 0.142, $F_{1,88}$ = 9.826, p = 0.002; remaining interactions non-significant). Similarly, the egg-larval development time showed the same effects (Table 2, MS origin = 0.147, $F_{1,88}$ = 23.124, p < 0.001; MS host = 0.205, $F_{1,88}$ = 32.294, p < 0.001; MS sex = 0.005, $F_{1,88}$ = 0.764, p = 0.385; MS origin × host = 0.145, $F_{1,88}$ = 22.824, p < 0.001; remaining interactions non-significant). The pupal development time of the parasitoids was also significantly higher on *S.avenae* than on *A. pisum*, the difference being mostly explained by females from the *S. avenae* - wheat system taking longer to eclose from *S. avenae* than from *A. pisum* (Table 2, MS origin = 0.010, $F_{1,88}$ = 0.655, p =0.421; MS host = 0.186, $F_{1,88}$ = 12.485, p < 0.001; MS sex = 0.035, $F_{1,88}$ = 2.350, p = 0.129; all interactions non-significant).

Regardless of parasitoid origin, body size of parasitoids was significantly smaller when the host aphid was *S.*

TABLE 1. Behavioural events in host recognition and acceptance of *Acyrthosiphon pisum* and *Sitobion avenae* by the parasitoid *Aphidius ervi* [a]

Parasitoid origin	Host aphid	A. ervi (N=20)				Aphid (N=20)	
		Body size (µg dry mass)	Encounter	Attack	Stab	Body size (µg dry mass)	Kick
S. avenae/wheat	S. avenae	109 a (2.4)	2.95 ab (0.21)	2.7 ab (0.24)	1.05 a (0.15)	29 a (1.1)	2.15 a (0.26)
	A. pisum	102 a (2.2)	3.65 bc (0.25)	3.95 b (0.29)	1.25 ab (0.14)	60 b (1.8)	5.7 b (0.32)
A. pisum/alfalfa	S. avenae	178 b (3.2)	2.1 a (0.18)	1.7 a (0.22)	1.85 b (0.18)	31a (0.7)	0.55 a (0.14)
	A. pisum	177 b (3.3)	5.45 c (0.49)	4.65 c (0.43)	5.85 c (0.59)	60 b (1.7)	8.35 b (0.80)

[a]Mean values or number of events are shown with standard errors in parenthesis. Values in each column followed by the same letter are not significantly different according to Kruskal–Wallis test with $\alpha = 0.05$.

avenae (Table 2, MS origin = 677.344, $H_{1,88} = 0.875$, p = 0.350; MS host = 47259.375, $H_{1,88} = 61.052$, p < 0.001; MS sex = 3026.261, $H_{1,88} = 3.910$, p = 0.048; MS host × sex = 3577.042, $H_{1,88} = 4.621$, p = 0.032; remaining interactions non-significant). There were marginally significant differences in parasitoid body size in relation to sex, mainly because of the smaller males obtained from *S. avenae*, when their origin was the *S. avenae* - wheat system. Furthermore, regardless of parasitoid origin there were no significant differences in sex ratio between parasitoids reared on *S. avenae* and on *A. pisum* (0.90 and 1.15, respectively, *G*-test, p > 0.05). Survival to the adult stage was significantly lower in parasitoids from the *A. pisum* - alfalfa system reared on *S. avenae* than those reared on *A. pisum* (75 and 100%, respectively, *G*-test, p < 0.05). No significant differences in survival were detected in parasitoids from the *S. avenae* - wheat system

(95 % survival on *S. avenae*, and 90% on *A. pisum*, *G*-test, p > 0.05).

DISCUSSION

A. ervi from alfalfa encountered, attacked and stabbed less frequently *S. avenae* than *A. pisum*. On the other hand, *A. ervi* from wheat did not show significant differences in its response to the two aphid hosts. Kicking was more frequently performed by *A. pisum* than by *S. avenae*, regardless of the origin of the parasitoid (i.e. from *A. pisum* on alfalfa or *S. avenae* on wheat), in spite of the smaller body size of parasitoids reared on *S. avenae* - wheat than on *A. pisum* - alfalfa. Differences in encounter, attack and stabbing may be related to aphid body size: *A. pisum* is larger than *S. avenae* and thus more likely to be encountered, attacked and stabbed by *A. ervi*. As expected from the increased rate of encounters, and

TABLE 2. Performance of *Aphidius ervi* parasitoids (females and males) on the host aphids *Acyrthosiphon pisum* and *Sitobion avenae*[a]

Sex	Parasitoid origin	Host aphid	Development time (day)			Body size (µg dry mass)
			Egg - larval	Pupal	Total	
Females (N=12)	S. avenae wheat	S. avenae	7.3 a (0.19)	6.1 b (0.19)	13.4 c (0.31)	129 c (9.4)
		A. pisum	6.3 b (0.13)	5.1 a (0.08)	11.3 a (0.14)	176 d (4.2)
	A. pisum alfalfa	S. avenae	7.3 a (0.13)	5.4 ab (0.23)	12.6 bc (0.34)	95 b (5.1)
		A. pisum	7.2 a (0.11)	5.3 a (0.13)	12.3 abc (0.22)	167 d (3.1)
Males (N=12)	S. avenae wheat	S. avenae	7.0 a (0.0)	5.4 ab (0.19)	12.4 bc (0.19)	60 a (2.1)
		A. pisum	6.4 b (0.16)	5.1 a (0.23)	11.5 a (0.27)	177 d (2.8)
	A. pisum alfalfa	S. avenae	7.2 a (0.11)	5.5 ab (0.19)	12.9 bc (0.34)	84 ab (5.4)
		A. pisum	7.1 a (0.08)	5.1 a (0.08)	12.2 abc (0.18)	165 d (5.6)

[a]Values given are means with standard errors in parenthesis. Values in each column followed by the same letter are not significantly different according to ANOVA with $\sqrt{(x + 0.5)}$ transformed data and $\alpha = 0.05$. Body size analysis was performed with the Scheirer-Ray-Hare extension of the Kruskal–Wallis test.

attacks and stabs received, *A. pisum* kicked more frequently *A. ervi* from alfalfa than *A. ervi* from wheat. In contrast, Kouamé & Mackauer (1991) recorded that small individuals of *A. pisum* are more frequently attacked and successfully oviposited in by *Ephedrus californicus* Baker, and Fuentes-Contreras & Niemeyer (1998) observed that small individuals of *S. avenae* are more frequently attacked and stabbed by *Aphidius rhopalosiphi* De Stefani-Perez. It is important to note that not only body size is involved in the interspecific comparisons between *A. pisum* and *S. avenae* described here. Other attributes, such as colour or semiochemicals present in the cuticle and in the cornicle secretions are also known to be involved in host recognition and acceptance by *A. ervi* (Battaglia et al., 1995, 2000; Mackauer et al. 1996), and may account for the higher number of encounters, attacks and stabs in the larger of the two aphid species (*A. pisum*) recorded in this study.

Performance of both sexes of the parasitoid showed that *A. ervi* from *A. pisum* - alfalfa was smaller when reared on *S. avenae* than on *A. pisum*, although there were no significant differences in their developmental times (Table 2). Despite the longer development time of *A. ervi* from *S. avenae* on wheat when reared on *S. avenae* than on *A. pisum*, the parasitoid attained smaller body size on *S. avenae* than on *A. pisum* (Table 2). Similar results, with longer developmental time when *A. ervi* is reared on *Sitobion fragariae* (Walker) rather than *A. pisum*, were also obtained by Christiansen-Weniger & Hardie (1997). *A. pisum* was larger than *S. avenae* in our experiments, and therefore should be a better host for *A. ervi* development (Sequeira & Mackauer, 1992, 1994). Again, not only body size is involved in this interspecific comparison. An important factor in the higher performance of *A. ervi* on *A. pisum* than on *S. avenae*, could be the well documented fact that *A. pisum* is the main host of *A. ervi* (Starý et al., 1985; Powell, 1994; Christiansen-Weniger & Hardie, 1997).

Pungerl (1984) successfully transferred *A. ervi* from *S. avenae* to *A. pisum*, as did Cameron et al. (1984), but Pungerl's efforts to transfer it in the opposite direction failed. In contrast, Cameron et al. (1984) successfully transferred *A. ervi* from *A. pisum* to *S. avenae*, but mummy production was greatly reduced in the first generation and recovered only after several generations on the new host. In our study both transfers were realised, although the lower survival of *A. ervi* from alfalfa reared on *S. avenae* support the low quality of *S. avenae* as a host for *A. ervi*.

In conclusion, although previous experiments have shown that *A. ervi* in wind tunnels prefers the aphid host - plant complex in which they were reared, we found that regardless of the origin of parasitoids (alfalfa or wheat) host acceptance and suitability of *A. pisum* on alfalfa was higher than that of *S. avenae* on wheat. This could be because *A. ervi* prefers *A. pisum* over *S. avenae* as a host.

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