Phytoparasitica
https://doi.org/10.1007/s12600-018-0637-y

Presence of less-preferred hosts of the aphid parasitoids *Aphidius ervi* and *Praon volucre* reduces parasitism efficiency

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Received: 16 January 2017 / Accepted: 2 January 2018

Abstract Parasitoids are characterized by a defined range of hosts, either more specialist or generalist. Under natural conditions, females may encounter different host species on the same plant or in the same location. In this case, their preference for one host could influence their choice. However, the presence of less suitable hosts may also affect their choice and, in some cases, may reduce their interest in a patch where both preferred and less preferred hosts are available. The aim of the present study was to test the consequences of the simultaneous presence of three cereal aphids (*Sitobion avenae* Fabricius, *Metopolophium dirhodum* Walker, and *Rhopalosiphum padi* Linnaeus) on the parasitism by two of their parasitoids, *Aphidius ervi* Haliday and *Praon volucre* Haliday. Firstly, in the no-choice experiment, *A. ervi* parasitized on *S. avenae* at a significantly higher rate as compared to *M. dirhodum*, whereas no parasitism on *R. padi* was observed. *P. volucre* parasitized the three species of cereal aphids with a significant preference for *S. avenae*. Interestingly, when two or three host species were offered simultaneously in the same quantity to pairs of parasitoids, the level of parasitism was less than that observed for one host species alone. This observation exhibits a distractive effect on non-host species, from the defense mechanism of a non-suitable host or from the perception of bad quality patches. These results raise the question of the practical application of inundative release of parasitoids for bio-control when several hosts are available simultaneously.

Keywords Host preference · Parasitic potential · Host specialist · Host generalist · Apparent mutualism and distraction effect

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Introduction

Parasitoids are the insects that develop on or in a single host and kill or paralyze it at the time of oviposition (idiobiont) or during its development (koinobiont) (Eggleton and Gaston 1990; Godfray 1994). They seem to have restricted host ranges (Memmott et al. 2000) and their specialization range may vary from a single host to all potential hosts of a particular habitat (Stilmant et al. 2008). The number of potential species and their taxonomic diversity define parasitoid host specificity (Futuyma and Moreno 1988). Host ranges of parasitoid in insects raise the question of competition, including apparent competition or coexistence between parasitoids (Hawkins and Sheehan 1994; Langer and Hance 2004; Stireman 2005), how parasitoid communities are functioning and have evolved (Shaw 1994; Stireman and Singer 2003a, b; Van Driesche 2004), and the ways

Published online: 13 January 2018

in which communities are structured (Begon et al. 2006). It is important to understand in applied point of view how shared parasitoid affects the population of phytophagous pests and the risk of attack on non-target species (Van Driesche 2004; Gassmann and Louda 2001). However, the actual host range of a particular parasitoid species, even if intensively studied, is not easy to assess (Shaw 1994).

In highly specialist parasitoids, their development and lifecycle are closely synchronized with those of their host species (Barrantes et al. 2008). Koinobionts are usually considered as more host-specific (Althoff 2003). Based on various host records during field and laboratory experiments, it appears that parasitoid host specificity is influenced by host ecology and phylogeny (Askew 1995; Stireman et al. 2006), particularly by the host's suitability for parasitoid development (Pennacchio and Strand 2006). According to Godfray (1994), the parasitoid host specificity relies on host recognition and acceptance by the female parasitoid. However, host's defense mechanism can limit the parasitoid's ability to utilize even the highly preferred hosts (De Farias and Hopper 1999).

In cultivated crops, natural enemies play a vital role in aphid control and some of them are actively used and marketed as biocontrol agents (Barahoei et al. 2010; Boivin et al. 2012). About 400 species of aphid parasitoids have been described worldwide (Rakhshani et al. 2007). Among them, species of the genus *Aphidius* (Hymenoptera; Braconidae) are powerful and efficient parasitoids in controlling the aphid population in cereal crops (Brewer and Elliott 2004; Levie et al. 2005a; Schmidt et al. 2003; Hance et al. 2017). Host preference and acceptance behavior of host specialised and generalised parasitoid were determined by Stilmant et al. (2008) using (1) the response of parasitoids to different hosts from antennation through oviposition, (2) the physiological suitability of different hosts for egg laying and immature development. These behaviors are regulated by semiochemical cues emitted by the host-species or the plant itself, induced or not by the feeding process of the phytophagous host (Rehman and Powell 2010; Albittar et al. 2016). In this context, under field conditions, several species of aphid host may be present on the same plant or on neighboring plants, particularly in cereal crops. In that case, the preference of the parasitoid for a species may reduce the rate of parasitism on the other aphid species and may thus favor the development of one aphid species, resulting in apparent mutualism (Frere et al. 2007), with negative consequences for crop protection in case of inundative release. On the contrary, when two aphid hosts share the same parasitoid, it may help one to build its population and may thus result in apparent competition between aphids. It is particularly the case for generalist parasitoids. It is thus essential to define whether in the presence of several host species a parasitoid will mainly affect one species to the benefit of the other or in the reverse if the presence of a less suitable host would reduce its efficiency on the preferred host. In both cases, such behavior may hamper an efficient biological control of all aphid pests present.

In cereal crops, *Aphidius ervi* Haliday (Hymenoptera: Braconidae) has been reported to parasitize a limited range of host species while *Praon volucre* Haliday (Hymenoptera: Braconidae) parasitizes most species of aphids (Stilmant 1994; Stilmant et al. 2008). The objective of this research was to determine the level of parasitism of a specialist or a generalist aphid parasitoids in the presence of less preferred or highly preferred hosts in a patch. We speculated that host choice by generalist parasitoids would result in lower apparent mutualism than specialist parasitoid. Therefore, we analyzed the level of parasitism produced by two aphid parasitoid species *Aphidius ervi* and *Praon volucre* that are commonly found in cereal crops against three species of cereal aphids, i.e. *Sitobion avenae* Fabricius (Hemiptera: Aphididae), *Metopolophium dirhodum* Walker (Hemiptera: Aphididae), and *Rhopalosiphum padi* L. (Hemiptera: Aphididae). To correspond to field conditions as much as possible, we used a cage experiment in choice and no-choice conditions. In general, cage experiments integrate the different steps of parasitization from host location to host suitability and thus give a good indication on the consequence in terms of host control (Levie et al. 2000). These three aphid species are indeed present in the field at the same time and even on the same plant (Hance 1995; Langer et al. 1997; Mushtaq et al. 2013).

Materials and methods

Collection and culturing of cereal aphids

The three host species, *S. avenae, M. dirhodum,* and *R. padi* were collected from cereal crops near the University College of Agriculture, University of Sargodha,

Punjab, Pakistan. It was ensured that these fields were not sprayed with pesticides. Aphids were placed in three cylindrical containers separately based on their species identification and then brought into the laboratory. Host species were mass-cultured separately under laboratory conditions (22 ± 2 °C, 65 ± 5% RH). Wheat (*Triticum aestivum* L.) variety Faisalabad-2008 was used as a host plant.

Collection and culturing of aphid parasitoids

To obtain parasitized aphids, field-gathered mummies (last stage of the parasitoid development inside the cuticle of their aphid host during which they spin their cocoon and undergo metamorphosis before emergence (Levie et al. 2005b) from cereal crops near the University College of Agriculture, University of Sargodha, Punjab, Pakistan or mummies from recently established greenhouse colonies reared on pea aphid were used. The collected mummies were placed in cylindrical containers with a layer of plaster of Paris at the bottom and shifted to the laboratory for rearing. As adult aphid parasitoids emerged from mummies, they were sorted out and identified (Wahl and Sharkey 1993). Parasitoid species, *A. ervi* and *P. volucre* were mass-cultured separately on *S. avenae* under laboratory conditions (22 ± 2 °C, 65 ± 5% RH, 16:08 h L:D). Adult parasitoids were fed with a honey water solution (50:50).

Host specificity of aphid parasitoids against wheat aphid species (no-choice test)

No-choice tests were performed to evaluate the host specificity of *A. ervi* and *P. volucre* against different host species. Twenty wheat seedlings (5 cm high) were transplanted into a pot and infested by 150 aphids (2–4 days old) of each species (*S. avenae, M. dirhodium* and *R. padi*). Pots were then individually placed in small cages (18 cm^3). We released mated and naive pairs of female *A. ervi* and *P. volucre* in each cage separately after six hours of aphid settlement on wheat seedlings. A solution of water and honey (50:50) was provided to adult parasitoid. After 72 h, parasitoids were removed from the cage. After 6–8 days when aphids turned into mummies, the number of mummies formed in each cage was recorded. The experiment was replicated 10 times for all parasitoid and aphid species. The number of mummies formed integrates the whole process of parasitism from host acceptance to host suitability and represents an adequate estimation of their impact on aphids in field condition as done by Legrand et al. (2004), Levie et al. (2005a, b) and Meisner et al. (2007).

Parasitic potential of aphid parasitoid in the complex population of three aphid species (multiple choice tests)

In order to evaluate the parasitic potential of *A. ervi* and *P. volucre* to parasitize and develop successfully in each host species, multiple choice tests were performed. Twenty wheat seedlings (5 cm high) were transplanted in each pot and then 150 aphids (2–4 days old) were released in the following combinations in each pot placed in a small cage as in the first experiments. The four treatments used were:

- T_1 75 L2 *S. avenae* + 75 L2 *M. dirhodum*
- T_2 75 L2 *S. avenae* + 75 L2 *R. padi*
- T_3 75 L2 *M. dirhodum* + 75 L2 *R. padi*
- T_4 50 L2 *S. avenae* + 50 L2 *M. dirhodum* + 50 L2 *R. padi*

Mated pairs of *A. ervi* and *P. volucre* were released in each cage. The food was provided to adult parasitoid as a solution of water and honey (50:50). After 72 h, parasitoid pairs were removed from the cages. Each aphid species was identified and reared separately on pots of fresh wheat seedlings placed in small cages. After 6–8 days, as the aphids turned into mummies, the number of mummies formed in each cage was recorded to check the parasitic potential of *A. ervi* and *P. volucre* against a complex population of three species of aphid. The experiment was replicated 10 times for each of the four treatments.

Statistical analysis

Experiments were performed under Two-factor factorial Completely Randomized Design (CRD) having 10 replications for each treatment. Data obtained from no choice and choice experiments were analyzed separately because in choice experiments we know the number of individuals of each aphid species that are parasitized, and the number of mummies due to each parasitoid but actually we cannot crossed these two aspects because it was not possible to distinguish without error a *M. dirhodum* from a *S. avenae* or a *R. padi* parasitized by *A. ervi* and the same for *P. volucre*. Significant

differences between two factors were computed with factorial ANOVA (parasitoids and aphid species as two factors) using SPSS v. 20. If significant differences were observed between two factors, Tukey's HSD post-hoc test was performed to compute mean differences.

Results

No-choice experiment

Even when specialized on a small range of species, aphid parasitoids usually thrive better on one species of aphids. In the no-choice experiment, the number of hosts parasitized differed significantly among the parasitoid species and among host species. Significant differences were observed among main effects and associated interaction (Aphid × Parasitoid) (Table 1) which indicates that different patterns of the capacity to parasitize aphids existed between the two parasitoid species.

It appeared clearly that in the no-choice experiment, *A. ervi* performed better on *S. avenae* (118.2 ± 3.65 mummies) followed by *P. volucre* against *S. avenae* (89.8 ± 4.85 mummies) whereas least parasitism or no parasitism was recorded by *A. ervi* against *R. padi* followed by *P. volucre* against *R. padi* (48.6 ± 2.35 mummies) (Table 2).

Choice experiment

Concerning the choice experiment, when *S. avenae* and *M. dirhodum* were offered as hosts, the number of mummies produced was significantly different for Aphid × Parasitoid interaction (Table 1). The pairwise comparison of means showed that the highest parasitism was observed by *A. ervi* against *S. avenae* (36.9 ± 3.16 mummies) followed by *P. volucre* against *S. avenae* (28.7 ± 0.66 mummies) whereas the least parasitism was recorded by *A. ervi* against *M. dirhodum* (16.3 ± 1.32 mummies) (Table 3).

When *S. avenae* and *R. padi* were offered as hosts, again the parasitoid, aphid and interaction effects were significant regarding the number of mummies produced (Table 1). Pairwise comparison of means showed that highest parasitism was observed by *A. ervi* against *S. avenae* (34.1 ± 2.56 mummies) followed by *P. volucre* against *S. avenae* (24.4 ± 0.34 mummies) whereas least parasitism was recorded by *A. ervi* against *R. padi* (Table 3).

The same trend was observed when *M. dirhodum* and *R. padi* were offered as hosts with significant differences linked to the aphid, the parasitoid, and the interaction (Aphid × Parasitoid) (Table 1). Pairwise comparison of means showed that the highest parasitism was observed by *A. ervi* against *M. dirhodum* (32.3 ± 2.96 mummies) followed by *P. volucre* against *M. dirhodum* (30.3 ± 0.62 mummies) whereas the least parasitism was recorded by *A. ervi* against *R. padi* (Table 3).

When all tested aphid species were offered simultaneously to each parasitoid, significant differences appeared between numbers of aphids parasitized and number of mummies produced by each parasitoid species as in the interaction between Aphid × Parasitoid (Table 1). Pairwise comparison of means showed that highest parasitism was observed by *P. volucre* against *S. avenae* (20.8 ± 0.83 mummies) followed by *A. ervi* against *S. avenae* (18.5 ± 1.48 mummies) whereas least parasitism was recorded by *A. ervi* against *R. padi* followed by *A. ervi* against *M. dirhodum* (8.1 ± 1.02 mummies). The parasitic potential of *A. ervi* and *P. volucre* decreased in the presence of a less specific host (Table 3).

Discussion

In the present study, we compared the parasitism of *A. ervi* and *P. volucre* against three species of cereal aphid, alone or presented simultaneously. In the no-choice experiment, the number of host preference and parasitization differed significantly among the parasitoid species and among host species (Table 1). A significant interaction between these two factors indicates that different patterns of the capacity to parasitize exist between the parasitoid species. *A. ervi* showed preference as a specialist parasitoid against *S. avenae* and generally parasitized *M. dirhodum*. For *A. ervi*, *S. avenae* is the only suitable host for its development (Stilmant et al. 2008). No parasitism was observed on *R. padi*. However, we observed that *A. ervi* showed antennal contact to distinguish between *R. padi* and *S. avenae* and to decide whether or not it will oviposit (Unpublished data). The present findings can be compared with Althoff (2003) and

Table 1 ANOVA parameters regarding parasitism by *A. ervi* and *P. volucre* against host aphid species in a no-choice and choice experiments

Experiment	Host species	SOV	DF	F	P
No-Choice	*S. avenae*, *M. dirhodum* and *R. padi*	Aphid	2	244.19	≤0.01
		Parasitoid	1	3.64	NS
		Aphid*Parasitoid	2	58.98	≤0.01
		Error	54		
		Total	59		
Choice	*S. avenae* and *M. dirhodum*	Aphid	1	45.68	≤0.01
		Parasitoid	1	0.06	NS
		Aphid*Parasitoid	1	23.93	≤0.01
		Error	36		
		Total	39		
	S. avenae and *R. padi*	Aphid	1	187.44	≤0.01
		Parasitoid	1	21.75	≤0.01
		Aphid*Parasitoid	1	143.06	≤0.01
		Error	36		
		Total	39		
	M. dirhodum and *R. padi*	Aphid	1	104.58	≤0.01
		Parasitoid	1	33.97	≤0.01
		Aphid*Parasitoid	1	47.45	≤0.01
		Error	36		
		Total	39		
	S. avenae, *M. dirhodum* and *R. padi*	Aphid	2	116.68	≤0.01
		Parasitoid	1	84.34	≤0.01
		Aphid*Parasitoid	2	10.71	≤0.01
		Error	54		
		Total	59		

Stilmant et al. (2008), who also reported similar results.

P. volucre acts as a generalist parasitoid against three hosts with a significantly higher level of parasitism on *S. avenae*. These findings confirmed those of Stilmant (1994) and Stilmant et al. (2008).

Table 2 Parasitism efficiency (Mean ± SEM) of *A. ervi* and *P. volucre* against host aphid species in a choice experiment

Parasitoid	Aphid species		
	M. dirhodum	*S. avenae*	*R. padi*
A. ervi	118.20 ± 3.85 a	60.90 ± 5.78 c	0.00 d
P. volucre	89.80 ± 4.85 b	57.60 ± 1.55 c	48.60 ± 2.35 c
HSD	15.11		

Means showing similar letters are not statistically significant at 5% level of significance

In the choice experiment, the parasitic potential of specialist *A. ervi* is lower (Table 3) in the presence of other aphid species than in non-choice experiments when aphid species were presented alone. The presence of less or unsuitable host *M. dirhodum* and *R. padi* in the same patch decreased the preference for suitable host *S. avenae* resulting in a decline of the parasitic potential of *A. ervi*. The parasitic potential of generalist *P. volucre* also decreased in the presence of other aphid species even though it usually parasitized three aphid species.

Thus, it seems that the presence of other less preferred species of aphids induces a strong distraction effect and an overall reduction of parasitism by the preferred species on other species (de Rijk et al. 2013). This kind of observation was already done by Meisner et al. (2007), who observed that the presence of alfalfa

Table 3 Parasitism efficiency (Mean ± SEM) of *A. ervi* and *P. volucre* against host aphid species in a choice experiment

Host species combination	Parasitoid	Number of parasitized aphids			HSD
		S. avenae	*M. dirhodum*	*R. padi*	
S. avenae and *M. dirhodum*	*A. ervi*	36.90 ± 3.16 a 34.39%	16.30 ± 1.32 c 15.19%	–	6.73
	P. volucre	28.70 ± 0.66 b 26.75%	25.40 ± 0.54 b 23.67%		
S. avenae and *R. padi*	*A. ervi*	34.10 ± 2.56 a 42.31%	–	0.00 c	5.06
	P. volucre	24.40 ± 0.34 b 30.27%		22.10 ± 0.60 b 27.42%	
M. dirhodum and *R. padi*	*A. ervi*	–	32.30 ± 2.96 a 37.29%	0.00 c	7.18
	P. volucre		30.30 ± 0.62ab 34.99%	24.00 ± 2.25 b 27.71%	
S. avenae, *M. dirhodum* and *R. padi*	*A. ervi*	18.50 ± 1.48ab 24.93%	8.10 ± 1.02 c 10.92%	0.00 d	3.90
	P. volucre	20.80 ± 0.83 a 28.03%	16.00 ± 0.65 b 21.56%	10.80 ± 0.93 c 14.56%	

Means showing similar letters are not statistically significant at 5% level of significance

aphid *Therioaphis maculata* Buckton (Hemiptera: Drepanosiphidae) reduced the level of parasitism on *Acyrthosuphum pisum* Harris (Hemiptera: Aphididae) by both *A. ervi* and *Praon pequodorum*. This behavior may, therefore, interfere with the biological control efficacy of parasitoid when multiple host species are present, resulting in apparent mutualism (Frere et al. 2007). Several mechanisms can be envisaged. The odor signals indicating inadequate or little-preferred host may decrease the perception of the preferred host or the overall quality of the patch. Defense mechanisms of the less suitable hosts could also affect the female parasitoid during its foraging behavior in a patch (kicking effect as a defense mechanism of aphid, fall down, and honeydew secretions). Parasitoid females may also waste time by discrimination behavior towards unsuitable hosts. Some of the differences observed for host preference may be related to differences in aphid defense reactions. The defense reactions may vary among aphid instars (Hågvar and Hofsvang 1991) and species. *S. avenae* reacted to parasitoid presence by kicking and emitting cornicular droplets, while *R. padi* produced an alarm pheromone causing the other individuals to disperse. *M. dirhodum* showed little reaction upon the first contact but increases its defensive response when re-encountered by a parasitoid (Gardner et al. 1984).

An indirect effect via the plant should also be investigated by Albittar et al. (2016). Finally, a reduction in the residence time in the patch is also possible if female parasitoid encounters less suitable or non-suitable hosts when foraging in a patch. These aspects should be tested more deeply using laboratory experiments.

Under actual field conditions, patterns observed may be biased by changes in both the relative abundance of host species and the relative abundance of the parasitoid species observed. Moreover, results may be influenced by learning process and local strain adaptations.

The major trade-off observed by generalists is that they can parasitize more resources; they are generally less efficient at using them as suggested by "jack-of-all-trades" hypothesis (Egas 2005). It was noticed that the generalist *P. volucre* did not distinguish rapidly against the less suitable *R. padi*, which indicates that generalist parasitoid was less efficient in its selection of host, compared to a host specialist such as *A. ervi* that was able to reject unsuitable hosts more rapidly. According to Meisner et al. (2007), generalist predators can be less effective at controlling a target aphid species when a second host species is present.

In conclusion, the level of host preference and parasitism of parasitoid not only depends on female choice and availability of resources (presence of suitable and unsuitable host in a patch) but also on the presence of a

less preferred or even unsuitable host. Our results are of tremendous importance for biological control and lead to thinking whether, in the case of multiple hosts, the use of generalist parasitoid is preferable or not. In future, studies can be performed by using multiple specialist parasitoids and generalist parasitoids for controlling target preferred host species in the presence of less preferred hosts.

Acknowledgements The author(s) are highly indebted to the Higher Education Commission of Pakistan for providing financial support throughout the study period and the Biodiversity Research Center, UCL, Belgium, for providing the necessary facilities to carry out the research. This paper is publication BRC n° 370 of the Biodiversity Research Center, Université catholique de Louvain, and an essential requirement for correspondence author for degree award. The authors are also thankful to the anonymous reviewers for their valuable comments to improve the manuscript.

Compliance with ethical standards

Conflict of interest The author(s) declare that there is no conflict of interest.

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