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# Inter-specific variation in the reactive distance of different aphid-parasitoid associations: analysis from automatic tracking of the walking path

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**Abstract**

The distance from which hosts are perceived by foraging parasitoid females has been repeatedly considered to be an important behavioural trait that is supposed to be related to their efficiency as biological control agents. In the present study, such a 'reactive distance' was quantified using the automatic analysis of video-recorded females' walking paths. Inter-specific variation of this trait was analysed by comparison between *Aphis gossypii* Glover, *Myzus persicae* Sulzer, and *Sitobion avenae* Fabricius, and three of their parasitoid species known to present different levels of specificity to these hosts: *Aphelinus abdominalis* Dalman, *Aphidius colemani* Viereck, and *Aphidius picipes* Nees. Responses to two different host instars of different size were also compared in each combination. On average, parasitoid females were able to perceive aphids from a distance of about 3 to 4 mm. The only significant difference observed was between the *Aphelinus* and the two *Aphidius* parasitoid species. No difference was detected between the different host instars or species tested. Females seem to be unable to discriminate between host and non-host species from a distance. These results seem to confirm the hypothesis of the use of a cuticular contact kairomone for host recognition at the species level.

**Key words:** Reactive distance; inter-specific variation; aphid parasitoids; video tracking

## INTRODUCTION

The ability of parasitoid females to discover hosts during their foraging behaviour has always been considered to be an important feature in estimating their efficiency to control phytophagous pests in biological control programs (Vinson, 1977; Powell, 1986; Bigler, 1994). Biological traits involved in host searching behaviour have been regularly included in the list of important criteria that have to be taken into account in order to select good-quality biocontrol agents (van Lenteren, 1991; Bigler, 1989, 1994). The corresponding biological mechanisms are usually based on the ability of foraging wasp females to perceive both long-range and short-range visual and/or chemical cues, leading to suitable hosts (Doutt, 1959; Vinson, 1976, 1984; Weseloh, 1981; van Alphen and Vet, 1986; Bell, 1990, 1991; Wellings, 1991; Godfray, 1994; Mackauer et al., 1996).

Among the different behavioural traits involved, the distance from which hosts are perceived (i.e., 'Reactive Distance'; Holling, 1966; Roitberg, 1985; Pak et al., 1991; Wajnberg and Colazza, 1998) is likely to play an important part. Using a stochastic model simulating the walking path of isolated parasitoid females during their searching behaviour, Bruins et al. (1994) have shown that this trait is indeed correlated with the wasp's efficiency to discover new hosts. These authors demonstrated that, whatever the host spatial distribution, an increase in the reactive distance leads to a strongly significant increase in the number of hosts discovered per unit of time. This trait was estimated by several authors usually using indirect methods based on percentage parasitism (Laing, 1937, 1938; Edwards, 1961; Holling, 1966; Yano, 1978). More recently, a more direct way to estimate this trait was proposed after analyzing the recorded walking paths of foraging females (Pak et al.,

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1991; Bruins et al., 1994; Wajnberg and Colazza, 1998).

Several studies demonstrated that reactive distance can be under different sources of variability. Holling (1966) found that the distance from which the praying mantis (*Hierodula crassa*) responds to a housefly increases with hunger, thus leading to an increase in searching efficiency. Bruins et al. (1994), working on egg parasitoids, demonstrated that this trait also shows significant genetic variation within a population used for biological control programs against lepidopterous pests. More generally, parasitoids' searching efficiency is usually known to vary according to the quality and distribution of hosts (Bell, 1991; Bruins et al., 1994) and to the previous experience of foraging females (e.g., Papaj and Vet, 1990). Since host detection can be based on the perception of chemical as well as visual cues (Goff and Nault, 1984; Michaud and Mackauer, 1994; Battaglia et al., 1995), reactive distance should also vary according to the size and/or colour of the host to be discovered (Pak et al., 1991; Bruins et al., 1994). Inter-specific variation is also expected since different wasp species probably detect different types of stimuli with different accuracy (Pak et al., 1991). Finally, such inter-specific variation might be influenced by phylogenetic constraints (Harvey and Pagel, 1991; Martins, 1996). Thus, the distance from which hosts are perceived could be a key trait in the determination of host specificity.

In the present study, different sources of variability in reactive distance were studied in three parasitoid species known to differ in their level of specificity to three different aphid species. The trait under study was quantified from an automatic analysis of video-recorded walking paths of isolated females in the presence of hosts. The nine host-parasitoid combinations were compared. For each combination, the difference in reactive distance to two host instars of different size was also analysed.

## MATERIALS AND METHODS

**Insects.** All host and parasitoid species studied were reared for many years in the laboratory before the experiment. The three different host species were all aphids (Homoptera: Aphididae): (1) The cotton aphid *Aphis gossypii* Glover, reared on cucumber; (2) the peach-potato aphid *Myzus persicae* Sulzer, reared on eggplant; and (3) the English grain aphid *Sitobion avenae* Fabricius, reared on wheat. In order to determine if host size influences parasitoid reactive distance, for each of these host species two different instars were compared: third larval instar (L3) and virginipare apterous adults (VA). For the three host species, the VA were about 30% bigger than L3 (average±SE length of VA vs. L3 ($n=10$ in each case): *A. gossypii*: 1.69±0.03 mm vs. 1.22±0.02 mm; *M. persicae*: 1.52±0.03 mm vs. 1.13±0.02 mm; *S. avenae*: 1.57±0.04 mm vs. 1.45±0.03 mm). All hosts were isolated in the morning and kept at 4°C until the beginning of the experiment.

The parasitoid species were all oligophagous solitary endoparasites of aphids: (1) *Aphelinus abdominalis* Dalman (Aphelinidae), (2) *Aphidius colemani* Viereck (Braconidae, Aphidiinae), and (3) *Aphidius picipes* Nees (Braconidae, Aphidiinae). They were chosen because they are known to show different levels of specificity with the three aphid species tested (Starý, 1974, 1975; Messing and Rabasse, 1995). These three wasp species can successfully attack *M. persicae*. However, neither *A. abdominalis* nor *A. picipes* attack *A. gossypii*, and *S. avenae* is not attacked by *A. colemani*. So, *A. abdominalis* and *A. picipes* were reared on *S. avenae*, while *A. colemani* was reared on *A. gossypii*. This choice also allowed a comparison between two main groups of aphid parasitoids, the genus *Aphelinus* and the genus *Aphidius* (sub-family Aphidiinae). Average sizes of the female parasitoids, estimated by the body length were respectively *A. abdominalis*, 1.21±0.05 ($n=10$); *A. colemani*, 1.89±0.06 ($n=6$); and *A. picipes*, 1.98±0.04 ($n=5$).

**Experiments.** The reactive distance was estimated from the automatic analysis of video-recorded females' motion in the presence of fixed hosts. Host-searching behaviour is known to change according to egg depletion (Collins and Dixon, 1986; Völk and Mackauer, 1990), the previous experience of the females (Bell, 1990), and the presence of other foraging conspecifics (see Godfray, 1994). Thus, in order to estimate reactive distances under conditions that were as standardised as possible, experiments were based on video recordings of isolated, naive females.

The two *Aphidius* species are proovigenic (i.e., they already have fully matured eggs at emergence), whereas *A. abdominalis* is synovigenic (i.e., emergence with no matured eggs available) (Le Ralec, 1991, 1995). Therefore, in order to analyse specimens with enough matured eggs ready to be laid, the tested females were 24 h and 48 h old, respectively. During this period, females were provided with water and diluted honey and kept at 20°C. After 48 h under these conditions, the ovaries of the *A. abdominalis* females contained a large amount of fully mature eggs (Le Ralec, 1991). Aphid mummies containing parasitoid pupae were individually isolated a few days before the experiment with a drop of honey for the emerging adults. Tested females were either virgin or mated (a previous experiment did not show any difference between these two conditions for the three species studied) and were placed individually in experimental conditions for 30 min before the experiment started.

The method used for estimating reactive distance was described by Pak et al. (1991) and Bruins et al. (1994). Because this method works only with fixed hosts, each experiment consisted of releasing one female in an open 9 cm-diameter arena (Petri dish) containing 21 aphids, all of the same species and instar, glued according to a regular pattern with Arabic gum on a disc of tracing paper. Hosts were always spaced 15 mm apart from each other. This distance was controlled by placing the Petri dish over a 1 mm grid paper. The Arabic gum was assumed to be harmless to aphids because glued VA females were still able to deposit larvae. A video camera (RCA-TC 1005/U01X) with a 55 mm lens (diaphragm 5.6) was placed about 70 cm above the arena, and the walking path of the female was video-recorded for 10 min or up to the moment when 10 hosts were attacked. All experiments were performed in the afternoon (from 2:00 pm to 6:00 pm) at 25±1°C, and under a light of about 1,700 lx. On average, 32 females (range: 24–36) were recorded per wasp species, and they were randomly allocated to each host species and instar condition. The 18 combinations (i.e., 3 host species × 3 wasp species × 2 host instars) were randomly distributed over all the days of the experiment. Hosts were considered to be attacked as soon as the female wasp adopted a typical sting position: *A. abdominalis* turns round, with the abdomen towards the host, while the two other species bend their abdomen forward, beneath the head. Under such conditions, an average of 5.47±3.25 attack behaviours were observed per female (only hosts attacked for the first time were taken into account).

From the video records obtained, an automatic computerized tracking device was used to transform each walking path into X-Y co-ordinates with an accuracy of 25 points per second (Coulon et al., 1983; Varley et al., 1994). As soon as a female perceives a host, she turns to it and walks more or less straight to it to attack it. So, at this moment, the angle between the path direction and the wasp-host direction drops sharply to zero. Following Pak et al. (1991) and Bruins et al. (1994), the reactive distance was estimated by the distance at which this turning behaviour appears. As a whole, 520 reactive distances were estimated this way, and the effect of "host species", "wasp species", "host instar" and all interactions were tested with an analysis of variance. Variation between females was also analysed as a random effect in the analysis of variance model. When necessary, a Fisher's least-significant-difference test was used to separate different means. All the corresponding statistical computations were done using PROC GLM of the SAS/STAT package (SAS Institute Inc., 1999).

Despite the fact that the Arabic gum used to fix hosts is odourless and colourless, it is possible that it does show some attractive or repelling effect on foraging females, thus producing a bias in the estimation of reactive distances. Therefore, the absence of attractive or repellent effect was first tested using the following statistical procedure: 104 females (i.e., 38 *A. abdominalis*, 28 *A. colemani* and 38 *A. picipes*) were video-tracked according to the method described above, but on arenas containing only the 21 Arabic gum dots. For each female, the number of observed gum dots encountered was counted. In case of a repellent (respectively attractive) effect, the number of gum dots encountered will be smaller (respectively bigger) than the average number of encounters under the hypothesis of no effect. The statistical distribution of the number of encounters under no effect was estimated using a Monte Carlo procedure (Rubinstein, 1981). For each female's walking path, 1,000 simulations were run. For each of them, 21 gum dot positions were randomly drawn over the whole surface offered to the female, and the corresponding number of encounters was counted. For each fe-

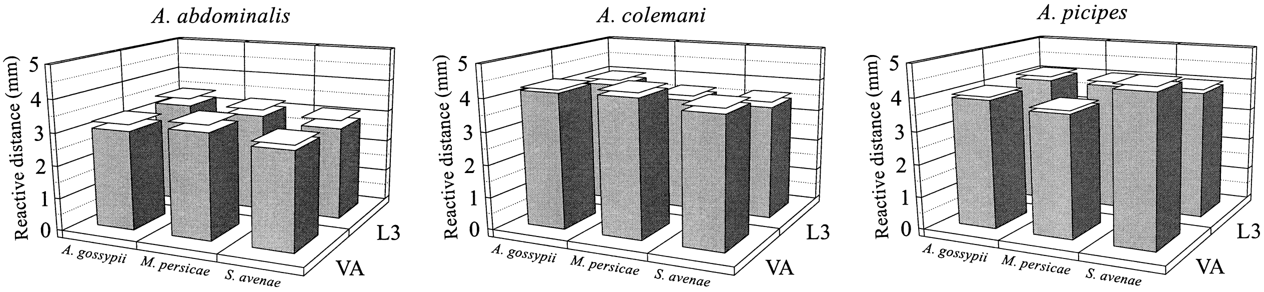

Fig. 1. Average reactive distances of the three aphid parasitoids studied for each of the host/instar combinations tested. Additional upper limits correspond to standard errors. L3: Third instar larvae; VA: Virginipare apterous adults.

male, the first-level risk of rejecting the hypothesis of no attractive (respectively repellent) effect was estimated by the proportion of simulated numbers of encounters above (respectively below) or equal to the observed real value. Such tests are know to be exact (Diggle, 1983), and the number of values generated here is far above those recommended by Hope (1968) and Marriot (1979). Finally, the results were combined over all the females tested using a Fisher's omnibus test (Fisher, 1954). In no case (i.e., for both hypotheses tested, and for the three wasp species) were the computed tests significant. The Arabic gum used did not have any effect on the foraging behaviour of female wasps. Therefore, reactive distances estimated using this experimental design probably have real biological meaning. It must be noted that this design limits the ability of the aphids to exhibit defensive behaviours, which can have an affect on female responses. However, this kind of defensive behaviour often occurs after first contact, and is probably not involved in host recognition but, at least for some species, in host acceptance only (Mackauer et al., 1996).

Table 1. Analysis of variance used to compare the average reactive distances of three aphid parasitoids to three host species and two host instars. The "wasp female" effect (tested as a random effect) is nested within the three-level interaction

| Source of variation | d.f. | Variance | *F* |
|---|---|---|---|
| Wasp species (1) | 2 | 31.623 | 28.14 ** |
| Host species (2) | 2 | 0.241 | <1 (NS) |
| Host instar (3) | 1 | 2.455 | 2.15 (NS) |
| Wasp female (4) | 79 | 1.315 | 1.94 ** |
| Interaction (1)–(2) | 4 | 1.870 | 1.62 (NS) |
| Interaction (1)–(3) | 2 | 1.194 | 1.08 (NS) |
| Interaction (2)–(3) | 2 | 1.353 | 1.21 (NS) |
| Interaction (1)–(2)–(3) | 2 | 1.472 | 1.29 (NS) |
| Error | 425 | 0.679 | |
| Total | 519 | 0.958 | |

NS: non significant; **: $p<0.01$.

Table 2. Overall average (±SE) reactive distances (mm) of the three aphid parasitoid species pooled over all the host species and instars they were offered. Values followed by the same letter did not differ significantly at the 5% level

| | *N* | Reactive distance |
|---|---|---|
| *A. abdominalis* | 141 | 3.1±0.1 a |
| *A. colemani* | 214 | 3.9±0.1 b |
| *A. picipes* | 165 | 3.9±0.1 b |

## RESULTS

The average reactive distances obtained for the 18 combinations studied are given in Fig. 1. It appears that, on average, *A. abdominalis* females had to be closer to the aphids to perceive them (i.e., smaller reactive distance) compared to the two other wasp species regardless of the aphid species or instar they were offered. This was statistically confirmed by the analysis of variance (Table 1) showing a significant "wasp species" effect. Table 2 presents the corresponding average values. However, no significant difference was found between the two *Aphidius* species.

The only other significant effect observed is the "wasp female" effect, demonstrating homogeneity among the different estimations of the measured trait within each female studied. All other effects were not statistically significant. More particularly, no difference was observed between the reactive distances to the three aphid species tested. Moreover, no significant difference was observed between the distance from which the two host instars were perceived regardless of the host species they belonged to (Table 1: Host instar effect, and interaction between host instar and host species). This suggests that the size of the aphid was probably not involved in the host perception process for the three wasp species compared. More interestingly, the interaction between the "wasp species" and the "host species" effects was not significant either. This suggests that the behavioural trait studied here did not differ according to a particular aphid-parasitoid association.

## DISCUSSION

Among the different behavioural traits involved in the efficiency of a biological control agent, the distance from which hosts are perceived is probably one of the most important characters to study (Bruins et al., 1994). In the present paper, using the automatic analysis of the video-recorded walking paths of foraging wasp females, this trait was estimated for different aphid-parasitoid associations known to present different levels of specificity. On average, wasp females perceived their hosts at a distance ranging from about 3 to 4 mm, a distance far greater than the length of the females' antennae. Therefore, responses to volatile chemical and/or visual stimuli are certainly involved in the way female parasitoids perceive their hosts. It is interesting to note that the average values obtained here are about twice as much as those obtained by Gerling et al. (1990) on *Aphelinus asychis* Walker, another aphelinid parasitoid attacking the pea aphid *Acyrthosiphon pisum* Harris. These authors visually estimated the perception distance by placing aphids on 1-mm grid paper. Such a strong difference might simply be explained by the fact that the species studied by Gerling et al. (1990) need to be closer to their hosts to perceive them. This difference may also be due to the fact that the video-tracking system used here gives much more accurate results than the visual estimation used by the other authors.

The distance from which hosts are perceived by insect parasitoids is known to be related to different sources of variability. Here, variations between different host and parasitoid species and between different host instars have been analysed. In addition to a significant variation between the different wasp females measured, demonstrating homogeneity among the different measures done for each female, the only significant effect observed was between the different wasp species compared. The distance from which the two *Aphidius* species reacted to their hosts was about 30% greater than the reactive distance obtained for *Aphelinus abdominalis* (see Table 2). Great differences between the behaviours of an *Aphelinus* and an *Aphidius* species were also found in olfactometer experiments (De Farias and Hopper, 1997). Such an intergeneric variation is likely related to a strong difference in the host attack behaviour. The *Aphelinus* species show a typical turning of the female's body, while the *Aphidius* species remain facing their hosts, bending their abdomen beneath their head. In order to test such a difference, which may be attributed to phylogenetic constraints, other wasp species belonging to different taxonomic units should be compared.

In all cases, such an inter-specific difference cannot be related to pre-imaginal conditioning since: (1) *A. abdominalis* and *A. picipes* were reared on the same host species and nevertheless showed a significantly different response, and (2) no difference was detected between *A. colemani* and *A. picipes* despite these two species being reared on different hosts.

For the three parasitoid species, no differences in the reactive distance were observed between the two host instars or the three host species. All types of host seemed equally attractive and recognised as potential hosts by the females. If it is known that both the *Aphidius* and *Aphelinus* species can attack all aphid instars (Starý, 1988) even if some of them are preferred, it could be expected that bigger hosts would be detected by females from a greater distance. Here, in spite of the different size of the two host instars compared, no significant difference was observed between the corresponding reactive distances, regardless of the host or parasitoid species studied. Such a result, also observed by Gerling et al. (1990) regarding the association between *A. asychis* and *A. pisum*, suggests that host size did not influence the host detection ability of the females.

For each parasitoid species, the reactive distance did not appear to differ between host and non-host aphids. This result indicates that host species recognition did not seem to be achieved from a distance in the three species compared. It can be hypothesised that visual cues, like shape and colour (Michaud and Mackauer, 1994; Battaglia et al., 1995), are likely implicated in the recognition of a potential host. Individuals of *A. gossypii*, *M. persicae* and *S. avenae* used in this study are all green or yellow-green, colours that have been shown to elicit an attack response from females of the parasitoid *Aphidius ervi* (Battaglia et al., 2000). However, recognition of a suitable host could only be achieved after antennal contact, probably by the perception of a cuticular kairomone. Our results confirm that such kind of chemical cues, derived from the aphid body, are non-volatile.

Lack of discrimination between host and non-host species from a distance could be costly for parasitoid females because of both the time lost in host examination and the risk resulting in aphid mechanical defences (Outreman et al., 2001). However, such a cost is likely lower for generalist parasitoids attacking many aphid species than for specialist species, which are attacking only one or a few aphid species. Indeed, the probability that the detected aphid is a suitable host is greater for generalist parasitoids (Michaud and Mackauer, 1995). The three species studied here are all oligophagous, but they all seem to need to be close to their hosts to recognise them as being suitable or not. However, under natural conditions, other perception mechanisms might be implicated in host recognition. For example, it is well known that olfactory cues coming from a host plant or from an aphid-plant complex can also be involved in host location (Schuster and Starks, 1974; Powell and Zhang, 1983; Bouchard and Cloutier, 1984; Sheehan and Shelton, 1989; Grasswitz and Paine, 1993; Guerrieri et al., 1993). It has also been shown recently that plants can release specific volatiles in response to aphid attacks and that the parasitoid *A. ervi* is able to distinguish chemicals emitted by plants attacked by its host aphid, *A. pisum*, from those attacked by a non-host aphid like *Aphis fabae* (Powell et al., 1998). Such types of cues could first lead females to be attracted by suitable hosts, reducing the cost associated to the need of contact for the discrimination between host and non-host aphids. Without such chemical cues, females of the three species tested here seem unable to discriminate between suitable and unsuitable hosts from a distance. Experiments are now being carried out with a four-arm olfactometer (Vet et al., 1983) in order to find out the importance of such chemical cues in the different aphid-parasitoid associations studied here.

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