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Comparative Studies on Foraging Behaviour of Two Aphid Parasitoid Species Attacking the Same Host Species on a Plant

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Abstract: The architecture of the Brussels sprout plant played a role in the host partitioning by the two parasitoid species. *D. rapae* mostly visited the middle and lower leaves, while *A. colemani* visited the upper leaves. This indicates that some factor (s) is involved in this type of host sharing. It was observed that *D. rapae* flew directly to the plant from the vial in a cage, while *A. colemani* first flew to the top of the cage (towards light) and then landed on the upper leaves of a plant. Attraction to plant chemicals for *A. colemani* is neither reported in the literature nor was it observed in the present study. These observations may lead to such questions; are *A. colemani* not responding to the chemicals of the host-plants? Is *A. colemani* visually attracted to host-plants in bright daylight? Another possible explanation of oviposition by the two parasitoid species at the different strata of the plant is that *D. rapae* was first attracted to honeydew on the upper surface of the lower leaves and then moved upwards to the lower side of the middle leaves, where they found the aphids, suggesting that females are not responding to honeydew. However, in the presence of other parasitoid species, *A. colemani* also oviposited more on upper leaves than the other leaves and *D. rapea* oviposited more on the middle/lower leaves than upper ones. This indicates that these two parasitioid species, when together, partition their hosts partly via plant architecture.

Key words: Parasitoids, aphids, *D. rapae*, *A. colemani*, *M. persicae*, foraging behaviour, brussels sprouts

Introduction

Diaeretiella rapae (McIntosh) and *Aphidius colemani* (Viereck) are important parasitoids of aphids. Their use can be improved by increased understanding of the underlying mechanisms of foraging behaviour through comparative behavioural and ecological studies.

Parasitoids often confine their searching to particular parts of a plant, resulting in different levels of parasitism among individuals of one victim species collected from different positions on a plant (Lawton, 1986). When closely related parasitoid species attack the same host species in the same micro habitat, differences in searching behaviour may result in the exploitation of different parts of the host population, i.e. in niche partitioning (van Alphen and Vet, 1986).

Qayyum (1999) found that fundamental niches (host stages as measured by host age) overlap for *D. rapae* and *A. colemani*. Both species oviposited in the less preferred as well as the preferred host stages. Moreover, the presence of hosts and mummified aphids on different parts of a plant indicates that the parasitoids search the whole plant. Therefore, it is possible that necessary conditions exist within a plant for resource partitioning by two or more parasitoid species.

The present study was therefore conducted on foraging behaviour of *D. rapae* and *A. colemani* foraging on *Myzus persicae* (Sulzer) in two experiments. In these experiments 'inexperienced' female parasitoids were used (Qayyum, 1999). Although conditioning parasitoids by allowing them to search and oviposit for some time before an experiment can be a sensible practice (van Alphen and Jervis, 1996), in choice experiment (such as this) the use of freshly emerged, 'inexperienced' females is more appropriate (van Alphen and Jervis, 1996) because through foraging, females can be expected to become more discriminating with respect to host stages or host location.

Section 2 of the present study deals with the searching behaviour of the two parasitoid species when released separately and together on a plant. Section 3 addresses the question: is there a different distribution of oviposition into aphids on a plant among two parasitoid species when alone and together? Such studies are important to gain insight into the foraging strategy of parasitoids in relation to plant directed host partitioning among two or more parasitoid species. The way in which differences in host search/inspection behaviour facilitate coexistence of two parasitoids species attacking the same hosts in the same plant is discussed.

Searching behaviour of *D. rapae* and *A. colemani* alone/separately and together on plants with *M. persicae*: The aim of this experiment was to determine if differences between the two parasitoid species in searching

behaviour would be evident when they searched alone or together for aphids on different parts of a plant and which of the two parasitoid species was more efficient in finding and attacking the host on these different plant parts.

Materials and Methods

The searching behaviour of *D. rapae* and *A. colemani* for *M. persicae* on whole Brussels sprout plants was observed. The plants were about 35 cm high, with 6 free leaves and 1-2 heart leaves. The leaf area ranged from 10.5 to 40.8 cm^2.

Both parasitoid species were allowed to search the plant first alone and then together for one hour after landing on the plant. The components of search behaviour recorded were: (1) first landing stratum on the plant, (2) relative success in discovering the hosts within one hour, (3) time to first encounter with aphid after landing, (4) time allocation to different sections of the plant, and (5) visits to different plant parts. In addition, the mode of host searching and inspection was observed for these two parasitoid species because differences in these behaviours can contribute to niche segregation (van Dijken and van Alphen, 1998).

To start with, four plant strata were distinguished: two lower true leaves, two middle leaves, two upper leaves and the heart (1-2 leaves). Each stratum was infested with twenty mixed-age aphids using clip-cage (Qayyum, 1999). The clip-cages were removed after the aphids were settled. The heartleaf was also infested with 20 aphids. Each infested plant was placed in the centre of a standard cage an experimental arena. Two sets of experiments were conducted.

In the first set of experiments one newly mated 'inexperienced' female parasitoid of a species was introduced in the cage. Before introduction the parasitoid had been kept in a glass vial with a cotton wool stopper. The vial was placed under the plant on the base of the experimental arena and the stopper was removed. The position of the introduced vial was changed north, west, south and east in each replication to avoid any experimental effect.

Searching was defined as starting when the parasitoid landed on the plant. Observation was stopped after one hour, or when the parasitoid terminated its search and left the plant for the cage walls. The time to first encounter with an aphid and the time allocation to different strata of the plant were recorded using a digital timer. The search time included all the activities of the parasitoid while on one stratum of the plant. Any subsequent return by a parasitoid to the same stratum of a plant was taken as a continuation of the previous search.

Fresh plants and aphids were used for each replication in order to avoid any effect of a plant having been searched previously. Fifteen female parasitoids (or more as indicated in the results) of each species were watched.

In the second set of experiments, two females one each parasitoid species, were introduced together into the experimental arena. The observations were similar to those in first experiment. However this time a second observer was used, so that the behaviour of two species of parasitoid could be recorded simultaneously. It is easy to distinguish the two species, *A. colemani* is generally smaller in size and of orange colour compared to *D. rapae* which is black. In this set of experiments also fifteen female parasitoids of each species were observed.

To examine the mode of host search/inspection, a Brussels sprout leaf, infested with about 10 fresh aphids, was placed in a small Petri dish (5 cm diameter). One newly mated 'inexperienced' female of a species was introduced into the Petri dish and watched under the microscope. Here, the aim was not to evaluate different searching/inspection modes but to check whether the two species of parasitoid use the same or different mode.

Results

The overall results show that *D. rapae* and *A. colemani* exploited different parts of a plant. Both species of parasitoid used a different searching strategy. The evidence for this is that *D. rapae* paid more visits to the heart-leaves while *A. colemani* confined itself almost entirely to other leaves.

After being introduced into the cage, the parasitoids landed on different parts of the plants. There was a significant ($P<0.05$) difference between the two parasitoid species in the distribution of their first landing between lower, middle or upper strata when released alone. Whereas 15% *D. rapae* landed on heart-leaves, no *A. colemani* did so (Table 1). When the parasitoid species were introduced together, *D. rapae* did not change its distribution of landing from that when it was alone, whereas *A. colemani* did change it distribution by landing on the upper stratum significantly more than the other strata (there was no significant difference when *A. colemani* was alone) (Table 1). This indicates that *A. colemani* changes its strategy from the very beginning in the presence of the other parasitoid species.

After landing on the plant both the species immediately started searching. *D. rapae* was significantly ($P<0.05$) more successful in discovering the host than *A. colemani*. (Table 2). *D. rapae* also took significantly ($P<0.01$) less time in reaching the host than *A. colemani* (Table 3). This shows that *D. rapae* is more efficient in finding the host than *A. colemani*.

D. rapae and *A. colemani* moved almost continuously

Table 1: First landing on a plant part by *D. rapae* and *A. colemani* when released alone and or together (n = 20)

	Number of parasitoids landed on				
Parasitoid	Lower leaves	Middle leaves	Upper leaves	Heart leaves	χ^2 (3 d.f.)
D. rapae alone	5	6	6	3	6.7 *
A. colemani alone	4	8	8	0	
Rapae+colemani	7	6	5	2	8.7 *
Colemani+rapae	4	5	11	0	

* P < 0.05

Table 2: Comparison of successes of host finding in *D. rapae* and *A. colemani* within one hour of their landing on the plant (n = 15)

	Number of parasitoids		
Parasitoid	Successful	Not successful	χ^2 (1 d.f.)
D. rapae alone	14.00	1.00	6.363*
A. colemani alone	8.00	7.00	0.441ns
Rapae + colemani	11.00	4.00	0.864*
Colemani + rapae	4.00	11.00	7.773*

* P < 0.05, ns Not significant, χ^2(3 d.f.) = 15.340, P < 0.01

Table 3: Time to first encounter of *D. rapae* and *A. colemani* (alone and or together) with the aphid when alighted on the plant (means of 15 replicates)

	Time (minutes) to first encounter by		
Status	*D. rapae*	*A. colemani*	t-value (28 d.f.)
Alone	12.02	35.33	3.109**
Together	22.93	47.56	2.879**
Alone vs. together (t-value, 28 d.f.)	1.517 ns	1.460 ns	

** = P <0.01, ns = Not significant

Table 4: Number of visits to different parts of the plant (20 aphids/leaf) by *D. rapae* and *A. colemani* when landed alone and or together on the plant (Figures are the total visits of 15 replicates in each treatment)

	Number of visits to				
Parasitoid	Lower leaves	Middle leaves	Upper leaves	Heart leaves	χ^2 (3 d.f.)
D. rapae alone	18	21	13	19	5.342 ns
Rapae+colemani	20	21	11	23	
A. colemani alone	10	22	24	3	39.731***
Colemani+rapae	6	20	18	1	

*** P < 0.001, ns Not significant

Table 5: Time allocation to different parts of the plant by the *D. rapae* and *A. colemani* when released alone and or together for 3600 seconds(all visits and activities inclusive). Figures are the means of 15 replicates

	Time (seconds) spent on			
Parasitoid	Lower leaves	Middle leaves	Upper leaves	Hearts
D. rapae alone	287.8d	985.7bc	457.0cd	1596.4a
A. colemani alone	217.9d	541.1cd	869.5c	27.7d
Rapae+Colemani	844.3c	921.3bc	462.7cd	517.7cd
Colemani+rapae	296.0d	241.7d	1431.0ab	30.0d

Means followed by the same letter are not significantly different from one another at P < 0.05

(Table 4), searching leaves. Some leaves were visited more than once (overall, both parasitoids visited middle leaves more than the other leaves). *D. rapae* showed the same distribution of visits to parts when alone or together with *A. colemani*. Again, it paid significantly (P<0.001) more visits to the heart-leaves than *A. colemani*. *A. colemani*, on the other hand, paid more visits to the upper leaves (P<0.001) than the other leaves in the presence of *D. rapae*.

The time allocation to different strata of a plant by the two species of parasitoid is given in Table 5. The analysis of variance gave an F-statistic value of 8.68 with nine degrees of freedom, suggesting that there is a significant interaction between the two variables (parasitoid and strata) and their combination. *D. rapae* when alone spent more time on heart-leaves than either of the other leaves (P<0.05). However *D. rapae*, in the presence of *A. colemani*, showed no significant preference in allocating time among the different strata of the plant (Table 5). *A. colemani*, on the other hand allocated more time to upper strata in the presence of *D. rapae* than when alone (P<0.05). These results indicate that the parasitoid species, when together, changed their searching behaviour.

D. rapae used both the antennae and the ovipositor in searching for the host. The females palpated regularly on the strata with the tips of their antennae and frequently probed the stratum with her ovipositor. Host inspection was mainly with the ovipositor. On approaching the host, the parasitoid curled her abdomen under her thorax, with the apex projecting forwards under her head, and appeared to wait for more movement from the aphid (sometimes it takes several seconds). This mode is known as vibrotaxis as described by van Dijken and van Alphen (1998). This mode was also adopted when the *D. rapae* female decided to examine the host further and to oviposit. By contrasts, *A. colemani* , did not touch the surface at all with her antennae while searching, but those were held straight ahead and were moved up and down. Host inspection was mainly with the antennae, sometimes followed by the ovipositor. *A. colemani* did not respond to vibrations caused by the host movement and also was not seen to probe the strata while walking.

Is there a different distribution of oviposition into aphids by the two parasitoid species among different strata of a plant?: In the previous experiment the searching behaviour of the two parasitoid species, once they had alighted on the experimental host plant, was studied. The searching behaviour related to plant strata suggested the two parasitoids have evolved to share the resources, given the expected distribution of aphids on the different strata of the plant. In the present section the experimental results that support this view were presented.

Materials and Methods

In this experiment three strata (lower, middle and upper

leaves), of a Brussels sprouts plant, were distinguished. The fourth stratum (heart-leaves) was not included since *A. colemani* appeared to avoid this stratum in the previous experiment. Prior to the start of the experiment, each plant was infested with 120 mixed-aged aphids from the aphid culture, equally distributed among the three strata. One such plant was used in a cage for each treatment. The treatments were *D. rapae* (alone), *A. colemani* (alone), *D. rapae* with (*A. colemani*) and *A. colemani* with (*D. rapae*). In each treatment four females of a parasitoid species were released (given some time to aphids to settle down) in the standard cage. However, in those treatments where both the species of parasitoid were released together, 2 females of each species were used. The parasitoids were removed after 48 hours. Parasitism was recorded by counting the number of mummified aphids (after 10 days) on lower, middle and upper leaves of the plant. This parasitism was used as criterion for the preferred plant strata of the two parasitoid species.

Results

The parasitism at different levels of the plant is given in Table 6. The ANOVA shows significant interaction between the two variables (parasitoids and plant strata) ($P<0.05$), indicating that the distribution of mummies on the plant strata varied with the parasitoid/s involved.

When alone, *D. rapae* parasitised most aphids on the middle leaves followed by the lower leaves. *A. colemani*, by contrast, parasitised more aphids on upper leaves followed by middle leaves ($P<0.05$). an almost similar trend was obtained when both the species were released together (Table 6). These results match with the overall searching behaviour of both the parasitoid species (Qayyum, 1999). However, the lower parasitism on upper leaves than the middle leaves by *D. rapae* (in spite of the intensive search of upper leaves) was presumably due to move or drop off of the parasitised aphids.

Table 6: Number of aphids mummified by *D. rapae* and *A. colemani* at different strata of a Brussels sprouts plant infested with *M. persicae* (means of 4 replicates)

	Number of mummified aphids on		
Parasitoid	Lower leaves	Middle leaves	Upper leaves
D. rapae alone	24.0b	32.0a	9.5c
A. colemani alone	17.0c	33.3b	52.8a
Rapae+colemani	36.8a	41.5a	5.8c
Colemani+rapae	8.8c	23.5b	44.5a

Means followed by the same letter in the rows are not significantly different from one another at $P < 0.05$

Discussion

The results of sections 2 and 3 (above) reveal that the two species of parasitoid attacking the same host species differ in the way they search a plant. The visits to a plant by *A. colemani* were not only fewer and shorter than by *D. rapae* but also fewer aphids were parasitised. Though this experiment did not show whether this difference was caused by direct recognition of parasitised aphids (Chow and Mackauer, 1986; Hofsvang, 1988) or by a strong defence reaction of parasitised aphids (Gardner *et al.*, 1984); both the parasitoid species did change their search behaviour when released together (Table 5). These differences indicate that the plant strata provide the necessary conditions for these two parasitoid species to coexist. The plant also provides the first cues in the chain of steps leading to the host (Vinson, 1975).

D. rapae was more efficient in finding the host than *A. colemani*. However, there was a great similarity in the immediate start of searching by the 'inexperienced' females of the two parasitoid species. In the first hour of their search, 60% ovipositional encounters (success) with aphids occurred (Table 2). This indicates that female parasitoids either gained in foraging experience very rapidly or that they both showed innate responses to a number of foraging stimuli. In the foraging strategy of *D. rapae* on *B. brassicae*, a searching pattern related to plant parts was shown, suggesting that the *D. rapae* has evolved to match the expected distribution of aphids and their secretions on different plant parts (Ayal, 1987).

In the present study, *D. rapae* generally visited the heart-leaves (Table 4). *A. colemani* mainly searched the other leaves, whereas *D. rapae* searched every part of the plant above ground. These observations clearly point to a pre-determined foraging strategy, probably genetically controlled (Vinson, 1975). In fact, *D rapae* were brought from a culture of *B. brassicae*, an aphid whose preferred feeding site is the plant heart-leaves (van Emden, 1965) and *A. colemani* was collected from *A. gossypii* on chrysanthemum leaves. The preferred feeding stratum of *A. gossypii* is on the upper part of the chrysanthemum plant (van Steenis, 1995). van Steenis and Khawass (1995) have found that the leaves from the middle and top layers of cucumber cultivars are the preferred feeding sites of *A. gossypii*. One obvious interpretation would be that *D. rapae* and *A. colemani* use the foraging strategy which their great-grand-parents had adopted.

The observations (Section 2) on searching and host inspection behaviour clearly show that *D. rapae* most probably uses vibrotaxis and the ovipositor in foraging, while *A. colemani* uses mainly the antennae. Moreover, host inspection/oviposition behaviour of *D. rapae* was more aggressive and with deeper probing, whereas *A. colemani* was always very gentle and shallowly probing (*A. colemani* sometimes used the ovipositor followed by the antennae for host inspection). This could be a major

difference between the two species, not only from the view point of host sharing, but also in relation to their effective use in the biological control of *M. persicae*, which is mostly found at low densities. The work of other researchers has shown that vibrotaxis is a better mode of host finding for low host densities than for high densities (van Alphen and Galis, 1983; van Dijken and van Alphen, 1998).

In the experiments reported here, the overall oviposition rate of *D. rapae* was always higher than that of *A. colemani* (Table 6), but it was not compared at different densities. This aspect needs to be further investigated. However, if parasitoids that use vibrotaxis to detect hosts are more efficient at low densities than those using ovipositor or antennae search, it could be suggested that *D. rapae* is more efficient at low densities than *A. colemani*.

Finally, Lewis *et al.* (1990) claimed that a primary determinant of the effectiveness of parasitoids as biological control agents was the behaviour of the ovipositing females. Two very important features of their behaviour are (1) efficient searching and attack behaviour and (2) retention of females in the target area. In the present experiments *D. rapae* showed overall superiority over *A. colemani* in searching and attack of hosts and allocation of time once it was on plant. From these results it could also be concluded that the plant architecture provides the necessary conditions for the coexistence (niche separation) of these two parasitoid species.

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