Bulletin of Entomological Research (2009) **99**, 299–306
doi:10.1017/S0007485308006342

How could host discrimination abilities influence the structure of a parasitoid community?

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Abstract

Three related *Aphidius* parasitoid species share the same host, the grain aphid *Sitobion avenae*. Among this parasitoid community, *Aphidius rhopalosiphi* is the most abundant species in the field. Both the interspecific host discrimination of *A. rhopalosiphi* towards hosts parasitized by the two other species (i.e. *A. avenae* and *A. ervi*) and the interspecific host discrimination of the two other species towards hosts parasitized by *A. rhopalosiphi* were studied here. Results showed that females of *A. rhopalosiphi* and *A. avenae* both discriminated between unparasitized hosts and hosts parasitized by the other species. This discrimination occurred only after ovipositor insertion, suggesting the perception of an internal marker of parasitism. Likewise, females of *A. rhopalosiphi* and *A. ervi* were able to discriminate between unparasitized hosts and hosts parasitized by the other species. However, in this combination of species, recognition of parasitized hosts occurred before ovipositor insertion, through an antennal perception, suggesting the presence an external cue indicating parasitism. Hence, interspecific host discrimination in the three *Aphidius* species is based on internal or external cues, which are used either alone or together. Our results showed that the cues used for interspecific host discrimination depend on the specific identity of the interaction. These differences seemed strongly linked to the way the different species respond to defensive behaviours of their aphid hosts. Results are discussed in the context of optimal foraging and possible consequences for community structure.

Keywords: host parasitoid interactions, interspecific competition, resource sharing, host discrimination costs, Aphidiinae

(Accepted 10 July 2008)

Introduction

Most organisms are hosts to a diverse community of parasites, and this raises all the classical ecological questions about the ways in which communities are structured and organised. One potential force shaping communities is interspecific competition. Interspecific competition between parasites may have shaped their behavioural strategies of host resource exploitation (Connell, 1980; Hawkins, 2000). In insect parasitoids (insects that develop inside another insect, their host, killing it as a consequence of their development), several species often exploit the same host population (Godfray, 1994; Hawkins, 2000). In contrast to predators, insect parasitoids do not remove parasitized hosts after

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attack; and thus these hosts remain vulnerable to subsequent attack by other parasitoid females, belonging to the same or a different species. In solitary parasitoids, usually only one adult parasitoid develops per host and when two different females oviposit in the same host (a behaviour called superparasitism if both females belong to the same species or multiparasitism if the second female belongs to a different species), supernumerary individuals are eliminated through physical combat between larvae or physiological suppression (Chow & Mackauer, 1986; Hubbard *et al*., 1987; Pexton & Mayhew, 2005). In the few studies where survival probabilities have been measured in endoparasitoids, the first egg had a marked advantage over later ones (Visser *et al*., 1992; van Baaren *et al*., 1994, 1995).

A parasitized host is, therefore, of lower quality for a parasitoid female compared to an unparasitized one; and, accordingly, even if super- and multiparasitism can be adaptive in some situations (for a review see van Alphen & Visser (1990)), most solitary wasps tend to avoid them. Avoidance of oviposition in already parasitized hosts generally implies the ability of female parasitoids to distinguish between unparasitized and parasitized ones, termed the host discrimination ability (van Lenteren, 1981). Such ability has a strong selective advantage, as females can avoid wasting eggs and/or time (Bakker *et al*., 1985), and is generally mediated through host markers present externally and/or internally, or on patch markers (Sugimoto *et al*., 1986; Hoffmeister & Roitberg, 1997). Some solitary parasitoids mark the host they just attacked externally with either a pheromone deposited during oviposition or a physical mark left on the host body (Mackauer, 1990). Internal cues for host discrimination can originate either from some parasitoid injected substances or from host quality changes associated with parasitism (Mackauer, 1990). Intraspecific host discrimination (i.e. the ability to recognize hosts parasitized by a conspecific) has been observed in more than 200 parasitoid species and has been found in most studied species (van Lenteren, 1981; van Alphen & Visser, 1990). In some species, host discrimination was qualified as imperfect (Outreman *et al*., 2001a) because only a part of the parasitized hosts encountered are rejected. In contrast to intraspecific host discrimination, interspecific host discrimination (i.e. ability to recognize hosts parasitized by another parasitoid species) has less often been detected among the parasitoid species studied, but it also has been less often studied (Turlings *et al*., 1985; van Baaren *et al*., 1994; van Baaren & Boivin, 1998). Both intra and interspecific host discrimination are important as a mechanism for partitioning the host resource between competitors; host discrimination provides information about the level of exploitation of the host population, and thus on the intensity of the intra- or interspecific competition.

In this study, the interspecific host discrimination ability has been investigated in a guild of *Aphidius* species sharing the same aphid host, *Sitobion avenae*. This guild consists of three closely related solitary parasitoids belonging to the genus *Aphidius* (*A. rhopalosiphi* De Stephani-Perez, *A. avenae* Haliday and *A. ervi* Haliday, Hymenoptera Braconidae) (Kambhampati *et al*., 2000), and it has been well documented that interspecific competition occurs frequently in this system (van Baaren *et al*., 2004). In cereal fields of Brittany (Western France), *A. rhopalosiphi* is the most abundant species and is present throughout the year, while both *A. avenae* and *A. ervi* appear later in the season (van Baaren *et al*., 2004). Since the fitness costs associated with multiparasitism might differ from costs associated with superparasitism, the ability of *A. avenae* or *A. ervi* females to recognize hosts parasitized by *A. rhopalosiphi* and *vice versa* has been tested here. It should be noted that this guild represents a particularly interesting case because the most abundant species, *A. rhopalosiphi*, often accepts hosts already parasitized by conspecifics (Outreman *et al*., 2001b), resulting in high superparasitism rates even in host-patches containing numerous unparasitized hosts (Outreman *et al*., 2001a, 2005). The interspecific host discrimination between *A. ervi* and *A. avenae* has not been tested here because both species are rare enough that the probability of attacking the same host is negligible.

Methods

Rearing

Aphidius rhopalosiphi and *A. avenae* originated from *S. avenae* mummies sampled in cereal crops around Rennes (Brittany, France) and were reared on a mixed-age culture of *S. avenae* originating from one parthenogenetic female collected in 1990 in the same area (SA1 clone, INRA-Zoology Collection). Aphids were reared on winter wheat, *Triticum aestivum*, cv. ‘Boston’, furnished by the society Saaton Union Recherche (France). Colonies of hosts and parasitoids were maintained in Plexiglas cages (50 × 50 × 50 cm) placed in climate-controlled rooms at 20 ± 1°C, 70 ± 10% RH and a 16L:8D photoperiod. *Aphidius ervi* mummies were bought from the Biobest Company and reared for several generations on *S. avenae* before the experiments were done, in similar conditions as the two other parasitoid species. For experiments, only second-instar aphid larvae isolated on a wheat leaf two hours before were used. This instar is the preferred one of all three species (Outreman, 2001a,b). To obtain parasitoid females, mummies were collected and placed individually in gelatine capsules. Newly-emerged females were isolated in plastic tubes containing moistened cotton, droplets of honey and a single male for mating. All the females used for the experiments were one day old and able to oviposit more than 50 eggs per day (Shirota *et al*., 1983 for *A. rhopalosiphi*; Starý, 1970 for *A. ervi*; personal observations for *A. avenae*). Each female had been allowed to oviposit in a single host placed on a piece of wheat leaf in a glass Petri dish (Ø = 5 cm) just before the experiment to eliminate females unable to oviposit.

Interspecific host discrimination experiment

A similar design was used to analyse interspecific host discrimination between *A. rhopalosiphi* and *A. avenae* (exp. 1 and 2) and between *A. rhopalosiphi* and *A. ervi* (exp. 3 and 4). For each experiment, 100 aphids parasitized by one of the parasitoid species were needed. They were obtained by being individually offered to parasitoid females. Each host was attacked only once; a host was considered as having been attacked when the female had stung and subsequently departed from it. Although it is not possible for either of the three parasitoid species to determine if an egg has been laid after ovipositor insertion, it is highly likely, since previous studies showed that 89–96% of healthy hosts contain a parasitoid immature after ovipositor insertion (van Baaren *et al*., 2004, for *A. rhopalosiphi* and *A. avenae*; Le Lann *et al*., in press, for *A. ervi*).

To test interspecific host discrimination, a single unparasitized host and a single host parasitized by a female of a given parasitoid species were exposed to a single heterospecific parasitoid female in a choice experiment until one of the two hosts had been stung with the ovipositor. With each parasitoid female, ten successive trials on a new pair of hosts were performed; and, for each combination of parasitoids, ten independent replicates were obtained. The following combinations were tested: aphids parasitized by *A. rhopalosiphi* were exposed to *A. avenae* females (exp. 1), aphids parasitized by *A. avenae* were exposed to *A. rhopalosiphi* females (exp. 2), aphids parasitized by *A. rhopalosiphi* were exposed to *A. ervi* females (exp. 3) and aphids parasitized by *A. ervi* were exposed to *A. rhopalosiphi* females (exp. 4). All the different experimental treatments were performed in random order. Care was taken that experiments were carried out within two hours after the host had been parasitized by the first parasitoid. This threshold time was chosen because external pheromonal marks disappear after several hours; and, when the host had been parasitized much earlier, the discrimination process is generally based on the recognition of physiological changes inside the host due to the development of the parasitoid and not on the recognition marks from the first female (Roitberg & Mangel, 1988, Outreman *et al*., 2001a).

For each host encounter, the behaviour of the female parasitoid was recorded (encounters, antennal rejections and ovipositor insertions). The number of encounters, therefore, represents the number of antennal rejections together with the number of stings. Three to four days after each experiment, the aphids were dissected in a drop of alcohol under a microscope and first-instar parasitoid larvae were counted. This latency between oviposition and dissection was chosen, since even larvae defeated in larval competition in multiparasitized hosts are still visible four days after oviposition (for all species, the development time is between 13 and 14 days in our rearing conditions) (van Baaren *et al*., 2004).

To test whether healthy and parasitized aphids were encountered at different rates in the choice tests, a binomial test was used. Subsequently, the effect of the host type (i.e. parasitized or unparasitized) on the probability for an aphid to be stung by a parasitic wasp was tested. Since each female was tested in ten repeated choice trials, generalized estimating equations (i.e. GEE) for correlated data, assuming a binomial error and using a logit-link function (Liang & Zeger, 1986) were used. Since no specific pattern for the correlation between single choices of the repeated test has to be assumed, an exchangeable working correlation matrix was used.

To analyse the avoidance rate of multiparasitism, the observed distributions of the number of larvae per host found at dissection were compared with an expected distribution built under the null assumption that the three species had no interspecific host discrimination ability. To compute the expected distribution of the number of eggs per host after two successive attacks under the null hypothesis (H_0) of no host discrimination ability, we assumed that (i) two successive encounters with the same host were independent (i.e. no host discrimination ability), (ii) a maximum of one egg can be laid per oviposition insertion (van Baaren *et al*., 2004) and (iii) all eggs laid survived until dissection. Let p_0 and p_1 be the probabilities of a host containing 0 or 1 parasitoid after a single attack, respectively. From separate experiments, we obtained the estimates $p_0 = 0.11$ and $p_1 = 0.89$ for *A. ervi* (Le Lann, unpublished data), $p_0 = 0.04$ and $p_1 = 0.96$ for *A. rhopalosiphi* (van Baaren *et al*., 2004) and $p_0 = 0.05$ and $p_1 = 0.95$ for *A. avenae* (van Baaren *et al*., 2004). Therefore, under H_0, in a sample of size n (number of ovipositor insertions), the expected frequencies $E(N_j)$ of the number of hosts containing j parasitoids at dissection after two successive attacks, by the two parasitoids x and y, are given by:

$$E(N_0) = n \times (p_0)_x \times (p_0)_y$$

$$E(N_1) = n \times (p_0)_x \times (p_1)_y + n \times (p_1)_x \times (p_0)_y$$

$$E(N_2) = n \times (p_1)_x \times (p_1)_y$$

For each treatment, a G-test with Williams' correction was used to compare the observed distribution of parasitoid eggs per host to the expected one.

Results

Interspecific host discrimination between A. rhopalosiphi *and* A. avenae

For all replicates, the number of unparasitized *S. avenae* hosts encountered 'rejected after antennal contact or stung by a female' did not differ from the number of parasitized hosts encountered (binomial tests, $P > 0.05$). *Aphidius rhopalosiphi* females encountered 5.5 ± 0.57 unparasitized hosts and 4.8 ± 0.56 parasitized hosts, whilst *A. avenae* females encountered 5.4 ± 0.39 unparasitized hosts and 4.3 ± 0.30 parasitized hosts (mean ± SE). About 90% of the encountered hosts were attacked by the female (i.e. ovipositor insertion), and this did not depend on their state (unparasitized or parasitized) (fig 1a; *A. rhopalosiphi*: GEE, $\chi^2 = 0.22$, df = 1, $P = 0.637$; *A. avenae*: GEE, $\chi^2 = 0.99$, df = 1, $P = 0.319$). However, the observed distributions of the parasitoid larvae found at dissections strongly departed from the distributions expected under the null hypothesis (i.e. no interspecific host discrimination) (fig. 2a) (*A. rhopalosiphi*: $G = 166.05$, df = 2, $P < 0.001$; *A. avenae*: $G = 204.3$, df = 2, $P < 0.001$). For both species, the majority of attacked hosts contained only a single parasitoid.

Interspecific host discrimination between A. rhopalosiphi *and* A. ervi

For all replicates, the number of unparasitized hosts encountered by a female did not differ from the number of parasitized hosts (binomial tests, $P > 0.05$): *Aphidius rhopalosiphi* females encountered 9.1 ± 1.07 unparasitized hosts and 9.2 ± 1.37 parasitized hosts, whilst *A. ervi* females encountered 7.6 ± 0.34 unparasitized hosts and 7.2 ± 0.89 parasitized hosts (mean ± SE). Among the host encountered, the proportion of ovipositor insertion (and, consequently, the number of antennal rejections) strongly depends on the type of host (fig 1b; *A. rhopalosiphi*: $\chi^2 = 43.85$; df = 1; $P < 0.001$; *A. ervi*: $\chi^2 = 28.32$; df = 1; $P < 0.001$). For both species, parasitized hosts were less often stung with the ovipositor. The observed distributions of parasitoid larvae also differed from distributions expected under the null hypothesis (i.e. no interspecific host discrimination) (fig. 2b) (*A. rhopalosiphi*: $G = 39.97$, df = 2, $P < 0.001$; *A. avenae*, $G = 10.09$, df = 2, $P = 0.039$). While the

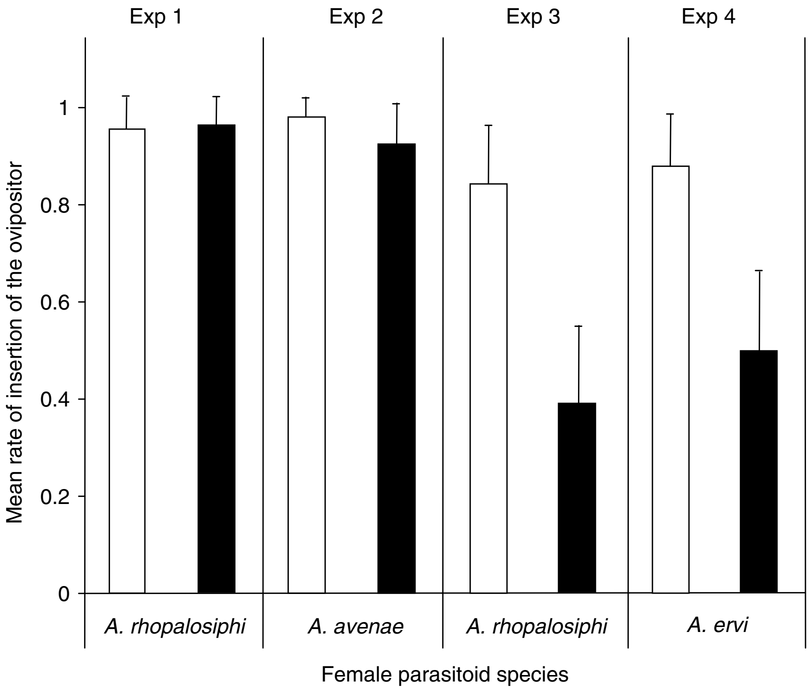

Fig. 1. Mean rate (±SEM) of insertion of the ovipositor in unparasitized *S. avenae* hosts (open bars) and in hosts parasitized by *A. rhopalosiphi* (exp 1, 3), *A. avenae* (exp 2) or *A. ervi* (exp 4) (filled bars). In all four experiments, a female was placed in a Petri dish with one unparasitized host and one host parasitized by another species, and ten pairs of hosts were successively presented. Each experiment was replicated with ten different females.

rates of multiparasitism in the *A. rhopalosiphi*-*A. avenae* interactions were very low (fig 2a), about 30% of hosts parasitized by *A. ervi* were accepted by *A. rhopalosiphi* females and about 60% of hosts parasitized by *A. rhopalosiphi* were accepted by *A. ervi* females (fig. 2b).

Discussion

Results showed that females of *A. rhopalosiphi* and *A. avenae* both discriminated between unparasitized *S. avenae* hosts and hosts parasitized by the other species. This host discrimination occurred only after an ovipositor insertion. Moreover, we found that females of *A. rhopalosiphi* and *A. ervi* discriminated between unparasitized hosts and hosts parasitized by the other species, but this recognition of hosts parasitized by the other species occurred before ovipositor insertion. Hence, interspecific host discrimination in the three *Aphidius* species studied here is based on either an internal mark only or on an external mark, which is used either alone or in combination with an internal mark. This is the first time that it has been shown that cues used for interspecific host discrimination depend on the specific identity of the competition.

Variation in the mechanisms of interspecific host discrimination

When *A. rhopalosiphi* females were exposed to hosts parasitized by *A. avenae*, almost all ovipositor insertions in parasitized hosts were rejections, as none or very few of these hosts contained two parasitoids larvae. This revealed that *A. rhopalosiphi* rejected hosts parasitized by *A. avenae* only on the basis of an internal factor. Females of *A. rhopalosiphi* probably used the internal mark left by *A. avenae*, which is also used in this species in intraspecific host discrimination (van Baaren *et al*., 2004). Discrimination on the basis of marks produced by closely related species has already been shown in other parasitoid species (Vet *et al*., 1984; van Baaren & Boivin, 1998). It is likely that closely related species produce similar marking substances and, hence, that they can recognize each other's marks. However, aphids can exude a small drop of yellowish fluid from cornicles; and, once emitted, this secretion rapidly solidifies in the air, remaining on the ends of the cornicles. Aphids with dried cornicle secretion on their body are often rejected by *A. rhopalosiphi* females. Rejecting hosts using this cue is safer and saves time although the cue is less reliable than the recognition of a pheromonal mark (Outreman *et al*., 2001a; Outreman & Pierre, 2005). Hosts parasitized by *A. avenae* rarely emitted cornicular secretion; and, thus, *A. rhopalosiphi* must insert its ovipositor in such hosts to recognize already parasitized hosts (van Baaren *et al*., 2004).

When *A. avenae* females were exposed to hosts parasitized by *A. rhopalosiphi*, they rejected these hosts using an internal mark only, as they do with hosts parasitized by females of their own species (van Baaren *et al*., 2004). Although hosts parasitized by *A. rhopalosiphi* show a high incidence of cornicular secretion emission, *A. avenae* does not induce further defensive behaviour when attacking such hosts (van Baaren *et al*., 2004). Hosts parasitized by *A. avenae* rarely emitted cornicular secretions (*A. avenae* stays in proximity of the hosts, fluttering the wings for several

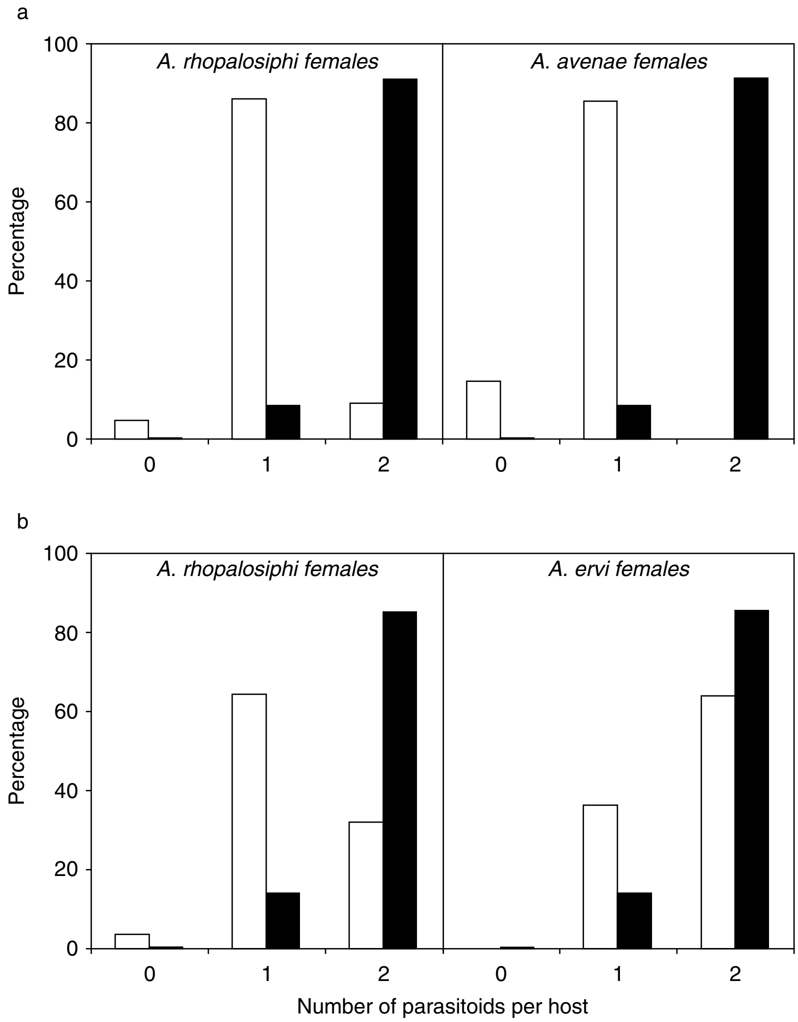

Fig. 2. Comparison of expected (under the null hypothesis of no host discrimination ability (filled bars)) and observed (open bars) egg distribution in *S. avenae* hosts that were stung successively by two females of different species. Figure 2a shows interspecific host discrimination between *A. rhopalosiphi* and *A. avenae*, and fig. 2b shows interspecific host discrimination between *A. rhopalosiphi* and *A. ervi*.

minutes before each oviposition, and this behaviour is linked to a low rate of cornicular secretion by the host (van Baaren *et al*., 2004)). Moreover, *A. avenae* is not repelled by hosts having emitted cornicular secretion. *Aphidius avenae* behaved towards hosts parasitized by *A. rhopalosiphi* as towards hosts parasitized by its own species.

When *A. rhopalosiphi* females were exposed to hosts parasitized by *A. ervi*, *A. rhopalosiphi* females rejected the majority of hosts parasitized by *A. ervi* after antennal examination. Sixty percent of the hosts parasitized by *A. ervi* emitted cornicular secretions (Le Lann, unpublished data). Thus, *A. rhopalosiphi* can reject these hosts because they have secreted, as they do with hosts parasitized by conspecific females. *Aphidius ervi* is known to use both external and internal marks to reject hosts parasitized by conspecifics (Bai, 1991: although in this publication the experiments did not allow specifying which kind of external mark was used, cornicular secretion or pheromonal mark (McBrien & Mackauer, 1990, 1991)), and it is not impossible that these external marks could be also recognized by *A. rhopalosiphi* females. A small number of parasitized hosts were not rejected upon antennal contact and are subsequently stung with the ovipositor. A number of these hosts were still rejected after the ovipositor insertion, suggesting that *A. rhopalosiphi* females also recognize the internal mark of *A. ervi* in rejecting parasitized hosts, as it is able to recognize the internal mark of *A. avenae* (see above).

When *A. ervi* females were exposed to hosts parasitized by *A. rhopalosiphi*, *A. ervi* rejected hosts parasitized by *A. rhopalosiphi*, both using external and internal cues. The nature of the external cue is not clear; *A. rhopalosiphi* either deposits an external mark as has been suggested for *A. ervi* (Bai, 1991) or it uses the host's cornicular secretion. *Aphidius ervi* also rejected hosts parasitized by *A. rhopalosiphi* using an internal mark, as it does in intraspecific host discrimination (McBrien & Mackauer, 1990; Bai, 1991). *Aphidius ervi* showed a high rate of multiparasitism although it is able to recognize parasitized hosts. This high rate of multiparasitism is adaptive because of the competitive superiority of this species when in competition with *A. rhopalosiphi* (*A. ervi* wins in 77% of the contests when the time interval between the two ovipositions is short: Le Lann, in press). Likewise, the avoidance of multiparasitism by *A. rhopalosiphi* is functional because it loses competition with *A. ervi* in 77% of the contests.

Potential impact of interspecific host discrimination on resource sharing

Interspecific host discrimination is adaptive whenever there is sufficient overlap in host exploitation between two parasitoid species, such that their offspring is affected by the competition with heterospecific larvae. The occurrence of interspecific host discrimination is less well documented than that of intraspecific host discrimination (Bolter & Laing, 1983; McBrien & Mackauer, 1991; Scholz & Höller, 1992; Agboka *et al*., 2002; Wang & Messing, 2004; Ardeh *et al*., 2005). Interspecific host discrimination is more difficult to show in a competitively superior species because females of such a species should accept hosts already parasitized by the inferior competitor at a high rate. Interspecific host discrimination may be absent between unrelated parasitoid species (e.g. van Strien-van Liempt & van Alphen, 1981). In such cases, parasitoids of both species may be unable to recognize each other's marking substances due to a phylogenetic constraint.

There, in *A. rhopalosiphi*, we found a more frequent rejection of hosts parasitized by one of the other species than has been found earlier for hosts parasitized by conspecifics (Outreman *et al*. 2001a). The reason for this rejection could be a different one for *A. ervi* and *A. avenae*. The rejection of hosts parasitized by *A. ervi* could be due to the fact that *A. rhopalosiphi* is inferior in contests for the host to *A. ervi* larvae; the fitness returns of multiparasitism are, therefore, smaller than that of conspecific superparasitism for *A. rhopalosiphi* (Le Lann *et al*., in press). These findings are in agreement with earlier work, showing *A. ervi* to be a superior competitor in larval fights against other *Aphidius* species, such as *A. smithi* (McBrien & Mackauer, 1990). The rejection of hosts parasitized by *A. avenae* is more difficult to understand. As the hosts are not alerted after parasitism by *A. avenae*, the fitness returns from oviposition in such hosts are larger than that of oviposition in a host already parasitized by a conspecific. Indeed, when encountering a host parasitized by a conspecific, a female of *A. rhopalosiphi* takes the risk of being glued by the aphid if it stings it (Outreman *et al*., 2001a); whereas, when encountering a host parasitized by a *A. avenae* female, a female *A. rhopalosiphi* does not take any risk in inserting its ovipositor, and its host discrimination ability saves eggs.

In the guild of three *Aphidius* species, *A. rhopalosiphi* is the most abundant. It is present in the field all year round and is abundant when the two other species arrive (van Baaren *et al*., 2004). It exploits patches only partially, and leaves a patch when the parasitized aphids have started to emit cornicular secretions (Outreman *et al*., 2001a). These secretions are known to act as a pheromonal signal, alerting the other aphids of the presence of a natural enemy (Montgomery & Nault, 1977). The two other species have developed different strategies to avoid the defensive behaviour of the aphids (van Baaren *et al*., 2004, for *A. avenae*; and Le Lann, unpublished data, for *A. ervi*). Both show interspecific host discrimination and exploit the unparasitized hosts in the patches already partially exploited by *A. rhopalosiphi*.

Numerous studies have documented that parasitoids sharing a single host species exhibit species-specific microhabitat preference and/or differences in spatial distribution (e.g. habitats with different microclimates, host plant species, plant clones or individuals and plant parts: Kaneko, 2004). The species studied here show only partial niche differentiation with sufficient overlap to expose them to the negative effects of interspecific competition. The interspecific host discrimination found here allows all those species to use the shared resource efficiently; both *A. ervi* and *A. avenae* avoided hosts already parasitized by the abundant species, *A. rhopalosiphi*. The latter abandons host patches long before all hosts have been parasitized, leaving these hosts available for *A. ervi* and *A. avenae*. Hence, *A. ervi* and *A. avenae* can use a part of the host population not exploited by *A. rhopalosiphi* (i.e. the residual resource) with no risk of multiparasitism because of their ability to discriminate hosts already parasitized by this dominant competitor. *Aphidius ervi* and *A. avenae* are both so rare that the probability that they attacked the same host is negligible.

Acknowledgements

We thank Jacques van Alphen, Thomas Hoffmeister and an anonymous referee for helpful comments on a previous version of this manuscript. The experiments comply with the current laws of France. This work was supported by the European Marie Curie Chair programme COMPAREVOL (http://comparevol.univ-rennes1.fr/) and by the Brittany region programme ECOCLIM.

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