

Odour-mediated long-range avoidance of interspecific competition by a solitary endoparasitoid: a time-saving foraging strategy

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Summary

1. In studies on optimal foraging strategies, long-range decisions in the pursuit of resource are rarely considered. This is also the case for sympatric parasitoids, which may be confronted with the decision to accept or reject host larvae that are already parasitized by a competing species. They can be expected to reject already parasitized hosts if it is likely that they will lose the resulting intrinsic competition. However, examples of such interspecific host discrimination are rare.

2. We propose that parasitoids that are not egg-limited should reject inferior hosts only if it saves them time, and that this will be achieved mainly when the parasitoids are able to detect competitors from a distance. We tested this hypothesis using the sympatric parasitoids *Cotesia marginiventris* (Cresson) and *Campoletis sonorensis* (Cameron).

3. *C. sonorensis* was found to be the superior intrinsic competitor but, upon contact with a host larva, both wasps readily accepted hosts that had already been parasitized by the other species. However, in an olfactometer experiment, *C. marginiventris* females were found to strongly avoid the odour of their superior competitor.

4. These results are in accordance with a time optimization scenario, whereby the inferior competitor accepts competition if it costs only an egg, but avoids competition if it may save time that can be allocated to the search for more profitable hosts.

5. Models on host discrimination strategies in parasitoids had not yet considered discrimination from a distance. Long-range foraging decisions can also be expected for other organisms that have to choose between resources of varying suitability and profitability.

Key-words: competition, host discrimination, olfaction, optimal foraging, parasitoids.

Introduction

Optimal foraging theory concerns the decisions that animals make while foraging for resources that contribute to their reproductive success. Parasitic wasps searching for suitable hosts for their offspring have been ideal models for such studies (Godfray 1994; Quicke 1997). Parasitoids frequently have to decide whether to lay eggs in already parasitized hosts, which may be inferior resources compared to unparasitized hosts. In case of multiparasitism by individuals of more

than one solitary endoparasitoid species, usually only one individual will successfully develop inside the host, after having eliminated the other(s). Parasitoid larvae can combat each other through physical attack, physiological suppression or both (Salt 1961; Vinson 1972; Vinson & Iwantsch 1980b; Bai & Mackauer 1991; Tillman & Powell 1992a, 1992b; van Baaren & Nenon 1996). The species that lays its egg first can be expected to win the competition (Bautista & Harris 1997; Wallner, Weseloh & Grinberg 1982; Collier, Kelly & Hunter 2002), but often the survival among same-aged parasitoid larvae is found to be independent of the oviposition sequence (Mackauer *et al.* 1992). The outcome of competition may also depend on the time elapsed between the two parasitization events (Isenhour 1988; Baur & Yeagan 1995; De Moraes *et al.* 1999; Ueno 1999).

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If female wasps can distinguish between already parasitized and unparasitized larvae they may reject the parasitized hosts to avoid competition. Rejection of hosts already parasitized by conspecifics (intraspecific host discrimination) is common in larval parasitoids (van Alphen & Visser 1990). Kin selection is likely to be one of the driving forces that has led to the recognition and avoidance of hosts that are already parasitized by conspecifics. Indeed, the likelihood of avoidance of superparasitism increases with the relatedness of the potentially competing parasitoids (Marris, Hubbard & Scrimgeour 1996). Kinship does not play a role in the avoidance of multiparasitism and therefore, in the absence of relatedness, it is expected that competitive ability (chance of surviving the competition), eggload and time are the key factors that determine the incidence of host discrimination (van Lenteren 1981; van Alphen & Visser 1990). It has been a topic of considerable discussion whether eggload or time is the principal limiting factor of fitness in parasitoids (Rosenheim 1996; Sevenster, Ellers & Driessen 1998), but it is clear that in nature the average life span of solitary parasitoids is often too short to deposit all their eggs (Rosenheim 1999). Therefore selection should strongly favour time optimization in parasitoid foraging strategies.

Interspecific host discrimination (avoidance of multiparasitism) has been rarely observed and mainly for closely related species (van Lenteren 1981; Vet *et al.* 1984; van Baaren, Boivin & Nenon 1994; Royer *et al.* 1999; Agboka *et al.* 2002; Ardeh, de Jong & van Lenteren 2005), in which cases it could be an artefact of still using the same cues to avoid superparasitism. Van Alphen & Vissen (1990) argue convincingly that interspecific host discrimination should only evolve in inferior competitors. As some parasitoid species are indeed very poor competitors inside the host (intrinsic), why then is interspecific host discrimination rarely observed among sympatric, non-related parasitoids? Here we argue that most studies have not considered host discrimination from a distance.

Solitary endoparasitoids that use lepidopteran larvae as host usually carry ample eggs and time is therefore expected to be their most important limiting factor. Based on a simulation model, Turlings, van Batenburg & van Strien van Liempt (1985) suggest that as long as a female parasitoid is not egg-limited and oviposition is not overly time-consuming she should accept a host already parasitized by another species, even if the chance of offspring survival is small. Based on results of a field study on parasitoids of *Drosophila* larvae, Janssen (1989) drew a similar conclusion. Things would be different if host rejection would result in considerable time gain, time that could be used to find more suitable hosts (Turlings *et al.* 1985). Such a time gain could be achieved if already parasitized hosts are detected and rejected from a distance.

Long-distance avoidance of possible competitors was first reported by Price (1970), who found that in the three ichneumonid genera *Pleolophus*, *Endasys* and

Mastrus, females avoid areas where other parasitoids had searched previously for hosts. Similarly, Janssen *et al.* (1995a, b) showed the ability of the parasitoid *Leptopilina heterotoma* to recognize and avoid patches with the superior competitor, *L. clavipes*, using volatiles substances. This avoidance occurs only when both hosts and competing parasitoids are present on the same patch and the competitors have had contact with the hosts. The exact source and identity of the avoidance-invoking odour remains unknown. The odours could be produced by parasitoids searching for hosts, by host larvae that are being attacked or they could be a side effect of the oviposition behaviour of the parasitoid (Janssen *et al.* 1995b). Interestingly, and in accordance with our hypothesis, *L. heterotoma* do not avoid laying eggs in hosts already parasitized by *L. clavipes*. Thus, Janssen and coworkers provide the first support for a time saving strategy. Such sophistication in parasitoid foraging behaviour can be expected only in closely coevolved systems, where parasitoids occupy similar niches.

Here we present a study on another closely coevolved system for which we specifically tested the hypothesis of time-saving competition avoidance. The solitary endoparasitoids *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) and *Campoletis sonorensis* (Cameron) (Hymenoptera: Ichneumonidae) are the main parasitoid species that attack larvae of *Spodoptera frugiperda* (Lepidoptera: Noctuidae), one of the most important insect pests of different crops in the Americas (Sparks 1979; Andrews 1988; Ashley *et al.* 1989). *C. marginiventris* and *C. sonorensis* co-occur throughout North America and have been collected frequently in the same maize fields (Pair *et al.* 1986; Andrews 1988; Riggins *et al.* 1993; Molina-Ochoa *et al.* 2001; Hoballah *et al.* 2004) and are expected to have a long history together, which may have led to traits that reduce competition between the wasps. They both attack second and third instar larvae (Isenhour 1985; Jalali, Singh & Ballal 1987), but neither *C. marginiventris* nor *C. sonorensis* seems to avoid to lay eggs in larvae already parasitized by conspecifics or by other species (Rajapakse, Ashley & Waddill 1991; Rajapakse, Waddill & Ashley 1992; Baur & Yeangan 1995; Escribano *et al.* 2000).

Several studies have evaluated how *C. marginiventris* (Isenhour 1988; Rajapakse *et al.* 1991; Rajapakse *et al.* 1992; Escribano *et al.* 2000; Sallam, Overholt & Kairu 2002) and *C. sonorensis* (Vinson 1972; Vinson & Ables 1980a; Escribano *et al.* 2000) compete with other parasitoid species, but no information exists on the competition between the two. Depending on the species they were competing with, both species were found to be either superior or inferior intrinsic competitors (Miller 1977; Isenhour 1988; Rajapakse *et al.* 1991; Baur & Yeangan 1995; Escribano *et al.* 2000). All the larval instars of both *C. marginiventris* and *C. sonorensis* possess mandibles that potentially could be used to attack other parasitoid larvae (Boling & Pitre 1970; Wilson & Ridgway 1975). The developmental time of *C. marginiventris* and

C. sonorensis is similar and depends strongly on temperature (Wilson & Ridgway 1975; Kunnalaca & Mueller 1979; Isenhour 1986).

Like many other parasitoids of herbivores (Turlings & Benrey 1998; Dicke & Vet 1999; Turlings & Wäckers 2004b), *C. marginiventris* and *C. sonorensis* are both attracted to the odours produced by the plants attacked by their hosts (Elzen, Williams & Vinson 1983, 1984; Turlings, Tumlinson & Lewis 1990; McAuslane, Vinson & Williams 1991; Turlings, Davison & Tamo 2004a). However, nothing is known about the long-range interaction and possible interference in the hosts searching process between the two species.

Here we show that *C. sonorensis* has the best chance to survive in case of multiparasitism and that this is affected neither by the sequence in which the two species parasitize the same host nor by the time difference between the respective ovipositions. The competitive superiority of *C. sonorensis* was confirmed in cage studies with host larvae on small maize plants, in which the wasps could forage freely together. A six-arm olfactometer was used to investigate if the wasps respond to the odour of competing females, with the expectation that the inferior competitor might avoid the odour of other species to optimize its time allocation in favour of the search for the most suitable hosts. *C. marginiventris* was indeed found to be repelled by the odour of *C. sonorensis*.

Methods

INSECTS

The rearing colony of *C. marginiventris* originated from the USDA-ARS, Biological Control and Mass Rearing Research Unit (Mississippi, USA). The *C. sonorensis* colony was established in 2001 from individuals collected from parasitized *S. frugiperda* larvae in maize fields in Mexico (Poza Rica, Veracruz, Mexico). That year the *C. marginiventris* was replenished with wasps from the same fields. Both parasitoids were reared on *S. littoralis*. For the rearing, 25 *S. littoralis* caterpillars (2–4 days old) were offered to two mated females (4–7 days old) for 3 h in a plastic container (9.5 cm diameter, 5 cm high). The parasitized caterpillars were then placed into transparent plastic boxes (15 × 13 × 5.5 cm) on a wheatgerm-based artificial diet until cocoon formation. Cocoons were kept in open Petri dishes, which were placed in Bugdorm-1 cages (30 × 30 × 30 cm) (MegaView Science Education Services Co. Ltd, Taiwan) at a sex ratio of 1 : 2 (male : female), with wet cotton wool and honey as a food source. Parasitized host larvae and adults of *C. marginiventris* were held until the experimental day in an incubator (25 °C and 16 L : 8D), whereas parasitized larvae and adults of *C. sonorensis* were held in the laboratory under ambient light and temperature conditions (19–24 °C). All experiments were conducted with 2–4-day-old naive mated females.

S. littoralis larvae were reared from eggs provided by Syngenta (Stein, Switzerland). The eggs were kept in the above-described incubator and after emergence larvae were placed on artificial diet at room temperature, until using them either for rearing or for the experiments.

PLANTS

For the cage experiment 10–11-day-old maize plants with four to five fully developed leaves (var. Delprim) were used, whereas 8–9-day-old maize plants of the same variety with three to four developed leaves were used for the olfactometer experiment. One seed (for the cage experiment) or two seeds (for the olfactometer experiment) were planted per pot (200 mL) in commercial soil (COOP, Switzerland) and grown in a climate chamber (23 °C, 60% r.h., 16D: 8 L, 50 000 L m⁻¹ m²). The day before an olfactometer experiment started, the plant pairs were transplanted into glass pots that fitted the olfactometer (250 mL, 4.5 cm diameter, 11 cm high).

INTRINSIC COMPETITION

To determine the intrinsic competitive ability of each species we set up the following experiment. Twenty-five second instar *S. littoralis* larvae were offered to two parasitoid females (2–4 days old) of one of the two parasitoid species in a plastic box (9.5 cm diameter, 5 cm high). If a female did not sting any larvae within 5 min, another female was used. As soon as stinging with the ovipositor was observed, the presumably parasitized larva was removed and transferred to another identical plastic box. After 25 larvae were parasitized they were either (1) kept on artificial diet or (2) offered to two parasitoid females of the other species after 5–10 min (0 days), 1 day or 2 days. During the second oviposition cycle the females were also observed and the multiparasitized larvae were removed immediately and transferred into a new plastic box with artificial diet. All the larvae that were assumed to have been singly parasitized or multiparasitized were then reared on artificial diet until cocoon development, in a separate box for each of the four treatments. The experiment was replicated six times for each combination of parasitoids and time delay between ovipositions. Unparasitized larvae were easily recognizable after 3–5 days, as they grew much larger than the parasitized larvae. They were counted and removed. The number of dead larvae was recorded daily, as were the number of cocoons of each parasitoids species that were formed.

CAGE EXPERIMENTS

To investigate possible competitive interactions in a simultaneous foraging situation, a second experiment was carried out where the females could interfere with each other either directly (disturbance, aggressive behaviour) or indirectly (interspecific host discrimination, multiparasitism, etc.). For each replication we

used six cages Bugdorm-2 (60 × 60 × 60 cm) (MegaView Science Education Services Co. Ltd, Taiwan), each holding five pots containing a 10–11-day-old maize plant. Fifteen second instar *S. littoralis* larvae were placed on each plant (75 larvae per cage) and were allowed to feed during one night before releasing the wasps. Each cage received a different combination of parasitoids: either eight *C. marginiventris*, eight *C. sonorensis*, four *C. marginiventris* + four *C. sonorensis*, four *C. marginiventris*, four *C. sonorensis* or two *C. marginiventris* + two *C. sonorensis*. The parasitoids were left with the plants and the larvae for 24 h. The hosts were collected, counted and kept in plastic boxes with artificial diet (one per cage). The experiment was replicated three times. We checked daily for dead and unparasitized larvae, and for the emergence of the cocoons.

For both the above experiments, a *G*-test with William's correction was used to test for differences between the species in the number of cocoons, unparasitized larvae, dead larvae and larvae that were not found back (the latter only for the cage experiment). In cases of significance, a pairwise comparison between treatments was performed after the *G*-values were subjected to a Yates' continuity correction.

OLFACTOMETER ASSAYS

A six-arm olfactometer (Turlings *et al.* 2004a) was used to test if the female wasps responded to the odour females of the competing species or to the odour of conspecifics. The olfactometer consists of six odour vessels that are connected to the six arms of a central chamber in which the parasitoids can choose between different odours. In this apparatus both species have shown to be attracted readily to the odours of plants damaged by their hosts (personal observations). The experiments tested if this attraction of the parasitoids to the induced plant odours was affected by the presence of females of their own species or of the competing species. Three odour sources were prepared, each with two maize plants on which 20 second instar *S. littoralis* larvae were allowed to feed during one night; vessels holding these plants were alternated with empty (control) vessels. One h before an assay, 10 females of *C. marginiventris* were placed in an arm connected to a vessel with caterpillar-damaged plants; to another such arm 10 *C. sonorensis* females were added, and no wasps were added to the third arm. During the first 0.5 h the females were trapped in the arms using plugs of cotton to prevent them from either walking up into the trapping bulb or out of the arm into the choice chamber (see Turlings *et al.* 2004a for a detailed drawing of the olfactometer). In this manner, any odour emitted by the females could adsorb onto the glass in the arm. After 0.5 h the cotton plugs were removed and the normal experimental airflows were passed through all arms. The wasps remained in the arm and were given 0.5 h to settle in the trapping bulb. On each test day, three groups of six naive females of each species were released alternately in the choice

chamber and their choices were recorded. Each group of females was given 0.5 h to make a choice and then removed. This experiment was replicated on 6 different days, with the different odours being introduced through different arms and alternating between the species that was first released in the olfactometer. A log-linear model assuming quasinormal distribution, thus allowing for overdispersion of the wasps, was used in statistical tests for odour preferences (Turlings *et al.* 2004a).

COLLECTION AND ANALYSES OF VOLATILES

During the 3-h bioassays, part of the volatile emissions from each odour source was collected by sucking 50% of the air flow out of each odour source vessel through a trapping filter containing 25 mg of 80–100 mesh Super Q adsorbent (Altech, Deerfield, IL, USA), as described by Turlings *et al.* (2004a). Immediately after each experiment, the volatiles collected on the filters were extracted with 150 µL of methylene chloride and two internal standards (n-octane and nonyl acetate, each 200 ng in 10 µL methylene chloride) were added to these extracts. Aliquots of these samples were analysed by gas chromatography and mass spectrometry, as described by Turlings *et al.* (2004a). Total quantities of the collected volatiles were calculated based on their peak areas compared to those of the internal standards. Analysis of variance (ANOVA) and Student–Newman–Keuls *post-hoc* tests were used to compare the total quantity of volatiles emitted among plant species.

Results

INTRINSIC COMPETITION

In all cases where the larvae were multiparasitized, significantly more *C. sonorensis* than *C. marginiventris* cocoons emerged from the parasitized larvae (Fig. 1). Larvae that were parasitized only by *C. sonorensis* yielded similar numbers of *C. sonorensis* cocoons as the multiparasitized larvae ($G_{\text{adj.}} = 3.42$, $P = 0.75$). In contrast, when larvae were parasitized by *C. marginiventris* only, significantly more *C. marginiventris* cocoons were produced than when larvae were multiparasitized ($G_{\text{adj.}} = 134.28$, $P < 0.001$). When the larvae were subjected to an oviposition by only one of the two species, significantly more *C. marginiventris* emerged than *C. sonorensis* ($G_{\text{adj.}} = 10.11$, $P < 0.01$). The number of parasitized larvae that died before forming a cocoon was also significantly different among treatments: there were fewer dead larvae when they were parasitized only once and in the cases of multiparasitism larval mortality increased with the number of days between the two parasitization events ($G_{\text{adj.}} = 16.69$, $P < 0.05$). The numbers of larvae that were found to be unparasitized (or survive parasitism) was significantly higher when they only had been stung by *C. sonorensis* ($G_{\text{adj.}} = 70.20$, $P < 0.001$).

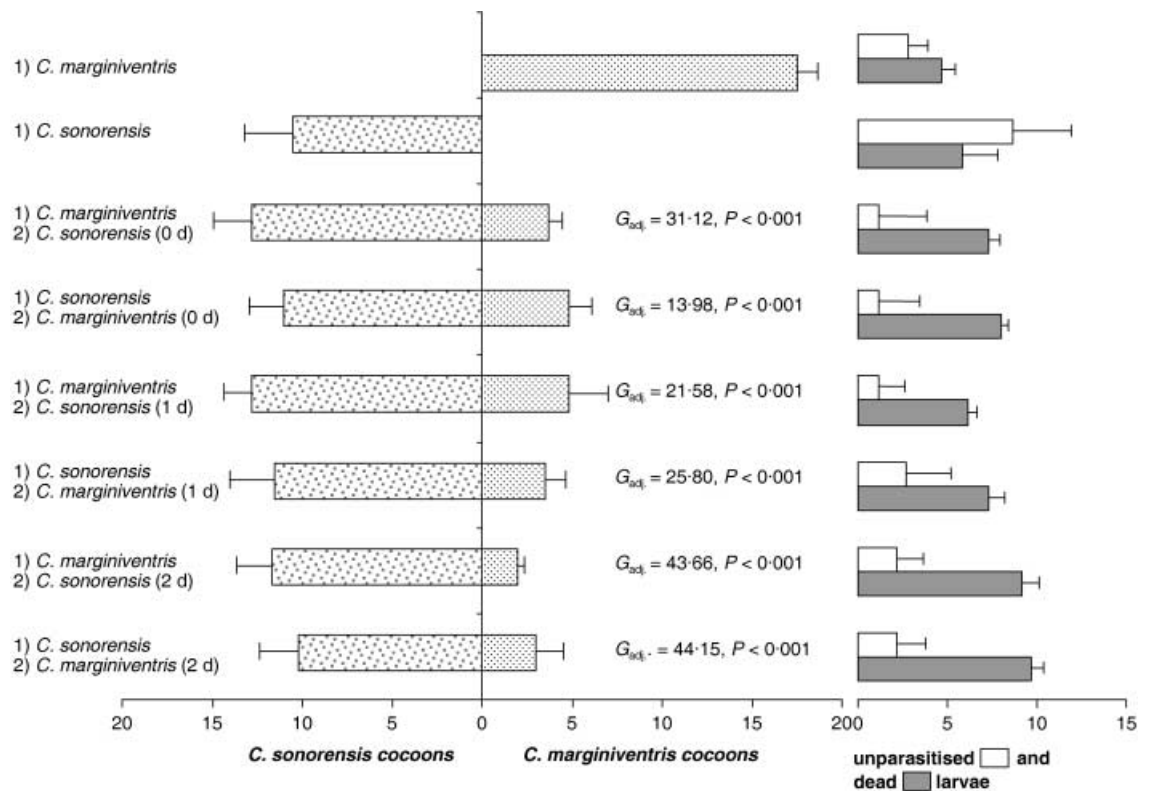


Fig. 1. Outcome of intrinsic competition experiments. Host larvae were parasitized by *C. marginiventris* and/or *C. sonorensis* and in case of parasitization by both species, the order in which the two species were allowed to oviposit and the time in between ovipositions varied (0, 1 or 2 days in between ovipositions). The bars on the left indicate the number of parasitoids that emerged from the host larvae (number of cocoons formed). Significant differences between the cocoons recorded for the two species are shown next to the bars. The bars on the right represent the larvae that died or survived parasitism.

CAGE EXPERIMENTS

In the cages where the two parasitoids foraged together significantly more *C. sonorensis* than *C. marginiventris* cocoons emerged from the larvae (Fig. 2: $G_{adj.} = 41.85$, $P < 0.001$); this was true in the cages with two *C. marginiventris* and two *C. sonorensis* females ($G_{adj.} = 21.44$, $P < 0.001$), as well as for the cages with four females of each species ($G_{adj.} = 19.29$, $P < 0.001$). The number of cocoons of *C. sonorensis* was significantly higher for the cage where four *C. sonorensis* females foraged alone compared with all the other treatments with *C. sonorensis* ($G_{adj.} = 13.95$, $P < 0.01$). Significantly fewer *C. marginiventris* cocoons were found in the cages where the two species were foraging together compared with the cages where *C. marginiventris* foraged alone ($G_{adj.} = 77.13$, $P < 0.001$), but no significant difference was found in the number of cocoons between cages with either four or eight females of this species foraging alone ($G_{adj.} = 0.74$, $P = 0.4$). There was no difference between *C. marginiventris* and *C. sonorensis* in parasitism effectiveness when they foraged alone ($G_{adj.} = 0.01$, $P = 0.9$).

The number of parasitized larvae that died before a cocoon was formed was significant different among treatments. Fewer larvae died from cages with only *C. sonorensis*, and larval mortality was highest for the cages in which four *C. marginiventris* and four *C. sonorensis* had foraged together ($G_{adj.} = 18.70$, $P < 0.01$). The

number of unparasitized larvae was highest in the two treatments with only *C. marginiventris* ($G_{adj.} = 31.82$, $P < 0.001$). Finally, the number of larvae that were not found back was significantly higher for the cages with eight *C. sonorensis* ($G_{adj.} = 16.99$, $P < 0.01$).

OLFACTOMETER ASSAYS

Females of both species were readily attracted to the arms that carried the odour of host-infested plants (Fig. 3). *C. marginiventris* females rarely entered the empty arms or the arm with *C. sonorensis* females plus maize odour, whereas they often chose the arm containing only maize odour or the arm with maize odour combined with *C. marginiventris* females (Fig. 3a). The *C. sonorensis* females also rarely entered the empty arms, but they chose equally well among the arms containing maize odour, independently of the presence of other female wasps (Fig. 3b). No significant differences were found between the total amounts of volatiles produced by the induced maize plants present in the different arm (Fig. 3c; $P = 0.22$).

Discussion

The intrinsic competition between *C. sonorensis* and *C. marginiventris* was almost always won by *C. sonorensis*, even if *C. marginiventris* had parasitized 2 days earlier

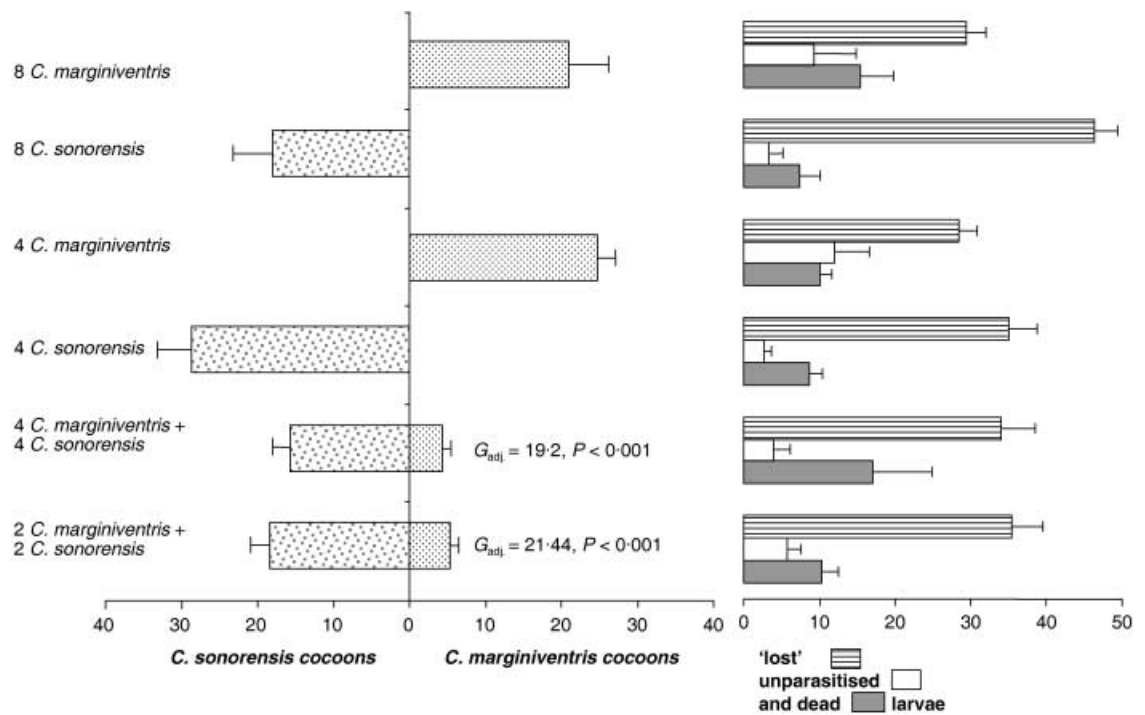


Fig. 2. Outcome of cage competition experiments. *C. marginiventris* and/or *C. sonorensis* wasps were placed for 24 h in cages with ample host larvae on maize plants. Numbers of wasps in the different cages varied as indicated. The bars on the left represent the number of parasitoids that emerged from the recollected host larvae (number of cocoons formed). Significant differences between the cocoons recorded for the two species are shown next to the bars. The bars on the right represent the larvae that were not found back, that died or that survived parasitism.

(Fig. 1). We did not establish whether this was a result of physical or physiological attack. However, cases of physical attack have been documented for *C. sonorensis* by Vinson & Ables (1980a). A closely related species, *C. perdistinctus*, employs both physical and physiological attack to suppress the larvae of *Cardiochiles nigriceps* in case of multiparasitism, depending on the time elapsed among the two parasitization events and on their sequence (Vinson 1972).

A large proportion of larvae was not successfully parasitized when *C. sonorensis* was the sole attacker (Fig. 1). This either means that there was not always an egg deposited when a sting was observed, or that some eggs or larvae did not survive inside the singly parasitized hosts. Therefore the competitive ability of *C. sonorensis* may have been under-estimated, because a certain proportion of the larvae that were assumed to be double-parasitized might not have contained a viable *C. sonorensis* larva. Indeed, *Spodoptera* species are not the most suitable hosts for *C. sonorensis*, as they may be able to resist parasitism by encapsulating a proportion of the parasitoid's eggs (Prevost, Davies & Vinson 1990; Cui, Soldevila & Webb 2000). In this context it should be noted that there was a consistent tendency that in the trials where *C. marginiventris* parasitized first, more *C. sonorensis* were produced. This suggests that *C. sonorensis* larvae may have benefited from the ability of *C. marginiventris* to suppress a host resistance factor. Various hymenopteran parasitoids, including *C. marginiventris* (Hamm,

Styer & Lewis 1990; Styer, Hamm & Nordlund 1987), suppress host resistance by injecting a polydnavirus in a host together with an egg and a study by Cusson *et al.* (2002) suggest that the injection of a polydnavirus by one parasitoid species may help a second parasitizing species. Hence, *C. sonorensis* may benefit from the presence of *C. marginiventris* and there would be no reason for the former to avoid the latter. In fact, *C. sonorensis* can be expected to prefer hosts larvae that have already been parasitized by *C. marginiventris*, which could explain why the olfactometer arm with *C. marginiventris* attracted slightly more *C. sonorensis* (Fig. 3b).

The cage experiments showed that when *C. marginiventris* and *C. sonorensis* were alone their parasitism rates were comparable. However, when the two species of parasitoids searched together for the hosts in the same cage, the proportion of *C. marginiventris* emerging was drastically reduced (Fig. 2). This is due probably to the superiority of *C. sonorensis* in the intrinsic competition, but could also in part be the result from a reduced oviposition rate caused by direct interference between the adults. The latter possibility is indicated by the results from the olfactometer experiment. Both species were equally attracted to the induced odours produced by the maize plants under caterpillar attack, but the *C. marginiventris* females avoided the arms containing females of *C. sonorensis*. This implies that *C. marginiventris* uses volatile cues to avoid patches where *C. sonorensis* females are already searching for

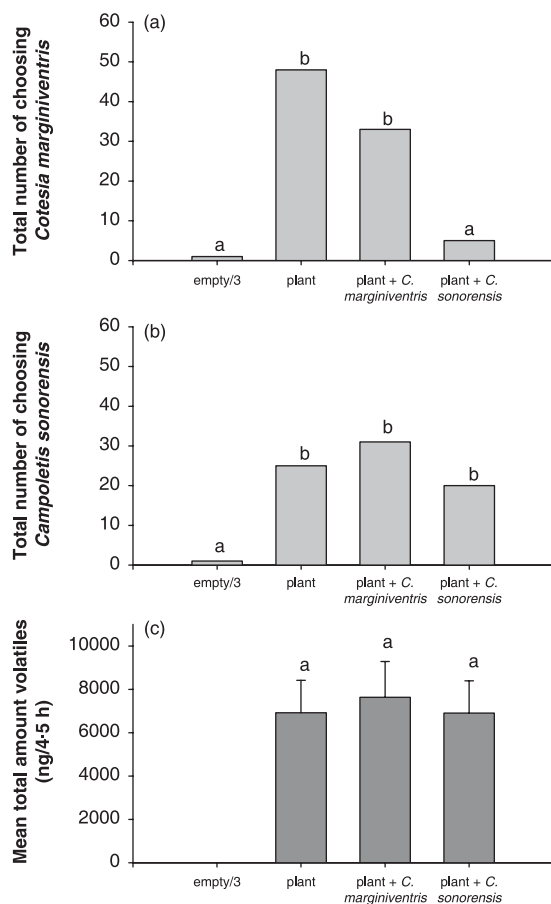


Fig. 3. Results from six-arm olfactometer experiments. Responses of females of (a) *C. marginiventris* or (b) *C. sonorensis* that were offered a choice between the odours of host-infested maize plants alone, host-infested maize plants plus 10 *C. marginiventris* females, host-infested maize plants plus 10 *C. sonorensis* females, and three olfactometer arms that carried clean air. The bars represent the totals of choices made over all replicates. The letters above the bars indicate significant differences calculated from a log-linear model, which used the values of each replicate ($n = 18$ groups of six wasps, $P < 0.001$). Graph (c) shows the total amounts of volatiles collected for each odour source during the bio-assays ($n = 6$). No significant differences were found among the arms that carried the odour of an infested maize plant.

hosts. This is similar to the interaction between the two *Drosophila* parasitoids *Leptopilina heterotoma* and *L. clavipes* (Janssen *et al.* 1995a). The inferior competitor, *L. heterotoma*, avoids stinkhorn patches where *L. clavipes* are present. Janssen *et al.* (1995b) also found that *L. heterotoma* avoids stinkhorn patches with conspecifics. *C. sonorensis* and *C. marginiventris* did not avoid the odour of conspecifics.

As in the studies by Janssen and colleagues the long-range avoidance of heterospecific competitors must be due to a repellent odour. In our case it can be excluded that the repellence was due to a change in the odours produced by the herbivores in the presence of the competing parasitoid, as has been suggested in the avoidance of the *Drosophila* parasitoid *L. clavipes* by its competitor *L. heterotoma* (Janssen *et al.* 1995b). In our

olfactometer assays, the plants and the hosts were separated from the parasitoids and there was no interaction with hosts possible.

Price (1970) noted that ichneumonid parasitoid females avoided areas that had previously been searched by conspecific and heterospecific parasitoids and suggested that this was due to the 'pungent' smell they emit. Ours appears to be the first study to demonstrate that indeed parasitoid-produced odours directly affect other members of the third trophic level. *C. sonorensis* is an ichneumonid and, as was the case for the wasps studied by Price (1970), produces a scent that is detectable by the human nose. Hence, an odourous signal is available that may be used by *C. marginiventris* to avoid its competitor. This avoidance of competition occurs only at a distance and not when a female contacts larvae that have already been parasitized. This may be because there are no contact signals that allow them to make the distinction between parasitized and unparasitized host, but given that various parasitoids can make such a distinction (van Alphen & Visser 1990), it is more likely that the wasps 'choose' to accept inferior hosts when they contact them. This is in accordance with our expectation that the wasps' foraging success is limited by time rather than by egg load. The wasps carry ample eggs and can waste some to poor-quality hosts. Moreover, an oviposition takes a few seconds at most, whereas the preceding location of the host can take considerably more time (personal field observations). Avoiding already parasitized hosts from a distance may therefore save them sufficient time to increase the likelihood of finding a larger number of more suitable hosts during their life span. Theoretical models used to predict whether or not parasitoids should discriminate between parasitized and unparasitized host have not yet considered discriminations from a distance (van Alphen & Visser 1990). These models predict that discrimination is more likely to occur if rejection time is much shorter than handling time (host recognition and oviposition time). Adding host recognition from a distance and subsequent host location time to the handling time in these models would greatly alter their outcome. Hence, interspecific host discrimination may be far more common than thus far assumed. Optimal foraging models developed for other systems should also consider the possibility of time saving foraging decisions from a distance.

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