Behaviour of male and female parasitoids in the field: influence of patch size, host density, and habitat complexity

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Bezemer, T.M.; Harvey, J.A.; Kamp, A.F.D.; Wagenaar, R.; Gols, R. et al

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T . M A R T I J N   B E Z E M E R ,[1,2] J E F F R E Y   A .   H A R V E Y ,[1] A N D R É   F .   D . K A M P ,[1] R O E L   W A G E N A A R ,[1] R I E T A   G O L S ,[3] O L G A   K O S T E N K O ,[1] T A I A D J A N A   F O R T U N A ,[1] T I M   E N G E L K E S ,[1] L O U I S E   E .   M .   V E T ,[1,3] W I M   H .   V A N   D E R   P U T T E N[1,2] and R O X I N A   S O L E R[1,3] [1]Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Heteren, The Netherlands, [2]Laboratory of Nematology, Wageningen University and Research Centre, Wageningen, The Netherlands and [3]Laboratory of Entomology, Wageningen University and Research Centre, Wageningen, The Netherlands

Abstract. 1. Two field experiments were carried out to examine the role of patch size, host density, and complexity of the surrounding habitat, on the foraging behaviour of the parasitoid wasp *Cotesia glomerata* in the field.

2. First, released parasitoids were recaptured on patches of one or four *Brassica nigra* plants, each containing 10 hosts that were placed in a mown grassland area. Recaptures of females were higher than males, and males and females aggregated at patches with four plants.

3. In experiment 2, plants containing 0, 5 or 10 hosts were placed in unmown grassland plots that differed in plant species composition, on bare soil, and on mown grassland. Very low numbers of parasitoids were recaptured in the vegetated plots, while high numbers of parasitoids were recaptured on plants placed on bare soil or in mown grassland. Recaptures were higher on plants on bare soil than on mown grassland, and highest on plants containing 10 hosts. The host density effect was significantly more apparent in mown grassland than on bare soil.

4. *Cotesia glomerata* responds in an aggregative way to host density in the field. However, host location success is determined mostly by habitat characteristics, and stronger host or host-plant cues are required when habitat complexity increases.

Key words. *Brassica nigra*, *Cotesia glomerata*, density dependency, habitat, *Pieris brassicae*, plant diversity, release–recapture, searching efficiency, spatial distribution.

Introduction

Parasitoids have long been used as model organisms in behavioural and evolutionary studies. Traditionally, host foraging by parasitoids is described through several steps that ultimately lead to successful parasitism. These are described through a hierarchical process of habitat location, host-plant location, and host location (Vinson, 1976), and parasitoids are known to use stimuli associated with the host, the host plant

or the microhabitat to locate their hosts (Godfray, 1994). A major limitation in parasitoid behavioural research is that by far most of what we know about host and host-plant location is derived from laboratory studies, whilst our knowledge about the behaviour of parasitoids in the field is still very limited (reviewed in Casas, 2000; Heimpel & Casas, 2007). In the field, parasitoid behaviour can differ greatly from what has been observed in the laboratory, where conditions are usually strictly controlled. For example, behaviour and activity can be influenced by abiotic, climatic factors such as wind speed, relative humidity, and precipitation that may vary over limited spatial and/or temporal scales (e.g. Casas, 1989; Fink & Völkl, 1995; Weisser *et al.*, 1997; Marchand & McNeil, 2000; Gu & Dorn, 2001).

In nature, the biotic and abiotic environment in which a parasitoid forages, can also significantly influence its behaviour and host location success. Parasitoid movement and host-finding abilities, for example, can be greatly influenced by habitat characteristics such as the structure or diversity of the vegetation in which the host plants are embedded (Andow, 1991; Bottrell *et al.*, 1998). Habitat structure can directly influence parasitoids, for example by physically hampering parasitoid movement or by masking host plants (e.g. Andow & Prokrym, 1990; Casas & Djemai, 2002; Gols *et al.*, 2005; Obermaier *et al.*, 2008). Apart from physical barriers, chemical cues used by searching parasitoids for host location may be disrupted by non-host plants (Sheehan, 1986; Perfecto & Vet, 2003; Bukovinszky *et al.*, 2007; Randlkofer *et al.*, 2007). A number of field studies have shown that specialist parasitoids are more abundant in simple plant communities than in complex ones, because their hosts are more abundant and easier to locate (Sheehan & Shelton, 1989; Coll & Bottrell, 1996). Diverse plant communities may also be more risky for searching parasitoids, since these communities often harbour higher densities of generalist natural enemies such as predators (enemies hypothesis; Root, 1973). On the other hand, nutritional resources such as nectar are frequently more abundant in diverse plant communities (Wäckers *et al.*, 2005). This can lead to a higher abundance of parasitoids in diverse plant communities (Andow, 1991), since the survival of many parasitoid species greatly depends on the availability of such food resources (Winkler *et al.*, 2006).

Within a specific habitat, the distribution of host plants and the density of hosts on a plant are typically highly variable. Parasitoids have evolved mechanisms that enable them to cope with these conditions, such as the ability to use chemical cues from herbivore-damaged plants and to adapt their behaviour based on previous experiences (Vet & Dicke, 1992). Theoretically this should lead to higher number of parasitoids and higher levels of parasitism in patches with more hosts. Data on behavioural responses of parasitoids to patch size or host density in the field are scarce (Waage, 1983; Casas, 1989; Sheehan & Shelton, 1989; Connor & Cargain, 1994; Völkl & Kraus, 1996; Legaspi & Legaspi, 2005; White & Andow, 2005). Some studies have reported that parasitoids aggregate at patches with high host densities (e.g. Umbanhowar *et al.*, 2003; White & Andow, 2005). However, true aggregative responses, where parasitoid numbers per unit host density increase, have rarely been reported. Moreover, most studies report inverse or independent relationships between host density and the level of parasitism in the field (Stiling, 1987; Hassell, 2000; Bezemer & Mills, 2001; Umbanhowar *et al.*, 2003; Pareja *et al.*, 2008). Thus, whether parasitoids display true positive density-dependent host location responses in the field remains unresolved (Hassell, 2000; Wajnberg *et al.*, 2007).

Studies of parasitoid foraging behaviour typically focus on female wasps. However, most parasitic wasps are haplodiploid, where fertilised eggs develop into females while unfertilised eggs produce males (Godfray, 1994). Consequently, mate finding in male parasitoids should also be an important determinant of parasitoid fitness (Fauvergue *et al.*, 1995, 2008; Schwörer *et al.*, 1999). To locate potential mates, male parasitoids are known to use volatiles or substrate borne sex pheromones (e.g. Fauvergue *et al.*, 1995; McNeil & Brodeur, 1995). Furthermore, they may use information to find cocoons where females are about to emerge, as well as sites where females aggregate to feed and forage for hosts (Nadel & Luck, 1992; Godfray, 1994; Gu & Dorn, 2003). However, whether males use host or habitat cues when searching for females has been little studied (Villagra *et al.*, 2005), although the results of some laboratory studies suggest that parasitoid males can use chemical cues from the host-plant complex to locate mates (McAuslane *et al.*, 1990; Villagra *et al.*, 2005, 2008). It is not known if male parasitoids respond to host patches in a density-dependent manner.

We used release–recapture studies to investigate host and host-plant finding behaviour in the field, using the parasitoid *Cotesia glomerata* and its most common host in Europe, *Pieris brassicae* larvae, which feed on wild and cultivated crucifer species. *Cotesia* species, including *C. glomerata* have been commonly used as a model species for behavioural studies (e.g. Mattiacci *et al.*, 1995; Geervliet *et al.*, 1996; Van Nouhuys & Via, 1999; Soler *et al.*, 2007). In the laboratory, females of this species orientate upwind towards herbivore-induced plant volatiles (e.g. Steinberg *et al.*, 1992, 1993; Geervliet *et al.*, 1996, 2000; Gu & Dorn, 2001), and they exhibit a density-dependent response to odours from cruciferous plants infested with different densities of their hosts (Geervliet *et al.*, 1998). A previous study conducted in large tents reported that the host finding behaviour of *C. glomerata* females was greatly influenced by the occurrence of root herbivory on neighbouring plants, indicating that females of this species can also use habitat-related information to locate hosts (Soler *et al.*, 2007). In the present study we specifically test: (i) whether female and male *C. glomerata* adults respond to host density and host-plant density in the field, (ii) whether male and female host location differs in the field, and (iii) what the influence is of the complexity of the habitat or vegetation on host or host-plant location behaviour of *C. glomerata*. We hypothesise that (i) female and male parasitoids will respond to host density and host-plant density in the field, but that (ii) females will show stronger responses than males, and that (iii) habitat complexity will have a negative impact on host location of parasitoids.

Materials and methods

General

We used a well studied tritrophic system consisting of the widely distributed wild annual crucifer, *Brassica nigra*, L. (Capparales), the chewing foliar insect herbivore *Pieris brassicae* L. (Lepidoptera, Pieridae), and the larval endoparasitoid *Cotesia glomerata* L. (Hymenoptera, Braconidae), a gregarious endoparasitoid that attacks young larvae of several species of pierid butterflies with *P. brassicae* being its preferred host (Brodeur *et al.*, 1996; Harvey *et al.*, 2003). The ecology of *C. glomerata* has been described elsewhere and this species can be found in meadow habitats (Sato & Ohsaki, 1987; Benson *et al.*, 2003). *Cotesia glomerata* is a relatively large parasitoid and is able to disperse quickly in

the fields (Wanner *et al.*, 2006). Damaged host plants become relatively quickly attractive to adult *C. glomerata* females, typically within less than 24 h after feeding damage occurs (Steinberg *et al.*, 1992). *Pieris brassicae* larvae were obtained from an insect culture maintained at the Laboratory of Entomology, Wageningen University, The Netherlands and had been reared on Brussels sprouts *B. oleracea* var. gemmifera cv. Cyrus. The culture of *C. glomerata* was maintained at the Netherlands Institute of Ecology, Heteren, The Netherlands on larvae of *P. brassicae*. *Brassica nigra* seeds were collected from a single population of wild plants growing northwest of Wageningen. Seeds were surface sterilised, germinated, and 1-week-old seedlings were transplanted into 1.2 l pots filled with sterilised potting compost. The plants were grown in a greenhouse at $22 \pm 1\,^{\circ}$C (day) and $16 \pm 1\,^{\circ}$C (night) at 70% RH and LD 16:8 h period. Natural daylight was supplemented by metal-halide lamps ($225\,\mu$mol s^{-1} m^{-2} PAR). Plants were watered daily and 6-week-old non-flowering plants were used in the release–recapture studies. For both release–recapture experiments, large numbers of adult *C. glomerata* were reared from *P. brassicae* larvae on Brussels sprouts plants. To synchronise emergence, *P. brassicae* larvae were parasitised on a single day and parasitised larvae were kept on plants in cages. Due to superparasitism, the sex ratio of the emerged adults was male biased. Released adults were 1–6 days old with the majority emerging 4–5 days prior to release. After emergence parasitoids were kept at $10\,^{\circ}$C, in large Petri dishes with diluted honey and water (100 adults in each Petri dish). The experiments were carried out during the summer of 2008.

Experiment 1

Experimental design. To study patch size responses and dispersal patterns of *C. glomerata*, we placed 401 potted *B. nigra* plants in a mown grassland (80 m × 40 m). The grassland was mown 7 days before the release–recapture study was performed. All plants were inoculated with 10 first-instar *P. brassicae* larvae on the youngest fully developed leaf 24 h prior to placing them in the field. We created two host-plant patch sizes by placing plants individually in the field or by placing four plants together. Within patch distance between the four individual plants was 40 cm, and distance between patches was 4 m (Fig. 1). Patches containing one and four plants were alternated. Sixty minutes after placing the plants in the field, all plants were inspected over a period of approximately 30 min by seven observers to obtain an indication of abundance of naturally occurring *C. glomerata* in the area. No *C. glomerata* adults were recaptured or observed during this time. After these observations were completed, 2700 *C. glomerata* wasps (86% males, based on a subsample of 250 individuals) were released in the centre of the grid, where no plants had been placed, so that the distance to the nearest plant patches from the release point was 4 m. Temperature was between 24 and 27 $^{\circ}$C, wind speed, measured every hour, was constant at 2–3 m s^{-1}, direction east–southeast. Five minutes after releasing the parasitoids, each plant was inspected carefully and all *C. glomerata* individuals that were observed on the

plants were caught using an aspirator and kept individually in Eppendorf tubes. Patch identity and time of recapture were recorded and in the laboratory the sex and hind tibia length (used as a proxy for body size) of each individual parasitoid was determined. Parasitoids were collected by seven observers, distributed evenly over the experimental field. Over a period of 75 min, all patches were inspected by all observers ensuring that an equal amount of time was spent at each patch. The same recapture procedure was repeated starting 2 and 4 h after release.

Data analysis. The spatial distributions of males and females were compared using two different methods: a non-parametric two-sample test following the procedure described in Syrjala (1996), and a Kolmogorov–Smirnov test based on individuals recaptured at different distances from the release point. The first test was carried out using the R 2.7.2 software (R Development Core Team, 2008). All other data were analysed in Genstat (11th edn). Subsequently, data from within each recapture period were pooled. For each patch the distance from the release point and the total number of males and females caught per patch and per plant was calculated. The effect of patch size (one or four plants), sex, and recapture period on the number of recaptures was analysed using accumulated analysis of deviance based on a generalised linear model with Poisson distribution and logarithmic link-function. This was done for the number of recaptures per patch and per plant. The effect of patch size on the proportion of all patches where adults were recaptured was analysed using a χ^2 test. Occurrences of males and females caught simultaneously and by the same person during a single inspection of a patch was also recorded. Sex ratios of released and recaptured adults were compared using a χ^2 test. Male and female drift from the release point was determined as the average displacement from the release point as described in Turchin and Thoeny (1993, see also Hougardy & Mills, 2006). The relationship between body size (hind tibia length) and distance from release point was analysed with linear regression analysis, and differences in body size between recapture periods or patch size were analysed using ANOVA.

Experiment 2

To determine the effect of vegetation diversity and structure, and host density per plant on host location behaviour of *C. glomerata*, we carried out a release–recapture experiment in a long-term biodiversity experiment with plots that differ in vegetation composition and diversity. The details of the experiment have been described elsewhere (Van der Putten *et al.*, 2000; Bezemer *et al.*, 2006; Harvey *et al.*, 2008). The experiment was set-up in a semi-natural grassland area where agricultural cropping practices were ceased in 1995 at the Mossel, near Ede, The Netherlands. Plots (10 m × 10 m each) were sown with 15 (S15), or 4 (S4) mid successional plant species in 1996, or not sown (N96) with five replicate plots per treatment. In a fourth set of five plots, agriculture was continued for three more years and from 1999 these plots were abandoned and not sown (N99). Plots were separated
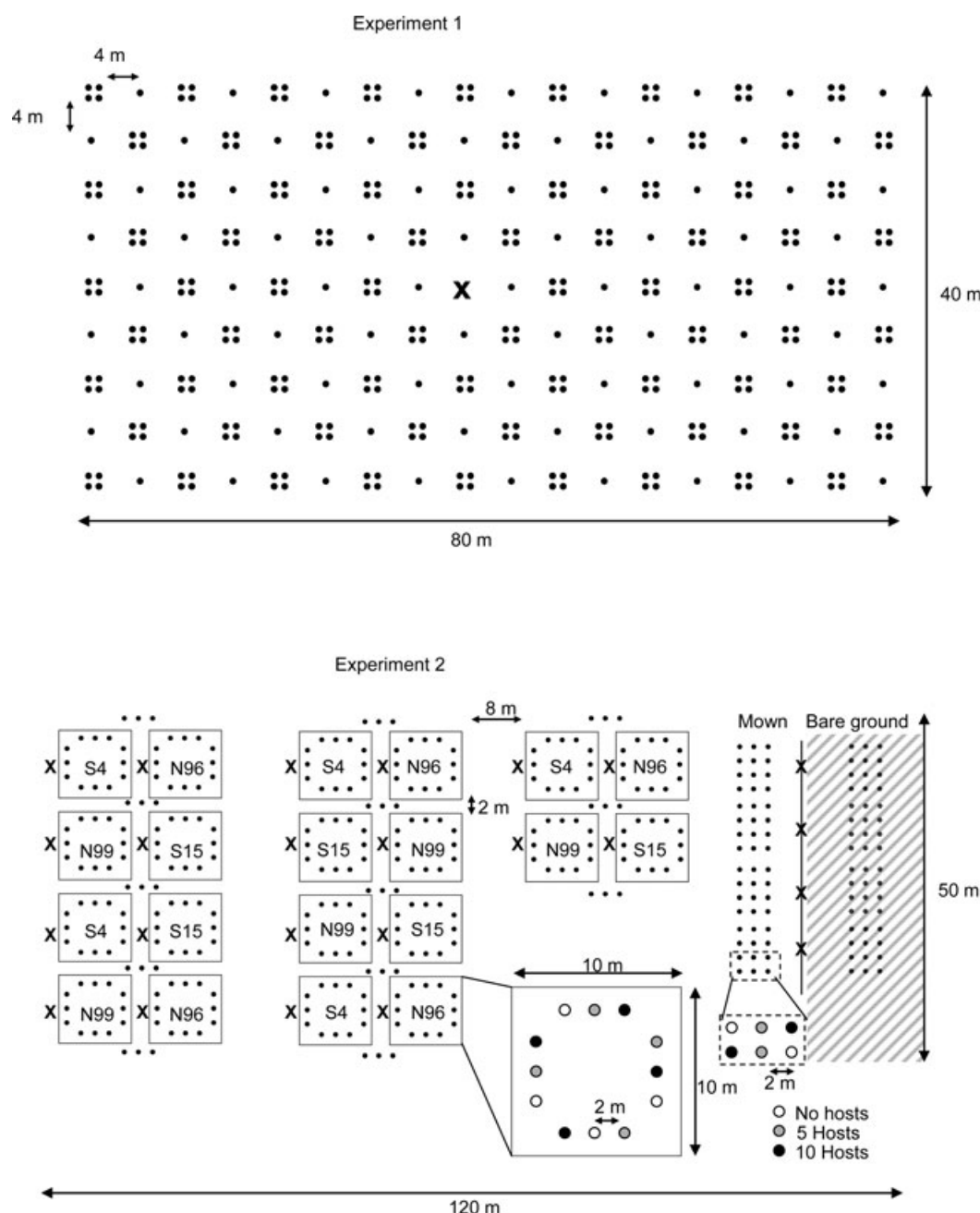
Fig. 1. Scheme of the set-up of experiments 1 and 2. Black dots indicate individual potted *Brassica nigra* plants. X indicates locations of parasitoid releases. In experiment 2, S15 and S4 indicate plots sown in 1996 with 15 or four plant species respectively, N96 and N99 indicate unsown plots since 1996 and 1999 respectively. Within each set of three plants, there was one randomly allocated plant with no hosts, one with five, and one with 10 hosts.

by 2 m wide paths and each year these paths were regularly mown during the growth season (Fig. 1). Although plots have not been weeded since 1996, plant communities of the four sowing treatments differ consistently in diversity, productivity, stability and composition (Bezemer & Van der Putten, 2007). In the Netherlands, *B. nigra* commonly occurs in semi-natural grasslands and on grasslands along road sites, but this species

was not present at the experimental site, although it had been recorded in very low densities some years earlier. The host, *P. brassicae* was also not present at the site but adult butterflies of this species had been recorded in the area surrounding the experimental site.

Four days prior to the release–recapture study, the paths were mown. Within the fenced area, and adjacent to the

experimental plots an area of 50 m × 20 m was also mown, next to which a second area of 50 m × 20 m was allocated where the soil was turned over 2 weeks earlier (bare soil). Three hundred and seventy-five *B. nigra* plants were used. One day prior to release of parasitoids, first-instar *P. brassicae* larvae were placed on the youngest mature leaf of the plant. Two host densities were used, 5 and 10 larvae per plant, while a third set of plants had no host larvae. Three hours after transferring the insects on the experimental plants, the plants were placed into the experimental field. Plants were placed 1 m from the edge inside each plot. On each of the four sides in each plot, one plant of each host density was placed and the three plants were then placed 2 m from each other (12 plants per plot). Vegetation height in the plots varied between 0.75 and 1.5 m, and the potted plants were about 40 cm in height. Thirteen sets of three plants were also placed in the mown paths in between the plots. Finally 16 sets of three plants were placed both in the open mown and cultivated area (Fig. 1). The distance between individual plants in the open and cultivated area was 2 m. The order of the three plants with different host densities at each location was randomised. The next day, at 24 positions homogeneously distributed over the experimental area, parasitoids were released (100 wasps per release point, 67% males). Temperature was between 22 and 25 °C, and wind speed was 5 m s^{-1}. Virtually all parasitoids dispersed from the release points. Fifteen minutes later, and for a period of 1 h, all parasitoids that were found on a plant were recaptured by seven observers who were distributed homogeneously over the experimental field. Each observer spent a fixed amount of time at each plant. This was repeated for two more 1-h periods starting 2 and 4 h after release. Each recaptured *C. glomerata* adult was kept individually into an Eppendorf tube and the location of the plant, and recapture period were recorded. In the laboratory all adults were sexed.

Data analysis. Male and female recaptures were calculated per plant. Very few adults were recaptured in the experimental unmown plots (see results). Therefore, the recaptures in the plots belonging to the different sowing treatments were grouped and habitat effects were compared using the following categories: (i) tall vegetation, (ii) mown vegetation between plots, (iii) mown vegetation in the open area, and (iv) bare soil. Statistical analyses were limited to data obtained from the open mown and cultivated area where almost all parasitoids were recaptured. Mean recaptures per plant in these two different habitat categories were analysed using a χ^2 test. The effects of host density and habitat on male and female density per plant were analysed using a generalised linear model with Poisson distribution and logarithmic link function.

Results

Experiment 1

A total of 112 females and 263 males were recaptured (Fig. 2). Relatively more females were recaptured than males. The sex ratio of the recaptured individuals was 70% males,

significantly lower than the release population which consisted of 86% males ($z = 4.51$, $P < 0.001$). The highest proportion of females was recaptured during the first period (sex ratio period 1:65%; period 2:78%; period 3:80% males; $\chi^2_2 = 8.06$; $P = 0.018$). Over the course of 5 h following release, 29.4% of released females and 14.7% of the males were recaptured. The spatial distribution ($\psi = 0.25$, $P = 0.9$) and distance to release point ($Z = 0.69$; $P = 0.72$) did not differ between males and females. Most adults were recaptured upwind (Fig. 2). Average movement from the release point during the first half-hour period was 2 m upwind, while at the end of the day adults were recaptured on average 12 m upwind. Most wasps were recaptured during the first period, and significantly more adults were recaptured on patches with four plants compared with patches with only one plant (Table 1, Fig. 3). When recaptures were analysed per plant rather than per patch, there was no difference between patches of one and four host plants during the first recapture period. During the second and third period more wasps were recaptured on patches consisting of four host plants, resulting in a significant interaction between patch size and period for this analysis (Table 1, Fig. 3). Parasitoid wasps were recaptured on 77 out of 161 patches, females on 54 and males on 63 patches. On the majority of patches (40) both females and males were recaptured during the course of the experiment. Remarkably, 54% of females were recaptured simultaneously with one or more males in a single patch. There was no significant relationship between body size and distance from the release point (females: $F_{1,109} = 1.09$; $P = 0.31$; males: $F_{1,260} = 0.019$; $P = 0.89$) and body size of the recaptured insects did not significantly differ between recapture periods (females: $F_{2,107} = 0.07$; $P = 0.93$; males: $F_{2,258} = 1.48$; $P = 0.23$), or large and small patches (females: $F_{1,109} = 0.00$; $P = 0.99$; males: $F_{1,260} = 0.46$; $P = 0.50$).

Table 1. Experiment 1: results are shown from a generalised linear model with Poisson distribution and logarithmic-link function, to test the effects of patch size, recapture period, and sex on the number of adult *Cotesia glomerata* wasps recaptured in patches consisting of one or four host plants.

Factor	d.f.	Number per patch		Number per plant	
		Wald χ^2	P	Wald χ^2	P
Patch size	1	59.3	<0.0001	20.0	<0.0001
Period	2	61.1	<0.0001	175.0	<0.0001
Sex	1	24.2	<0.0001	57.1	<0.0001
Patch size × period	2	5.2	0.07	16.5	<0.0001
Patch size × sex	1	0.03	0.87	0.08	0.77
Period × sex	2	4.3	0.11	11.2	0.004
Patch size × period × sex	2	0.2	0.70	0.4	0.51

Each plant contained 10 *Pieris brassicae*. Analyses were carried out on densities per patch and per plant. d.f. indicates degrees of freedom.
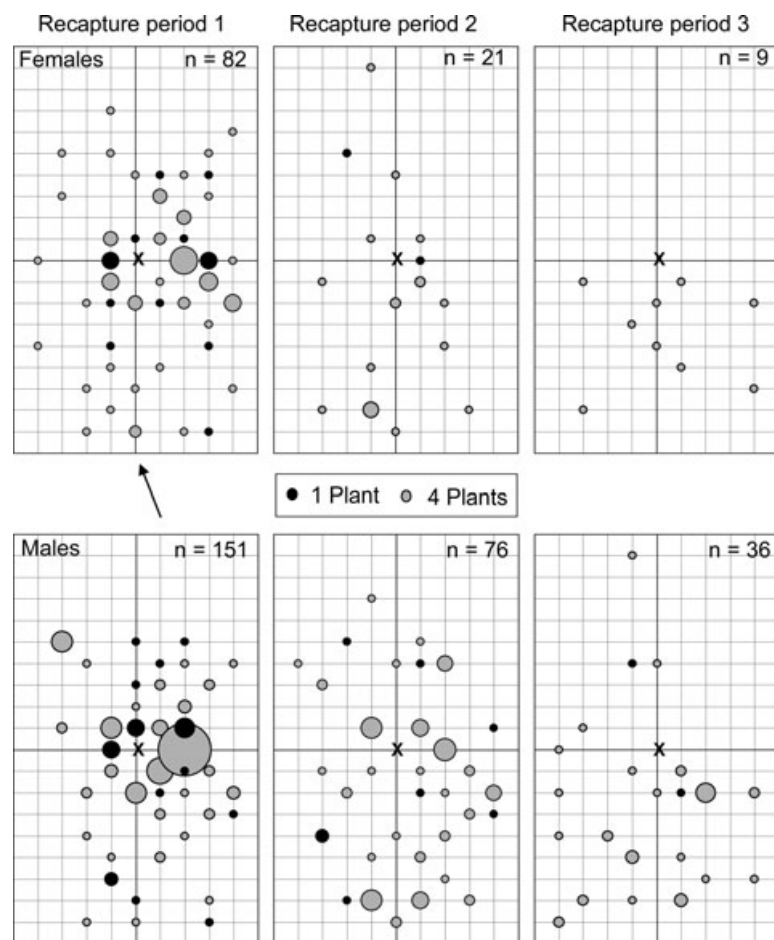
Fig. 2. Spatial and temporal distribution of adult female and male *Cotesia glomerata* wasps recaptured in experiment 1 on patches consisting of one (black circles) or four (grey circles) host plants with each plant containing 10 *Pieris brassicae* hosts. Recaptures were made during three periods of 75 min each (period 1 started 0.25 h, period 2 started 2 h, and period 3 started 4 h after parasitoid release). The total number of recaptured adults per period is also presented (*n*). Patches of one and four hosts plants were alternated and 4 m apart. The X indicates the release point where 2700 adults were released (87% males). One patch was located at each crossing of the grid lines but only patches with recaptures are shown. The size of the circle is representative of the number of recaptures. The arrow indicates the wind direction.

Experiment 2

Recapture rates were lower than in experiment 1; 44 females and 89 males were recaptured out of 2400 released wasps. Most adults were recaptured on plants placed on bare soil, followed by plants placed in mown vegetation in the open area. Only three adults were recaptured on plants placed in tall vegetation, and only four were recaptured on plants on the mown paths in between the plots with tall vegetation (Fig. 4). Analysis of host density responses were therefore restricted to plants placed in the open area that was mown or in bare soil. Significantly more adults were recaptured on plants placed in bare soil, compared to mown vegetation (females: $\chi_1^2 = 8.10$; $P = 0.004$; males: $\chi_1^2 = 4.35$; $P = 0.037$). Females were recaptured significantly more often on plants with 10 hosts than on plants without hosts or plants with five hosts both in bare soil ($\chi_2^2 = 10.13$, $P = 0.006$) and in mown vegetation ($\chi_2^2 = 10.67$; $P = 0.005$). Males were also recaptured most often on plants with 10 hosts but the difference between the three host densities was not significant (Bare soil: $\chi_2^2 = 4.80$, $P = 0.09$; mown vegetation: $\chi_2^2 = 4.66$; $P = 0.09$). The number of adults recaptured per plant was significantly affected by host density and by habitat (bare soil or mown), but there was also a significant interaction between host density and habitat (Table 2). In mown vegetation

Table 2. Experiment 2: results are shown from a generalised linear model with Poisson distribution and logarithmic-link function, to test the effects of host density (5 or 10 *Pieris brassicae* larvae per plant, or plants without hosts), parasitoid sex, and background habitat (mown vegetation or bare soil) on the number of adult *Cotesia glomerata* wasps recaptured per plant.

Factor	d.f.	Wald χ^2	P
Host density	2	23.0	<0.001
Sex	1	11.4	<0.001
Habitat	1	6.5	0.011
Host density × sex	2	0.6	0.75
Host density × habitat	2	8.4	0.016
Sex × habitat	1	1.7	0.19
Host density × sex × habitat	2	1.1	0.58

d.f. indicates degrees of freedom.

by far most adults were recaptured on plants with 10 hosts, while in bare soil adults were also recaptured relatively frequently on plants without hosts or plants with five hosts (Fig. 5). Remarkably, no females were recaptured on plants without hosts in mown vegetation, while they were recaptured on plants that were placed in bare soil.
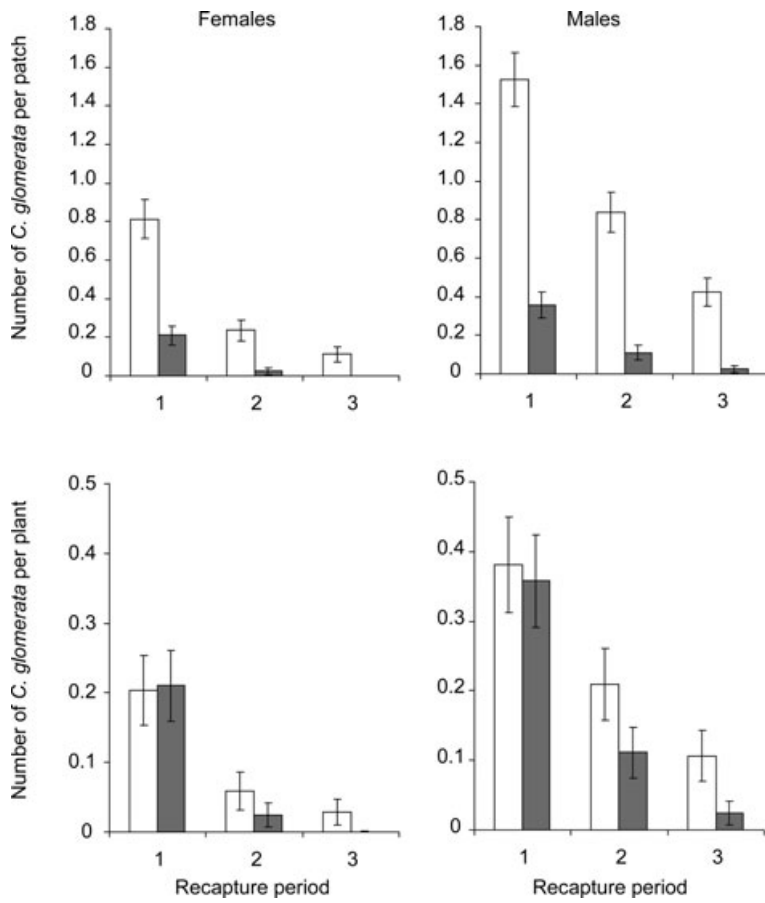
Fig. 3. Recaptured *Cotesia glomerata* females and males on patches consisting of four (open bars) or one (grey bars) host plant, in experiment 1 with each plant containing 10 *Pieris brassicae* hosts. Predicted means (± SE) are presented per patch and per plant for three recapture periods of 75 min each (period 1 started 0.25 h, period 2 started 2 h, and period 3 started 4 h after release). Statistical analyses are presented in Table 1.
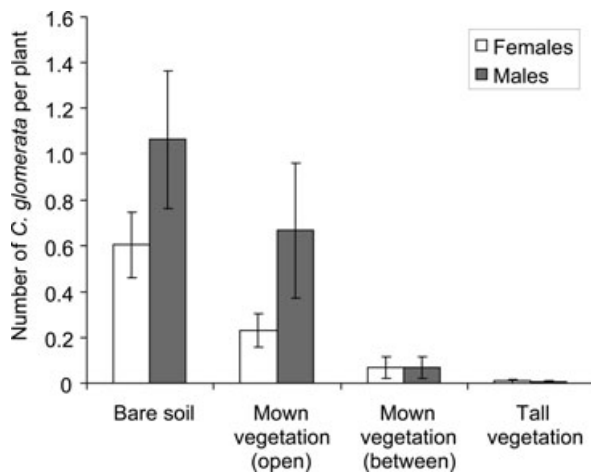

Fig. 4. Mean number (± SE) of recaptured *Cotesia glomerata* females and males per plant, on *Brassica nigra* plants placed on bare soil, on mown vegetation in the open area (open), on mown paths in between the tall vegetation (between), and in tall vegetation.

Discussion

This study shows that in the field both male and female *Cotesia glomerata* wasps exhibit positive responses to patch size and host density, but that behaviour of this parasitoid is most importantly influenced by habitat characteristics occurring at small scales. Aggregational responses in the field at larger patches have been shown for other species of parasitoids (e.g. Sheehan & Shelton, 1989; Bezemer & Mills, 2001; Umbanhowar *et al.*, 2003; Legaspi & Legaspi, 2005; White & Andow, 2005). In contrast with most other field studies, we recaptured more parasitoids per plant, as well as per patch in patches consisting of four plants than in single plant patches during the second and third recapture period in experiment 1. This shows that *C. glomerata* exhibits a true positive aggregational response to patch size. This effect was, however, only observed at later sampling times, indicating that *C. glomerata* adults first disperse more randomly, whilst later, they respond more precisely to cues from the host-plant complex and specifically locate large patches. Laboratory studies have also shown that the searching activity of *C. glomerata* females increases with host density (Geervliet *et al.*, 1998). Other studies have argued that patch size or host density can also influence retention of parasitoids, once they have entered these patches (Vos *et al.*, 1998). Clearly, both patch-level attraction and retention could have contributed to our results.

Cotesia glomerata is a gregarious parasitoid that in the field typically oviposits between 20 and 40 eggs in an individual host larva (Brodeur *et al.*, 1996; Harvey, 2000). It also attacks
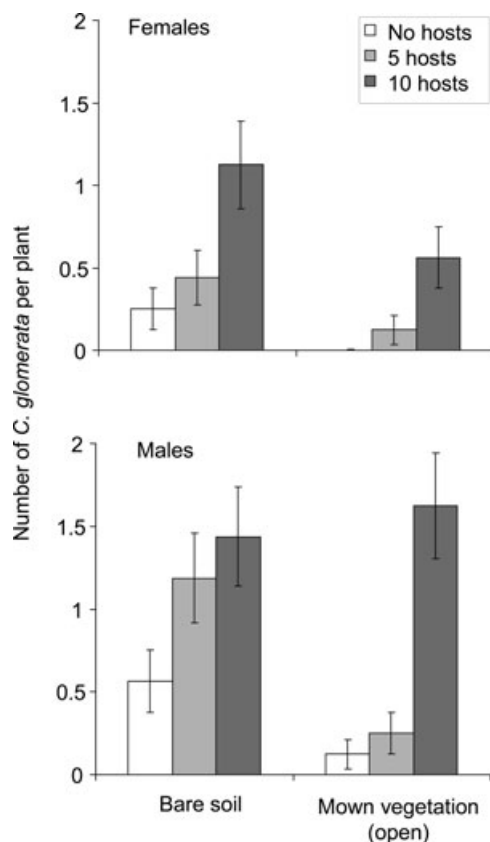
Fig. 5. Recaptured *Cotesia glomerata* females and males per plant on undamaged (clean) plants or on plants with 5 or 10 *Pieris brassicae* hosts. Predicted means (± SE) obtained from the generalised linear model (see Materials and methods) are shown. The plants were placed on bare soil or on mown vegetation in the open area.

several hosts within a single brood or patch, and laboratory studies have shown that it shows arrestment behaviour in host patches (Wiskerke & Vet, 1994; Vos *et al*., 1998). Larvae of *P. brassicae* feed gregariously during their first three instars before dispersing, and occur in clusters that are heterogeneously distributed in the field (Feltwell, 1982; Le Masurier, 1994). A positive response to host density or patch size as we observed here would therefore directly improve fitness in *C. glomerata*, as it would enable the wasp to parasitise most hosts per unit of time (Vos *et al*., 1998). It should be noted, however, that broods of *P. brassicae* in the field often exceed 40 individuals, much larger than the 5 or 10 hosts that were used in this study. In our study, under conditions where parasitoids probably experienced an array of different abiotic and biotic influences, *C. glomerata* still responded positively to differences in host density, even when these were low.

Remarkably, there was no difference in the response of male and female wasps to patch size in the field. One possible explanation for the positive aggregation response of males to patch size is that they are attracted to females which exhibit a positive response to host density. Several experiments conducted both in the laboratory and in the

field have reported that male *C. glomerata* wasps use sex pheromones to locate potential mates (Tagawa & Kitano, 1981; Field & Keller, 1993). In experiment 1, although there was no positive relationship between the number of males and females recaptured on a plant, almost half of all males were recaptured on a plant where, at the same time, one or more females were also recaptured. Moreover, although the response of males and females to host density did not differ, significantly higher proportions of females than males were recaptured on the host plants. This indicates that females were more responsive to hosts and host plants than males. However, we cannot exclude that males also responded directly to host or host-plant cues. This has rarely been explored, but there is some evidence that males of other parasitoid species respond positively to host and host-plant cues or that they can learn to explore these cues to locate potential mates (McAuslane *et al*., 1990; Villagra *et al*., 2008). Like most hymenopteran parasitoids, *C. glomerata* is a haploid/diploid species and thus only mated females can produce female offspring. Consequently, males play a prominent role in determining parasitoid fitness (Gu & Dorn, 2003). Behavioural studies have focused almost exclusively on females of this species and more work is needed to better understand the factors underlying behavioural responses of male *C. glomerata* wasps. This study suggests that cues influencing the behaviour of male and female parasitoids in the field may be more similar than previously assumed (Wajnberg *et al*., 2007; Schellhorn *et al*., 2008).

While we found distinct effects of host density and patch size on recapture rates of *C. glomerata*, experiment 2 clearly showed that host location success of this species most importantly depends on local habitat characteristics. Virtually no recaptures were made on plants placed in tall vegetation, independent of the composition of the vegetation. In the experiment, we used plants that had no reproductive stems or flowers, were generally not higher than 30–40 cm and, in the experimental plots were surrounded by much taller vegetation. This means that access to hosts in these plots was probably impeded by both the complex architecture and physical barriers offered by surrounding plants and possible interference from a diverse array of infochemicals emanating from them (Agrawal *et al*., 2006). However, recapture rates were also very low in plants placed in the mown paths that were 2 m wide in between the plots with tall vegetation. This was in spite of the fact that the vast majority of parasitoids were also released on these mown paths. These results reveal that *C. glomerata* habitually searches for hosts in open areas (Sato & Ohsaki, 1987; Benson *et al*., 2003). Other laboratory studies have also shown that vegetation characteristics such as height or density can interfere directly with the movement and host patch finding abilities of parasitoids (Andow & Prokrym, 1990; Gols *et al*., 2005; Bukovinszky *et al*., 2007; but see Coll & Botrell, 1996). The parasitoid *Diadegma semiclausum*, for example, located its host *Plutella xylostella* much more effectively when the host plant *Brassica oleracea* was surrounded by short compared to tall *Sinapis alba* plants (Gols *et al*., 2005). However, the reverse, where parasitoids prefer dense versus open vegetation, has also been reported (White & Andow, 2006). Therefore foraging behaviour and habitat preference in

parasitoids appears to be strongly dependent on the biology and ecology of the host species and its food plants and is probably association specific. Other work has shown that the susceptibility of *P. brassicae* caterpillars to parasitism by *C. glomerata* is directly related to the degree to which the plants are concealed by surrounding vegetation (Ohsaki & Sato, 1994). Given that *C. glomerata* avoids dense vegetation (this study) and forest habitats (Benson *et al.*, 2003), these parameters can provide enemy-free space for otherwise suitable hosts. Several authors have even argued that the avoidance of predation or parasitism may render intrinsically inferior plants more suitable for larval growth and development than plants of higher quality (Lawton & McNeil, 1979; Price *et al.*, 1980; Bernays & Graham, 1988).

The apparency of a host plant has been pointed out as an important factor for the degree of herbivory that the plant experiences (Chew & Courtney 1991; Agrawal *et al.*, 2006). Similarly, more apparent plants could also be visited more often by parasitoids. In our study plants placed in the open area were exposed from the surrounding habitat, while plants in the vegetated plots were more concealed. However, we have strong evidence that the foraging behaviour of *C. glomerata* that we observed cannot be explained solely by apparency. There were significant habitat effects on plant and host location when plants were placed in the open areas consisting of bare soil or mown grassland. Remarkably, although plants were similarly apparent in both areas, more adult parasitoids were recaptured on plants placed in bare soil than on plants placed in mown grassland. Moreover, in the bare soil area, where we assume that the influence of the background habitat was minimal, females were also recaptured on plants without hosts. Laboratory studies have also reported that undamaged *Brassica oleracea* plants are attractive to *C. glomerata* (Geervliet *et al.*, 1998). However, in our study, female parasitoids were not recaptured on undamaged plants when these were placed in the mown area. In the bare soil area, males were recaptured as frequently on plants with five hosts as on plants with 10 hosts, while in the mown grassland area the vast majority of males were recaptured on plants containing 10 hosts. All these results suggest an important role for chemical interference from the surrounding habitat. There appears to be a positive relationship between surrounding habitat complexity and the contrast and/or intensity of the plant or host signals required by *C. glomerata* to locate hosts or host plants (Hilker & McNeil, 2007). Laboratory studies have shown that parasitoids forage less efficiently in more complex habitats (Gols *et al.*, 2005; Bukovinszky *et al.*, 2007) and that non-host plants can also hamper host location behaviour in *C. glomerata* (Perfecto & Vet, 2003). However, to our knowledge no other study has shown that parasitoids require stronger host or host-plant cues when habitat complexity increases. A large body of literature shows that most parasitoid species exhibit associative learning to improve their foraging efficiency (Vet & Dicke, 1992; Vet *et al.*, 1995). Whether the foraging efficiency of *C. glomerata* in tall vegetation can be improved through associative learning of cues related to this habitat remains to be tested. However, given that the parasitoid habitually avoids shady habitats, this may be unlikely to happen.

In conclusion, we have shown that under field conditions, male and female *C. glomerata* wasps show positive responses to patch size and host density, and exhibit upwind searching behaviour, similarly to what has been found in wind tunnel trials. However, our study also clearly shows that host searching efficiency by *C. glomerata* in the field is most importantly influenced by the complexity of the surrounding habitat. Host plants are rarely located by the parasitoid in habitats with tall vegetation. The intensity of host related cues that is required by parasitoids to locate hosts increases with habitat complexity, and characteristics of the surrounding plant community can influence the aggregative response of parasitoids to their hosts.

Acknowledgements

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