Induced plant defences and their effects in complex communities:

from individual behaviour to field populations

André F.D. Kamp, 2007

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Cover illustration is an artist’s impression that represents the population dynamics and behavioural aspects of the studies described in this report. It shows the experimental fields, zoomed into the behaviour of individual insects. In the end it is the decision of the individual that drives the movements of the community.
The illustration was composed only and especially for this report by drs. N. van Hest.

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Induced plant defences and their effects in complex communities: from individual behaviour to field populations

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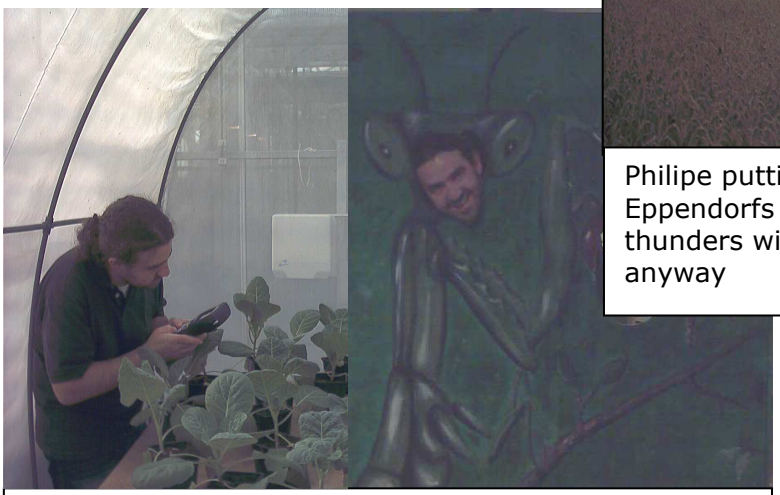
Preface

It feels almost like an epic journey such as they tell in ancient stories, but finally this final stage of me becoming an official scientist is almost at the end. Good journeys are seldom made alone and also with this one I would never have reached my destination without some important characters.
There is, of course, Philipe Severense from Portugal. Together we did al the monitoring of the field experiment. Patiently he taught me the names of all the insects we monitored. Together we suffered through weather extremities, listen to baseball-shaped ugly radios and had great fun with tea-bags and water proof markers. Currently I'm watching over his bike he sadly had to leave behind. Then there is Georgios Prekatsakis. With this Greek old-school philosopher-farmer I did the behavioural experiments. Hours of intensive wasp-staring truly changed our lives.
This journey was led by Tibor Bukovinszky, formally known as "Sensei", himself. With great patience and very nice Uganda thea he guided us over the slicky roads of research. Despite busy schedules that include born babies, annoying students such as ourselves and other stuff I don't want to know about, he managed to be always there when needed and be one of the most involved scientists I know, both people- and research-wise.
These three guys and of course, my girlfriend Nienke, for her cover illustrations, but even more important the endless support, endless flows of coffee and snacks during late hours; the people from Unifarm, who prepared the fields and took care of the plants and insect rearers; André Gidding and Frans van Aggelen, I owe you all great thanks. Without you all this would have been a bat trip and not the cool journey it is now.

Philipe putting very relaxed cocoons in Eppendorfs while knowing rain, hail and thunders will make us suffer that day anyway



To really observe insects, Georgios will be the insect

Abstract

Cabbage plants are well-known for their defences against herbivory. They have a large array of constitutive and induced defences that may be direct and indirect. Foraging herbivores affect the plant by inducing plants defences. In turn, the induced plant can affect insects as an individual and as a community, for example through changes in plants quality and volatile blends. In the field are simultaneously attacked by several herbivore species. Plants may respond to herbivore species in different ways, in turn affecting the insect community. Factors that influence community composition of herbivores (i.e. spatial heterogeneity of the habitat) will likely interact with effects of defences on insect communities, but this aspect has not been investigated. These effects are also likely to affect natural enemies that often use herbivore-induced plant volatiles, to successfully locate their victim. The responses of natural enemies of herbivores in response to a community of herbivores attacking a plant have howver received limited attention. Here, these plant-insect interactions are studied from two points of view: population dynamics and parasitoid behaviour.

In the first experiment, using a field-set-up, the effects of induction on the insect community were tested on two cabbage cultivars, white cabbage and Brussels sprouts, which were both planted in two field sizes. Plants were induced by a specialized herbivorous species, larvae of the large cabbage white. During a 13-week period abundances of cabbage-related insects were monitored to study differences in insect communities between induced and control plants, cultivars and field sizes.

In contradiction to the resource concentration hypothesis field size did not affect *Brevicoryne brassicae, Myzus persicae, Aleyrodes proletella, Pieris rapae, Mamaestra brassicae* and *Autographa gamma*. Only *Phylotretra undulata, Ph. atra* and *Thrips* were found in higher densities in large fields. One natural enemy, *Cotesia rubecula,* which is a parasitoid wasp, was found most in small fields. Other natural enemies were not affected. Parasitized *B. brassicae, Syrphids, Chrysoperla,* and *Diadegma semiclausum* were found equally in small and large fields. Preference for cultivar differed per species. *Thrips* and *Al. proletella* clearly preferred Brussels sprouts, while white cabbage was preferred by *Ph. undulata, Ph. atra* and *M. persicae*. *M. brassicae* and *P. xylostella* did not prefer either cultivar. Larvae of *Pi. rapae* and *Chrysoperla* was found equally distributed among the cultivars while their eggs were found more on white cabbage and Brussels sprouts respectively. *Chrosoperla* was the only species of the natural enemies that had a preference for a particular cultivar. Induction had a strong affect on insect abundances. Herbivores generally preferred not-induced plants, except for *Phylotretra spp.* which were found most in induced plants and *Pi. rapae* and *Pl. xylostella* which were both not affected by induction. Parasitized cabbage aphids were found most in induced plants while none of the other natural enemies preferred induced or control plants. Apparently, avoiding induced plants, which contain more toxins that hinder larval development, is profitable for most herbivores. They generally seem not to choose plants that are induced to profit from the encounter dilution effect. They also do not choose not-induced plants because it is enemy low space, since natural enemies generally were unaffected by induction. Since plants are not solely induced by *Pi. brassicae,* further research is needed to link species to each-other. Only via a complete interaction web, it can be determined what enemy low- or dense space is and can the development of the insect community be predicted.

Indirect defences of cabbage plants include the release of volatiles that guide parasitoids to their hosts. In field situations plants are often infested with more then one species. Different herbivores may elicit different volatiles. Volatile blends emitted by plants that are infested with, hosts and non-host herbivores may be more difficult to asses for parasitoids, meaning that non-hosts hinder host searching behaviour. Here, foraging behaviour of a gregarious fairly specialised endoparasitoid wasp, *Cotesia glomerata*, was analysed. Behaviour was observed in a lab experiment with white cabbage plants that were infested with either *P. rapae* (host), *Mamestra brassicae* (non-host) or both.

Most time was spent on patches with hosts and mixed patches. Total patch time, and durations and frequencies of searching, grooming, walking and flying did not differ between these treatments. Also percentages of attacked hosts and ovipositions did not differ. Patches with only non-hosts were left three times faster then hosts-only and mixed patches. Accordingly, frequencies and durations of all of the behavioural parameters were equally lower then in hosts-only and mixed patches. This suggests that there was no apparent affect of non-host in mixed patches hindering foraging efficiency. It also suggests that non-hosts can reduce host searching efficiency because, likely through an unspecific volatile blend, wasps can not distinguish between host and non-host infested plants at long range. However, in mixed patches it was observed that parasitoids oviposited in non-hosts, which costs time energy and eggs. I suggest that this phenomenon occurred because odours of hosts and non-hosts blended because larvae of both species touched and odour tracks crossed while feeding in the patches. The wasps used in this experiment were inexperienced. When the wasps get more experienced, this phenomenon may diminish. This, the consequences for the non-host as well as the ecological impact should be subject of further investigation.

Both studies were performed at Entomology Department of the University of Wageningen supervised by T. Bukovinszki and M. Dicke. This was an MSc-project for my Biology study at Radboud University, Nijmegen.

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1 Introduction

1.1 Plant-insect interactions

In the multitrophic environment in which insects live, plants play key roles (i.e. Price *et al.,* 1980). Plants do not only interact with herbivorous insects, but also with the antagonists of these herbivores (reviews Kessler & Baldwin, 2002; Dicke & Hilker, 2003). Plants have a wide array of possible direct and indirect defences against phytophagous insects that may be constitutive or herbivory induced. Direct defence strategies (reviewed by Wittstock and Gerhenzon, 2002) involve the production of morphological structures, such as trichomes, on the leaf surface that hinder herbivore colonization. Plants may also produce toxic compounds to deleteriously affect the development of herbivorous insects (Dicke and van Loon, 2000). Indirect defence mechanisms include plant cues that attract antagonists of herbivores. For example, volatiles that are produced when the plant is attacked by herbivores, can guide parasitoids to their hosts, thus, indirectly defend the plant (Dicke *et al., 1*990, Takabayashi *et al.,* 1994, Turlings *et al.,* 1990a,b, 1991a,b, De Moraes *et al*., 1998; Turlings *et al*., 2002).
I have here studied two aspects of plant defence. In a field experiment, I induced cabbage varieties with a specialist herbivorous species and investigated the effects of the induction on the development and composition of the insect community. In this experiment, two cabbage varieties and two field sizes were tested. Furthermore, in a series of behaviour experiments, I studied differences in within-patch behaviour of a parasitoid between patches with hosts, non-hosts and both hosts and non-hosts.

1.2 Field experiment: testing three factors that affect insect populations

Differences between cabbage cultivars
Brassica oleracea is well known for its inducible defensive mechanisms. Glucosinulates are secondary plant compounds produced to defend the plant against attackers. Several families of the order Capparales, of which the Brassicaceae are the most economically important (Charron *et al.,* 2005), produce glucosinulates. Volatile compounds that may be used as info-chemicals are degradation products of glucosinulates (Mithen, 2001). The degradation products are known to act against microbial pathogens, nematodes, and generalist herbivores, and are attractants for specialist feeders (Price *et al.*, 1980; Renwick *et al.,* 1992; Lazzeri *et al.*, 1993; Mari *et al.*, 1993; Lin *et al.*, 2000). Because *B. oleracea* demonstrates such an apparent response to herbivory, it is particularly suitable to study the differences in response of the insect community with respect to induced or not induced plants.
In *Brassica spp,* release of volatile compounds depends not just on the foraging species but vary between cultivars and part of the season (Charron *et al.*, 2005). Also architectural differences between cultivars may affect for example natural enemy foraging efficiency (e.g. Kareiva and Sahakian, 1990; van Lenteren and de Ponti, 1990). It is however yet unknown how development of insect populations may differ between cultivars. In the field experiment, I compared insect densities of two cabbage cultivars, Brussels sprouts (*Brassica oleracea gemmifera* cv Cyrus) and a white cabbage (*Brassica oleracea capitata* cv Christmas Drumhead).

Effects of field size
Herbivores are generally thought to be more abundant in larger fields according to the resource hypothesis (Root, 1973). Although insect abundances are correlated to landscape heterogeneity, recent experiments have demonstrated that responses to field sizes vary considerably. Banks (1998) for example, found that vegetation composition influences cabbage aphid densities, flea beetle densities depended on scale of fragmentation, while small cabbage whites were influenced by neither of them. This may because of differences in migration capabilities (e.g. Bowman *et al.,* 2002), but also may be related to differences in search modalities used by herbivore species (Bukovinszki *et al.,* 2005), local growth rates and temporal trajectories (Hämback and Englund, 2005). Field size was therefore included in the field set-up. Effect of field size was studied by comparing insect abundances of the two cultivars planted in both large fields and small fields.

Induction
A single plant is likely to be visited by a multitude of herbivores during its lifespan. Each of these herbivores may affect the plant's responses differently, for example in terms of physiology and release of volatiles. Such changes in plant qualities, resulting from induction, are likely to affect the preference and performance of subsequent herbivores (Hunter, 1987; Hudsen and Stiling, 1997; van Zandt, 2004). This means that interactions between, but also within, trophic levels become more complex when the number of insects that feed on the plant increases (see also Vos *et al.,* 2006). While parasitoids may be attracted to induced volatiles, herbivores that attempt to escape parasitoids are likely to avoid plants that are already induced. This is because induced plants often have higher levels of toxins, hindering the development of herbivores (e.g. Sznajder and Harvey, 2003) and avoid enemy dense space (e.g. Sato *et al.,* 1999). Herbivores are known to use volatiles to detect host plant quality (i.e. Oshaki and Sato, 1994) and avoidance of enemies (Price *et al.,* 1980; Oshaki and Sato, 1994) or competition (Pallini *et al.,* 1997). Responses of herbivores to induced plants may however vary considerably. In some cases herbivores are attracted to induced plants. When volatile-cues are unspecific, heterospecific herbivores on the same plant can render protection, providing an encounter-dilution effect (Shiojiri and Takabayashi, 2003). For example, *Cotesia plutellae*, a specialised parasitoid wasp is attracted to cabbage plants that are attacked by its host *Plutella xylostella.* However, when besides its host a non-host species (here *Pieris rapae*), feeds on the plant, the attractiveness is reduced through changes in the emitted volatile blend (Shiojiri *et al*., 2001). This emphasizes that behavioural studies, limited to single plant – host complexes, are simplifications of what actually happens in the field, where a multitude of insect species feed on a single plant. The variability of independent colonization events of a plant by different herbivores further complicate what happens in the field. It has been acknowledged that such lab studies do not always translate to the field (Gurevitch and Collins, 1994, Hunter, 2002). For example, Gols *et al.,* (2005) found a reduction of foraging efficiency of a parasitoid wasp, *Diadegma semiclausum*, in habitats under more diverse plant composition. Studying population processes on the other hand will disregard behavioural differences between individual insects (reviewed by Vet, 2001). Although new techniques and models are promising in linking information webs to interactions in field situations (Vos *et al.,* 2006), a study by Karimzadeh *et al.,* (2004) shows that differences in individual performance does not necessarily translate into differences in population dynamics.
Despite evidence of apparent effects of induction on insect populations, there are only few studies that have examined this (see i.e. Viswanathan *et al.,* 2005).

Here, I investigated how initial induction by herbivory affects subsequent insect populations during a season. The cabbage varieties were thereto induced, using a specialist herbivore, *Pieris brassicae* (large cabbage white). The gregarious larvae of this butterfly feed exclusively on glucosinulates producing plants such as *Brassicae oleracea*. Insect densities on induced plants were then compared with densities on not induced cultivars.

1.3 Behaviour experiment: Non-hosts affecting within patch behaviour of a parasitoid

In general, the herbivore-induced release of volatile compounds is thought to be a reliable cue for parasitoids to locate their host species (Dicke and Vet 1999). The number and types of volatiles that is produced is diverse (i.e. Mithen, 2001). Parasitoid species are not only found to detect the host presence but also distinguish, to a certain extend, between host type (Micha *et al.*, 2000; Fatouros *et al.,* 2005), age (Matticacci and Dicke, 1995) and whether a host already is been parasitized (Fatouros *et al.,* 2005). However, when infested with more then one herbivore species, specificity of plant cues may be reduced. Foraging efficiency of a parasitoid wasp, *C. glomerata*, is reduced when non-host plants are mixed with host plants (Perfecto and Vet, 2003). In some cases, parasitoids are also attracted to host plants that are infested with non-host herbivores (Agelopoulos and Keller, 1994; Geervliet *et al.,* 1996). Vos *et al.,* (2001) showed that *C. glomerata*, did not discriminate between host and non-host infested *B. oleracea* plants while time spent on a patch of the latter was much lower.
In such cases, when volatile-cues are unspecific, heterospecific herbivores on the same plant can render protection, providing an encounter-dilution effect (Shiojiri and Takabayashi, 2003). For example, *C. plutellae*, a specialised wasp, is attracted to cabbage plants that are attacked by its host *Plutella xylostella.* However, when besides its host, *Pieris rapae*, which is a non-host species, feeds on the plant, the attractiveness is reduced through changes in the emitted volatile blend (Shiojiri *et al*., 2001). Irrespective of how volatiles influence parasitoids, they do directly affect their behaviour (see e.g. Vet 2001; van Zandt and Agrawal, 2004). After locating an infested plant, parasitoids have to exploit the patch to pinpoint the host's exact location. For *C. glomerata,* patch exploitation behaviour is a well studied subject. (see Wiskerke and Vet, 1994; Vos *et al.,* 1998), but only with host species on the plant. Leaving tendency for instance, is related to host type (Shiojri *et al.,* 2000) and host distribution (Vos *et al*., 1998; Wiskerke and Vet, 1994). How behaviour is affected when non-hosts are present amongst hosts is however mostly unknown territory.
We examined the foraging behaviour of *Cotesia glomerata* (Hymenoptera: Braconidae) under influence by non-host presence. *C. glomerata* is a fairly specialised, gregarious endoparasitoid that parsitizes young larvae of *P. brassicae* and *P. rapae*. *Mamestra brassicae* also feeds on *B. oleracea* (although not exclusively) and is a non-host species for *C. glomerata*. Geervliet *et al.,* (1996) already demonstrated that *C. glomerata* does not discriminate between both Lepidopteran species. Despite, how *C. glomerata* spends its time on the patch is likely to be affected by non-host presence since it foraging behaviour seems to be related to patch quality. Here I investigated how patch allocation time differs between patches containing hosts only, non-hosts only and both species together.

2 Materials and methods

2.1 Field experiment

Species
Two cabbage varieties were used, white cabbage (*Brassica oleracea capitata* cv Christmas Drumhead) and Brussels sprouts (*Brassica oleracea gemmifera* cv Cyras). Four week old plants of both cultivars were breed biologically and transplanted to the field on May, 5th. The wheat *(Triticum aestivum)* was sown on April, 21st. Fields were fertilized with dry manure. The herbivore used for initial induction of the cabbage, larvae of large cabbage white (*Pieris brassicae, Lepidoptera: Pieridae*), were reared and maintained at the Entomology department of Wageningen University, The Netherlands.

Setup
In a field set-up, eight treatments were tested in six replicates. Hereto, a total of 24 fields (figure 1) were each sown with 144 plants of one of the two cabbage cultivars. Two field sizes were used, twelve fields of 8 x 8 m (large fields) with 10.5m isolation distance between them, and twelve fields that were divided into nine of 3 x 3 m (small fields) with 5m isolation distance between them. Each large field and small field contained 144 and 16 plants respectively. One (randomly chosen) side of each large and each small field was induced twice by the *P. brassicae* larvae. First induction took place on June, 13th, 2006. Per plant a patch was placed, consisting of approximately 15 eggs. Plants were checked the next two days for number of surviving larvae and, when necessary, extra 1 - 2 day-old larvae were added to the patch. Larvae were manually removed after ten days. The second induction was took place on June, 28th, 2006. Here, 8 to 12 larvae were placed on a plant, to homogenise the amount of surviving larvae. Again, all *P. brassicae* larvae were removed ten days after induction.

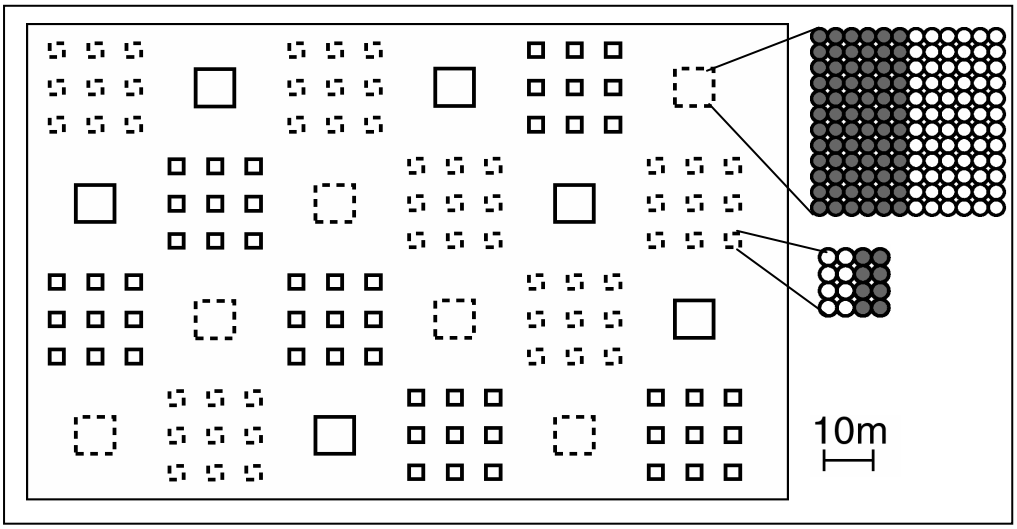


Figure 1; *setup of the fields. Dotted squares are fields sown with white cabbage, straight lines are fields sown with Brussels sprouts. Dark circles indicate induced plants; light circles indicate not-induced plants*

Any *P. brassicae* caterpillars found on control plants were removed. *P. brassicae*-infested control plants were marked and no longer monitored. Plants that were supposedly induced but showed no evidence of damage by *P. brassicae* were also marked and no longer recorded.

Measurements

Each week, beginning in week 23, plants (18 out of a total of 144) were monitored for cabbage related insect species, (see table 1). Between week 32 and 35, the number of monitored plants was reduced to 12 per plot, due to the increasing numbers of insects that were found on the plants. The number of monitored plants was equally divided between the induced and not induced sides of each field. The same was done for the fields that were divided into nine sub-fields. Plants were always selected pair-wise, meaning that, later in the season when 12 plants per plot were selected, two plants were chosen in six (randomly chosen) subfields. Each week a new set of plants was selected for monitoring. Plants were randomly monitored without replacement.
Depending on the species, it was also recorded in which state the species were found, that is, as an adult, larvae, egg or pupae and whether it was parasitized. Monitoring was done non–destructively; all insects were left on the plant. Only cocoons and mummies were sampled to construct quantitative food webs, a study that is included in this report.

Table 1; *Species found with the discriminated life stages. For some, it was recorded whether they were parasitized (P).*

Species	**guild**	**recorded**
Cabbage aphid (*Brevicoryne brassicae*)	herbivore	individuals, P
Green peach aphid (*Myzus persicae*)	herbivore	individuals, P
Small cabbage white (*Pieris rapae*)	herbivore	eggs, larvae, P
Cabbage moth (*Mamestra brassicae*)	herbivore	eggs, larvae
Silver Y moth (*Autographa gamma*)	herbivore	eggs, larvae, pupae
Diamondback moth (*Plutella xylostella*)	herbivore	eggs, larvae, pupae, P
Flea beetles (*Phyllotreta undulata, P. atra*)	herbivore	adult
Pollen beetle (*Meligethes aeneus*)	herbivore	adults
Thrips ssp.	herbivore	larvae
White fly (*Aleyrodes proletella*)	herbivore	individuals
Harlequin ladybeetle (*Harmonia axyridis*)	carnivore	egg, larvae, adult
Hoverflies (*Syrphid spp.*)	carnivore	larvae
Lacewing larvae (*Chrysoperla sp.*)	carnivore	eggs, larvae
Seven-spotted lady beetle (*Coccinella septempunctata*)	carnivore	eggs, larvae, adult
Cotesia glomerata	parasitoid	cocoon clutches
Cotesia rubecula[*]	parasitoid	cocoons
Diadegma sp.	parasitoid	cocoons

* For *C. rubecula,* the number of cocoons was calculated as a percentage of the total number of *P. rapae-larvae* on the plant.

Data analysis

The number of the species found per week was compared between the eight treatments with a repeated measures analysis. The mean of insect counts per plant in an induced or control part of a field was taken as experimental units. To achieve normality, count data was log transformed, whereas data on parasitism has been arcsine square-root transformed. A mixed model was used where each weeks of monitoring have been considered as repeated measurements on the induced-control side of a field. Because the measurements in induced and control sides of a field were dependent from each other, this has been included as a random factor in the model. Different covariance matrices have been fitted to the dataset, i.e. compound symmetry, autoregressive and Toeplitz, because the error variance associated with the measurements was not equal across the time points and between the treatments (homoscedasticity was not met). The selection of the best fitting model was based on Akaike's information criterion and Schwarz's Bayesian criterion. Data was analysed using SAS 8.2.

2.2 Behaviour experiment

Species

The plant species, *B. oleracea cv capitata* Christmas Drumhead, were obtained from Unifarm Wageningen. The plants were grown in a greenhouse in which humidity (60% RH), temperature (22 ± 1 °C) and light were controlled. Metal halide bulbs of 400 W supplemented natural light. Plants were given sufficient water and were fertilised (Crystalon®). For our experiments, two month (± 1 week) old equally sized plants were used.

All insect species were reared and maintained at the entomology department of Wageningen University. The herbivores used were larvae of *P. rapae (Lepidoptera: Pieridae)* (host) and *M. brassicae (Lepidoptera: Noctuidae)* (non-host). Both herbivores were placed together, using different brushes, on the first extended leaf of the plants one day before each test. When placed on the plants, larvae of *P. rapae* were in their second instar and *M. brassicae* were selected to be one or two days older, to compensate for the lower amount of foliar damage they cause at the same age.

The parasitoid wasps were 4- to 7-day-old, mated, inexperienced *C. glomerata* females. The wasps were reared on *Pieris brassicae*. Cocoons from this rearing were placed in rearing boxes and stored in a climate chamber (16/8 LD, 24 °C and 60 % RH) with sufficient honey and water supply. Prior to the testing, a selection of 'active' female wasps was made. Hereto, a *B. oleracea* leaf, previously damaged by *P. rapae* larvae was offered to the wasps. Attracted wasps, which additionally showed active searching behaviour, were placed in Petri dishes. Before releasing them into the test room, wasps were allowed to acclimatize to test room conditions for approximately one hour.

Setup

All experiments took place inside a transparent cloth tent (figure 2) in a greenhouse compartment at the Entomology department of Wageningen University, (t = 22 ± 1 °C, RH = 60 %). Light was provided by metal halide bulbs of 400 W in addition to natural light. For each observation, plants with herbivores were placed on a table at a distance of 50 cm to each other. All plants, on which an oviposition took place, were replaced. Plants were used one day only. Wasps were released individually from the Petri dishes at 50 cm from the first row of plants at 15 cm above the table (= release station). From the moment of release, behaviour of the wasps was monitored and recorded continuously, using a TRS-80 Model 100 portable computer with the event-recording program The Observer (Noldus, 1991).

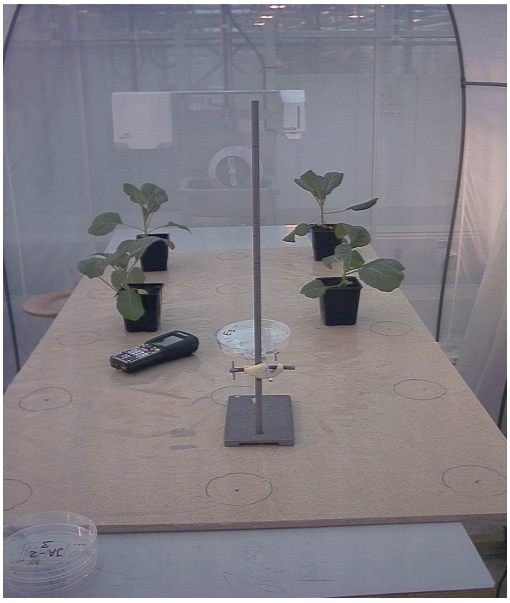


***Figure 2**; Experimental setup*

Treatments consisted of a set of four plants with a combination of host and non-host herbivores (hereafter, mixed patch). Three treatments were tested: plants with 10 hosts only (34 replicates), 10 non-hosts only (14 replicates) and mixed patches of 5 hosts and 5 non-hosts (25 replicates).

Behavioural observations
Behavioural parameters were defined according to Wiskerke & Vet (1994) with some minor adjustments. Time allocation of the following parameters was measured (table 2).

Table 2; *Behavioural parameters*

Parameter	Description
Fly	the wasp is airborne
Landing	the moment of touch down on a plant
Ceiling	landing on the ceiling of the tent or any object other than the plant
Walk	the antennae are extended in front of the head and are alternately moved up and down
Search	the antennae are bent and sweeping along the leaf surface; when searching, moving speed and direction is slower and more erratic than walking
Attack host	inserting the ovipositor into a host larva for short time (< 1 s), antennae and wings are raised
Attack non-host	inserting the ovipositor into a non-host larva for short time (< 1 s), antennae and wings are raised
Oviposit host	inserting the ovipositor into a host larva for a longer time (≥ 5 s), antennae and wings are raised
Oviposit non-host	inserting the ovipositor into a non-host larva for a longer time (≥ 5 s), antennae and wings are raised
Stop	motionless, except for some antennal movement, although antennae do not touch the leaf surface
Stop at silk	wasp is waiting at the leaf near a larva that is hanging on a silk wire in an attempt to escape the wasps attack
Groom	The wasp repeatedly draws the antennae through her fore legs and/or brushes the thorax and the abdomen with the midlegs, and the ovipositor and wings with the hind legs
Other plant	Wasp landed at another plant and oviposited or remained there for at least one minute

Wasps that instantly flew to the ceiling of the tent and stayed there for 5 or more minutes were recaptured and considered non-responsive. Observations ended when a wasp either remained on the plant she first landed on for one hour, or when the wasp left the plant. A plant (patch) was considered left when the wasp landed on another plant (or any other object) and oviposited or stayed at least one minute.

Data analysis
From the data obtained by the Observer, duration and frequency of all types of behaviour was calculated. Additionally the total time spent on the patch was calculated by adding durations of all displayed behaviour. Treatment-effect on these parameters was analysed using a Kruskal-Wallis non-parametric test. Any significant effect ($p < 0.05$) was then tested pair-wise between treatments with a Mann-Whitney test ($p < 0.05$). These statistics were performed using SPSS 12.01 for Windows. The fraction of hosts parasitized was analysed by a generalized linear model (Proc Genmod) using SAS 8.2. The fraction was modelled in logits: $\text{logit}(p)=\log(p/(1-p))$, assuming a binomial distribution for errors. Pairwise comparison of treatment groups was carried out by requesting linear contrasts.

3 Results

3.1 Field experiment

General patterns
Sampling moment (week number) had an overall significant effect on abundances on all of the analysed species ($p < 0.0001$, see appendix I). Generally, abundances increased continuously from the starting point of monitoring (week 23) and reached peak densities between week 29 and 31, followed by rapid decrease. In the first period, temperatures were high. July's day-averages were approximately 5° C above normal, which broke Dutch weather records. From week 32 a period of excessive rainfall started, which broke August's precipitation records. From that point on, insect numbers decreased. Only white flies and *D. semiclausum* increased throughout the monitoring series.

Herbivores
Cabbage aphids were found in relative high densities compared to other herbivores (± 20 per plant). They tended to be more abundant on Brussels sprouts then on white cabbage but differences were not significant ($F_{1,493} = 3.28$, $p = 0.071$). Abundances also tended to be affected by induction ($F_{1,493} = 3.22$, $p = 0.073$). There were slightly more cabbage aphids on control plants (21,4 per plant) then on induced plants (18,8 per plant). Field size had no apparent effect ($F_{1,493} = 0.04$, $p = 0.840$).
Green peach aphids were affected by induction ($F_{1,492} = 6.39$, $p = 0.0118$) and had a strong tendency of preferring white cabbage ($F_{1,492} = 3.71$, $p = 0.0545$). Although field size as an individual factor had no apparent affect ($F_{1,492} = 0.62$, $p = 0.4321$), there was a significant interaction between field size and induction ($F_{1,492} = 5.49$, $p = 0.0195$, figure 3), indicating that differences between induced and not-induced plants were increased in large fields.

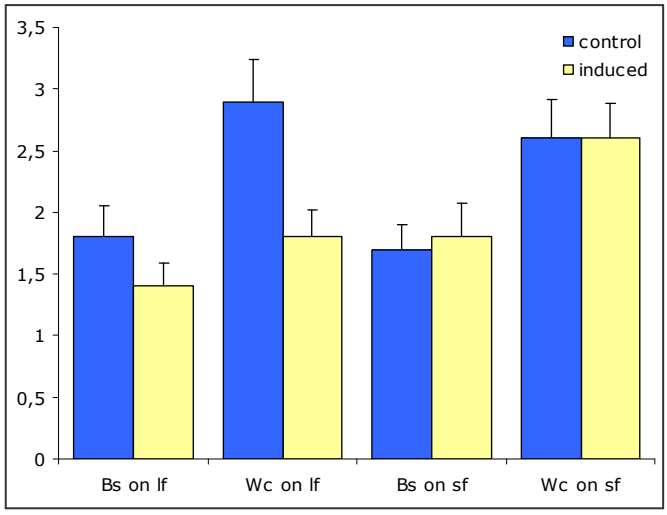


***Figure 3;**, Average numbers of peach aphids per plant, on control and induced Brussels sprouts (Bs) and white cabbage (Wc) in either large fields (lf) or small fields (sm)*

More small cabbage white-eggs were found on white cabbage ($F_{1,493}$ = 7.16, p = 0.008). Densities of larvae did however not differ between both cultivars ($F_{1,493}$ = 0.03, p = 0.856). Field size did not influence numbers of eggs ($F_{1,493}$ = 2.61, p = 0.107) or larvae ($F_{1,493}$ = 0.48, p = 0.491). Also induction did not affect number of eggs ($F_{1,493}$ = 0.10, p = 0.751) or larvae ($F_{1,493}$ = 2.29, p = 0.131).
Cabbage moth-eggs were not affected by field size ($F_{1,493}$ = 0.02, p = 0.890), cultivar ($F_{1,493}$ = 0.59, p = 0.442) or induction ($F_{1,493}$ = 0.11, p = 0.737). Larvae were found more on not induced plants than on induced plants ($F_{1,493}$ = 20.12, p < 0.0001). No effect was found for field size ($F_{1,493}$ = 2.49, p = 0.115) and crucifer ($F_{1,493}$ = 2.64, p = 0.105).
Diamond back moths tended to lay more on Brussels sprouts then white cabbage ($F_{1,493}$ = 3.42, p = 0.065). Number of larvae were however not effected by crucifer ($F_{1,493}$ = 0.56, p = 0.455). Neither eggs ($F_{1,493}$ = 0.56, p = 0.455) nor larvae ($F_{1,493}$ = 0.43, p = 0.511) were effected by field size. Also induction did not affect number of eggs ($F_{1,493}$ = 0.34, p = 0.561) or larvae ($F_{1,493}$ = 0.84, p = 0.361).
Flea beetles *P. undulata* and *P. atra* showed similar responses to treatments (figure 4) although the former were found in approximately ten times higher densities. *P. undulata* preferred large over small fields ($F_{1,488}$ = 12.86, p = 0.0004) white cabbage over Brussels sprouts ($F_{1,488}$ = 34.96, p < 0.0001), and induced over not-induced plants ($F_{1,488}$ = 61.94, p < 0.0001). Similarly, *P. atra* preferred white cabbage ($F_{1,493}$ = 14.16, p = 0.0002), and induced plants ($F_{1,493}$ = 9.79, p = 0.0019) over Brussels sprouts and not-induced plants, respectively. There was a tendency ($F_{1,493}$ = 3.55, p = 0.060) of preference for large fields. For both species there were significant interaction effects between field size and cultivar (*P. undulata*: $F_{1,488}$ = 6.02, p < 0.0145; *P. atra*: $F_{1,488}$ = 4.52, p < 0.0340), indicating that in large fields the difference between cultivars increased. Furthermore, interaction effects were found between induction and cultivar (*P. undulata*: $F_{1,488}$ = 6.89, p < 0.0090; *P. atra*: $F_{1,488}$ = 4.76, p < 0.0297), indicating that the differences between cultivars increased as a result of induction.

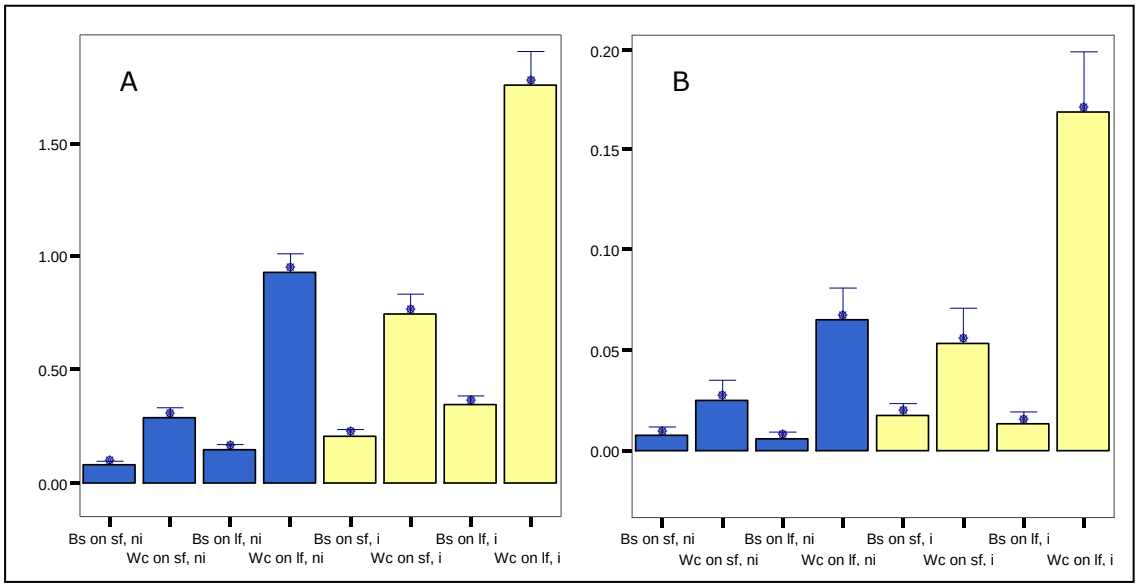


Figure 4; *Total numbers of* P. undulata *(graph A) and* P. atra *(graph B) on Brussels sprouts (Bs) and white cabbage (Wc) in small fields (sf) or large fields (lf) that were either induced (I, yellow bars) or not-induced (blue bars, ni)*

Thrips preferred Brussels sprouts over white cabbage ($F_{1,489}$ = 9.00, p = 0.0028). They were marginally more abundant in large fields then in small ones ($F_{1,489}$ = 3.67, p = 0.0558) and also more on not-induced plants then induced plants ($F_{1,489}$ = 3.29, p = 0.0701).

White flies preferred not induced plants over induced plants ($F_{1,479}$ = 3.93, p = 0.0481). Cultivar tended to affect abundances as well. Most whiteflies were recorded on Brussels sprouts ($F_{1,479}$ = 3.58, p = 0.0592). There was a significant interaction between week and cultivar ($F_{10,479}$ = 2.42, p = 0.0081), suggesting that the effects that cultivars had changed during the season (figure 5). White flies were not affected by field size ($F_{1,479}$ = 0.23, p = 0.6299).

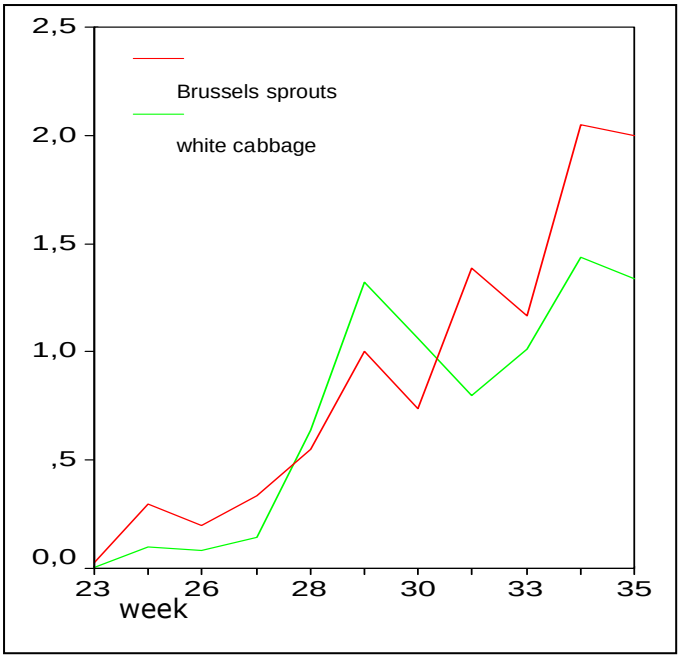


Figure 5; *Differences between numbers of* Aleyrodes proletella *on Brussels sprouts and white cabbage over time*

Natural enemies

More parasitized cabbage aphids (mummies) were found on induced plants ($F_{1,381}$ = 5.27, p = 0.0222). Field size and cultivar had no apparent effect (resp., $F_{1,381}$ = 0.91, p = 0.3398 and $F_{1,381}$ = 0.19, p = 0.6657).

Syrphid-larvae had a tendency of being more abundant on Brussels sprouts then on white cabbage ($F_{1,493}$ = 3.39, p = 0.066). Field size and induction had no effects ($F_{1,493}$ = 0.20, p = 0.655 and $F_{1,493}$ = 0.41, p = 0.525, respectively).

Chrysoperla-eggs were more found on Brussels sprouts compared to white cabbages ($F_{1,493}$ = 4.90, p = 0.027). Neither field size ($F_{1,493}$ = 0.00, p = 0.959) nor induction ($F_{1,493}$ = 0.09, p = 0.759) had an effect. Larvae were not affected by field ($F_{1,493}$ = 0.54, p = 0.465), cultivar ($F_{1,493}$ = 0.81, p = 0.369) and induction ($F_{1,493}$ = 0.39, p = 0.534).

C. rubecula parasitized more small cabbage whites in small fields then in large ones ($F_{1,340}$ = 9.21, p = 0.0026). Neither cultivar nor induction affected percentages of parasitized larvae (resp. $F_{1,340}$ = 1.93, p = 0.1661 and $F_{1,340}$ = 0.02, p = 0.8746).

Diadegma semiclausum, parasitoid of diamond back moths, were not significantly affected by field size ($F_{1,373}$ = 0.62, p = 0.4324), cultivar ($F_{1,373}$ = 0.27, p = 0.6050) or induction ($F_{1,373}$ = 0.02, p = 0.8884). There was however a significant interaction between induction and cultivar ($F_{1,373}$ = 5.20, p = 0.0232), which suggests that induction amplifies the differences between both cultivars. Smallest percentages of parasitized diamond back moths were found on induced white cabbage plants.

Other species
Several other species were found, but in densities that were to low (average less then 0.05 per plant, per week) for adequate statistical analysis. That were, of the herbivores, silver Y moth and pollen beetle and of the natural enemies, *Coccinella septempunctata* (in egg-form), *Harmonia axyridis,* cocoon clutches of *C. glomerata* and parasitized peach aphids.

3.2 Behaviour experiment

Patch time allocation
Treatment effected total time spent on the patch (figure 6, appendix II). Overall, wasps spent most time on plants when there were hosts present (table x). Wasps spent approximately one-fifth of the time on patches with only non-hosts compared to patches with 10 hosts only and the mixed patches (appendix II). There was no difference in patch time between the latter two treatments. Furthermore, durations of all behaviour types was effected by treatment, except 'stop' on which treatment had no apparent effect (appendix II).

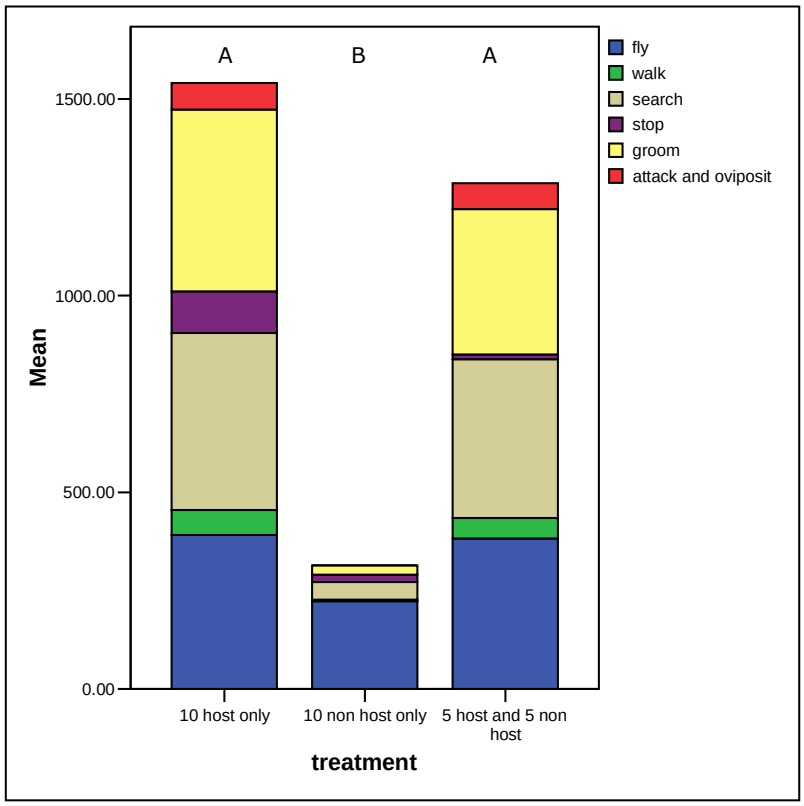


Figure 6; *patch time allocation per treatment. Bars represent sums of total durations of each behavioural parameter. "attack and oviposit" shows the duration of all attacks and ovipositions in hosts and non-hosts. Different letters indicate significant difference in total patch time ($p < 0.05$)*

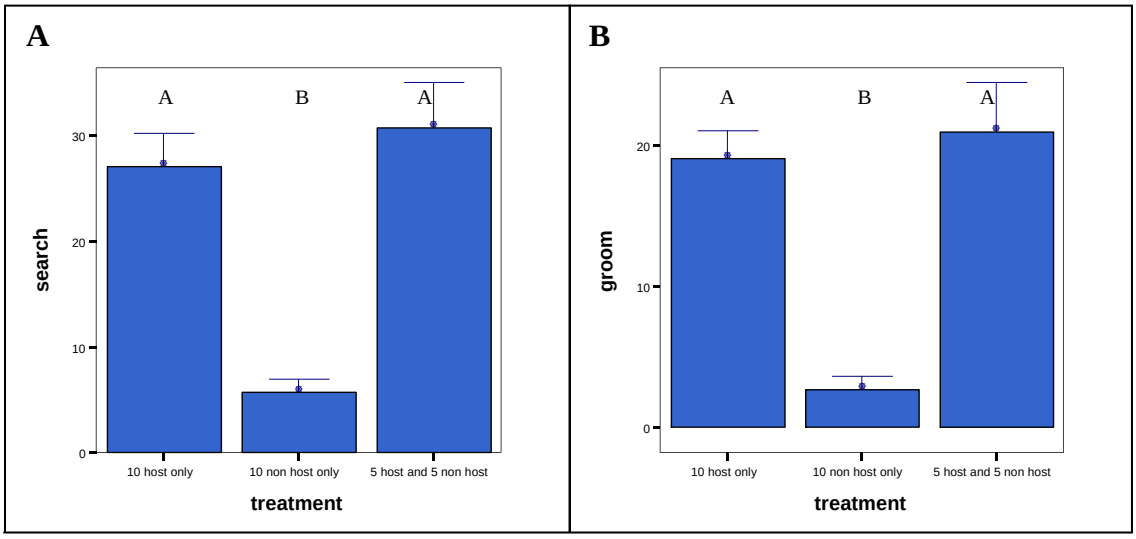
The other types of behaviour followed the same trends as total patch time; wasps spent shortest times displaying these types of behaviour on plants with only non-hosts present and longest on plants with hosts and plants with hosts and non-hosts (table 3). Of these, smallest difference was found in flying around the plant, 233 s around plants with only non-hosts and 392 s for both other treatments.

Wasps generally spent most time grooming and searching. Here I found also the largest differences between treatments. Only one-tenth of the time was spent searching, and time spent grooming was reduced close one-twentieth.
Differences in walking were even more pronounced. Wasps spent 63 and 56 seconds walking on host-only patches and mixed patches, respectively, while on non-host patches time spent on walking was only four seconds. Oviposition and attack did not differ between treatments, except oviposition in non-hosts which occupied more time on plants with hosts-non-hosts mixtures then with non-hosts alone.

Table 3; *patch allocation times.*

Treatment	**10 host only**		**10 non-host only**		**5 host + 5 non-host**	
Behaviour	*Mean*	*S.E.*	*Mean*	*S.E.*	*Mean*	*S.E.*
total patch time	1542.77	162.45	314.54	47.51	1440.31	159.49
fly	391.54	44.43	223.49	33.11	392.41	49.58
walk	63.17	12.12	4.02	1.82	56.04	10.63
search	450.58	54.25	44.37	9.95	410.90	50.69
stop	105.36	45.96	18.47	10.96	30.04	10.73
groom	462.09	59.07	24.09	9.11	461.73	76.34

Frequencies in which behavioural parameters were displayed on a patch followed the same trend as for durations of these behaviours (figures 7 A-D, appendix II). No differences were found between 10 hosts only and 5 hosts and 5 non-hosts treatments, while 10 non-hosts was significantly lower in all cases. Again, 'stop' was not significantly different between treatments (appendix II). Searching behaviour was most frequent in all treatments, 27 times in patches with 10 hosts only, 31 times in mixed patches and 6 in patches with non-hosts only.



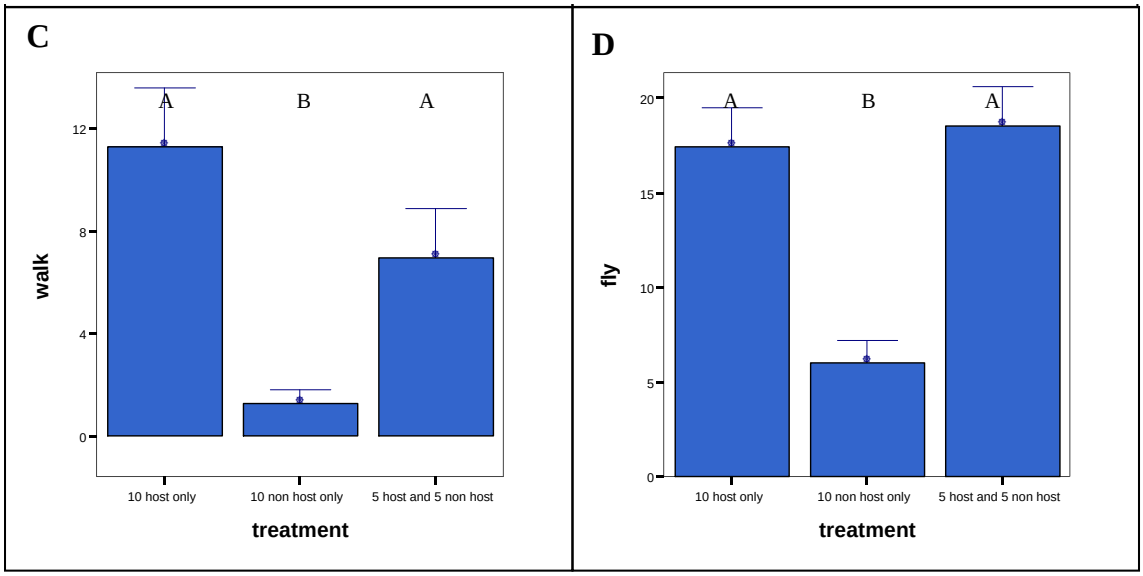


Figure 7*; freqencies of searching (A), grooming (B), walking (C) and flying (D). Different letters in graphs indicate significant differences (Mann-Whitney U: p < 0.05, df =2)*

Host en non-host encounters

In several observations *C. glomerata* was observed ovipositing in non-host caterpillars (as shown in figure 8).

Figure 8; *Oviposition of C. glomerata in P. rapae (left) and M. brassicae (right)*

Through dissection after observations, eggs of *C. glomerata* were found in apparently parasitized larvae of *M. brassicae* larvae, confirming that actual oviposition had taken place. Ovipositions in non-hosts occurred only in mixed patches (figure 9, appendix II).

Duration of attacks and ovipositions (table 4) did not differ between treatments (see appendix II), except for oviposition in non-hosts, since it was only observed in mixed patches. Therefore, also frequency of non-host parasitization differed in the same between both treatments (figure 9 D). Number of attacks non-host attacks did however not differ significantly, although there was a tendency of more non-hosts being attacked in mixed patches (figure 9 C).

The percentage of ovipositions in hosts was significantly higher in the mixed patches (40 %) then in patches with hosts only (30 %). Number of superparasitisms occurred in approximately 50 % per observation and did not differ between mixed patches and patches with 10 hosts only.

Table 4; *durations of attacks and ovipositions*

Treatment	**10 host only**		**10 non-host only**		**5 host + 5 non-host**	
Behaviour	*Mean*	*S.E.*	*Mean*	*S.E.*	*Mean*	*S.E.*
attack host	4.72	1.32	x	x	8.29	4.66
oviposit host	61.27	7.75	x	x	62.03	12.86
attack non-host	x	x	0.09	0.09	2.79	1.65
oviposit non-host	x	x	0.00	0.00	15.17	5.23

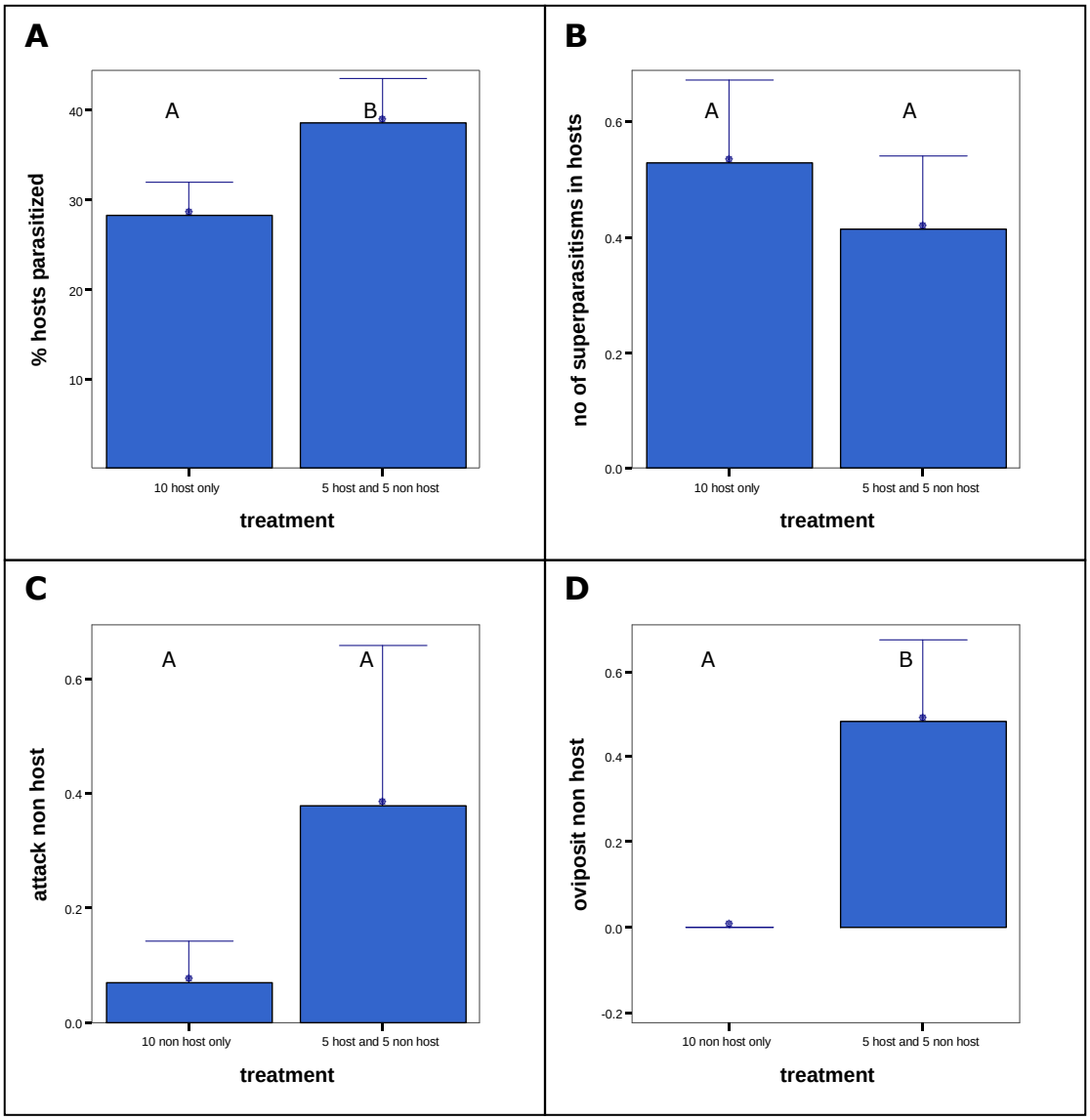


Figure 9; *percentage of hosts parasitized (A), number of super parasitisms in hosts (B), attacked non-hosts (C) and ovipositions in non-hosts (D). Different letters in graphs indicate significant differences (Mann-Whitney U: $p < 0.05$, df =2)*

4 Discussion and conclusions

4.1 Field experiment

Population fluctuations
Sampling moment (week number) had a strong effect on the number of insects found. Naturally, insect population fluctuate between seasons and within a season because of a large variety of abiotic and biotic factors. Weather extremities such as the heat in the first part and the excessive rainfall in the second part of the monitoring series must have had some impact on the insect community. Leite *et al.,* (2006), demonstrated that increases in temperature favour *Thrips* and white flies, while heavy rain and high humidity are deleterious for these insects. It is likely that abundances in general, would have decreased later or at slower rates when the rain-period was less extreme.

Cultivar
Of the herbivores, *Thrips* and white flies showed clear preferences for Brussels sprouts, while white cabbage was preferred by leaf beetles and peach aphids. Cabbage moths and diamond back moths had no preference for either cultivar. Some species laid their eggs on one cultivar while their larvae were found in equal numbers on both cultivars. This was the case for small cabbage white which laid most eggs on white cabbage and *Chrysoperla* which laid most eggs on Brussels sprouts. *Chrosperla* was the only species of the natural enemies that showed preference for a particular cultivar. Parasitized cabbage aphids, *C. rubecula*, *D. semiclausum* and *Syrphids* were found equally distributed between cultivars, although the latter tended to prefer Brussels sprouts.
The differences in insect abundances between both cultivars are likely to be the result of physiological differences. For example, the interaction effect between cultivar and week number that was found for white flies may be because of a difference in the leaves of the cultivars. White cabbage leaves have a thick fatty layer which enables rainwater to flush off insects more easily. This occurred intensive in the rain period in the last part of the monitoring series. Other insects were then found in the dense crops of the white cabbage plants, which protected them against rainfall.

Field size
According to Root (1973), specialist herbivores should be more abundant in large fields. However in this experiment, field size had little influence on the herbivore densities. Only flea beetles were affected by field size and it tended to affect *Thrips.* A study by Banks (1998) also showed relations between flea beetle abundances and field sizes. Although both flea beetles and *Thrips* were most abundant in large fields, this results hardly support Roots resource concentration hypotheses, since none of the other herbivores were apparently affected by field size.
Other studies support the idea that field size can affect herbivores in very different ways. Grez & Gonzáles (1995) for example also found equal densities of cabbage aphids, peach aphids and diamond back moths in different sizes *B. oleracea* fields and Banks (1998) found no field size effect for small cabbage whites. Another study, by Bukovinszky *et al.,* (2005) furthermore supports the results for aphids, but found higher densities of *P. rapae*-eggs, in contradiction to my observations. Since the same field sizes were used, this may be due to a difference isolation distance, which is supported by a study of Fahrig and Paloheimo (1988). Apparently, the resource concentration hypothesis does not apply to all herbivores and differs per species.

Recently it is been suggested that foraging strategies in combination with displacement speed and arrestment response affect herbivore responses to field sizes (see Bukovinszky *et al.,* 2005; Hambäck and Englund, 2005). Bukovinszky *et al.,* (2005) compared cabbage aphids, cabbage butterflies and diamondback moths. Cabbage aphids, use short range (post alighting) cues while cabbage butterflies and diamondback moths use long range cues. Another difference between these species is that cabbage aphids and diamondback moths show a high arrestment response when a host plant is found while cabbage butterflies engage long flights between ovipositions (i.e. Bukovinszky *et al.,* 2005).
My results do not support this theory either, since herbivores with different search modalities and displacement speeds, such as cabbage aphids, diamondback moths and cabbage butterflies, were all not affected by field size. The strong response of the flea beetles is explained by Hambäck and Englund (2005). Flea beetles have a predominantly olfactory search mode, which in combined with aggregation pheromones can lead to high numbers. First individuals have the highest change to land in large fields and subsequently attract other individuals. Therefore highest densities may be found in large fields. Field size furthermore affected one of the natural enemies. *C. rubecula* was found most in small fields. The number of this parasitoid was calculated as a percentage of parasitized small cabbage whites, because its abundance is directly linked on the presence of its host. This means that in small fields, percentage wise more larvae were parasitized, while, between field sizes, the total number of larvae did not differ. Overall, it is evident that the mechanisms trough which field size affects population dynamics are still open for debate.

Induction
Induction took place at only two moments, so it was not a continuous process. However, since there was no interaction found between induction and week for any recorded species, it can be assumed that the affects of both inductions lasted during the monitoring series. A variety of herbivores and natural enemies were affected by induction. The majority of the herbivores preferred control plants over induced plants. That is, peach aphids, white flies, cabbage aphids and thrips were most found on not-induced plants, although for the latter two only a tendency was found. Flea beetles were the only herbivores that were found most on induced plants. Small cabbage whites cabbage and diamond back moths were not affected by induction. Cabbage specialists are thought to be less affected by increased levels of toxins of induced plants then generalists (e.g. Sznajder and Harvey, 2003). Growth efficiecy of small cabbage whites for example were not affected by induction of wild radish plants, but the plants experienced less colonisation by leaf miners and grasshoppers (Agrawal, 1999).
Interestingly, cabbage moth females deposit their eggs irrespective of induction, while the larvae apparently prefer not induced plants. These larvae are however relatively mobile. This enables them to switch plants in contrast to, for example, early instar cabbage whites that are restricted to the plant of choice of the adult females. Diamond back moths are also mobile but did not prefer control plants over induced plants, although it has been well documented that feeding preference decisions by first-instar P. xylostella larvae is the principal mechanism of host-plant resistance (Eigenbrode & Shelton, 1990; Verkerk & Wright, 1996b; Eigenbrode & Pillai, 1998). Interestingly, none of the natural enemies was found more on induced plants except parasitized cabbage aphids. From herbivores point of view that means that avoiding induced plants, which contain more toxins that hinder larval development (e.g. Sznajder and Harvey, 2003), may be more effective then chose either induced (encounter dilution effect) or not-induced (enemy low space) plants to avoid enemies.

In this field experiment plants were not just affected by the induction of large cabbage whites, but also by other herbivores that colonized the plant. Although induction by large cabbage whites clearly affects insect composition of the insect community, it should be kept in mind that induction by other herbivores seems to affect the community in different ways (Agrawal, 1999). Some insects that were not affected by the induction as a result of feeding large cabbage whites may have been influenced by other inducers. Although flea beetles were the only herbivores that preferred cabbage-white induced plants, it can therefore not simply be said that, herbivores prefer enemy-low space. Also, only parasitized cabbage aphids were found more on induced plants then control plants. None of the other natural enemies were found more on induced plants.
Avoiding enemy-dense space can only be effective if herbivores share common enemies that can be avoided by feeding on plants that are not colonized by the other herbivore(s). To study this, a multi-trophic interaction web should be constructed to link species to each other. Since different inducers affect the same plant differently, development of the insect community may depend on all other herbivores that colonize and induce the plant. In that case, insects that first colonize a plant have the largest impact on how the insect community develops. Plant preference of primary and subsequent colonizers should be subject of further investigation because it may reveal links between insect behaviour and population dynamics.

4.2 Behaviour experiment

The results of these experiments clearly reveal a differential effect of hosts and non-hosts presence in a patch on searching behaviour of *C. glomerata*. Time spent on a patch with non-hosts only is much lower then on patches were there are hosts only. This was also found by Vos (2001). Host derived stimuli are reliable cues but are difficult to detect at long distances, whereas plant-derived stimuli may be less reliable but easier to detect (Vet *et al.,* 1991; Vet and Dicke, 1992). Generally, it can be concluded that plants with only non-hosts reduce foraging efficiency because they have to investigate plants without hosts. Wasps seem to detect an induced plant and link it to potential host presence. Then they have to search on the plant and investigate if and where they are. Wasps spent little time searching and walking on plants with non-hosts only, so apparently they have little trouble in close-range detecting the absence of hosts. Although the time spent on plants with only non-hosts is short, they still have to search on useless patches in order to determine no hosts are present which costs precious time and energy. If learning capabilities of *C. glomerata* can, in time, increase foraging efficiency by neglecting or further reduce searching time on plants with non-hosts only should be further investigated.
Mixed patches, that contain hosts and non-hosts, may be more difficult to asses for parasitoids due to changes in volatile compounds (e.g. Micha *et al.,* 2000; Fatouros *et al.*, 2005). I predicted a confusing effect, in which non-hosts reduce foraging efficiency. This was not the case since neither duration nor frequency of flight, search, walk, stop, and groom were affected. Also, percentages of hosts attacks and ovipositions were not affected by non-host presence. It did affect however the wasps behaviour in an intriguing way. The wasps also attacked and oviposited in non-hosts. Attacking occurred in both mixed and non-hosts only patches, while ovipositions occurred only in mixed patches. It is generally thought that the wasps are capable of discriminating between hosts and non-hosts (see e.g. Vet *et al.,* 1991), which apparently is not always true. I noticed that the wasps tend to search holes in the leaf intensively first and then followed a trail to locate the caterpillar.

In this set-up, host and non-host caterpillars were able to move across and feed on the entire plant. *M. brassicae,* the non-host, is relatively mobile. It is therefore likely that odour-tracks of hosts and non-hosts have crossed and mixed during the 24-hour feeding time. Caterpillars often touched each other while moving and foraging, which may have caused a dilution effect for the wasps. The response to the volatile or contact stimuli associated with presence of hosts was strong. In some cases, when wasps were already agitated, they showed attacking behaviour on faeces of their hosts. Nevertheless, wasps attacked and oviposited in a non-host before and after encountering and ovipositing in host-caterpillars. Since ovipositions in non-hosts only occurred in mixed patches, their must be some host-related mechanism that alter the response of the wasps to the non-hosts and perhaps their discriminating ability. When, however hosts and non-hosts share a patch, non-hosts seemed not negatively affect host foraging efficiency of *C. glomerata*, although it can be stated that it does affect its response to non-hosts. Whatever the impact of this phenomenon is in a field-situation depends on host and non-host distributions and densities. Furthermore, these tests were performed with naïve wasps. Experience can greatly increase foraging efficiency of these wasps (review Vet *et al.,* 1995). Although in some cases wasps oviposited in multiple non-hosts this effect may diminish when the number of host-encounters increases over time. Again, the effects of learning should be studied more closely. Also different host / non-host ratios may have different effects as well as different, less related non-hosts. It is interesting study what the effects will be when, for example, aphids are on the plant in stead of another Lepidopteran. Parasitoids are thought to be energy, time and/or egg limited, which means that attacking and ovipositing in non-hosts may have a great ecological impact. It is evident that non-host attacks deserve more study. Not only is it yet unknown whether it occurs in a field-situation, also what its ecological impacts are, and how it affects the non-host itself should be subjects for more studies.

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Appendix I, Week effects on recorded species

Species	Num Df	Den Df	F	p
Brevicoryne brassicae	10	493	247.45	<0.0001
Brevicoryne brassicae-parasitized	8	381	28.89	<0.0001
Myzus persicae	10	492	77.51	<0.0001
Pieris rapae-eggs	10	493	72.62	<0.0001
Pieris rapae-larvae	10	493	72.62	<0.0001
Mamestra brassicae-eggs	10	493	3.66	<0.0001
Mamestra brassicae-larvae	10	493	25.95	<0.0001
Plutella xylostella-eggs	10	493	31.34	<0.0001
Plutella xylostella-larvae	10	493	114.25	<0.0001
Phyllotreta undulata	10	488	12.68	<0.0001
Phylotreta atra	10	488	4.64	<0.0001
Thrips ssp.	10	489	29.92	<0.0001
Aleyrodes proletella	10	479	27.34	<0.0001
Syrphid spp.	10	493	25.85	<0.0001
Chrysoperla-eggs	10	492	38.37	<0.0001
Coccinella septempunctata-larvae	10	493	28.29	<0.0001
Cotesia rubecula	8	340	18.91	<0.0001
Diadegma sp.	9	373	30.18	<0.0001

Appendix II, Analysis of behavioural parameters

Statistical analysis of durations per behaviour is presented in tables 1 - 6. Mean values with standard errors of frequencies of all behaviours are shown in table 7. Statistical analysis of frequencies is presented in tables 8 – 11.

Table 1; Kruskal Wallis analysis of durations

Behaviour	patch type	Mean	S.D.	Chi^2	p
time on patch	hosts only	1542.7668	947.24978	25.879	0.000
	non-hosts only	314.5379	177.77900		
	mixed	1440.3128	797.45505		
fly	hosts only	391.5415	259.07396	6.361	0.042
	non-hosts only	223.4900	123.87274		
	mixed	392.4128	247.91023		
walk	hosts only	63.1653	70.67451	16.962	0.000
	non-hosts only	4.0236	6.79196		
	mixed	56.0388	53.12614		
search	hosts only	450.5788	316.35829	28.840	0.000
	non-hosts only	44.3664	37.22308		
	mixed	410.8960	253.44573		
stop	hosts only	105.3641	267.96154	3.90	0.142
	non-hosts only	18.4750	40.99989		
	mixed	30.0440	53.63146		
groom	hosts only	462.0874	344.43439	29.461	0.000
	non-hosts only	24.0914	34.06966		
	mixed	461.7296	381.68108		
attack host	hosts-only	4.7176	7.70276	16.282	0.000
	mixed	8.2944	23.28682		
attack non host	non-hosts only	0.0914	0.34209	9.850	0.007
	mixed	2.7868	8.26604		
oviposit host	hosts-only	61.2703	45.21104	25.995	0.000
	mixed	62.0304	64.32338		
oviposit non host	non-hosts only	0.0000	0.00000	15.215	0.000
	mixed	15.1676	26.16440		

P values and Chi^2 were calculated with a Kruskal Wallis test, with df = 2 in all cases

Table 2; Mann-Whitney Test for durations in host and non-host patches

Behaviour	t patch	fly	walk	search	groom
Mann-Whitney U	30.000	136.000	93.000	14.000	8.000
Wilcoxon W	135.000	241.000	198.000	119.000	113.000
Z	-4.718	-2.314	-3.364	-5.081	-5.217
Asymp. Sig. (2-tailed)	0.000	0.021	0.001	0.000	0.000

Table 3; Mann-Whitney Test for durations in host and mixed patches

Behaviour	t patch	fly	walk	search	groom
Mann-Whitney U	416.000	423.000	405.000	412.000	413.000
Wilcoxon W	741.000	748.000	1000.000	737.000	738.000
Z	-0.138	-0.031	-0.308	-0.199	-0.184
Asymp. Sig. (2-tailed)	0.890	0.976	0.758	0.842	0.854

Table 4; Mann-Whitney Test for durations in host and mixed patches

Behaviour	attack host	oviposit host
Mann-Whitney U	357.000	388.000
Wilcoxon W	682.000	713.000
Z	-1.071	-0.568
Asymp. Sig. (2-tailed)	0.284	0.570

Table 5; Mann-Whitney Test for durations in mixed and non-host patches

Behaviour	t patch	fly	walk	search	groom
Mann-Whitney U	20.000	97.000	31.000	16.000	18.000
Wilcoxon W	125.000	202.000	136.000	121.000	123.000
Z	-4.538	-2.284	-4.264	-4.655	-4.597
Asymp. Sig. (2-tailed)	0.000	0.022	0.000	0.000	0.000

Table 6; Mann-Whitney Test for durations in mixed and non-host patches

Behaviour	attack non host	oviposit non host
Mann-Whitney U	142.500	112.000
Wilcoxon W	247.500	217.000
Z	-1.422	-2.498
Asymp. Sig. (2-tailed)	0.155	0.012

Table 7; frequencies of each recorded behaviour

patch type	hosts only		non hosts only		mixed	
Behaviour	*Mean*	*S.E.*	*Mean*	*S.E.*	*Mean*	*S.E.*
fly	17	2	6	1	19	2
walk	11	2	1	1	7	2
search	27	3	6	1	31	4
stop	4	1	1	0	2	1
groom	19	2	3	1	21	3
landing	17	2	6	1	19	2
superparasitism	1	0	0	0	0	0
attack host	2	0	x	x	2	0
attack non host	x	x	0	0	0	0
oviposit host	3	0	x	x	2	0
oviposit non host	x	x	0	0	0	0

Table 8; Kruskal Wallis test for frequencies of recorded behaviour

Behaviour	fly	walk	search	groom	stop	parasi-tism	super-parasitism
Chi-Square	16.783	10.245	25.213	26.841	5.205	30.067	6.424
df	2	2	2	2	2	2	2
Asymp. Sig.	0.000	0.006	0.000	0.000	0.074	0.040	0.000

Table 9; Mann-Whitney Test for frequencies in host and non-host patches

Behaviour	fly	walk	search	groom
Mann-Whitney U	84.000	113.500	45.500	29.000
Wilcoxon W	189.000	218.500	150.500	134.000
Z	-3.498	-2.892	-4.374	-4.749
Asymp. Sig. (2-tailed)	0.000	0.004	0.000	0.001

Table 10; Mann-Whitney Test for frequencies in host and mixed patches

Behaviour	fly	walk	search	groom	attack host	oviposit host
Mann-Whitney U	727.000	710.000	688.500	719.500	691.500	616.000
Wilcoxon W	1673.000	1656.000	1283.50	1665.500	1637.500	1562.000
Z	-0.041	-0.217	-0.436	-0.118	-0.418	-1.192
Asymp. Sig. (2-tailed)	0.967	0.828	0.683	0.906	0.676	0.233

Table 11; Mann-Whitney Test for frequencies in mixed and non-host patches

Behaviour	fly	walk	search	groom	attack non host	oviposit non host
Mann-Whitney U	83.000	139.000	39.000	39.500	258.000	49.000
Wilcoxon W	188.000	244.000	144.000	144.500	363.000	154.000
Z	-4.048	-3.063	-4.859	-4.854	-1.205	-4.819
Asymp. Sig. (2-tailed)	0.000	0.002	0.000	0.000	.228	0.000