



Abundance of syrphid larvae in willow plantations:
-Role of habitat type, prey (*Phratora vulgatissima*) availability and interactions with other natural enemies

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Abstract

A large number of hover fly species are as larvae effective predators and often feed on insect pests in plantations. The leaf-beetle *Phratora vulgatissima* is a common pest in willow plantations and the aim of this study is to study what may affect the presence of hover flies in this system. The quality of the surrounding habitats, prey availability and interactions with other natural enemies are parameters that may explain variances in densities of hover flies and was here investigated at five localities whereas a total of 40 plots of 5 x 5 meters have been studied in detail. The heteropterans *Anthocoris nemorum* and *Orthotylus marginalis* are two natural enemies to *P. vulgatissima* and whose foraging behaviour differs and their interactions with the hover fly may therefore differ. The syrphid larva and the mirid display a similar foraging behaviour and interactions, e.g. competition and predation, between these two species are thus likely to occur. Experiments were performed in the laboratory to study if there were any differences in proportion of consumed syrphid eggs and in time to consumption of eggs between anthocorids and mirids. The results showed that all plots in field where syrphid eggs were found were surrounded by a high proportion of forest while no eggs were found in plots next to arable land. Leaf beetle egg clutches with syrphid eggs were in average larger in size compared with clutches without. The variation in density of leaf beetle eggs was small between localities and plots, which could explain the lack of association between high densities and abundance of syrphid eggs. The abundance of other enemies, e.g. heteropterans, seemed to have a negative effect on the hover fly since no hover fly eggs were found in plots with high densities of other enemies. Both species of heteropterans consumed a large proportion of syrphid eggs. Contrary to my expectations none of the species had a larger negative impact on the survival of the syrphid neither when considering time to consumption of the egg nor the proportion of consumed syrphid eggs. This study shows that a higher diversity within the enemy-complex may have negative effects on the biological control of pests and that predators within the same guild are susceptible to predation in certain developmental stages. Hover flies are probably of little importance in the biocontrol of leaf beetles in situations with high densities of other natural enemies but have the potential to be particularly important as predators in recently harvested plantations i.e. plantations with low densities of heteropterans.

Sammanfattning

Ett flertal arter av blomflugor är, som larver, effektiva predatorer och äter ofta insektskadegörare i odlingar. Bladbaggen *Phratora vulgatissima* (Coleoptera:Chrysomelidae) är en vanlig skadegörare i Salix-odlingar och målet med denna studie är att undersöka vad som kan påverka förekomsten av blomflugor i detta system. Kvalitén på omgivande habitat, tillgång på föda och interaktioner med andra predatorer är faktorer som kan förklara skillnader i täthet av blomflugor och undersöktes här på fem lokaler där totalt 40 ytor om 5 x 5 meter detaljstuderades. Skinnbaggarna *Anthocoris nemorum* och *Orthotylus marginalis* är två naturliga fiender till *P. vulgatissima* och vars födosöksbeteende skiljer sig åt, vilket gör att deras interaktion med blomflugor kan skilja. Blomflugelarven uppvisar ett födosöksbeteende som mest liknar miridens och interaktioner, såsom konkurrens och predation, mellan dessa två är därför troligast. Experiment utfördes på lab för att undersöka om det fanns någon skillnad i andel uppätta blomflugeägg och tid tills ägget ätits upp mellan anthocorider och mirider. Resultaten visade att alla ytor i fält där blomflugeägg hittades var omgivna av en hög andel skog medan inga ägg hittades i anslutning till odlad mark. Bladbaggeägg-samlingar med blomflugeägg var i genomsnitt större än de utan. Variationen i täthet av bladbaggeägg var liten mellan såväl ytor som lokaler, vilket kan förklara varför inget samband mellan höga tätheter och förekomst av blomflugeägg kunde konstateras. Förekomst av andra fiender, skinnbaggar, tycktes ha en negativ effekt på blomflugan då inga ägg av blomflugor hittades i ytor med höga tätheter av andra fiender. Båda arterna av skinnbaggar åt en stor andel blomflugeägg och i motsats till vad som förutspått hade ingen art större negativ inverkan på blomflugans överlevnad varken i fråga om tid till ägget blivit uppätet eller andelen ättna blomflugeägg. Denna studie visar att närvaro av flera predatorer inte alltid är positivt för biologisk kontroll av skadegörare utan att predatorer som annars delar byte i vissa stadier är känsliga för predation. Blomflugor är troligen av mindre betydelse för kontroll av bladbaggar i närvaro av andra fiender men har goda möjligheter att bli viktiga bekämpare i nyskördade fält, där det är låga tätheter av skinnbaggar.

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1 Introduction

Suppression of herbivores is in several cases strengthened by a high diversity within the enemy-complex (Aquilino *et al.*, 2005; Snyder *et al.*, 2007). This could be explained by the complementary action of predators with different foraging strategies. Several predator species could also make the defensive behaviour among the herbivores less effective (Sih *et al.*, 1998). A higher diversity among predators increases the chance that the enemy-complex will contain an effective and strong competitive species (Ives *et al.*, 2005). It may also lead to an increased competition for food among predators and even that predators prey on each other (Straub *et al.*, 2007). Interactions as competition and predation within an enemy-complex are called intraguild predation (IGP). IGP is not an uncommon phenomenon and is reported in several organisms that share prey and may compete in several ecological systems (Polis *et al.*, 1989; Bampfylde & Lewis, 2006).

A factor that may affect intraguild predation is that predation in insects often is stage-specific where a predatory species may be more vulnerable to predation in their immobile stages, like eggs and young larvae, but less vulnerable in later developmental stages (Hindayana *et al.*, 2000; Fréchette *et al.*, 2007). If predators also have overlapping niches and display a similar foraging behaviour, especially in active predators, they are more likely to compete for resources and interactions among these species are therefore negative (Sih *et al.*, 1998). IGP is more likely to occur in species that compete for limited resources and thus decrease the effectiveness of biocontrol in plantations (Polis *et al.*, 1989; Rosenheim *et al.*, 1999).

Fréchette *et al.* (2007) investigated the interactions between two natural enemies of aphids that display similar hunting modes and which are within the same guild; a mirid (Heteroptera:Miridae) and a hover fly (Diptera:Syrphidae). Their study confirms that hover flies are highly susceptible to predation as eggs by the mirid nymphs since all eggs were consumed in the experiments.

Although a majority of hover fly larvae are effective predators on aphids and other insects, which makes them interesting in suppression of pests in plantations (Sommaggio, 1999), almost all species of hover flies feed on pollen and nectar from plants in their adult stage. The pollen is also necessary for producing eggs. Presumably as a consequence of the adult life style, studies have shown that the quality of habitats surrounding the plantations is important for existence of adult hover flies in plantations (Sutherland *et al.*, 2001). Oviposition in gravid females is induced via olfaction of infested plants and the eggs are often placed in or close to large aggregations of prey (Scholz and Poehling, 2000; Ambrosino *et al.*, 2006).

In willow plantations, usually planted for biomass production, the leaf beetle *Phratora vulgatissima* is a major pest. Since willow plantations are rarely sprayed with pesticides, insect pest densities are mainly affected by weather, harvesting and natural enemies. Studies have shown that heteropterans are the most important predators on leaf beetles in this system (Björkman *et al.*, 2003).

However, there is another common predator on *P. vulgatissima*, a hover fly, that has not been studied as detailed as the heteropterans. The female hover flies oviposit in *P. vulgatissima* egg clutches and when the larva has hatched it starts to consume adjacent beetle eggs and larvae. Some years hover fly eggs have been found in high densities in some fields, in 25% of the egg clutches, while other years they have been absent in the same fields (Björkman *et al.*, 2003). The mechanisms behind these fluctuations in population densities between fields and years are still unknown and are in need of investigations. Parameters that could explain these fluctuating patterns in the field are (1) the abundance of other predatory insects (2) the supply of food for the adults and larvae and (3) the quality of the habitats surrounding the plantation.

The syrphid larvae are slow moving and relatively inactive predators, a foraging behaviour they share with mirid nymphs of *Orthotylus marginalis* (Heteroptera:Miridae). Syrphid larvae and mirid nymphs are thus likely to interact since they have overlapping niches and display similar feeding behaviour. These two predators both differ from the more active and fast moving anthocorid *Anthocoris nemorum* (Heteroptera:Anthocoridae), which visits more egg clutches than the two others. The interactions between *O. marginalis* and *A. nemorum* have been experimentally investigated and the study showed that there were no negative interactions between these species (Björkman & Liman, 2005).

One aim of this study was to examine how the amount and availability of food for both hover fly adults and larvae, in willow plantations and adjacent environment, affect their abundance in the field. Existence of other predators in the plantations may also increase the risk of predation of syrphid eggs and larvae and their densities in the field were therefore also estimated.

Another aim of this investigation was to study the interactions between syrphids and heteropterans with different feeding strategies in laboratory experiments.

1) To address the first aim of this study, *i.e.* to sample and measure a number of parameters in the field and estimate their effect on the abundance and presence of syrphid eggs. The parameters that have been used and their expected effects are:

- a) Existence of other natural enemies, the three species of heteropterans. Abundances of syrphid eggs were expected to decrease with increasing densities of other enemies
- b) Leaf-carrying willow shoots with leaf beetle eggs. The abundances of syrphid eggs were expected to increase with increasing densities of leaf beetle egg clutches
- c) The size of the leaf beetle egg clutches. A higher proportion of syrphid eggs was expected to be found in large clutches
- d) The habitats surrounding a sampled field. Forests and grasslands were expected to have a positive effect on the abundance of syrphid eggs while arable land were expected to have a negative effect

2) To address the second aim of the study, *i.e.* studying how the different feeding behaviour of *A. nemorum* and *O. marginalis* affect their response when exposed to a *Phratora* sp. egg clutch containing a *Syrphus* sp. egg. Proportion of consumed syrphid eggs and time to consumption are estimated. The mirid *O. marginalis* are expected to feed more readily and affect the syrphid more

negatively than the anthocorid *A. nemorum* since the mirid and the syrphid larvae have more similar foraging strategies.

2 Materials and methods

2.1 Study organisms

2.1.1 The leaf beetle

Phratora vulgatissima L oviposits on the lower side of willow leaves in clutches of 10-50 eggs and one female is able to produce several hundred eggs. Both adults and larvae feed on leaves and are major pests in willow plantations. The adult females start to lay their eggs from late May until middle of July. In the autumn the adult beetles disperse in search for suitable places for overwintering like cracks and crevices in buildings and plants (Björkman *et al.*, 2004).

2.1.2 The heteropterans

There are three species of heteropterans which are common predators on *Phratora* beetles; two species of mirids, *Orthotylus marginalis* Reuter and *Closterotomus fulvomaculatus* DeGeer and one anthocorid, *Anthocoris nemorum* L (Björkman *et al.*, 2003). The heteropterans pierce the eggs and larvae with their mouthparts and suck out the contents of eggs and bodies. When the mirids find a clutch of eggs they often consume all eggs before they start to search for a new one and this relatively inactive foraging behaviour is called 'find and stay'. The behaviour of the anthocorid differs significantly from the two mirids and they are more active predators and only eat a few eggs before searching for a new egg clutch and are called 'run and eat' predators. All three species often overwinter in the willow plantations. Therefore the harvesting of the fields, which takes place in the winter every third to fifth year, affects the natural enemies more negatively compared with the leaf beetles since they usually overwinter outside the plantation (Björkman *et al.*, 2004).



Photo 1. A chrysomelid egg clutch containing a syrphid egg which is marked with a black ring (Photo taken by Karin Eklund, Department of Ecology in Ultuna, SLU).

2.1.3 The hover fly

Among the predatory hover fly larvae there are species, e.g. *Parasyrphus nigratarsis* Zetterstedt, that are specialized on leaf beetle eggs and larvae and which may have a large impact on their numbers (Köpf *et al.*, 1997). The gravid females, like the species of hover fly that are found in willow plantations, place one or in some cases two or three eggs within or next to the clutches of chrysomelid eggs to facilitate for their offspring to find food (Photo 1). Hover fly larvae are slow moving predators and have a relatively inactive foraging behaviour (Köpf *et al.*, 1997). In the beginning of autumn some species could be overwintering as larvae in leaf litter or in cracks in bark (Rank & Smiley, 1994; Hart & Bale, 1997), as adults in larval galleries created by other insects in trees (Georgiev *et al.*, 2004) or as pupae in the soil (Cornell University's New York State Agricultural Experiment Station's website; 2008-10-01).

2.2 Field studies

To determine the association between syrphid egg abundance and (1) density of other natural enemies (i.e. heteropterans), (2) density of leaf beetle eggs, (3) the average size of beetle egg clutches and (4) the surrounding habitats, five willow plantations around Uppsala were visited; Buskvreten, Granby, Kroksta, Tullstugan and Varpsund. All localities had been visited earlier during the same season and were considered to have high densities of the leaf beetle *P. vulgatissima*. In these areas a number of plots (5 x 5 metres) were sampled at the edge of the plantations and at a distance of 90 metres between the plots. This distance was used to minimize the risk that the same hover fly individual would appear in more than one plot and relies on an article that investigated movement of hover flies in different environments investigating the gut contents of the hover flies to determine the distance travelled from the food source (Wratten *et al.*, 2003).

Table 1. Information about the five sampled willow plantations

Locality	Geographic coordinates	Perimeter field	Area field	Number of plots	Last harvest(year)
Buskvreten	59°37'N, 17°27'E	1940	7.6	7	2005
Varpsund	59°37'N, 17°29'E	964	5.2	3	2007
Tullstugan	59°38'N, 17°48'E	1164	3.5	7	
Granby	58°39'N, 17°38'E	2300	16.7	10	2007
Kroksta	59°56'N, 17°27'E	2420	15.0	13	2004

The plantations at the different localities differed in size and, therefore, the number of plots varied between them. The size of the plots sometimes had to be increased since the goal was to find at least 20 leaf-carrying shoots with eggs in each plot. The sampling took place between 24 and 26 of May in year 2008. For more information about the plots and localities see Table 1.

2.2.1 Density of heteropterans

Each plot was censused to estimate the density of other natural enemies and assess to the abundance of syrphids. The density of natural enemies was estimated by knockdown sampling, a method described by Björkman *et al.* (2003), where the top part (35 cm) was shaken above a plastic bowl and the enemies were counted and determined to species. In this study the heteropterans mentioned above were counted; *O. marginalis*, *C. fulvomaculatus* and *A. nemorum*. Thirty samples were taken per plot and the size of the plot could be adjusted like in the sampling of chrysomelid eggs.

2.2.2 Density and size of egg clutches

All plots censused for heteropterans were also systematically examined for leaf beetle eggs. In each plot 5-10 leaf-carrying shoots per stem were censused for egg clutches at a height of 0.5-2 metres above the ground. The aim was to find 20 egg clutches per plot. All sampled shoots per plot were counted and leaves with eggs were put in a plastic bag and kept cold to avoid hatching of the eggs. Finally the number of eggs in each clutch was counted in the laboratory and clutches with syrphid eggs were kept in the fridge for future experiments.

2.2.3 Habitat effects

Apart from sufficient supply of food for the larvae, the adult hover fly also needs food in form of nectar and pollen to be able to produce eggs and to find a suitable egg clutch where to put their eggs. Therefore the edge habitats along each plot were described and classified into four different categories; forest, grassland, arable land and other. Willow plantations were classified as arable land while streams, lakes, buildings and roads were included into the category other. Previous studies have shown that forests and grasslands with tall vegetation have positive effects on the abundance of hoverflies (Sjödin *et al.*, 2008) while arable land is expected to have an opposite effect.

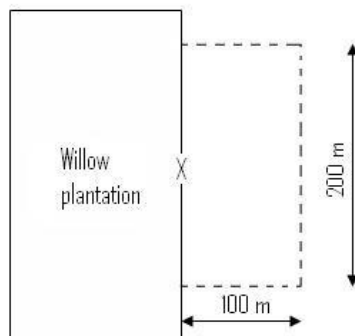


Figure 1. Illustration of a willow plantation and the habitat types around the plot. X marks the plot, situated at the edge of the plantation, and the broken lines illustrate the analyzed area in term of habitat types.

Outside the edge of each plot the surrounding habitat was analysed in an area of 200 x 100 metres, a rectangle with 100 metres sides along the edges in both directions (100 x 2) and with a width of 100 metres (Fig 1). The used distance was considered as the distance travelled by the hover flies from their food source (cf. reasoning in 2.2 above and Wratten *et al.* (2003)).

2.3 Laboratory experiments

2.3.1 Intraguild predation between heteropterans and hover flies

Nymphs of *O. marginalis* and *A. nemorum* were collected in field and starved in the fridge for 24 hours before the experiments to increase their motivation to predate. To maximize feeding rate heteropterans in their fourth or fifth developmental nymphal stage were used in the experiments as consumption rate has been observed to be high in these stages (Björkman *et al.*, 2003). Egg clutches containing hover fly eggs that were collected in the field experiment were too few and additional egg clutches with fly eggs were gathered from both willow plantations and wild populations around Uppsala. Several clutches from wild populations were not *P. vulgatissima* eggs but instead belonging to the species *P. vitellinae* L and were therefore only called *Phratora* spp. in this experiment. All beetle egg clutches containing fly eggs were kept cold until the experiments started.

Predation on hover fly eggs was studied to determine if the tendency to predate was higher in the immobile nymphs of the mirid *O. marginalis* than in the more mobile nymphs of the anthocorid *A. nemorum*. The egg clutches with hover fly eggs were kept individually in Petri dishes (Ø8.5 cm) with a moist filter paper as heteropterans are sensitive to drought. One predator of either the mirid or the anthocorid was introduced to this arena. The egg clutches differed in size but clutch sizes were evenly distributed between the two species. The time for the start of the experiment was noted and the number of remaining eggs was noted once a day. If no eggs were consumed within a day, the nymph was replaced and a new experiment was carried out. The experiments were finished when the fly egg was consumed, if the fly egg hatched or after three days (72 hours).

2.3.2. Nitrogen analysis of eggs

If syrphid eggs contain more energy for the predator than leaf beetle eggs then this could be an alternative explanation for any observed preference for syrphid eggs. Therefore an analysis was conducted to compare nitrogen content in syrphid eggs with leaf beetle eggs. Eggs were weighed before they were analyzed in an Elemental Analyzer. In the analyzer oxygen was added and the eggs were combusted. The excess of oxygen that was formed during the oxidation process was reduced in later processes and the total nitrogen (Tot-N) content in the eggs as the dry weight of the eggs was measured. For more information about the elemental analysis see Verardo *et al.* (1990).

2.4 Statistical analyses

Plot was the experimental unit in all analyses of field data. A general linear model (ANOVA) was used to evaluate possible differences between localities and plots (with and respectively without syrphid eggs) in mean densities of beetle egg clutches and the size of these clutches.

When analysing the association between other natural enemies and presence of syrphid eggs a non-parametric Kruskal-Wallis test was used between localities and a non-parametric Mann-Whitney test was used to evaluate the results between plots with and plots without syrphid eggs. A Kruskal-Wallis test was performed to evaluate differences in the edge habitat types among localities and a Mann-Whitney test was used to test for differences between plots with absence and presence of hoverfly eggs.

In the laboratory experiment a Mann-Whitney test was used to compare the predation rate of the two heteropteran species and a Pearson correlation was used to test if the size of the egg clutch had any impacts on the time to consumption of the fly egg within the two species *O. marginalis* and *A. nemorum*.

All statistics were carried out in the program Minitab.v14 for Windows (®).

3 Results

3.1 Field studies

3.1.1 The density of natural enemies

The three species of heteropterans did not occur in all plots so their total effect on abundance and presence of syrphid eggs were evaluated. The density of natural enemies was higher at Tullstugan and Kroksta, the two localities where the hover fly was absent, compared with Buskvreten Varpsund and Granby (Fig. 2a). There was a significant difference in density between the localities (Kruskal-Wallis test: $H=21.2$, $p<0.01$) and in comparison between plots the density were lower in plots with presence compared with plots in absence of syrphid eggs (Fig. 2b. Mann-Whitney test: $W=695.5$, $n_1=10$, $n_2=30$, $p=0.01$).

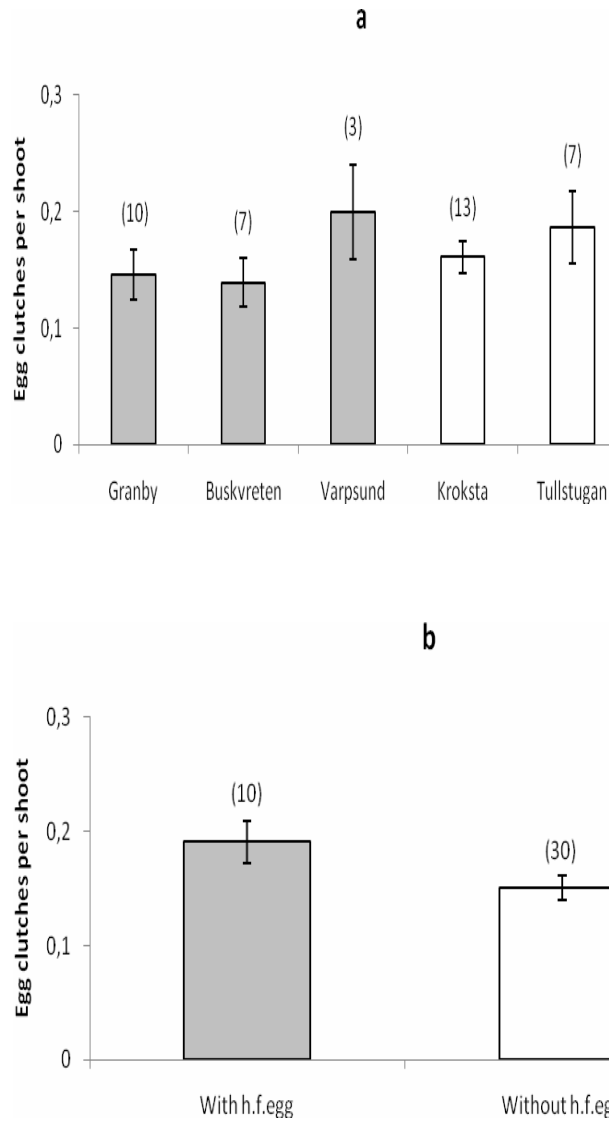


Figure 2. Densities of egg clutches among localities (a) and between plots with and without hover fly eggs (b). Localities with presence of hover fly eggs are marked with grey bars. Number of plots is presented as numbers over the bars. Mean values and SE are shown in the figures.

3.1.2. Density and size of egg clutches

The density of hover flies was low in the field and eggs were only found in 13 of 880 investigated leaf beetle egg clutches (1.5 %) and in 10 of 40 plots (25 %).

Hover fly eggs were found at three localities; Buskvreten (n=8 eggs), Granby (n=4) and Varpund (n=5). In Varpund eggs were found in all three plots (100 %), in Buskvreten in four of seven plots (57 %) and in Granby in three of ten plots (30 %). The density of leaf-carrying shoots with egg clutches was slightly higher in Varpund (Fig 3. Mean=0.2 eggclutches/shoot, SE=0.01) than the other localities but there were no significant differences between neither localities nor plots with hover flies compared with the remaining plots (Fig 3b. ANOVA: $F_{1,38}=3.2$, $p=0.08$).

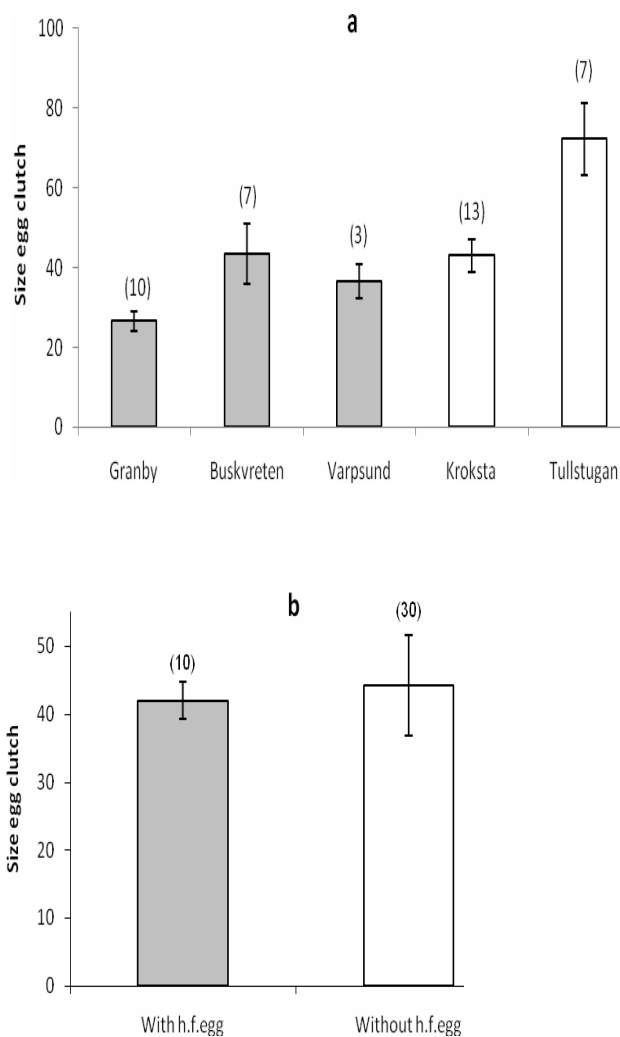


Figure 3. Size of egg clutches among localities (a) and between all plots with and without hover fly eggs (b). Localities with presence of hover fly eggs are marked with grey bars. Number of plots is presented as numbers over the bars. Mean values and SE are shown in the figures.

Mean size of egg clutches differed significantly between the five localities ($F_{4,35}=7.4$, $p<0.01$) and was largest at Tullstugan (Fig 4a. Mean=72.2eggs/clutch, SE=9.1). However there was no difference in size of egg clutches between plots with and without hover fly eggs (Fig 4b. $F_{1,38}=0.02$, $p=0.9$).

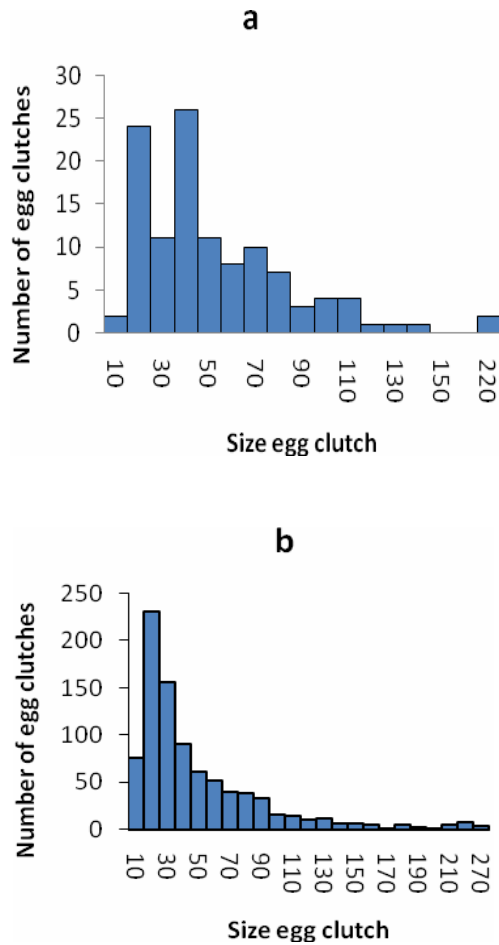


Figure 4. Size frequency distribution of leaf beetle egg clutches with (a) and without (b) syrphid eggs.

3.1.3 Size of egg clutches with presence of syrphid eggs

A large amount of egg clutches was collected in field and the size of clutches with syrphid eggs was compared with the remaining egg clutches. Clutches with syrphid eggs contained on average more eggs (Fig 5a. $n=115$, 37; median) than clutches consisting of only *Phratora*. sp. eggs (fig 5b. $n=849$, 27; median) and the resulting

differences was significant (Mann-Whitney $W=400925.5$, $n_1=115$, $n_2=849$, $p<0.01$).

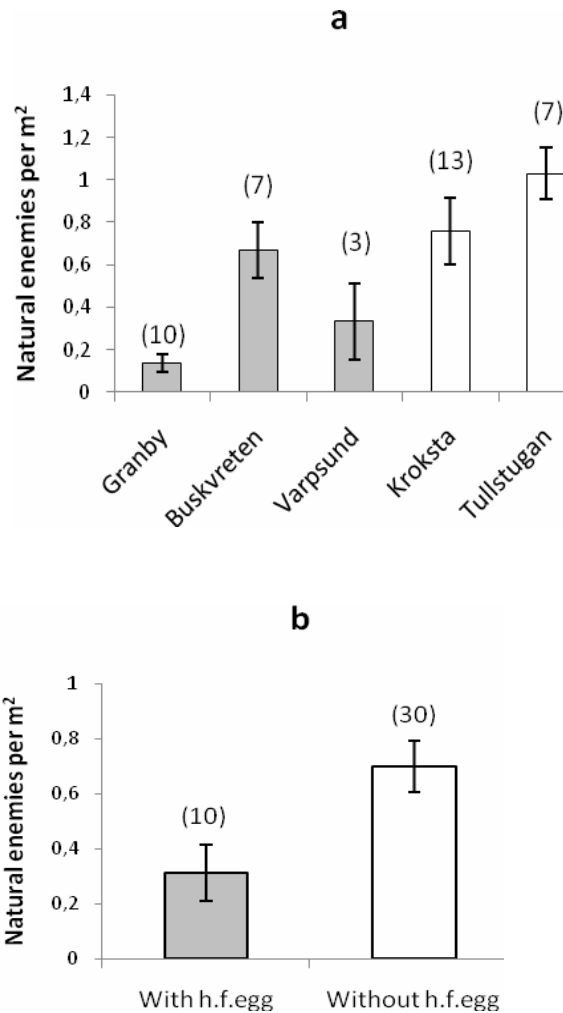


Figure 5. Densities of natural enemies i.e. heteropterans among the five localities (a) and between all plots with and without hover fly eggs (b). Localities where syrphid eggs were present are marked with grey bars. Number of plots is presented as numbers over the bars. Mean values and SE are shown in the figures.

3.1.4 The surrounding habitat

Forests had a positive effect on the presence of syrphid eggs and the proportion of surrounding forests differed between the localities (Fig. 6a). The proportion of

arable land, on the other hand, was highest at Tullstugan and Kroksta, the two localities where no syrphid eggs were found (Fig. 6a). Higher amounts of forest and lower amounts of arable land were recorded in plots with syrphid eggs compared with the rest of the plots (Fig. 6b) and these two categories differed significantly between the groups (Mann-Whitney test: $W_{\text{forest}}=481.5$, $n_1=10$, $n_2=30$ $p<0.01$, $W_{\text{arable land}}=737.0$, $n_1=10$, $n_2=30$, $p<0.01$). There was no difference in amount of grassland surrounding the plots and the last category other was not analysed further in this study.

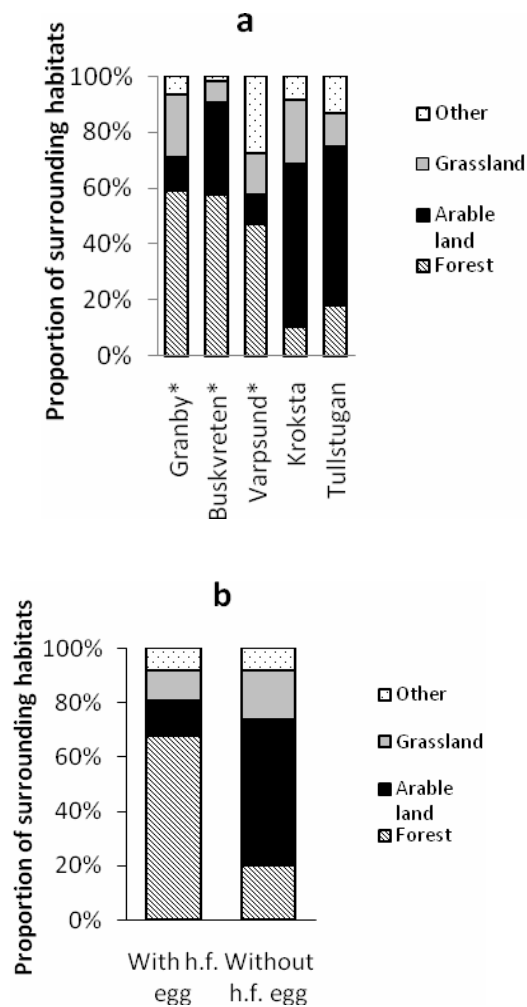


Figure 6. a) Composition of four habitat types surrounding the willow plantation in the five localities. Localities with presence of hover fly eggs are marked with *. b) Composition of four habitat types surrounding groups of plots with and without hover fly eggs. Mean values are shown in the figure.

3.2 Laboratory experiments

3.2.1 Predation on syrphid eggs

Both species of heteropterans consumed syrphid eggs as expected. The mirid *O. marginalis* consumed 19 of 20 syrphid eggs (95%) and the anthocorid *A. nemorum* 18 of 19 eggs (95%). The mean time to consumption of the syrphid eggs was about a day in both *O. marginalis* (Fig 7. 22.0 hours SE=1.2) and *A. nemorum* (27.3 SE=2.8). These similar patterns explained why there were no significant differences in either time to consumption of syrphid eggs (Mann-Whitney test: $W=341.5$, $n_1=19$, $n_2=18$, $p=0.6$) or the proportion of consumed syrphid eggs ($W=400.5$, $n_1=20$, $n_2=19$, $p=1$) between *O. marginalis* and *A. nemorum*.

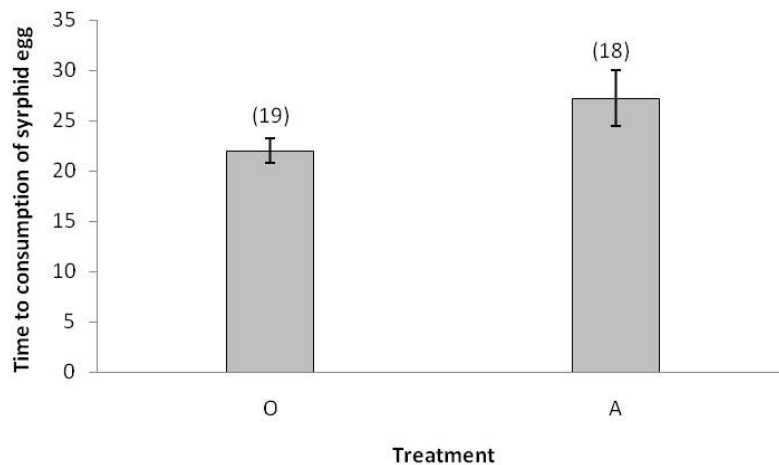


Figure 7. Time to consumption of syrphid eggs in leaf beetle egg clutches between the mirid *Orthotylylus marginalis* (O) and the anthocorid *Anthocoris nemorum* (A). Number of eaten eggs is presented as numbers over the bars. Mean values and SE are shown in the figure.

Although the heteropterans also consumed beetle eggs in this experiment, the sizes of these egg clutches had no impact on time to consumption of fly eggs in neither of the species (Pearson correlation: *O. marginalis*: $r=-0.004$, $n=19$, $p=1.0$; *A. nemorum*: $r=0.2$, $n=18$, $p=0.5$).

In the design of the method in this experiment a number of time intervals were tested before a day was chosen as standard and one egg was consumed by an anthocorid after 2 hours. This measurement together with an observation of unusual long time before consumption of egg in a mirid ($t=69$ hours) were considered as outliers and left out from the analysis. Statistical analysis were also done with these two outliers included in the dataset but had no significant impact on the result.

3.2.2 Nitrogen content of eggs

There were no differences between in total nitrogen content between syrphid eggs and leaf beetle eggs (Mean Tot-N=92.7mg/g, SE=5.5, $n_1=3$ and mean Tot-

N=99.0mg/g, SE=2.7, $n_2=7$). Syrphid eggs weighed half as much as leaf beetle eggs (Mean=0.02mg, SE=0.003 and mean=0.04, SE=0.002 respectively). There were too few eggs to do any statistical analyses.

4 Discussion

My study indicated that syrphid eggs are susceptible to predation by at least two species of heteropteran bugs in willow plantations as shown by the lower syrphid egg density in plots with high densities of heteropteran predators. Few syrphid eggs were though found in field and there were no evidence of correlations between low densities of enemies and high number of syrphid eggs in the clutches. The mechanisms behind predation were studied in detail in my laboratory experiments and showed that both species of heteropterans had a large impact on the survival of the eggs. Both species were able to identify syrphid eggs in an egg clutch independent of its size and affected the survival of syrphids.

What type of foraging strategy the predators use will affect the prey in different ways. Mirids of the 'find and stay type' are more likely to reduce the increase in abundance of prey than the anthocorids of the 'run and eat type' (Dalin *et al.*, 2006) The behaviour of hover fly resemble that of mirids were therefore considered to have great potential to be important natural enemies to leaf beetles in willow plantations.

In contrast to my expectations anthocorids may consume predators and will visit more egg clutches with hover fly eggs (Björkman and Liman, 2005). Because the foraging behaviour significantly differs between anthocorids and syrphid larvae there may be another reason behind their consumption of syrphids, *e.g.* characteristics of the eggs. Both studied species of heteropterans are generalist predators and through consuming nitrogen-rich predators they can enhance their uptake of nitrogen (Denno and Fagan, 2003). Anthocorids may consume more eggs than the mirids since they are more active predators.

Although few eggs were analysed it is unlikely that the nutrient content of eggs that make syrphid eggs more favourable than leaf beetle eggs since they were similar. Other characteristics like softness of the eggshell or defensive chemicals within the eggs affect predators (Eisner *et al.*, 1999) and could not be excluded since they have not been studied in this study.

Comparisons of foraging behaviour in closed arenas are both simpler and more practical than experiments on living plants which may, however, be more appropriate. In a small arena neither of the species has to search actively to find an egg clutch and all clutches contained a syrphid egg which is a significant higher proportion than what is found in willow plantations. The proportion of eaten syrphid eggs would be lower if experiments would be conducted in natural environments.

My study showed that syrphid eggs were found more frequently in larger than smaller leaf beetle egg clutches and were rarely found in small aggregations (<10 eggs). Hover fly eggs are unlikely laid in larger clutches to decrease the risk of predation but instead to insure that the larva has a sufficient supply of food (Scholz

& Poehling, 2000). On the other hand more eggs were not found in the largest clutches and the median size of an egg clutch with syrphid egg is slightly higher than the median size for clutches collected from the five localities. Some of the clutches without syrphid eggs have probably been preyed upon unlike clutches with syrphid eggs which also could be an explanation to these size differences.

I found no evidences for higher densities of syrphid eggs with increasing densities of leaf beetle egg clutches. This is not surprising since the densities did not differ among the five investigated plantations and all were considered to have high densities before the study. Otherwise hover flies are able to sense semiochemicals emitted from plants as an answer of attacks by herbivores and these signals are probably stronger in fields with high densities of herbivores (Scholz & Poehling, 1999; Verheggen *et al.*, 2008). Hover fly females spend less energy to find a place for oviposition in plantations with high densities of leaf beetle eggs.

I conclude that forests had a positive impact on existence of hover flies. All plots and localities with syrphid eggs were surrounded by a high proportion of forests. In addition to provide food sources for adult hover flies, forests also have the potential to offer shelter from wind, overwintering sites and shelter from predators (Sutherland *et al.*, 2001). Even if adult hover flies are good fliers there is always a risk of being exposed to predation when lekking, feeding and ovipositing and this risk is increased in arable land where there are few places to hide.

The fact that all sampled plots were situated at the edge of all plantations could result in a biased image of measured parameters. However, no significant differences in abundance of *P. vulgatissima* eggs have previously been detected within willow plantations (unpublished data) and adult hover flies are known to avoid flying long distances in dense vegetation as willow plantations (Wratten *et al.*, 2003).

It is still unclear which species of hover fly that are active in willow plantations but there are several characteristics that they share with *Parasyrphus nigrirarsis*. This species' larvae eats leaf beetle eggs and larvae and the adult females lay one to three eggs in egg clutches of *Phratora vitellinae*, often on leaves of *Salix cinerea* (Köpf *et al.*, 1997). In my study I also found a number of *P. vitellinae* egg clutches containing hover fly eggs on *S. cinerea* clones in a forest. In future studies it would be interesting to rear a number of syrphid eggs from willow plantations in the same manner as Köpf *et al.* (1997) with larvae and eggs of *P. nigrirarsis*.

The role of hover flies in biocontrol of pests in willow plantations can be discussed. Scarcity of food is unlikely to have been the limiting factor for hover flies. Predation from other predators seems as a much more likely explanation for the observed variation in syrphid numbers. Presence of hover fly adults seemed to depend largely on the habitats surrounding the plantation, especially the amount of forest showed a positive association with syrphid abundance. It seems likely that syrphid larvae have the potential to be particularly important as predators in recently harvested willow plantations, plantations with low densities of heteropterans. The adult hover flies are mobile and are therefore able to find younger and recently harvested fields. Studies have shown that heteropterans are less frequent in wild populations of willow found in forests compared with open landscapes, like willow plantations (Dalín *et al.*, 2006). When I conducted my study I spent less time searching and found more syrphid eggs in forests compared

with plantations and I found few heteropterans in these forests. This indicates that forests are important habitats for this hover fly and where competition from heteropterans is low.

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