

# Biology and performance on different diets of an omnivorous insect predator, *Psallus haematodes* (Heteroptera: Miridae)

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Omnivorous mirids (Heteroptera: Miridae) seem to be important biological control agents of willow leaf beetles. Here we describe the biology, the performance and survival on different diets of a mirid recently discovered to be relatively common in willow plantations, *Psallus haematodes*. Unlike some other mirids on willows, *P. haematodes* was found to feed only on leaf beetle (*Phratora vulgatissima*) eggs and not on larvae. In a series of greenhouse experiments we found also that the feeding rate increased gradually to reach its maximum in the last instar and adult stage, i.e. 1.9 eggs per day. Mirids provided with leaf beetle eggs developed faster ( $24 \pm 0.7$  vs.  $29 \pm 0.5$  days), survived better (55 vs. 30 %) and lived longer ( $10.1 \pm 1.1$  vs.  $5.7 \pm 1.2$  days) than mirids only provided with willow shoots. Females provided with eggs also attained a higher weight than females without eggs ( $709 \pm 79$  vs.  $307 \pm 85$   $\mu\text{g}$ ). Mirids provided with eggs, attained a lower final weight on detached shoots than on growing plants; males ( $453 \pm 28$  vs.  $602 \pm 41$   $\mu\text{g}$ ) and females ( $709 \pm 79$  vs.  $898 \pm 30$   $\mu\text{g}$ ). The fact that *P. haematodes* occurs later in the season than a predatory mirid (*Orthotylus marginalis*) known to play a key role in the biological control of leaf beetles makes it likely that these two mirids may act complementarily in biological control, despite many similarities in biology.

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A large number of insects are omnivorous but the habit of feeding both on plants and animals is especially common among heteropterans. Omnivores are potentially harmful to plants (Burgess et al. 1983, Gabarra et al. 1988, Alomar et al. 1991, Kohno & Hirose 1997, Coll & Guershon 2002, Rosenheim et al. 2006) at the same time as they may play an important role as predators (Coll & Guershon, 2002, Björkman et al. 2004, Hunt-Joshi et al. 2005, Zhi et al. 2006, Magalhaes et al.

2007). A consequence of the broad diet of omnivores is that they can survive even when prey is in short supply, supposedly resulting in less variation in abundance (Coll & Guershon, 2002). Stability in abundance is particularly interesting for agents to be used in biological control. Omnivory seems to have a potentially stabilizing effect especially on the community level (Krivan & Schmitz 2003, Krivan & Diehl 2005, McCann et al. 2005, Beckerman et al. 2006) whereas its role

on the population level is more uncertain (Morin & Lawler 1995, Coll & Guershon 2002). To unravel this uncertainty is of particular interest in applied ecology, e.g. biological control.

In biological control of pests it has recently been acknowledged that an effective control often depends on the combined effect of several natural enemy species, acting in concert (e.g. Symondson et al. 2002, Finke & Denno 2004, Snyder et al. 2006). However, it is important that the species involved are not too similar with respect to e.g. food preference, spatial distribution, phenology, etc. (e.g. Losey & Denno 1998, Symondson et al. 2002, Björkman & Liman 2005). One of the most critical phases in biological control is the early increase phase of the pest (Walter 2003, Larsson et al. 1993, 2000). A rapid and accurate response of any biocontrol agent when the pest starts to increase in number, increases the likelihood of successful control and thus reduces the risk for reaching unacceptable damage levels. However, most specialized (e.g. parasitoids) and generalist (e.g. predators) natural enemies may be too slow in their response to early increases in pest density: The parasitoids because they respond with a numerical time-lag, the predators because they respond with a numerical or functional (e.g. switching) lag. Omnivorous predators that spend at least part of their life cycle on the same host plant as the target pest should have greater potential than other enemies to be quick in their response to increases in pest density.

A basic assumption behind this hypothesis – that omnivorous predators sharing the same host plant as their prey should be especially effective biocontrol agents in the early pest phase – is that the omnivore survives periods with low pest densities. In this paper we present results that challenge this assumption. In addition, we here explore whether an omnivorous insect predator that recently was discovered to be common in willow plantations show characteristics that makes it a likely complement to other known biocontrol agents of leaf beetles.

We have previously shown that omnivorous mirid bugs (Heteroptera: Miridae), especially *Orthotylus marginalis*, are important predators on willow leaf beetles (Björkman et al. 2003, 2004). Our data indicate that this mirid actu-

ally may have a regulatory function of the leaf beetles (Björkman et al. 2004). The leaf beetles, especially their larvae, may defoliate coppicing willow plantations severely and reduce biomass production up to 40% (Björkman et al. 2000). Such losses are not economically acceptable in this bioenergy crop. Spraying with insecticides against this pest is not acceptable either from an economic or an environmental perspective. Biological control is the most attractive alternative for controlling the pest. In the coppicing willow system, the use of moderately resistant willow clones in combination with means that promote natural enemies, such as predatory mirids, seem as a realistic and sustainable method for biocontrol.

In the willow system we have recently discovered mirid species that are active later in spring than *O. marginalis*. The most common species seem to be *Psallus haematodes* (Gmelin) (Heteroptera: Miridae) (Fig. 1). Little is known about the biology of this species (Kullenberg 1944, Wachmann et al. 2004). For example, Kullenberg (1944) only refers to *P. haematodes* (*P. roseus*) being a predator of aphid and galling insects. The aims of this paper were (1) to find out whether *P. haematodes* is a predator of eggs and larvae of the willow leaf beetle (*Phratora vulgatissima*) that causes most damage to willow plantations, (2) to quantify its feeding rate in different instars, and (3) to investigate the effect of different diets (pure vegetarian vs. vegetarian plus prey) on the survival and performance of male and female *P. haematodes*. In addition, observations describing the morphology, oviposition and phenology are reported. A question of general interest for omnivores is whether there is any difference between females and males in their responses to presence of prey. It could be hypothesized that females should suffer more from a pure vegetarian diet than males because their reproductive effort is higher and more dependent on food sources high in N (Awmack & Leather 2002).

#### *System and previous knowledge*

Willow plantations grown to produce biofuel are harvested every 3<sup>rd</sup> to 5<sup>th</sup> year. This means that natural enemies have a better opportunity to establish and increase in density compared to

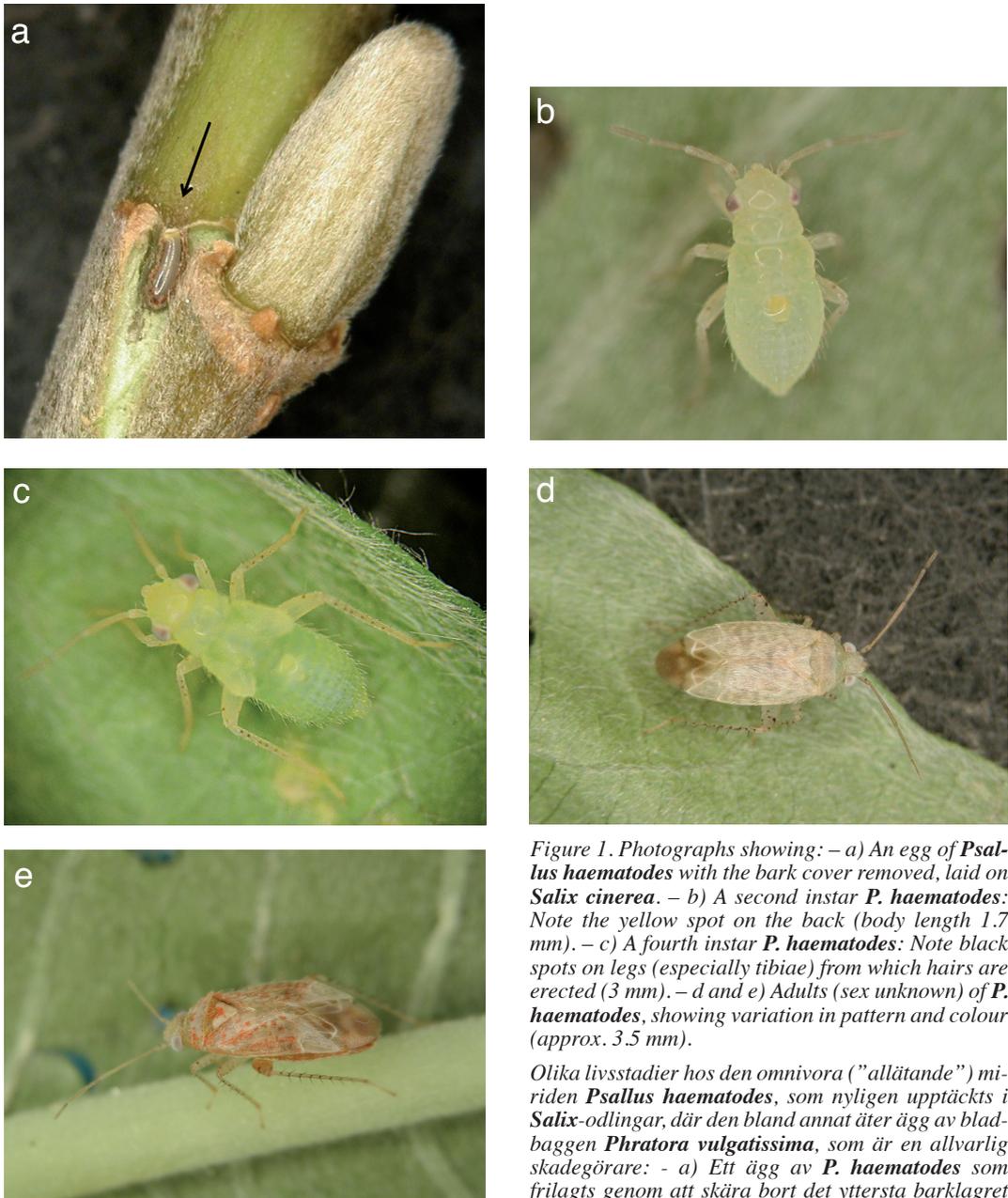


Figure 1. Photographs showing: – a) An egg of *Psallus haematodes* with the bark cover removed, laid on *Salix cinerea*. – b) A second instar *P. haematodes*: Note the yellow spot on the back (body length 1.7 mm). – c) A fourth instar *P. haematodes*: Note black spots on legs (especially tibiae) from which hairs are erected (3 mm). – d and e) Adults (sex unknown) of *P. haematodes*, showing variation in pattern and colour (approx. 3.5 mm).

Olika livsstadier hos den omnivora ("allätande") miriden *Psallus haematodes*, som nyligen upptäckts i *Salix*-odlingar, där den bland annat äter ägg av bladbaggen *Phratora vulgatissima*, som är en allvarlig skadegörare: – a) Ett ägg av *P. haematodes* som frilagts genom att skära bort det yttersta barklagret på en *Salix cinerea*-kvist. – b) En andrastadienymf av *P. haematodes*: Notera de den gula fläcken på ryggen (kroppslängd: 1.7 mm). – c) En fjärdestadienymf av *P. haematodes*: Notera de svarta prickarna på benen (särskilt tibiorna) vid hårens bas (3 mm). – d och e) Adulter (kön okänt) av *P. haematodes*, som visar variation i utseende (ca 3.5 mm).

plantations harvested every year. But harvesting disrupts biological control also in this short rotation coppice system (Björkman et al. 2004). The mechanism seems to be that most of the main natural enemies (i.e. mirid bugs) are removed at harvesting because they overwinter as eggs inserted in the willow shoots and buds. The leaf beetles overwinter mainly outside the plantations and are less affected by the harvesting than the natural enemies (Björkman et al. 2004, Björkman & Eklund 2006)

The predation during egg and larval stages of the leaf beetle *Phratora vulgatissima* is important for the population dynamics of this species (Björkman et al. 2004). The more common natural enemies have been identified (Björkman et al. 2003): Apart from syrphids (*Syrphus* sp.), three species of stinkbugs (Heteroptera) seem to be important; *Anthocoris nemorum* (Anthocoridae), *Closterotomus fulvomaculatus* (Miridae) and *Orthotylus marginalis* (Miridae). These insects have two types of behaviours; ‘run and eat’ and ‘find and stay’ (Björkman et al. 2003). *Anthocoris nemorum* represents the first type, which is very active and normally eats only one or two eggs in a batch before moving on. The two mirids represent the second type, which is more stationary. The mirids normally eat all eggs in a batch before leaving to find a new site.

The samplings in which the above described knowledge is based were conducted in late May to mid-June. The results presented here focus on a mirid species that may have been overseen in these “early” samplings.

## Materials and methods

### Field samplings

Branches of *Salix cinerea*, the willow on which the highest *P. haematodes* densities were found, were brought to the laboratory to hatch nymphs to be used in the experiments. The first nymphs appeared after 15 days in the greenhouse (mean temperature: 18°C, RH: 70 %). The branch sampling was done in early spring of 2006 from *S. cinerea* bushes growing a few kilometers south of Uppsala (59°48'N, 17°39'E).

### Oviposition, phenology and morphology

The oviposition sites of *P. haematodes* were determined by examining a large number of wil-

low shoots through removing the upper layer of the bark and cutting the buds.

The phenology was determined by weekly samplings with a vacuum machine (d-vac, STIHL BG 85) on different commercial willow clones and on natural *S. cinerea*. The sampling continued during the whole developmental period from first instar to adult.

By following individuals from first instar to adulthood it is possible to present photographs illustrating the appearance of the different stages of *P. haematodes*.

A thorough description of *P. haematodes* (*P. roseus*) morphology and biology is presented in Kullenberg (1944) where it e.g. is noted that the colour of adults seem to be affected by their age and weather conditions.

### Experiments with *P. vulgatissima* eggs as prey

Newly hatched *P. haematodes* first instar nymphs (n=40) collected from *S. cinerea* in the field were placed individually in plastic vials (6.5 cm long and with a diameter of 2.6 cm, resulting in a volume of 34.5 cm<sup>3</sup>). The vials contained a piece of wet filter paper and a willow leaf (clone 78021 *S. viminalis*). The lid of the vial was pierced several times with a needle for air circulation. The leaves were changed every Monday, Wednesday and Friday. Before changing the leaf, the vial was inspected to make clear whether the mirid was alive or dead. For the mirids provided also with leaf beetle eggs (n=20), the number of eggs fed upon was noted. Nymphs were categorized to instar by observing for moulted skins. The weight of the mirids reaching adulthood was measured as soon as possible after they had died.

In order to always have fresh leaf beetle eggs to provide the mirids with, adults of *P. vulgatissima* were kept on potted *S. viminalis* (clone 78021) saplings in large cages in the greenhouse. The plants were changed every Monday, Wednesday and Friday. Leaves of these plants (with or without eggs) were checked before being offered to the mirids: damaged leaves were not used and any arthropods (e.g. thrips) found were removed.

The experiments lasted during the entire development of the mirids, from egg hatch until death. Dead nymphs were stored in alcohol

whereas specimens that reached adulthood were stored in the freezer for later weight measurements.

The studies described here were all done in the greenhouse (mean temperature = 25°C; Light:Dark, 20:4h).

**Feeding rate in different instars.** The number of eggs consumed per day was estimated by dividing number of eggs eaten by number of days between observations. The instars were identified by observing size of the mirids and occurrence of moulted skins. The feeding rate differed markedly among instars (Fig. 2).

**Survival and performance.** The survival, developmental rate and proportion of nymphs reaching adulthood were all estimated by noting if mirid individuals were still alive and in what instar they were when changing leaves.

**Effect of plant condition.** In order to evaluate to what extent detached leaves differ in quality as food for *P. haematodes* compared with intact leaves on actively growing plants, we conducted an additional experiment. Twenty mirids were raised from first instar to adulthood on potted *S. viminalis* (clone 78021) saplings and were provided with *P. vulgatissima* eggs *ad libitum*. The potted plants were kept individually in cages (40 x 40 x 70 cm). The mirids provided with

detached leaves (n=20) were kept in vials (H: 6.5 and D: 2.6 cm) containing a moist piece of filter paper. The final weight of males and females was recorded.

**Experiments with *P. vulgatissima* larvae as prey**  
Large nymphs (n=6) and adult males (n=6) and females (n=6) of *P. haematodes* were offered *P. vulgatissima* first instar larvae *ad libitum* for 96 h. The same type of vials and experimental set up as described for the main experiment with eggs was used here.

## Results

### *Oviposition, phenology and morphology*

The mirid *P. haematodes* lays its eggs under the bark adjacent to the buds of willows (*Salix* spp.) (Fig. 1a). Eggs are laid singular or in small batches (2-3 eggs) at each oviposition site. However, one egg per site is most common. The eggs are white with a flattened top, oval in shape (cf. Kullenberg 1942).

The first nymphs (Fig. 1b) hatch from eggs in the middle of June. In 2006, the first nymphs were observed on 12 June. The first adults were observed on 3 July. In the greenhouse, the average time to reach the adult stage from egg hatch was 24 days. The mean temperature during this period was 23±2°C. Eggs of the leaf beetle *P. vulgatissima* are normally found until the end of June, although the maximum densities often

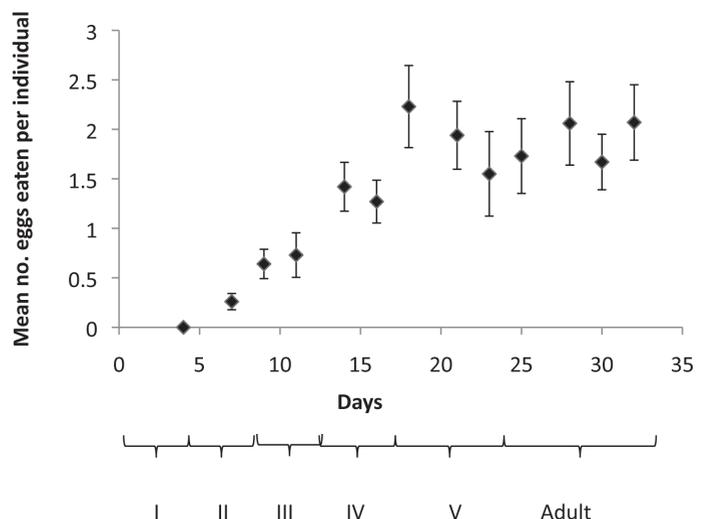


Figure 2. Consumption rate by the mirid *Psallus haematodes* on eggs of the willow leaf beetle *Phratora vulgatissima*. Means (±SE) for each day is presented.

Hastighet med vilken miriden *Psallus haematodes* äter ägg av bladbaggen *Phratora vulgatissima*. Medelantalet (±SE) ägg per individ per dag redovisas. Hastigheten ökar med storleken upp till sista nymfstadiet. Medelhastigheten under hela perioden var 1,3 ägg per dag per individ.

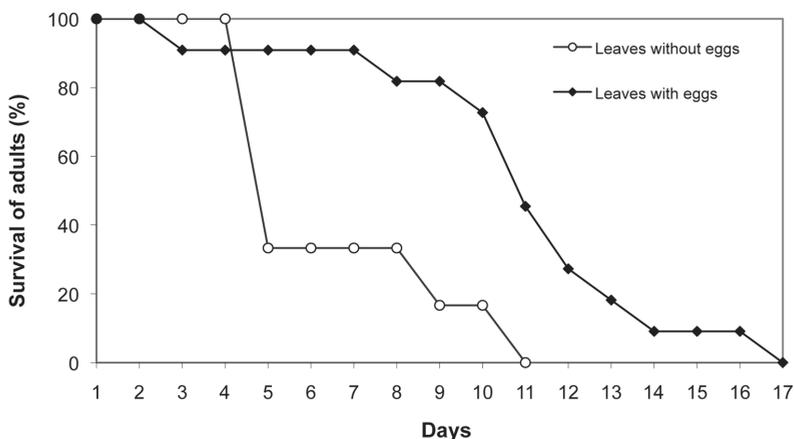


Figure 3. Survivorship of adult *Psallus haematodes* provided either with eggs of the leaf beetle *Phratora vulgatissima* and willow leaves or only with willow leaves.

Överlevnaden hos adulta *Psallus haematodes* som försågs med såväl ägg av bladbaggen *Phratora vulgatissima* som *Salix*-blad var väsentligt bättre än hos adulta mirider som enbart fick äta på *Salix*-blad.

occur in late May.

All nymphal stages have a yellow spot on the back (Fig. 1b-c). After the first instar, nymphs and the adults have black spots on the legs, especially on the tibiae, with black hairs erected from these points (Fig. 1c-e). The colour of nymphs is pale green. The adults vary in colour from whitish to redbrownish. The black spots on the legs is a character that can be used to distinguish *P. haematodes* nymphs from the nymphs of the more common mirid *Orthotylus marginalis* also occurring on *Salix*.

**Experiments with *P. vulgatissima* eggs as prey**  
**Feeding rate in different instars.** *Psallus haematodes* feeds on *P. vulgatissima* eggs in all nymphal stages and as adult. Consumption rates increased with time (i.e. size) and stabilized to reach its maximum in the last (5<sup>th</sup>) nymphal instar and adult stage (Fig. 2). Feeding rates differed markedly among instars, with the exception of last instar and adult stage (Fig. 2). On average, an individual consumed 1.3 eggs per day during the 32 days of the experiment.

**Survival and performance.** The development from egg hatch to adult stage was significantly shorter for mirids with eggs than for mirids without eggs (mean no. days  $\pm$  S.E. was  $24 \pm 0.7$  vs.

$29 \pm 0.5$ ;  $X^2 = 10.4$ ,  $p = 0.0013$ , d.f. = 1). Nymphal survival was higher among mirids with eggs than for mirids without eggs (0.55 vs. 0.30;  $X^2 = 15.1$ ,  $p < 0.001$ , d.f. = 1). Adult survival was also higher when leaf beetle eggs were present (Fig. 3); adults with prey survived on average 10.1 days (S.E. = 1.1) compared with 5.7 days (S.E. = 1.2) without eggs ( $F_{1,16} = 7.11$ ,  $p = 0.0176$ ).

**Effect of plant condition and egg provision.** The weight of adults provided with eggs that were held on actively growing willow saplings was significantly higher than that of adults provided with detached leaves (Fig. 4;  $F_{1,29} = 16.7$ ,  $p = 0.004$ ). Females weighed significantly more than males (Fig. 4;  $F_{1,29} = 43.4$ ,  $p < 0.0001$ ). Female weight differed significantly among all three treatments, i.e. with eggs on saplings ( $898 \pm 30 \mu\text{g}$ ), with eggs on detached leaves ( $709 \pm 79 \mu\text{g}$ ) and without eggs on detached leaves ( $307 \pm 85 \mu\text{g}$ ) (Fig. 4;  $F_{2,18} = 30.6$ ,  $p < 0.0001$ ). No such comparison was possible for males because only one male individual survived in the treatment without prey. The surviving male weighed  $237 \mu\text{g}$ , to be compared with the average  $453 \pm 28 \mu\text{g}$  (lowest value:  $402 \mu\text{g}$ ) among males in small containers with eggs and  $602 \pm 41 \mu\text{g}$  among males in large cages with eggs (Fig. 4). The two

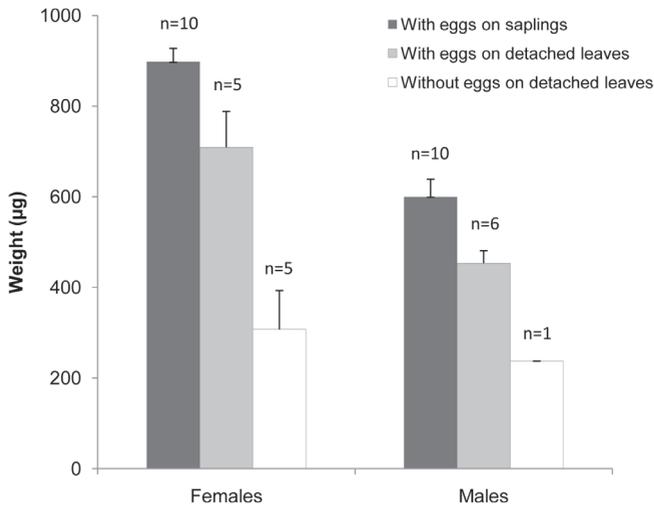


Figure 4. Weight (mean $\pm$ SE) of *Psallus haematodes* females and males reared on either actively growing willow saplings and provided with eggs of the willow leaf beetle *Phratora vulgatissima* or reared on detached willow leaves with or without leaf beetle eggs.

Vikt (medelvärde $\pm$ SE) hos honor respektive hanar av miriden *Psallus haematodes* som fått leva på *Salix*-plantor med ägg av bladbaggen *Phratora vulgatissima* eller som fått leva på *Salix*-blad med eller utan bladbaggeägg. Att ges möjlighet att äta på bladbaggeägg hade störst positiv effekt på miridens slutvikt men en viss positiv effekt av att äta på *Salix*-plantor jämfört med lösa blad kunde också konstateras.

latter groups differed significantly ( $F_{1,16} = 21.1$ ,  $p < 0.0001$ ).

**Experiments with *P. vulgatissima* larvae as prey**  
None of the tested *P. haematodes* nymphs or adults had consumed any first instar *P. vulgatissima* larvae within 72 h, when the first mirids started to die, nor after 96 h.

## Discussion

The results showed that *Psallus haematodes* feeds readily on *Phratora vulgatissima* eggs, and thus may play a role in the biological control of this willow leaf beetle. The feeding rate increased between larval instar but was stable within instars. Females and especially males of the mirid benefited from having prey included in the diet. Both sexes benefitted also, expressed as a higher final weight, by feeding on growing willow saplings compared to feeding on detached leaves.

The feeding rate of *P. haematodes* was shown to be on the level with that of the mirid (*O. marginalis*) shown to play a significant role in the population dynamics of the willow leaf beetle *P. vulgatissima* (Björkman et al. 2003, 2004; Fig. 2). This means that *P. haematodes*, in theory, could also be of importance in the biological

control. In addition, the fact that the phenology of *P. haematodes* shows little overlap with that of *O. marginalis* implies that the two species may act complementarily with little negative inference. The only concern is that *P. haematodes* only feeds on eggs and not on larvae of the leaf beetle (cf. Reitz et al. 2006). The relative difference in timing between emergence of *P. haematodes* and oviposition in *P. vulgatissima* will affect how important *P. haematodes* can be in biological control. We have no detailed data on this but observations indicate that the temporal overlap may vary considerably between years. The extended oviposition period of *P. vulgatissima* (Björkman et al. unpublished data) ensures that at least some eggs are available for *P. haematodes* but significant effects on *P. vulgatissima* dynamics is probably only materialized under certain conditions.

The difference between males and females with respect to how addition of prey affected survival was surprising; intuitively, one would expect the larger females to suffer more from a nitrogen poor diet. It is possible that a greater energy demand by males, e.g. more active flyers, than females may explain why males were more dependent on prey in the diet than females (cf. Stockhoff 1993). However, there are to our

knowledge no data or observations indicating that males of *P. haematodes* or other mirids are much more active than females (Wheeler 2001). Thus, the greater dependence of male than female in this mirid species remains a mystery.

In this study we also found evidence that plant quality affects the growth (i.e. final weight) of *P. haematodes*: both male and female mirids attained a weight that was approximately 30 % higher when feeding on saplings than when feeding on detached leaves. A confounding factor making it difficult to draw firm conclusions was that the mirids feeding on actively growing willow saplings were kept in larger containers than the mirids feeding on detached shoots. It is, for example, possible that a mirid experiencing a stressful environment (here small vial) may decide to finish development earlier than necessary. The rationale would be that the next generation could hatch earlier and possibly compete for a better place than the parent experienced. Whether plant quality (e.g. water content) affects prey feeding rate in *P. haematodes* as shown for other omnivores (e.g. Janssen et al. 2003, Sinia et al. 2004) was not studied here but is a factor that needs further attention.

To conclude, adding prey to the diet of *P. haematodes* improves the performance of both males and females. The strong negative response among males to the absence of prey, with respect to survival, remains unexplained. If the result reported here is representative and also apply to other species, the general assumption that omnivores are especially good at surviving periods when prey is in short supply may be questioned. For good reasons, in most studies where results are separated between the sexes, the focus has been on the females (but cf. Haukioja & Neuvonen 1985). If males die to a great extent in the absence of prey, the stabilizing role of omnivory may be less often realized in nature than predicted by models. However, more studies are needed of the effect of animal diet on the survival and performance of - male and female - omnivores before we can put the hypotheses to a real test. It is possible that the results presented here are unrepresentative or that they suffer from some unknown methodological problem. Nevertheless, the results suggest that the mirid *P. haematodes* may be a good comple-

ment to other mirids in the biological control of the leaf beetle *P. vulgatissima* and possibly other potential pests on willows.

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### Sammanfattning

Omnivora ("allätande") mirider eller ängsstinkflyn (Heteroptera: Miridae) tycks spela en viktig roll i den biologiska kontrollen av bladbaggar som lever på *Salix*. I den här uppsatsen beskriver vi biologin och utvecklingen på olika dieter hos en mirid som nyligen upptäckts i *Salix*-odlingar, *Psallus haematodes*. Till skillnad mot andra mirider så fann vi att *P. haematodes* enbart åt ägg och inte larver av bladbaggen *Phratora vulgatissima*. I en serie växthusförsök kunde vi konstatera att äthastigheten ökade successivt för att nå sitt maximum (1.9 ägg per dygn) i sista nymf och adultstadiet. Mirider som fick såväl bladbagge-ägg som *Salix*-blad utvecklades snabbare (24±0.7 vs. 29±0.5 dagar), överlevde bättre (55 vs. 30 %) och levde längre (10.1±1.1 vs. 5.7±1.2 dagar) än mirider som enbart fick *Salix*-blad. Honor som fick ägg nådde en slutvikt som var högre än honor som inte fick ägg (709±79 vs. 307±85 µg). Bland mirider som fick ägg så påverkades slutvikten hos såväl hanar (453±28 vs. 602±41 µg) som honor (709±79 vs. 898±30 µg) positivt av att äta på en levande *Salix*-planta jämfört med att äta på löstagna blad. Att *P. haematodes* förekommer senare på säsongen än den mirid (*Orthotylus marginalis*) som visat sig spela en viktig roll i kontrollen av bladbaggar tyder på att denna nyupptäckta art kan fungera som ett komplement i biologisk kontroll, trots många likheter i biologi.