Behavioural Mechanisms behind Aggregation in a Tritrophic Perspective

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Abstract

Gregarious organisms need to handle the trade-off between positive effects of group living and increasing food competition. The gregarious *Phratora vulgatissima*, a specialist leaf beetle on willow in Europe and Asia, frequently reaches outbreak densities in natural stands and short rotation coppices. Outbreaks threaten the yield and plantations therefore rely on omnivorous predators as biocontrol agents, like *Anthocoris nemorum* and *Orthotylus marginalis*. I aimed to elucidate behavioural mechanisms of the beetle and the predators to understand how and why species aggregate. The beetle's aggregation behaviour was studied by looking at key reproductive traits like oviposition rate, clutch size, and oviposition site choice on willow shoots. Both predators were characterized further by examining where on the vertical shoot they preferentially hunt for the beetle's eggs and how the quality of alternative food (different plant genotypes) alters their effects on the beetle. I so revealed how the reproduction of the beetle is modulated by lateral (conspecific density), bottom-up (plant genotypes), and top-down (omnivorous predators) effects. To lower exploitative competition among larvae females increase the distances between clutches on a plant and lower their oviposition rate if too many, or too few (too few confirmations of own decision) conspecifics visited a shoot. Observed bottom-up effects include lowering clutch size and number of eggs on a shoot with plant genotype unsuitability, initially selecting large leaves for oviposition/feeding, and increasing clutch distances due to larger leaf area of a willow genotype. Three top-down effects in form of predator avoidance behaviours were observed. Females lowered median clutch size and oviposition rate leading to fewer eggs in presence of the predators/their combination. Females also preferentially feed in the shoot canopy but oviposit in the lower part. In combination with the observation that both predators show contrasting vertical preferences on the shoot I argue that females try to avoid the area were the predators are consuming more eggs. In general I contributed to the ecological concept of habitat domain, attack-abatement, clutch size, cognitive maps, and nonconsumptive effects. I hope the results facilitate our understanding of insect outbreaks and species aggregation, possibly leading to better control of those in economic relevant systems.

Keywords: clutch size, cognitive map, kin recognition, non-consumptive effects, oviposition rate, neutral interference, selfish herd, habitat quality, dilution, omnivore

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Dedication

To my wonderful wife and daughter

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Stephan JG, Stenberg JA, Björkman C (2015). How far away is the next basket of eggs? Spatial memory and perceived cues shape aggregation patterns in a leaf beetle. *Ecology* 96(4), 908-914.

II Stephan JG, Low M, Stenberg JA, Björkman C (2016). Habitat quality and predator hunting mode interactively affect attack-abatement patterns of predation risk. *Ecology* (submitted).

III Stephan JG, Stenberg JA, Björkman C. Consumptive and nonconsumptive effect ratio depends on local resource quality – a story about host plants, leaf beetles, and omnivorous predators (manuscript).

IV Stephan JG, Stenberg JA, Björkman C. Moving up and down the shoot: how ovipositing leaf beetles avoid habitat domains of different predators (manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of Jörg Stephan to the papers included in this thesis was as follows:

I Developed research questions and design, performed data collection, did the statistical analyses and wrote the paper with assistance from Johan Stenberg and Christer Björkman.

II Developed research questions and wrote the paper together with Matt Low with assistance from Johan Stenberg and Christer Björkman.

III Developed research questions, performed data collection together with Johan Stenberg, did the statistical analyses and wrote the paper with assistance from Johan Stenberg and Christer Björkman.

IV Developed research questions, performed data collection together with Johan Stenberg, did the statistical analyses and wrote the paper with assistance from Johan Stenberg and Christer Björkman.

Abbreviations

1 AN + 1 OM	Predator treatment with one *Anthocoris nemorum* and one *Orthotylus marginalis* caged on individual willow shoots
2 AN	Predator treatment with two *A. nemorum* caged on individual willow shoots
2 OM	Predator treatment with two *O. marginalis* caged on individual willow shoots
4 OM	Predator treatment with four *O. marginalis* caged on individual willow shoots

1 Introduction

The aim of this thesis was to shed light on the questions how and why species aggregate. These questions were approached with controlled lab experiments utilizing a leaf beetle, different host plant species/genotypes and two omnivorous predators. I tried to include three levels within the trophic system in investigating how predators (top-down the food chain), how the host plant (bottom-up), and lateral (on the same trophic level) effects shape the beetles´ behaviour. I aim to understand if and how the reproductive behaviour of the herbivore is modulated by these mechanism on all these trophic levels as this early phase during beetle life time is critical for the fitness and the population dynamics of the species with the potential to get insights on the occurrence of insect outbreaks.

1.1 Oviposition and aggregation in response to intraspecific competition

Due to exploitative competition (Mitchell, 1975) and increased risk of predation while searching for alternative feeding sites (Matsumoto, 1990) survival of insect larvae normally decreases with increasing egg numbers in an aggregation. On the other hand, larval aggregation may improve thermoregulation (Joos *et al.*, 1988), increase predator protection (Denno & Benrey, 1997; Hunter, 2000), and help to overcome plant defences (Clark & Faeth, 1997). Larvae are aggregated because mothers chose where to place the eggs on a plant (Whitham, 1978; Silva & Furlong, 2012) and within the landscape (Heisswolf *et al.*, 2006). This oviposition site choice can be modulated by e.g. vegetation structure (Meiners & Obermaier, 2004), predators/parasitoids (Higashiura, 1989), and the availability and quality of host plants (Obermaier & Zwölfer, 1999). Information about presence of conspecific eggs might also influence the oviposition choice, with some species preferring egg-free hosts (Vasconcellos-Neto & Monteiro, 1993), while other prefer the presence of conspecific eggs (Navasero & Ramaswamy, 1993; Raitanen *et al.*, 2013). Some species may even balance parasitism threats and larval feeding competition (Meiners *et al.*, 2005). Here we investigated how the leaf beetle *P. vulgatissima* (Coleoptera: Chrysomelidae) is distributing its eggs on individual host plants with special focus on how they respond to the presence of conspecific egg clutches.

On the individual plant the second decision by the female is how many eggs to oviposit in a clutch, which can depend on resource quality (Bergström *et al.*, 2006), resource size (Godfray, 1986), and predation/parasitism (Subinprasert & Svensson, 1988; Siemens & Johnson, 1992). Similar predation and competition as for progeny from a single clutch could arise from siblings/non-siblings from different clutches that are on the same shared plant. Comparable to the optimal clutch size that produces the highest progeny survival (Lack's clutch-size hypothesis; Lack, 1947; Godfray *et al.*, 1991), one could imagine an optimal distance between clutches as an additional behavioural component to increase egg survival. It has been shown that the dispersal distance in spider mites populations can be driven by relatedness (Bitume *et al.*, 2013) and the spatial distribution of adults on a plant increases with inbreeding (Le Goff *et al.*, 2009). Some insects are also able to recognize conspecific eggs (Loeb *et al.*, 2000; Zink, 2003). However, how this affects distances between clutches has been unknown and is addressed in this thesis.

Insects may not only perceive eggs directly, but also indirectly via cues like sex pheromones, aggregation pheromones, faeces, and larval defence secretions (Fernandez and Hilker 2007), as well as induced plant volatiles due to feeding and oviposition (Dicke & Baldwin, 2010). At the same time insects are able to learn and memorize (Dukas, 2008; Wright & Schiestl, 2009) including spatial memory (Srinivasan, 2010; Collett *et al.*, 2013). However, these studies are performed on bees, wasps, and ants, while studies on beetles have focused on conditioning (Held *et al.*, 2001) and how larval experience influences adult behaviour (Rausher, 1983). Here we investigated for the first time the spatial memory of a leaf beetle. The existence of such cognitive capabilities should help to better understand the behaviour of this beetle on individual plants and this knowledge will aid to understand the population dynamics in this species.

1.2 Oviposition and aggregation in response to host plants and predators

Besides the direct consumptive effect on their prey, predators exhibit another indirect top-down effect. This nonconsumptive effect is associated with changes in prey traits due to scaring the prey and altering its behaviour. Nonconsumptive effects can have far-reaching impacts on trophic cascades (Beckerman *et al.*, 1997; Trussell *et al.*, 2003), ecosystem functions (Schmitz *et al.*, 2008; Matassa & Trussell, 2011), and often equals or exceeds the effects of direct consumption (Schmitz *et al.*, 2004; Preisser *et al.*, 2005). Within the system consisting of two predators, *Anthocoris nemorum* (Heteroptera: Anthocoridae) and *Orthotylus marginalis* (Heteroptera: Miridae), the leaf beetle *P. vulgatissima* and different *Salix* spp. genotypes (Malpighiales: Salicaceae) we addressed two nonconsumptive effects. First, we focused on the effect of predator presence on the clutch size and the oviposition rate of the leaf beetle. Second, the oviposition site selection due to predator presence was investigated. More specifically, we looked at the distribution of herbivore eggs and hunting efforts of predators on the vertical axis of willow shoots and if the beetles changed their oviposition site preferences due to predators.

1.2.1 Not laying eggs as a nonconsumptive effect

The presence of predators can for example generate physiological stress resulting in energetic costs cascading an negative impact on reproductive output (Nelson, 2007). This should represent the strongest nonconsumptive effect because it lowers fitness of the prey. This effect is for example exerted via higher conspicuousness of males attracting females (Uzendoski *et al.*, 1993), mating interruption (Travers & Sih, 1991), or changes in prey behaviour that result in lower weight gain or poorer provision of progeny (Harfenist & Ydenberg, 1995).

Besides nutritional value the herbivores behaviour can be affected by the plant quality expressed as different combinations of defence traits (Agrawal, 2007; Schaller, 2008; Karban, 2011) in form of structural features like trichomes (Mulatu *et al.*, 2006) and chemical features like volatiles (Degen *et al.*, 2004). These difference not only exist among species but also among plant genotypes (Kaplan & Thaler, 2010; Stenberg *et al.*, 2011a) affecting herbivore performance (Kaplan & Thaler, 2010), fitness (Lehrman *et al.*, 2012) and community composition (Schmitz *et al.*, 2008; Wimp *et al.*, 2010).

Plant genotype also affects higher trophic levels (Underwood & Rausher, 2000; Bailey *et al.*, 2006; Tack *et al.*, 2010), and efforts have been made to connect nonconsumptive effects of predators to the plant genotype the interaction occurs on (Thaler *et al.*, 2014; Kersch-Becker & Thaler, 2015).

Even if the omnivore is not affected by structural defences, variation in plant sap quality can alter the means of satisfying nutritional needs leading to higher or lower consumption of herbivores (Lundgren *et al.*, 2009; Stenberg *et al.*, 2011b). However, no attempts have been made to tease apart the contributions of consumptive and nonconsumptive effect on fitness of an individual herbivore and the combined effects of different predators. We therefore explored if the oviposition rate is altered by host plant genotype, predator presence and how different host plants genotypes interact with this nonconsumptive effect because the omnivorous predator is also affected by host plant quality.

Whether herbivores lay fewer eggs within a certain time (lower oviposition rate) can depend on plant species richness in the habitat (Unsicker *et al.*, 2010), temperature (Tammaru *et al.*, 1996), or intraspecific exploitative competition (Hemptinne *et al.*, 1992). Oviposition rate can also be a proxy for host plant (genotype) acceptance in the *P. vulgatissima*-willow system (Lehrman *et al.*, 2012) and we used this observation to investigate how different predators and different willow genotypes modulate this nonconsumptive effect.

In addition to how many eggs are laid on an individual plant, how many eggs are laid in a certain location is important in determining egg aggregation. These egg clutches (also: batch, cluster, patch) have contact with each other and bottom-up like resource size and quality (Godfray, 1986; Pilson & Rausher, 1988; Kagata & Ohgushi, 2002) and top-down factors like predator/parasitoid attack (Subinprasert & Svensson, 1988; Siemens & Johnson, 1992) have been shown to be important in determining their size. Females would increase fitness by laying more eggs in the same clutch as it could increase the ability to overcome different plant defences (Young & Moffett, 1979; Clark & Faeth, 1997), or lower the encounter probability of predators (Paper II). On the other hand large clutches will increase exploitative competition between the hatching larvae (Mitchell, 1975) forcing them to migrate, which in turn can increase predation risk (Matsumoto, 1990). How the predator is foraging on the herbivore eggs is also determining if larger clutch sizes are advantageous. Differences in this predator hunting mode (Miller et al., 2014) increased survival chance in larger clutches in cases were the predator is not immediately consuming all encountered eggs (Paper II). Therefore if the clutch size of the leaf beetle is interactively affected by top-down and bottom-up effects was investigated.

1.2.2 Changing the oviposition site on an individual willow shoot

Oviposition site choice is a key life history trait in insect ecology (Refsnider & Janzen, 2010), important at different spatial scales (Kessler & Baldwin, 2002;

Meiners & Obermaier, 2004; Silva & Furlong, 2012). Females have to balance sufficient food availability for the larvae and predation risk in their choice where to lay their eggs on individual plants (Kessler & Baldwin, 2002). The predators can differ in the danger that they present to the progeny as they exhibit different hunting modes and habitat domains (Miller *et al.*, 2014). *A. nemorum* shows a 'run and eat' hunting mode, while *O. marginalis* is less mobile and can be considered as a 'find and stay' predator (Björkman *et al.*, 2003). These contrasting modes were used to explain how the predation on leaf beetle eggs and larvae is negatively affected via intraspecific interactions in the mobile predator *A. nemorum* but not in the less mobile predator *O. marginalis* (Björkman & Liman, 2005). Hunting mode also served as explanation for the neutral interspecific interactions between the two predators (Björkman & Liman, 2005). However, different habitat domains on the vertical willow shoot axis could play an additional role in explaining intra- and interspecific interaction and were, therefore, addressed here.

More significantly, the leaf beetle may perceive some parts of the shoot less dangerous because of a small domain overlay with a predator leading to lower chances of encountering the predator. Here we investigated the habitat domains of the leaf beetle and the two predators, their overlay, and if the anticipation of predation on the beetle eggs can change the oviposition site selection by beetle females (Vonesh & Blaustein, 2010; Lee *et al.*, 2014). Investigating where on the shoot the leaf beetle is ovipositing and where important predators in the system hunt for these eggs should help to understand if predation pressure could have been involved in the evolution of the oviposition site selection of the leaf beetle. We investigated the nonconsumptive effect of changing oviposition site in a set up were the predators is actually an omnivores which may be more affected by plant quality than the herbivorous prey they consume (Eubanks & Denno, 1999). Thus, we investigated how different plant genotypes change these vertical preferences of the predators and the leaf beetle and if it also changes the responses of the leaf beetle to the respective predators and their combination.

2 Thesis aims

The aim of this thesis was to understand how and why an herbivore, the leaf beetle *P. vulgatissima*, is grouping on individual host plants. Understanding the behavioural mechanisms during oviposition by individual beetle females on individual plants should help to understand how this species is aggregating. Because population dynamics are shaped by decisions of each individual the understanding of individual behaviour ultimately contributes to the understanding of insect outbreaks. We specifically aimed:

- to investigate if leaf beetle females use spatial memory during oviposition on individual plants (Paper I)
- to connect egg predation within clutches to general predator effects on prey grouping (Paper II)
- to identify and quantify plastic behavioural responses of ovipositing leaf beetles to predators and host plants (Paper III, IV)

3 Study system

3.1 The leaf beetle

Phratora vulgatissima (Coleoptera: Chrysomelidae) [L.] adults and larvae skeletonize willow leaves (Malpighiales: Salicaceae: *Salix* spp.)[L.], and this beetle is the most common specialist herbivore of willow in Europe (Peacock & Herrick, 2000). Adults emerge in April, feed for about two weeks, mate, and subsequently lay hundreds of eggs on the undersides of leaves in clutches of 1–50 eggs. The larvae feed gregariously during the first and second instar and then solitarily on different leaves during the third instar (Kendall *et al.*, 1996) followed by pupation in the soil. Adults emerge in August, feed shortly, and find hibernation sites in reeds or under the bark of trees (Björkman & Eklund, 2006). Although the species is considered to be univoltine in Sweden it has a second generation in the Uppsala area if the first generation is completed before August (Dalin, 2011). Adults probably excrete pheromones that attract other individuals (Peacock *et al.*, 2001). Because its oviposition shows no apparent link to the survival of adults oviposition rate is a valid proxy for leaf beetle fitness (Lehrman *et al.*, 2012).

From an economical perspective this beetle is the most important insect pest in willow short rotation coppices because it can reduce the stem wood production up to 40% (Björkman *et al.*, 2000) and frequently reaches high densities (Björkman *et al.*, 2004).

3.2 Willow as host plant

The host plant of this leaf beetle is willow. Willows are grown in short-rotation coppices and have become an important system for growing renewable feedstock for bioenergy production in many countries (Keoleian & Volk, 2005; Karp & Shield, 2008).

The four *Salix* genotypes used for the experiments were chosen because they differ in chemical composition (Lehrman *et al.*, 2012) and have been used in previous experiments establishing a narrow but distinct suitability gradient for both the leaf beetle and the omnivorous predator *A. nemorum*. The suitability of these genotypes for the leaf beetle increase in the order Gudrun < Loden < 78021 < 78183 (Stenberg *et al.*, 2010). The suitability for *A. nemorum* in the absence of prey follows the reverse order. In presence of additional prey the most suitable of these genotypes for *A. nemorum* is genotype 78183 and the suitability's of the genotypes Gudrun, Loden, and 78021 are similar (Stenberg *et al.*, 2011a).

3.3 The omnivorous predators

Within the well investigated tritrophic system of the host plant willow, the leaf beetle *P. vulgatissima* and its omnivorous predators several species have been found to be important for biocontrol within willow short rotation coppices and in natural willow stands. Among them are the mirids (Heteroptera: Miridae) *Orthotylus marginalis* [Reut.] and *Closterotomus fulvomaculatus* [De Geer] (Björkman *et al.*, 2004; Dalin, 2006) and the anthocorid *Anthocoris nemorum* (Hemiptera: Anthocoridae) [L.] (Björkman et al., 2004), which is also an important biocontrol agent in apple orchards (Sigsgaard 2010). *O. marginalis* is mainly predacious (Lehman 1932). Other observations suggest that it can survive on a minimal amount of animal food but has a preference for such food (Kullenberg 1944). *A. nemorum* is mostly regarded as a predator, but it also feeds on shallowly located fluids from the green parts of host plants (Lauenstein 1979).

4 Methods

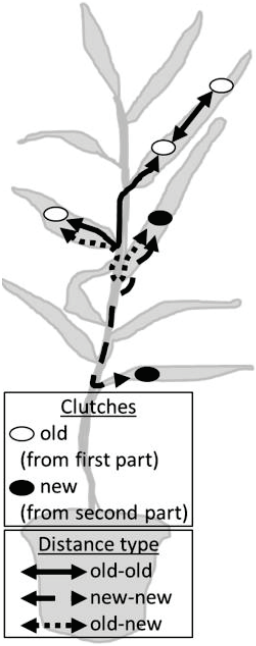
In all three experiments shown here, 20-cm winter cuttings were used to grow shoots of around 60 cm height. Growing the plants and all experiments were performed in the green house (23°C, relative humidity of 80%, light regime 18 h light/6 h dark). Some days before the experiment we removed side shoots, dried leaves, and leaves not fully expanded at the top and the individual plants were placed in cylindrical transparent plastic cages (70 cm height, 30 cm diameter) with a net on top (Fig. 1). Except for the first experiment where we also used individuals from the rearing the used leaf beetles were collected in the Uppsala area, Sweden.

Figure 1: Caged individual plants (in the middle: uncaged plant of *Salix* genotype 78183) where leaf beetles and predators where released in.

4.1 Beetle oviposition in presence of conspecific eggs

With this experiment we aimed to investigate if female beetle modulate the distances between egg clutches and if they use cognitive capabilities for doing so. Besides the general preparation, we here further standardized the plants in this experiment by additionally removing all leaves except 10 within 25 cm of the shoot. We therefore gained similar distances along the shoot between the leaves. The experimental procedure was the following: (1) in the first part we allowed each female to lay eggs for four days on the same plant (treatment: *first release*); (2) we measured the distances between the clutches (distance type: *old–old*); (3) for the second part we randomly assigned plants that had received eggs to either of the two treatments: *experienced* (releasing the same female again) or *naïve* (releasing new females that had not yet laid any eggs on any of the plants); (4) after three days all distances between these new clutches (*new–new*) and between the new clutches and the old clutches (*old–new*) where measured. Because the distances between clutches decreased with increasing number of clutches on a plant (adding points in a defined space decrease the mean distances between them; see Paper I) these distances were standardized by dividing each by the number of clutches on the respective plant.

Figure 2: Females were allowed to lay egg clutches (old) where after the distances between these clutches were measured. Then either the same female or a female from the rearing was released again and laid clutches (new) where after the distances between these new clutches (new-new) and their relation to the already established clutches (old-new) were measured.



4.2 Oviposition in response to host plants and predators

With the following experiments we aimed to understand if predator presences compared to predator absence and host plant quality alters the oviposition behaviour of the leaf beetle.

4.2.1 Clutch size and number of eggs laid on a shoot

First we were interested in the number of eggs that females lay on different plant genotypes and in presence of different predators. This experiment was divided in two parts. The first part was performed in 2009, with a complementary second part in 2015. The first part of this experiment involved all four *Salix* genotypes with either two ovipositing *P. vulgatissima* females released on individual plants for six days (Control) and one treatment with additionally two *A. nemorum* individuals (2 AN). In the second part of the experiment only the genotypes 78183 and Loden were used and we added the following predators to the plants with ovipositing females: two *O. marginalis*

(2 OM), one *A. nemorum* and one *O. marginalis* (1 AN + 1 OM), or four *O. marginalis* (4 OM). At the end of each experiment the clutch size, the number of consumed eggs, and the position of each clutch were recorded. Because genotypes had different numbers of leaves we divided each shoot into 13 equally sized parts (lowest position was part 1).

4.2.2 Vertical position of eggs on the shoot

In order to understand the behaviour of the leaf beetles we investigated the behaviour of the predators with respect to where they preferentially hunt on the shoot. Because natural oviposition does not result in a homogeneous distribution of eggs on the shoot (Paper IV) we distributed leaf beetle egg clutches along shoots on the *Salix* genotypes Gudrun, Loden, 78183 and 78021. Each plant was again divided into 13 equally sized parts (lowest position was part 1). We then attached leaves that had egg clutches with insect pins on the underside of the leaves of the experimental shoots. These clutches were previously manipulated to three size classes (5, 15, or 45 eggs per clutch). All 13 vertical positions of the experimental plants received one clutch. Three *A. nemorum* individuals or three *O. marginalis* individuals were then allowed to consume eggs for three days, and then we counted the number of empty egg shells and their locations. In addition to the gained information about the preferred vertical hunting area on the shoot, the positions of egg clutches in the previous experiment provided the information on the vertical preferences of the leaf beetles and how it is affected if the predators are present during oviposition.

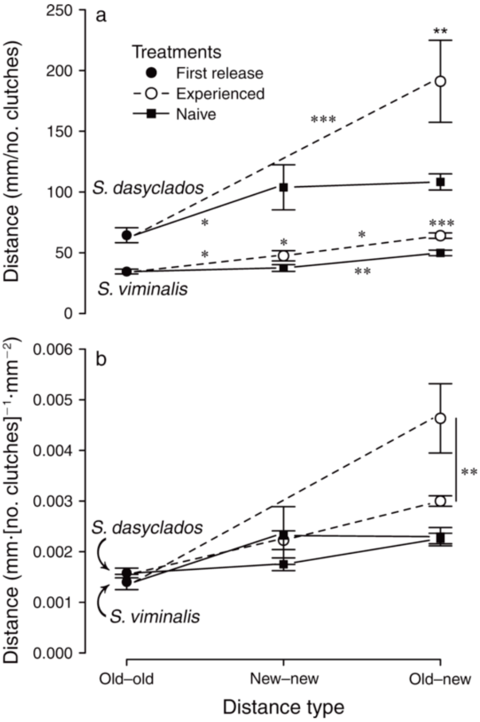
5 Results and Discussion

5.1 Beetle oviposition in presence of conspecific eggs

In this experiment we used the mean distance between clutches to describe the intra-plant clutch distribution because we were interested in the beetle's cognitive capabilities. We found the largest clutch distances for experienced females (Fig. 3) that can rely on perceived cues and memory because they themselves established the already existing clutches on a plant. Because experiences females increased the distances between clutches further than naïve females this behaviour indicates that this species must use some kind of spatial memory (or a cognitive map) to improve its egg distribution. Memory and learning involve costs (Dukas, 2008), but increased fitness due to optimized aggregation should be a strong evolutionary driver and should compensate for these. Because *P. vulgatissima* can memorize spatial information about previous oviposition on a plant it is able to reduce competition between sibling/non-sibling larvae. Because the larvae from nearby clutches will form a group the increase in larval survival would be due to known mechanisms relevant to aggregating organisms (Paper I). In addition, the terms egg pooling/egg clumping/egg clustering that normally refers to eggs that have contact with at least one other conspecific egg could be extended considering this fine-tuned distance modulation. Therefore, arguments for the existence of such modulation should be similar to those related to egg pooling, like host-plant nutrient distribution (Chew & Courtney, 1991) and increased female fecundity (Courtney, 1984).

Intra-plant egg distribution can vary on host plant species due to different suitability (Silva & Furlong, 2012). Here we showed that leaf morphology in itself can also be important, because females increased the distances between clutches on a less suitable host plant due to differences in leaf area and not host suitability (Fig. 3b).

Figure 3: Distances (mean ± SE) between egg clutches of the leaf beetle on a shoot after (a) correcting for shoots with different numbers of clutches and (b) additional correcting for *Salix* species with different total leaf areas. Largest clutch distances were found among new–new and old–new clutches in part two of the experiment for experienced females that were released on the same respective plants as in part one, and could rely on perceived cues and memory (compare to old–old clutches; old clutches are those laid in part one, new clutches were laid in part two). Naive females released in part two that had not encountered the respective plant before could only rely on cues. Significant differences were determined via a Kolmogorov- Smirnov test. * P < 0.05; ** P < 0.01; *** P < 0.001.



The distance modulations might represent a previously unknown behavioural element of insect oviposition that increases the chances of offspring survival. How exactly these beetles use their memory during oviposition, however, remains unknown. Nevertheless, cognitive capabilities are assumed to alter trophic interactions and population dynamics (Kondoh, 2010), which is probably especially important for gregarious out-breaking species like *P. vulgatissima*. In identifying these new behavioural component of oviposition we so contribute to the mechanistic understanding of the spread of insect outbreaks because population dynamics are shaped by individual decisions.

5.2 Oviposition in response to host plants and predators

5.2.1 Clutch size and number of eggs laid on a shoot

It appears that the mean clutch size of *P. vulgatissima* is driven by the plant genotype because size increases with increasing plant suitability (Fig. 4a, b). This beetle therefore showed similar plasticity found in other herbivorous insects (Pilson & Rausher, 1988), while other may not be able to alter this behavioural trait (Janz & Thompson, 2002). Clutch size may also increase with

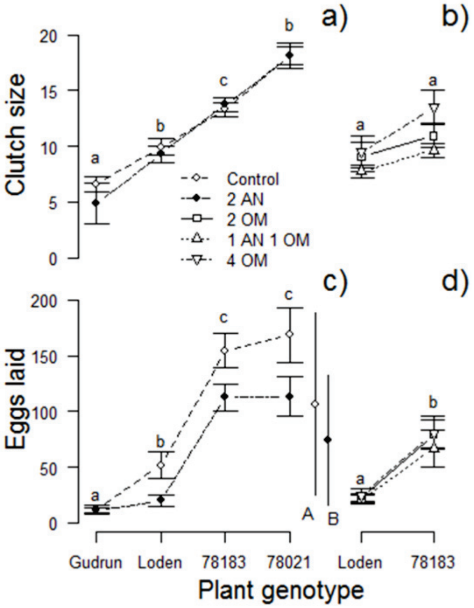


Figure 4: Mean (±SE) clutch size and eggs laid on individual plants by two *Phratora vulgatissima* females depending on the Salix genotype (*S. dasyclados*: Gudrun, Loden; *S. viminalis*: 78183, 78021) and the predator treatment (Control = only leaf beetles, AN = *Anthocoris nemorum*, OM = *Orthotylus marginalis*) for the first (a, c) and second (b, d) experimental part. Lowercase letters indicate differences between genotypes and upper case letters differences between overall means (±SD) of treatments ($p < 0.05$; Tukey contrast).

leaf area (Kagata & Ohgushi, 2002) and we showed previously that *P. vulgatissima* increases its distances between clutches on a plant due to higher leaf area of the unsuitable genotype, not the unsuitability itself (Stephan *et al.*, 2015). In contrast, the *S. dasyclados* genotypes (Loden and Gudrun) with twice as large leaves as the *S. viminalis* genotypes (78183 and 78021) received considerably smaller clutches. Although females more frequently initially select larger leaves for oviposition and feeding (Paper IV) there seems to be no relation between clutch size and leaf area of particular leaves and mean clutch size is modulated by plant suitability. Similar to the increase of distances between clutches the adaptive mechanism would be to avoid intraspecific exploitative competition. Before moving to other plant parts the larvae feed gregariously, close to the hatching site, until the 3rd instar. This means that competition is lower on suitable plant genotypes that can support more larvae in an equivalent feeding area (Pilson & Rausher, 1988; Freese & Zwölfer, 1996; Roitberg *et al.*, 1999). Suitable plant genotypes that provide ample food provision therefore sustains larger clutches, suggesting that females match the number of larvae hatching from an egg clutch to the food quality to reduce the risk of larval aggregation problems.

Contrary to the plant genotype *P. vulgatissima* did not follow our expectations regarding the predators. Predator presence did not change the mean clutch size, which was especially surprising for the presence of *A. nemorum* as larger clutch size increase individual egg survival in case where only this predator is foraging on the eggs (Paper II, Paper IV). However, investigating the actual clutch size distribution showed that either of the predator types/combinations lowered the median and the variation in clutch sizes with smaller sizes becoming more frequent (Paper III). This change in size distribution appeared for both predators meaning the leaf beetle females may not discriminate between the predators.

The other behavioural response becomes apparent by comparing the mean total number of eggs laid on the different genotypes in predator absence and presence (Fig. 4 c, d). We evaluated the oviposition choice with a no-choice assay, not in a field set up (Tschanz *et al.*, 2005) or with alternative host plants. However, oviposition rate is a good indicator for life time fitness in this species and our results confirm previous findings that lower egg numbers are laid on less suitable plant genotypes (Stenberg *et al.*, 2010; Lehrman *et al.*, 2012). We can also conclude that host plant acceptance was due to suitability not larger leaf/feeding area because the cumulative leaf area of all plants was similar.

Most interestingly was the finding that the predator presence also lowers oviposition rate. In the presence of *A. nemorum* the oviposition rate decreased compared to the predator absence treatment and it also seems to decrease in the second part of the experiment for all predator treatments in similar strength. It may be difficult to detect lower oviposition rate on a high predation risk plants in the field (Tschanz *et al.*, 2005) or specific plant genotypes (Stephan *et al.*, 2016) as many other aspects like valuing own performance higher than that of the offspring (Mayhew, 2001), habitat heterogeneity (Andersson *et al.*, 2013), or higher predation risk on otherwise suitable hosts (Egusa *et al.*, 2008) could be more important for egg survival. However, we found first evidence that *P. vulgatissima* could lower its oviposition rate to avoid predation.

The number of eggs not laid on a plant due to predator presence and plant genotype represent a strong non-consumptive effect (Paper III). As a result, complicated interactions arise because the predators and their consumption of eggs and disturbance of the females are also depending on the plant genotype. For example increased time spent on egg consumption by the predators due to lower plant sap quality is accompanied with less time spent searching for prey and thus disturbing the beetle females less. Consequently, although the plant gains protection through egg consumption by the omnivorous predator, there might be also a "cost" in form of lower benefit from the nonconsumptive effect as the predator will disturb the herbivorous beetles less. This may ultimately increasing damage to plants, depending on the ration between consumptive and nonconsumptive effect on a plant genotype (Paper III). Also, assays investigating indirect defences of plants via `bodyguards´ should include foraging kairomones from beetles (Fernandez & Hilker, 2007) or plant volatile induction due to feeding or oviposition (Dicke & Baldwin, 2010). This will ensure that possible differences in the nonconsumptive effect of the omnivorous predators due to the host plant are included as they may result in differently strong effects on the herbivore reproductive behaviour (Paper III).

5.2.2 Vertical position of eggs on the shoot

We found that both omnivores have contrasting preferred hunting areas at individual plants (Fig. 5). *A. nemorum* mainly consumed eggs in the upper part of the plant, whereas *O. marginalis* preferentially foraged in the lower part. Neither of the four plant genotypes interfered with these contrasting preferences and therefore strengthen our interpretation that these are general attributes. We believe that these different preferences are another important factor contributing to the neutral relationship between the two predator species, which was previously attributed solely to their different foraging strategies (Björkman & Liman, 2005). However, the details of the different preferences remain unexplored and still have to be confirmed in the field. The fact that *A. nemorum* (overwintering as adult) feeds on flower nectar in the shoot canopy (Sigsgaard & Kollmann, 2007) and that *O. marginalis* hatches after willow flowering (overwinters as eggs) and mainly feeds on sap maybe relevant here. Also the very active *A. nemorum* might pass the area occupied by *O. marginalis* as we also have the impression that *O. marginalis* is more territorial because it lays its eggs in the lower part of the shoot and actively defends them. Dominant species are often avoided by less dominant species (Binz *et al.*, 2014) and *A. nemorum* may evade time- and energy-consuming confrontations.

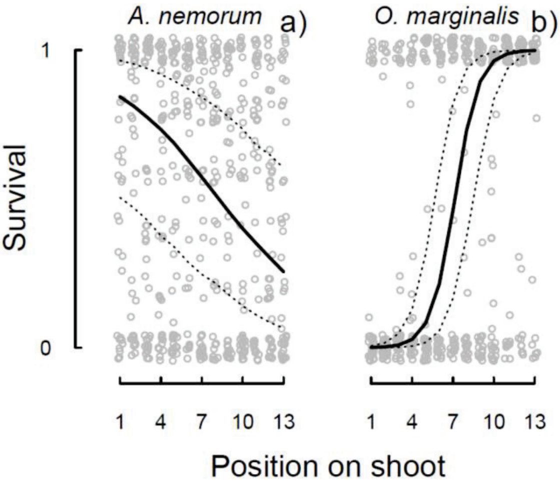


Figure 5: Survival of *Phratora vulgatissima* eggs within a clutch after being exposed to three *Anthocoris nemorum* (a) or three *Orthotylus marginalis* predators (b) in relation to vertical position of the clutch on the shoot (1 = lowest part along the shoot). The survival probability increased down the shoot if *A. nemorum* was released, whereas it increased up the shoot if *O. marginalis* was in the cage. Circles show the proportion survived eggs within clutch (shifted to increase visibility), and the lines indicate the model predictions with bootstrapped confidence limits.

Leaf beetle females preferred to oviposit in the lower part of the shoot, despite the fact that leaves are smaller on the top and bottom of the plant with leaf area also being an important determinant for beetle oviposition (Paper IV). The individual females preferentially feed in the upper shoot part (Paper IV), which may be explained by higher leaf nitrogen concentration in the shoot canopy (Weih & Rönnberg-Wästjung, 2007), but move to the lower shoot part for oviposition. This is surprising, and because we may be able to rule out other explanations (Paper IV) we believe this represents predator avoidance behaviour.

This plastic avoidance was differently strong among predator treatments and plant genotypes. On three of the four plant genotypes we could observe that the presence of *A. nemorum* amplified the behaviour of choosing leaves for oviposition in the lower plant part where this predator is hunting less frequently (Fig. 6). In presence of *O. marginalis*, however, the leaf beetles did not respond strongly (Fig, 7a, d). This may be due to the previously mentioned shorter temporary overlap early in the spring in combination with the believe that time to first reproduction and the survival of herbivore eggs laid early in the season are very important (Parry *et al.*, 1998). Additionally, the lower mobility of *O. marginalis* may lead to less frequent encounters by the beetles compared to *A. nemorum* with its ‘run and eat’ behaviour. The shoot canopy

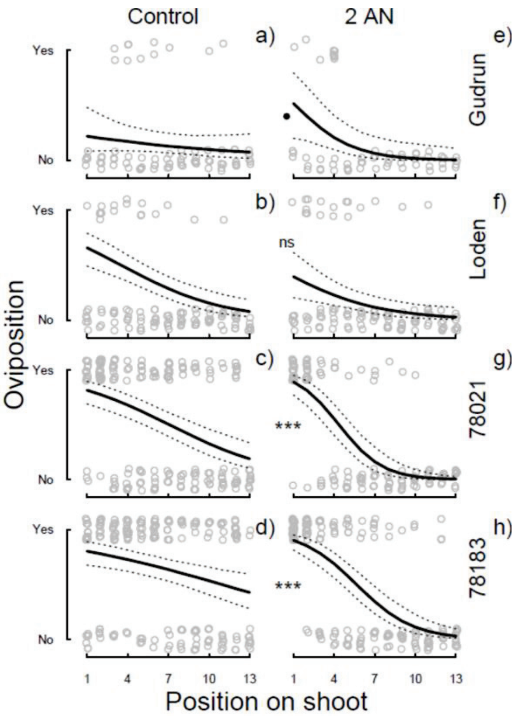


Figure 6: Oviposition of two *Phratora vulgatissima* females in relation to vertical position on the shoot (1 = lowest part along the shoot) with respect to different predator treatments (Control = only leaf beetles females, 2 AN = leaf beetles and two *Anthocoris nemorum* individuals) and plant genotype (*Salix dasyclados*: Gudrun, Loden; *Salix viminalis*: 78021, 78183). Circles show the incidence of oviposition (shifted to increase visibility), and the lines show the model predictions with bootstrapped confidence limits (comparisons to slope of respective Control: *** = $p < 0.001$; ● = $p < 0.09$; ns = $p \geq 0.05$).

may therefor appear more dangerous and the fact that alarm substances produce by Anthocoridae (Evans, 1976), that may be used by the leaf beetle as a foraging kairomone, could contribute to this interpretation. In confronting the ovipositing leaf beetles with both predators simultaneously we found a tendency for a weakened preference on Loden and no position preference on 78183 (Fig. 7b, e). This last result validates that the females are able to perceive both predators, try to avoid their respective habitat domains, and anticipate future predation on their eggs/larvae because the predators are not harmful to the adult females themselves. For the last treatment we doubled the number of *O. marginalis* and we expected that the leaf beetles preference for the lower shoot part would be even more weakened. This was true for the genotype Loden, but not 78183 where we observed the exact opposite. This interaction between predator density and plant genotype is puzzling at the moment and will be investigated further.

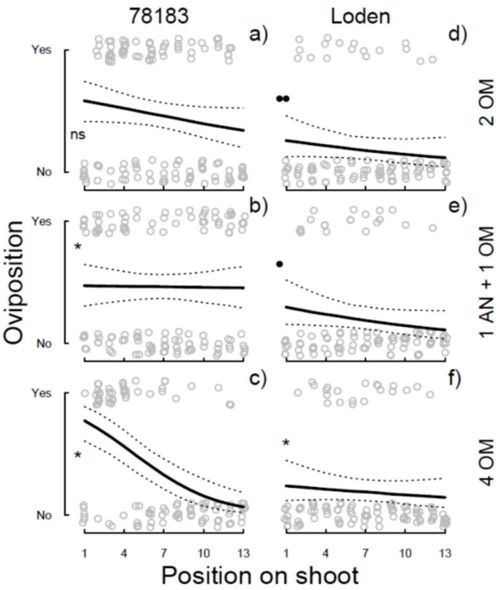


Figure 7: Oviposition of two *Phratora vulgatissima* females in relation to vertical position on the shoot (1 = lowest part along the shoot) with respect to plant genotype (*Salix dasyclados*: Loden; *Salix viminalis*: 78183) and different predator treatments (Control = only leaf beetles (see Fig. 4b and 4d, respectively), AN = *Anthocoris nemorum*, OM = *Orthotylus marginalis*). Circles show the incidence of oviposition (shifted to increase visibility), and the lines show the model prediction with bootstrapped confidence limits (comparisons to slope of respective Control: * = $p < 0.05$; ●● = $p < 0.06$; ● = $p < 0.09$; ns = $p \geq 0.05$).

6 Conclusion

We showed that the leaf beetle *P. vulgatissima* possesses sophisticated strategies to respond to a changing environment during egg laying. The changes in the environment(s) are set by the presence of conspecifics on host plant and its quality, the predators that are present during oviposition, and the direct and indirect interactions among these tree factors within this tritrophic system. It is believed that one element that may contribute to the occurrence of insect outbreaks is gregariousness because this form of living is shared among most outbreaking species. Furthermore, due to the number and complexity of mechanisms accompanied, it is believed that this form of living increases the variability of survival chances making insect outbreaks and their causes hard to explain or even predict. We illustrated which factors might modulate this variability and explored some behavioural mechanisms of the outbreaking herbivore and two omnivorous predators. We hope we contributed to the understanding on group living behaviour and (may) inspired new interesting ecological questions.

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