

**Intra- and interspecific interactions among natural enemies  
and consequences for biological control of arthropods**

Habilitationsschrift

von

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## General introduction

Use of natural enemies developed over the last decades to an important plant protection strategy in biological control (van Lenteren 2007) as well as in integrated pest management (Abrol 2014). Reasons behind are manifold and range from restricted approval of pesticides, pest resistance, health concerns and increased sensibility for environmentally friendly strategies to consumer demands for residue free produce. But also increased market demands for organic production contributes to high interest in biological plant protection strategies (Bale et al. 2008; van Lenteren 2000a). Agricultural and horticultural production takes place mainly in two different environments, either in the open field or under protected cultivation. The later can be further divided into greenhouse cultivation and cultivation of crops in polytunnels. The difference between these systems is the degree of isolation from the natural environment, which decreases from open field to polytunnels to greenhouse cultivation of crops. In that sense greenhouses are (almost) completely isolated from environmental factors. The greenhouse climate, water and nutrients are adjusted to optimise growing conditions and crop yield. Incidences of pest and diseases are at a rather low level mostly due to phytosanitary processes. If pest control is necessary only a few key pest species are of major importance and growers frequently face the comfortable situation to select among several natural enemy species which are commercially available (van Lenteren 2007; Pilkington et al. 2010). For example in tomato growing in the greenhouse the greenhouse whitefly is one of the most important pests, which can be controlled either by the whitefly parasitoid *Encarsia formosa* (Hymenoptera, Aphelinidae) or several predatory bugs (*Macrolophus pygmaeus*, *Dicyphus hesperus*; Heteroptera, Miridae). The optimal strategy depends on tomato growing period and if both antagonists are present, interspecific interactions cannot be excluded (Sohrabi et al. 2013). However, not all arthropod pests are easy to control in the greenhouse. For example Western flower thrips, *Frankliniella occidentalis* (Thripidae) is difficult to control in many crops (cucumber, roses, chrysanthemum etc.) and integrated approaches are need for successful strategies (Mouden et al. 2017). The possibility to control the environment, changes partly if crops are grown in poly-tunnels. The crop still is rain protected, but temperature can be controlled only marginally. More important is that arthropod pests and natural enemies can emigrate more easily into poly-tunnels compared to greenhouses, which leads to numerous additional interactions among natural enemies released to control a specific pest

(Messelink et al. 2014; Gabarra et al. 2004) and with natural enemies from the surrounding environment (Pineda, Marcos-Garcia 2008). Even more complex is the situation in the open field. Annual crops are colonised each year again by several pest species and natural enemies emigrate from source habitats (Ludwig et al. 2017; Alomar et al. 2002). Whether or not many pest species and natural enemies are present depends on availability and quality of alternative habitats (Bianchi et al. 2006) as well as on the dispersal behaviour of the arthropods (Muller, Brodeur 2002). In perennial crops similar factors as in annual crops are important, but additionally crop management strategies play an important role (Rusch et al. 2010) and will influence the foodweb structure (Denno, Finke 2006). Additionally functional biodiversity can be manipulated in the field by several approaches, i.e. trap plants, banker plants, flowering strips, pheromones (mating disruption) etc., which increase not only number but also the abundance of interacting species. Interactions among natural enemies in the field are therefore at its highest level of complexity (Hooks, Johnson 2003; Schellhorn et al. 2015) and most likely contribute substantially to the high variability and low predictability of biological pest control in general (Wyckhuys et al. 2013). For the simple greenhouse ecosystem the analysis of multitrophic interactions is already on a good way and will quickly lead to further improvements in biological control strategies, but for the complex agricultural ecosystem interdisciplinary approaches are needed.

In general the impact of natural enemies depends on the efficiency of each antagonist species to suppress a pest species, but recently the importance of omnivores, i.e. feeding at different trophic levels, came into the focus (Rosenheim, Harmon 2006). On the one hand predators might feed as herbivores and predators (Coll, Guershon 2002), and on the other hand predators feed on various prey species in the arthropod community, i.e. detritivores and herbivores insects as well as other predatory arthropods. For biological control of pest species, interactions among antagonists which compete for shared resource, termed intraguild predation (Polis et al. 1989), are of particular interest. For example, numerous natural enemy species are commercially available for biological control of key pests in greenhouse crops, i.e. 6 parasitoid species and 5 predator species, without specific recommendations of compatibility (Tab. 1). Although the relevance of intraguild predation (IGP) was unclear for a long time, it is now recognised as a widespread interaction in general (Arim, Marquet 2004) and in communities of biological control agents (Janssen et al. 1998; Brodeur,

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Rosenheim 2000; Snyder et al. 2005). Two types of intraguild predation can be distinguished (Polis et al. 1989).

Tab. 1 Number of commercially available parasitoid and predator species in Germany for biological control of important greenhouse pests (Jehle et al. 2014).

Pest Species	Parasitic Wasps	Predatory Species	$\Sigma$
<b>Aphids</b>	6	5	11
<b>Leafminer</b>	2	1	3
<b>Lepidoptera</b>	2	-	2
<b>Scale insects</b>	5	4	9
<b>Spider mites</b>	-	5	5
<b>Thrips</b>	-	9	9
<b>Fungus gnats</b>	-	1	1
<b>Whiteflies</b>	3	4	7
<b>Mealy bugs</b>	5	1	6

The first type of IGP is coincidental and occurs mainly when the intraguild predator feeds on an herbivore that was previously attacked by a parasitoid or pathogen, the intermediate predator. In that case, the intraguild predator unintentionally consumes the intermediate predator together with the herbivore prey item. The second type is termed omnivorous IGP, and occurs when one predator (intraguild predator) encounters and consumes another predator (intermediate predator). The first type of IGP can be interpreted also as an asymmetric or unidirectional relationship, since only the intraguild predator is able to consume the parasitoid, while the second type is a symmetric or bidirectional relationship, because each of the antagonists has the potential to prey on the other (Fig 1).

Based on theoretical understanding of interactions among three species, i.e. intraguild predator, intermediate predator and herbivorous prey, the equilibrium densities were analysed by differential equation models (Rosenheim, Harmon 2006; Borer et al. 2007). For the first type of interaction, the superior competitor (sustained at lowest equilibrium density of the herbivore) will outcompete the inferior. The superior competitor in that case is also the best biocontrol agent. For the second type of interaction three species equilibrium can be reached only if the intermediate predator is the superior biological control agent. The intraguild predator in that case only exists if the equilibrium density of the herbivore is increased, which is not the preferred scenario in pest control. However, does intraguild predation always disrupt biological control? In practice the outcome of IGP in biological control is highly variable and

frequently not disrupted as predicted by theory (Janssen et al. 2006). Based on a recent meta-analysis on the influence of IGP on suppression of a shared prey the main differences between theory and practice were summarised (Rosenheim, Harmon 2006).

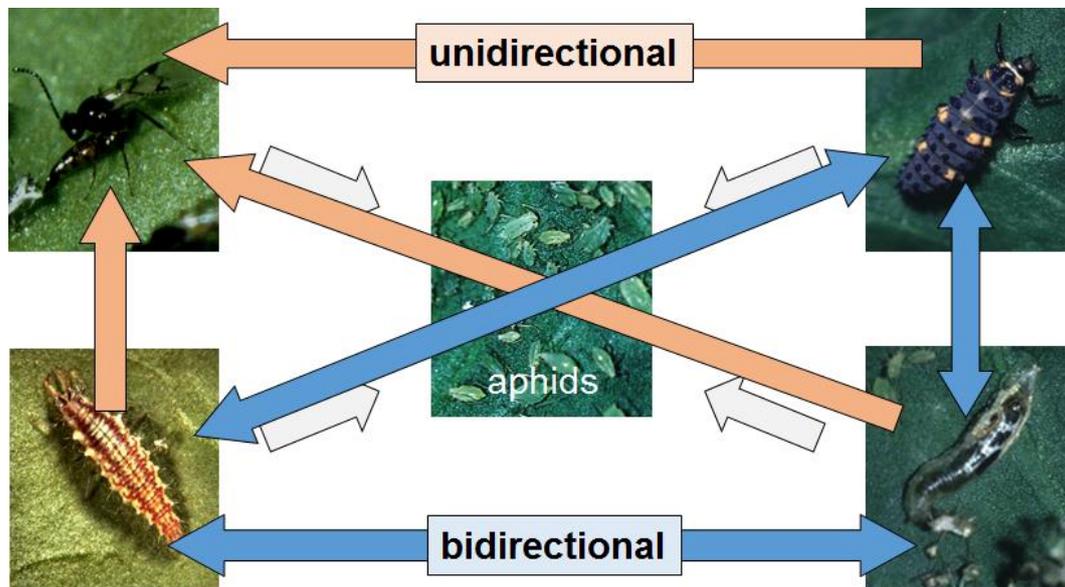


Figure 1 Types of intraguild predation within the guild of aphidophagous species. All natural enemies (parasitoids and predators) attack the common aphid herbivore (  $\leftarrow$  ). IG-predators (e.g. coccinellid, syrphid, chrysopid larva) show the potential to feed on each other (bidirectional or symmetric IGP  $\leftrightarrow$ ). In contrast, parasitoids are not able to kill predatory species and therefore the IGP relationship is unidirectional or asymmetric (  $\rightarrow$  ).

Basically, theory considers only equilibrium densities while empirical studies focus on transient dynamics on much shorter time scales and additionally theory excludes the possibility that alternative prey are important for omnivorous predators. Authors conclude that a better understanding of transient dynamics as well as a better causal analysis of the variability of interactions between intraguild predator species and the impact on herbivore prey is needed (Rosenheim, Harmon 2006). A key determinant for the impact of intraguild predation is the preference of the intraguild predator to consume the intermediate predator or the herbivore. Therefore many interactions in the guild of natural enemies are shaped by optimal foraging by adults during host habitat and host searching as well as decisions when and where to reproduce. For example, female syrphids decide in which aphid colony offspring has the best survival probability (Pineda et al. 2007). Similarly, parasitoids sense the environment before parasitism of hosts and are likely to balance decisions based on its physiological state and environmental factors including intra- and interspecific competitors (Cotes et al. 2015; Martinou et al. 2010).

## **Outline of the Work**

The principal goal was to investigate multitrophic interactions among natural enemies to understand the impact of intraguild predation on the overall impact of natural enemies on pest population development in the complex field as well as in the simplified greenhouse environment. Based on the results implications for biological control of pests in different production systems, agricultural and horticultural crops in the field as well as in the greenhouse, are discussed.

In **Chapter 2**, the effect of intraguild predation on survival of aphid parasitoids was investigated. To assess the impact in a realistic scenario a field study was designed where the natural community of aphidophagous predators had access to the intraguild prey, i.e. aphids parasitized by *Lysiphlebus fabarum* (Hymenoptera, Aphidiidae). Besides monitoring the insect population dynamics, extraguild prey density was manipulated to investigate impact on parasitoid survival. Taking into account the specific foraging of the aphid parasitoid the in-depth insights on the selection pressure of aphidophagous predators is provided.

In **Chapter 3**, a new video technique was developed for field observations, which allows continuous recording of behavioural interactions between intraguild predator and prey. The use of a multiple video camera set-up equipped with infrared night vision and in combination with time-lapse recording allows continuous observations over several month, restricted only by storage capacity and power supply. Continuous observation of aphid patches in the field revealed not only a broad spectrum of intraguild predators attacking parasitoids but also specific functional relationships between extraguild prey density and predator species

In **Chapter 4**, the mortality risks for different developmental stages of the parasitoid *Lysiphlebus fabarum* in confrontations with 4 different aphidophagous predators, *Coccinella septempunctata* (larva and adult), *Chrysoperla carnea* and *Episyrphus balteatus* were analysed. On the one hand, pathological effects of the endoparasitoid on its host might reduce defensive behaviour of the aphid on predator attack, but on the other hand, selection pressure might also minimize the risk of predation. For the adult parasitoid, the high mobility could be a guaranty for escape behaviour but only interpretation of the behaviour in an ecological context will finally help to understand the results.

In **Chapter 5**, the interactions between two important parasitoid species for aphid biocontrol in greenhouses and several intraguild predators are compared. Based on

the assumption that female adult parasitoids should minimize the risk of predation for themselves and for their offspring, behavioural decisions made during foraging should be adapted. Since direct and indirect interactions between organisms are hard to separate a standardised bio-test setup was developed which allowed comparison of behavioural reactions in confrontation with several intraguild predators.

In **Chapter 6**, the indirect impact of aphid population density, i.e. extraguild prey, on survival of parasitized aphids was investigated. Endoparasitoids partly rely on efficient escape behaviour of its host, which can be manipulated also by the developing parasitoid larva. However, optimal foraging and patch use of females might also be influenced by perceived predation risks. In consequence parasitized aphids profit from dilution effects in combination with physical defence against attacking intraguild predators.

In **Chapter 7**, the capacity of associative learning of parasitoids in the context of intraguild interactions was investigated. For many parasitoid species, associative learning of herbivore induced plant cues plays an important role to optimise host location. But whether negative experience with an intraguild predator can be exploited by associative learning has rarely been investigated.

In **Chapter 8**, the suitability of microsatellite marker for sib ship reconstruction of the aphid parasitoid *Diaeretiella rapae* was investigated. Especially if relatedness of individuals collected in the field can be identified at family level, it will be possible to traces foraging decisions made by females in the field under unbiased conditions. The technique might offers high potential for experimental studies with small species impossible to follow directly. More specifically the impact of IG-predator on the foraging behaviour of the parasitoid can be studied in the field non-destructive and without any methodological interference.

In **Chapter 9**, intraguild predation between the aphidophagous hoverfly, *Episyrphus balteatus* and other aphidophagous predators was explored. Predators frequently aggregate at places with high prey densities, which leads to numerous interactions among developmental stages and different predator species. The outcome of direct confrontations is hard to predict and depends not only on the physical strength but also on camouflage and defence behaviour of the aggressors.

In **Chapter 10**, the intraspecific interactions of two predatory soil mites of the genus *Hypoaspis*, i.e. *H. aculeifer* and *H. miles*, were investigated. Both species are important soil predators, which prey not only on soil arthropods but also on Western

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flower thrips completing the development as pre-pupa and pupa in the soil. Whether or not cannibalism could be a reason for low impact on western flower thrips was investigated in detail.

In **Chapter 11**, combined effect of two predatory mites on western flower thrips was investigated. *Amblyseius cucumeris* attacks western flower thrips on the plant canopy while *Hypoaspis miles* attacks developmental stages in the soil. Although predators do not interact directly with each other, the soil predatory mites has to compete with other predatory mites in the soil and the effect on thrips depends largely on availability of alternative prey.

Finally, **Chapter 12** summarizes and discusses the main results of the previous chapters and gives an outline for future research.

## Effects of intraguild predation on parasitoid survival

(based on Meyhöfer R., Hindayana D., 2000)

### **Abstract**

To assess the potential selection pressure caused by intraguild predation between predators and parasitoids of aphids an estimate was made of the predation risk to *Aphis fabae* Scop. mummified by *Lysiphlebus fabarum* (Marshall 1896) on sugar beet. Mummified aphids were exposed to a natural community of predators. Their survival time was estimated during a 10-day field survey. Additionally, the role of alternative prey on parasitoid survival was investigated by adding unparasitized aphids to half of the mummy aggregations.

The field data were evaluated by survival analysis. Two covariates were tested within a Cox proportional hazard model: (i) the presence of the alternative prey and (ii) the patch structure (number of proximal mummies attacked). Within 4-5 days after exposure predators destroyed approx. 50 % of the mummies. The model with both covariates revealed a significant difference concerning survival of the mummies in the two treatments (Likelihood ratio test,  $\chi^2=78.03$ ,  $P=0.0001$ ). Alternative prey reduced the predation risk on mummies by 29 %, while a high level of predation on proximal mummies increased the individual predation risk by 4 %. The results are discussed in the context of prey location by predators and the evolution of anti-predator mechanisms.

## **Intraguild predation by aphidophagous predators on parasitised aphids: the use of multiple video cameras**

(based on Meyhöfer R., 2001)

### ***Abstract***

A video technique that allows simultaneous behavioural observations of several experimental replicates under field and laboratory conditions is described. The technique was used to analyse predation risk of parasitised aphids in a sugar beet field. The images of 16 black and white video cameras were recorded by a video multiplexer in combination with a time-lapse video recorder. Each camera was weather protected and equipped with a single infrared diode to allow observations during night times. Single leaves carrying aphid mummies only or mummies and unparasitised aphids were monitored. All colonies were exposed to predation and parasitism by the community of natural enemies in the field. Colonies with mummies and unparasitised aphids were visited significantly more often than those without additional aphids. Predators also stayed significantly longer in patches with unparasitised aphids. Although an equal proportion of aphid mummies were destroyed in both treatments, the video analysis showed differences in predator species spectrum between treatments. In patches with aphids, coccinellid and hemipteran predators preyed on mummies, while in patches with only mummies, chrysopids accounted for most of the damage. The decrease in parasitoid survival could be attributed to the increasing number of predator visits in aphid patches and to a lesser extent to the decreasing number of unparasitised aphids (alternative prey). Parasitoid survival in colonies without alternative prey was correlated with the number of predator visits and the time predators spent on a leaf.

Continuous video observations gave additional behavioural information for the interpretation of field data. Other prospective research fields for the use of the multi video camera technique are outlined and general advantages and disadvantages are discussed.

## **Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum*: Mortality risks and behavioural decisions made under the risk of predation.**

(based on Meyhöfer R., Klug T., 2002)

### ***Abstract***

Intraguild predation (IGP) is a primordial mortality factor that generates consequences for the coexistence of species in natural communities as well as for the implementation of antagonists in biological control programs. Among parasitoids and predators the most frequent form of IGP is asymmetric. Because it exerts a strong selection pressure on the inferior parasitoids it seems to be likely that these antagonists have evolved strategies to minimize IGP.

Our study traced the behaviour of aphid parasitoid *Lysiphlebus fabarum* (Marshall), which is able to exploit the enemy free space in ant protected aphid colonies. In the agricultural landscape *L. fabarum* frequently forages in aphid colonies without ant protection where it is exposed to situations with an extraordinary high risk of predation by aphidophagous predators. In the current study we investigated predation risks for different developmental stages of *L. fabarum* and behavioural decisions made under the risk of predation by foraging females.

All developmental stages of *L. fabarum* suffered from a high risk of predation in confrontations with most of the tested aphidophagous predators. Only aphid mummies turned out to be a less frequent IG-prey compared to unparasitized aphids when found simultaneously with adult *Coccinella septempunctata* L. and larvae of *Episyrphus balteatus* de Geer. Nevertheless, foraging females of *L. fabarum* did not avoid the presence of predators nor displayed an effective defence behaviour in direct confrontations with any of the tested predator species. Coccinellids, syrphids as well as chrysopids proved capable of killing an adult parasitoid.

The discrepancies between the observed predation risks and the lack of behavioural adaptations of adult *L. fabarum* are discussed in different contexts.

## Impact of intraguild predators on behavioural decisions made by foraging parasitoids

(based on Meyhöfer R., Klug T., unpublished)

### **Abstract**

Predation is one of the key mortality factors for most species and influences many behavioural decisions. In aphid antagonist guilds, trophic interactions among natural enemies are widespread and is termed intraguild predation (IGP). The specific relationship between parasitoids and predators is asymmetric, i.e. the former is always IG-prey and the latter always IG-predator. Theory predicts that prey individuals, i.e. parasitoids, should avoid foraging in or near patches that are already exploited by predators, to minimize the predation risk. In the current study we investigated behavioural decisions made by two aphid parasitoid species, *Aphidius colemani* and *Aphidius ervi*, under the risk of predation, i.e. in presence of different aphidophagous predator species. The results show that both parasitoid species were affected by the presence of predatory *C. carnea* larvae on the plant, and significantly reduced their patch residence time as well as the time they allocated to searching activities, with *A. ervi* being more sensitive than *A. colemani*. Behavioural decisions made by *A. colemani* and *A. ervi*, in confrontations with different species of aphidophagous predator, did not allow simple conclusions. Based on our observations, we hypothesize that coccinellids are perceived as the major mortality risk, followed by ants and chrysopids, while syrphid larvae only seemed to be perceived as a minor risk to foraging parasitoid females. Although adult parasitoid mortality was low during direct confrontations with aphidophagous predators, foraging females strongly underestimated the predation risk for their offspring. Results are discussed in the context of optimal foraging and possible consequences for population development.

## ***Introduction***

Any decision made by arthropods during the foraging process is influenced by both abiotic, i.e. wind, rain, temperature and humidity, and biotic factors, i.e. physiological state, host plants, hosts, competitors, natural enemies (Price, 1997; Godfray, 1994). The impact of most of these factors on foraging behaviour has been well investigated, at least for certain species, such as antagonists of pests with economic importance, which are model organisms in many lab and field studies (Jervis, 2005; Bellows & Fisher, 1999; Van Alphen & Jervis, 1996). An important but less studied biotic factor for most arthropods is predation (Werner, 1992; Abrams, 2000). The occurrence of predators commonly influences prey decisions about feeding, activity levels and reproduction, to a diverse array of vertebrate and invertebrate prey (Lima & Dill, 1990; Sih, 1994). In response to heightened perceived predation risk, prey curtail feeding effort, increase anti-predator activity (e.g. vigilance behaviour) and shift activity to less risky and usually less rewarding habitats (Lima, 1998b). Behavioural non-lethal interactions are pronounced, especially in species rich guilds with different life history strategies. For example, host plant – aphid systems frequently include different aphid species, as well as several predatory, primary parasitoid and secondary parasitoid species, all interacting in space and time (ref). Natural enemies competing for the same resource are likely to engage in trophic interactions, termed intraguild predation (IGP) (Polis *et al.*, 1989; Polis & Holt, 1992; Rosenheim *et al.* 1995). In particular, predator and parasitoid relationships are asymmetric, since only the predator is able to attack the parasitoid and not vice versa. Moreover, all developmental stages of parasitoids are at a high risk of predation, e.g. larval stages developing as endoparasitoids in aphids (Brodeur & Rosenheim, 2000; Meyhöfer & Hindayana, 2000; Colfer & Rosenheim, 2001; Meyhöfer & Klug, 2002) and adult parasitoids engaged in foraging activities (Heimpel *et al.*, 1997; Meyhöfer & Klug, 2002).

Many authors hypothesize that, on evolutionary timescales, predators shaped the foraging behaviour of parasitoids (Brodeur & Rosenheim, 2000; Müller & Brodeur, 2002; Weisser *et al.*, 1994). In a comparative study, Völkl and Mackauer (2000) suggested that the main driving forces in oviposition behaviour of parasitoids were aphid defensive behaviour and aggression of trophobiotic ants. Parasitoids should weigh up the risk of predation against various benefits (i.e. lost feeding/oviposition opportunities) when deciding which behavioural option to pursue. To minimize predation risk for themselves and their offspring, female parasitoids should avoid

foraging in or near aphid patches that are already exploited by other natural enemies. In this respect behavioural decisions made by IG prey do not differ from decisions made by primary prey. From the perspective of primary prey and IG-prey the best defence against predation is to avoid detection and, if detected, to escape, or if escape is not a reasonable possibility to counterattack. For example, many studies show how primary parasitoids and hyperparasitoids deal with predator aggression in ant protected aphid colonies (Mackauer & Völkl, 1994; Völkl & Mackauer, 2000). The spectrum of specific defences range from chemical camouflage in *Lysiphlebus* species (Liepert & Dettner, 1996), to morphological adaptations in hyperparasitoids (Hübner & Völkl, 1996) and use of defensive glands. Moreover, when foraging for pine aphids, the aphid parasitoid *Pauesia sylvestris* showed behavioural responses to ant presence and concentrated foraging efforts in ant-attended aphid colonies on less valuable but safer pine-needle microhabitats (Völkl & Kroupa, 1997). Obviously, total avoidance of predator detection is almost impossible for parasitoids and usually conflicts with other interests, such as feeding, reproducing, and dispersing. Thus, an evolutionary trade-off between predator avoidance and other requirements must occur (Steiner & Pfeiffer 2007).

In the current study we investigated behavioural decisions the made by aphid parasitoids under the risk of predation. We focus on two koinobiotic endoparasitoids, *Aphidius colemani* and *Aphidius ervi*, which are specialised on aphids but parasitize a broad range of host species. In several regions they are temporally contiguous, parasitizing the same aphid species (ref). Their host ranges include more than 15 aphid species, among them several species of the genus *Aphis*, *Myzus* and *Rhopalosiphum* (Stary, 1995). It is known that both parasitoid species use semiochemicals to locate host infested plants (Powell *et al.*, 1998) and patch leaving decisions of *Aphidius* species are influenced by patch quality (Outreman *et al.*, 2005). Both species are time limited, i.e. they usually die before they have laid all their eggs (van Steenis *et al.*, 1996; Wajnberg, 2006). Because of their broad host range, both parasitoid species not only have to compete with conspecific and heterospecific parasitoids but also with many different predator species. The guild of aphidophagous predator species normally comprises several species of the Families Coccinellidae, Syrphidae, Chrysopidae, Anthomyiidae and Cecidomyiidae, as well as aphid honeydew collecting trophobiotic ant species. Among them are mandibulate species (Coccinellidae, Chrysopidae, Formicidae), as well as species with sucking mouthparts (Anthocoridae)

and mouthparts adapted for piercing aphids (Syrphidae, Cecidomyiidae). Each group has a specific foraging strategy and it is likely that they constitute different mortality risks to foraging parasitoid species. Moreover, both parasitoid species, as well as several of the mentioned aphidophagous predator species, are frequently found in the same habitat and released for aphid biological control in commercial greenhouses (ref).

In a series of manipulative experiments we investigated behavioural responses of both parasitoid species in direct confrontations with different aphidophagous predator species. Since direct and indirect effects, i.e. via the shared resource, are likely to be involved in interactions, we first studied the impact of the predator *C. carnea* on various levels and developed a standardised bioassay. In a second step we compared behavioural responses of both parasitoid species in confrontations with different predator species in the bioassay set-up, to investigate the plasticity in behavioural responses by parasitoids. We predict that female parasitoids would adapt their foraging strategy to minimize predation risk for themselves as well as for their offspring, with immediate departure from the patch if assessment of predation risk would be high. Being generalists with a broad host range we further predict that risk assessment by both parasitoid species should be similar.

### **Material and Methods**

All experiments were performed with the tritrophic system of sweet pepper, *Capsicum annuum* (c.v. Mazurka), as host plants, the green peach aphid, *M. persicae* Sulzer (Homoptera: Aphididae), as the herbivore, the parasitoids *A. ervi* and *A. colemani* as IG-prey and four different species of aphidophagous predator (*Coccinella septempunctata*-adult, *Chrysoperla carnea*-L3, *Episyrphus balteatus*-L3, *Myrmica rubra*-adult) as IG-predators. A stock colony of both parasitoid species was maintained under growth chamber conditions of 20 °C, 70% RH, and L:D (16:8) h with *M. persicae* on sweet pepper as their host.

The aphidophagous predator *C. carnea* was supplied by a commercial breeder (Neudorff Ltd., Emmerthal, Germany). The predators, *E. balteatus* and *C. septempunctata*, were reared at the Institute of Plant Diseases and Plant Protection, Leibniz University Hannover (Bargen *et al.*, 1998) under the same rearing conditions as parasitoids (see above). *M. rubra* (worker ant), was collected in June at a field site in front of the institute directly before the experiments took place. All predators were

fed *M. persicae* until experiments started. Before experimental use, the predators were standardized by a 4 h starving and 1 d old, mated parasitoids experienced the host plant complex for approximately 20h.

For all experiments *M. persicae* aphids of the same age cohort were used. To obtain the same aged aphids, 20 adult aphids were allowed to settle on a sweet pepper plant and reproduce for 24 h. Adults were then removed and offspring were allowed to grow for two additional days before use in the experiment (see below). Presence of aphids in the patch was necessary to keep natural enemies in the patch and motivate them for prey/host searching. Therefore, experiments without aphids in the patch were not conducted.

We predict that the behavioural decisions made by the parasitoids might be influenced by direct, i.e. physical contact, visual and olfactory stimuli emanating from the predator, as well as indirect effects, i.e. disturbance and killing of aphids by the predator. Therefore, we first investigated both direct and indirect effects on the parasitoids during confrontations with the predator *C. carnea* only. In a second set of experiments, the impact of five different predator species on both parasitoid species was investigated in a standardised bioassay set-up.

Overall impact of the predator *C. carnea* on behavioural decisions made by parasitoids  
The aim of this experiment was to compare behavioural responses of the parasitoids *A. colemani* and *A. ervi* in confrontations with larvae of the predator *C. carnea*. Aphids, parasitoids and predators were allowed to move freely on a sweet pepper plant in this set-up. Observed effects were a result of direct and indirect impacts of *C. carnea* on parasitoid species.

The behavioural interactions between individual adult female parasitoids and the predator *C. carnea* were tested on potted sweet pepper plants, each with a single pair of leaves. 3 h prior to the experiments 15 *M. persicae* (developmental stage L2-L3) were allowed to settle on the lower side of one of the top leaves of the plant. A clip cage was used to establish a single aphid colony per plant. At the beginning of the experiment an individual *C. carnea* larva (L3) was released on the upper side of the leaf with the aphid colony. To hinder predator from leaving the plant a ring of insect glue (Temmen-Insektenleim™) was placed on the stem of the experimental plant. One minute later either a single *A. colemani* or a single *A. ervi* female was released near the aphid colony. In the control treatments only female parasitoids were tested and in test treatments *C. carnea* – parasitoid combinations were tested and each replicated

ten times. Experiments ended either with the death of the parasitoid or its departure from the experimental plant. The behavioural responses of the parasitoid were recorded with a multiple video camera set-up described by Meyhöfer (2001) and later analysed with the Observer Video-Pro system (Noldus Technology, 1996). Since only 10 video cameras were available for simultaneous recordings, five replicates of the control treatment and five replicates of the predator treatment were recorded at the same time.

### *Direct effects of the predator C. carnea on behavioural decisions made by parasitoids in an bioassay set-up*

The first experiment demonstrated that the parasitoid behaviour was altered in presence of the predator, but the results did not allow conclusions on direct and indirect effects. Therefore, a bioassay set-up was developed where, movement of the prey and predator were standardized, i.e. immobilized aphids and simulated predator attacks. Nevertheless chemical and physical sensing was still possible, since prey was alive and predator was freshly killed.

For the bioassay set-up, 20 *M. persicae* L2 aphids were fixed in a regular pattern on the lower side of a sweet pepper leaf with an adhesive glue (Roll'n glue®, Pentel of America). *C. carnea* larva were attached to a thin wire and killed by dipping into liquid nitrogen immediately before experiments took place. Predator searching in the aphid colony was simulated by moving the dead *C. carnea* 5 times within five minutes slowly in front of the head of the female parasitoid. Because *M. persicae* colonies can be found on both sides of the sweet pepper leaf, behavioural response of the parasitoid were investigated first on intact plants on the lower side of a sweet pepper leaf and second on leaves turned upside down floating in a Petri dish filled with water. Leaf size in the later case was standardized to discs with a 4 cm diameter. Two treatments, parasitoids with and without predator movement, were each replicated 20 times with *A. colemani* and *A. ervi*, for each experimental set-up. Parasitoid females were released near the artificial aphid colony. Behavioural responses were recorded for 5 min on video tape (Meyhöfer 2001) and analysed later with the Observer Video-Pro system (Noldus Technology, 1996).

### *Behavioural responses of parasitoids to different aphidophagous predator species in a bioassay set-up*

In this set-up the behavioural response of *A. colemani* and *A. ervi* to different aphidophagous predator species was investigated. For direct comparison across species the experimental conditions were again standardised (see above). To investigate the species specific foraging behaviour, predator individuals were alive and allowed to move freely on the sweet pepper leaf with the aphid colony. As a host patch, 20 L2 aphids were fixed in a regular pattern with the adhesive glue on the lower side of sweet pepper leaf discs (see above). One minute after the introduction of the female parasitoid the predator was released and interactions were recorded during the following five minutes. Control treatments, without predators, and experimental treatments, with *E. balteatus*, *C. carnea*, *C. septempunctata* or the ant species *M. rubra*, were each replicated 10 times. To hinder predators from leaving the single leaf discs were floated in Petri dishes full with water. Parasitoid behaviour was recorded again with a multiple video camera set-up, described by Meyhöfer (2001), and later analysed with the Observer Video-Pro system (Noldus Technology, 1996).

### *Analysis of behavioural interactions*

To analyse the impact of predators on parasitoids, we compared all behaviours that the parasitoid performed in treatments without the predator (control) with behaviours in treatments with the predator present.

The different parasitoid behaviours recorded were: A) foraging activity on the plant (female present on the experimental plant but not on the leaf with the aphid colony); B) foraging activity on the leaf with the aphid colony: B.1) searching (parasitoid moves), B.2) pausing (periods the parasitoid spent motionless), B.3) attacking aphids (includes attack of aphids and ovipositor insertions, starts with antennation of the aphid and bending of the abdomen for ovipositor insertion), B.4) contact with predator (physical contact), and B.5) attacking predator (ovipositor attempts towards the predator); C) leaving the experimental arena by flying away.

The time the female parasitoid spent in and the frequency of the different behavioural states in the presence of the predator was compared with the time budget in absence of the predator (control). Statistical analysis was conducted using a series of non parametric Mann-Whitney U Tests. Comparison of direct behavioural responses to

predator contacts in the standardized bioassay set-up was conducted by a series of  $\chi^2$  tests. Additionally, transition probabilities between behavioural states were compared by log likelihood ratio tests.

## **Results**

### *Overall impact of the predator *C. carnea* on behavioural decisions made by parasitoids*

Aphids, parasitoid and predator were allowed to move freely on a sweet pepper plant and interact with each other during this experiment. The focus in the following results was on the foraging female parasitoid.

On average the parasitoid *A. colemani* spent 87.08 min ( $\pm$  49.02 SD) on the aphid-infested and predator free plants. In the presence of the predator the residence time decreased significantly to 24.01 min ( $\pm$  23.73 SD) (Mann-Whitney-U-Test, N = 10, U = 7, p = 0.001).

The behavioural analysis shows that the presence of the predator *C. carnea* influenced mainly the searching behaviour of the parasitoid *A. colemani*. While the frequency of its searching activity per minute on the leaf with the aphid patch increased two-fold, the average duration decreased two-fold (Fig. 1).

Direct contacts between the predator *C. carnea* and the parasitoid *A. colemani* occurred at a frequency of 0.042 times per minute and were of a short duration (1.62 s). In total the parasitoid *A. colemani* attempted to attack the predator with its ovipositor three times (average duration 4.8 s  $\pm$  2.91 SD). The parasitoid left the plant by flight in nine replicates and was killed by the predator in only a single replicate.

In contrast to *A. colemani*, the total time the parasitoid *A. ervi* spent on the experimental plant was not influenced by the presence of the predator, although the average residence time decreased from 44.75 min ( $\pm$  29.97 SD) to 27.90 min ( $\pm$  25.05 SD) (Mann-Whitney-U-Test, N = 10, U = 34, p = 0.226). Moreover, the different behaviours displayed by the parasitoid *A. ervi* were observed at similar frequencies and average durations (Fig. 1) in presence and absence of the predator, respectively. Parasitoid-predator contacts occurred 0.032 ( $\pm$  0.056 SD) times per minute and lasted 2.8 s ( $\pm$  3.83 SD). The predator killed none of the parasitoids. All *A. ervi* females left the plant by flight. In two replicates the parasitoid left the plant immediately after contact with *C. carnea*.

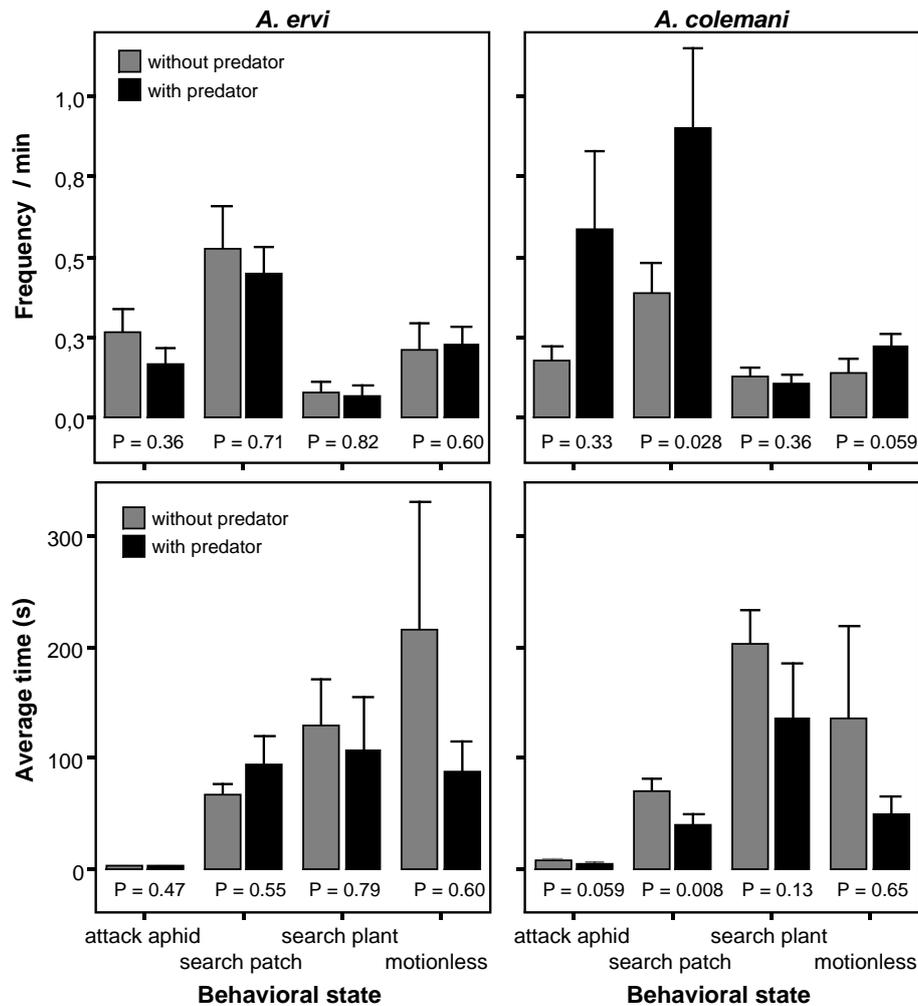


Figure 1. Average frequency ( $\pm$  SE) of, and average time ( $s \pm$  SE) spent in, different behavioural states by the aphid parasitoids *A. ervi* and *A. colemani*, in presence and in absence of the predator *C. carnea*, on sweet pepper plants infested with the aphid *M. persicae*. Data represent variation in means for individual parasitoid females (Mann-Whitney U-Test,  $n=10$  for each group of data).

#### *Direct effects of the predator C. carnea on behavioural decisions made by parasitoids in a bioassay set-up*

The first experiment showed that parasitoid behaviour was altered in the presence of the predator. Since predator and prey were allowed to move freely on the plant, predator activity and patch quality, i.e. number of hosts, changed continuously throughout the experiment. To exclude host movements and standardise predator - parasitoid contacts, aphids were immobilized and predator movement was simulated. Frequency and duration of most behavioural elements displayed by the parasitoid *A. colemani* were not influenced by contact with or the presence of the predator *C. carnea* (Fig. 2b, 2d).

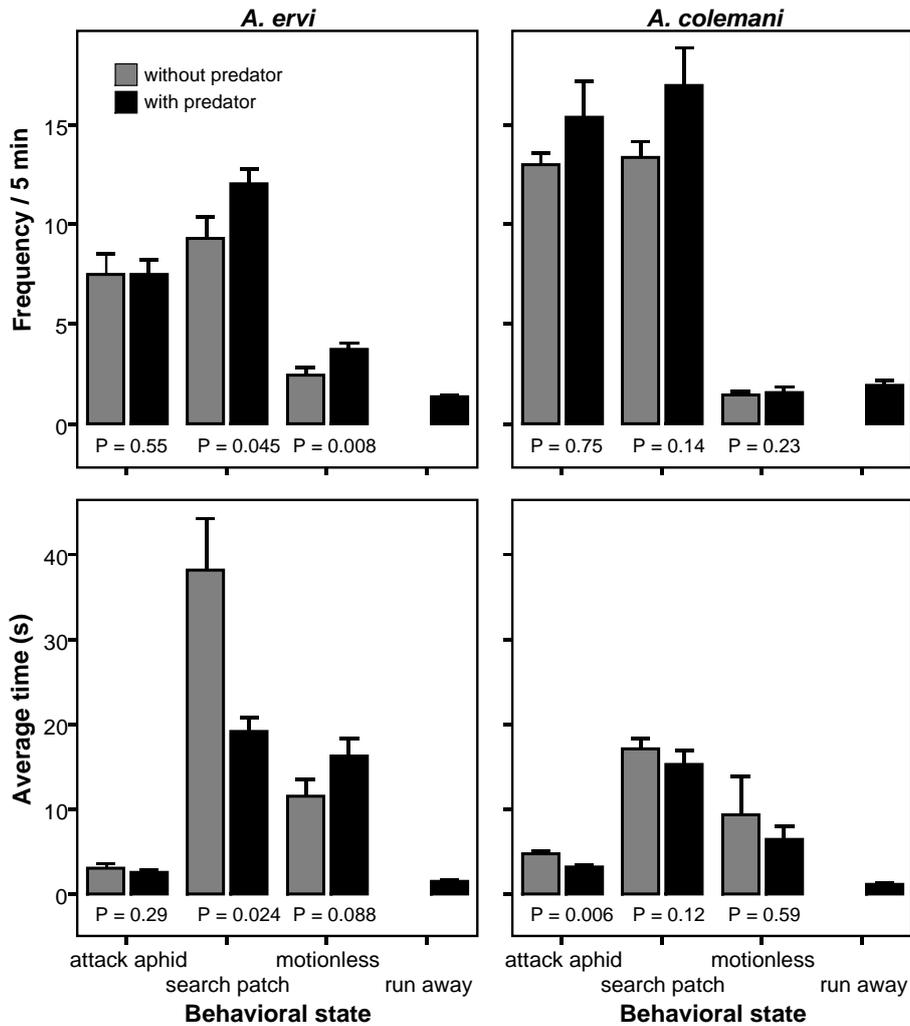


Figure 2. Average frequency ( $\pm$  SD) of, and average time (s  $\pm$  SD) spent in, different behavioural states by the aphid parasitoids *A. ervi* and *A. colemani*, in presence and in absence of the predator *C. carnea*, on sweet pepper leaf discs infested with the aphid *M. persicae*. In this standardized bioassay set-up aphids were fixed and predator parasitoid contacts were established artificially once every minute during a five minute time interval (Mann-Whitney U-Test, n=20 for each group of data).

Only the average time females spent on oviposition attempts was significantly reduced compared to the control treatment without predator activity (Fig. 2d). In contrast, *A. ervi* parasitoid females show in the presence of the predator more frequent and shorter host searching sequences than in the control treatment without the predator (Fig. 2a, 2c). Moreover, the frequency of the resting behaviour was significantly increased in the predator treatment (Fig. 2a).

Both parasitoid species displayed unique behaviours in direct response to predator contacts, which were not observed in the control treatments. They showed a fast but short running behaviour, flew off (short take offs) from the leaf or flew away from the leaf. Sixty seven percent of the predator approaches took place while the parasitoid species were searching for hosts, 17 % while attacking aphids and 15 % while being motionless. A behavioural change after confrontation with the predator was more likely

for the parasitoid *A. colemani* (81/87) than for *A. ervi* (78/95; Likelihood Ratio Test = 4.071,  $df = 1$ ,  $p = 0.044$ ).

The immediate behavioural response of searching parasitoids to artificial predator contacts was analysed by transition probabilities. For example, *A. colemani* parasitoids, engaged in host searching, switched to the behavioural state run away, i.e. escape from predator, with a probability of 0.24 (Fig. 3). Comparison of behavioural responses of the two parasitoid species indicated that transitions from host searching behaviour to the behavioural states run away (0.24 *A. colemani*; 0.28 *A. ervi*), fly away (0.08 *A. colemani*; 0.14 *A. ervi*) and fly off (0.05 *A. colemani*; 0.01 *A. ervi*) were observed at similar frequencies for both parasitoid species. In contrast, the transition probability from host searching behaviour to the behavioural state attack host increased more than two-fold for *A. colemani* (0.32) compared to *A. ervi* (0.14). When predator contacts took place while the parasitoid was searching for hosts, the probability to continue with host searching increased more than two-fold for *A. ervi* compared to *A. colemani* (Fig. 3).

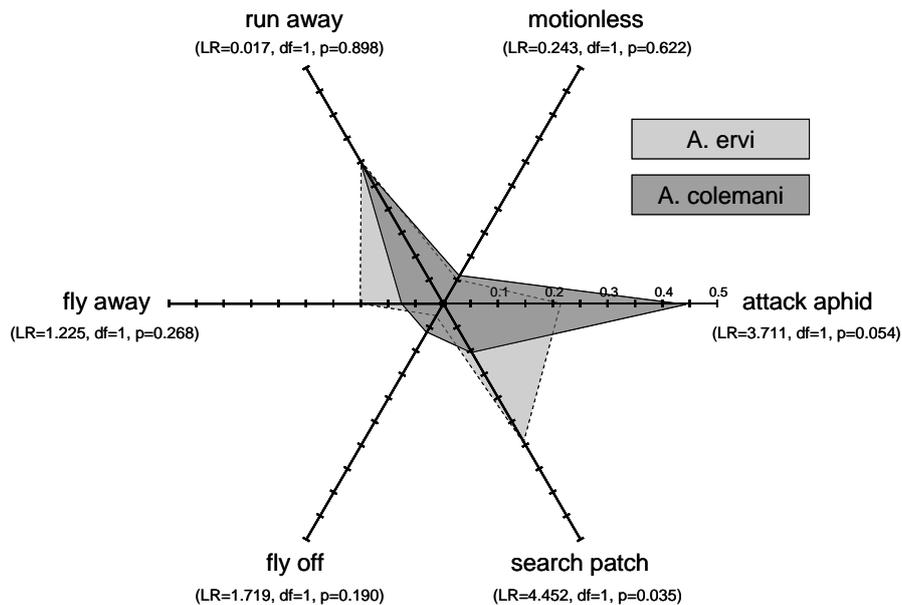


Figure 3. Behavioural responses of searching *A. colemani* and *A. ervi* female parasitoids to five consecutive predator contacts, in a bioassay set-up. Transition probabilities are calculated as the proportion of individual females responding to contacts either with continued foraging (attack aphid, search patch, motionless) or defensive behaviours (run away, fly off, fly away) (LR = Likelihood Ratio,  $n > 15$  for each group of data).

In contrast, if predator – parasitoid contacts took place on the lower side of the leaf, all parasitoid species flew off the plant in response to direct contact with the predator, compared to the control where only 10 % of the parasitoid females (4/40) left the plant spontaneously. The majority of the parasitoid females left the plant on the first or

second direct encounter with the predator (32/40), while only 8 parasitoid individuals remained for a longer period of time on the plant. *A. colemani* and *A. ervi* parasitoid females did not differ in their response (Likelihood Ratio = 0.70, df = 1, p = 0.792).

*Comparison of parasitoids behavioural responses to different aphidophagous species*

Behavioural responses of the parasitoids *A. colemani* and *A. ervi* to four different aphidophagous predator species was compared in the bioassay set-up. Host aphids were immobile and host density was constant in all experiments.

All of the tested predator species spent most of the experimental time performing prey searching activity. The proportion of the total time the different predator species spent performing searching activity ranged from 20 % (*C. carnea*) to 60 % (*M. rubra*). Predator species killed no more than 2 aphids during the 5 min experimental period. Contacts between antagonists were observed frequently and initiated either by the predator or the parasitoid (Tab. 1). Interactions between the predator species *C. carnea* or *C. septempunctata* and the parasitoid *A. colemani* were initiated by both antagonists at similar rates. In contrast, approximately 100 % of the contacts between *A. ervi* (parasitoid) & *C. carnea* (predator), *A. ervi* (parasitoid) & *E. balteatus* (predator), and *A. colemani* (parasitoid) & *E. balteatus* (predator) were made by the parasitoids while more than 70 % of the contacts between *A. ervi* (parasitoid) & *M. rubra* (predator), *A. ervi* (parasitoid) & *C. septempunctata* (predator) and *A. colemani* (parasitoid) & *M. rubra* (predator) were made by the predator. Both parasitoid species showed defensive behavioural responses in approximately 50 % of the contacts with the predator species *C. septempunctata* and *M. rubra*. In contrast, contacts between parasitoid and the predator species *C. carnea* or *E. balteatus* led to behavioural responses in less than 13 % of the total number of contacts (Tab. 1). Behavioural responses of the parasitoid species included fast movements away from the predator, flying off or flying away from the experimental arena. Overall departures of parasitoids from the experimental arena as a direct response to predator contact were observed in 12.5 % (10/80), and as an indirect response to predator contact in 11.25 % (9/80) of the replicates. The highest proportion (70 %, i.e. 7/10) of immediate departures from the experimental arena was observed for the parasitoid *A. ervi* in contacts with the predatory ant species *M. rubra* (Tab. 1).

Table 1. Number of contacts between different predator and parasitoid species during a 5 min interval. Both antagonists foraged freely on a patch with 25 aphid which were immobilized. Contacts were initiated either by the predator (Predator-Parasitoid Contact) or by the parasitoid (Parasitoid-Predator

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Contact) and frequently resulted in direct defensive behavioural responses of the parasitoid (Parasitoid Response to Contact). Response behaviour includes the defensive behavioural states run away, fly away, and fly off. The number of female parasitoids which left the patch by flight by choice (numbers in brackets) or in direct response to predator contacts (numbers without brackets) are displayed in the last column.

<i>Predator</i>	<i>Parasitoid</i>	Predator-Parasitoid Contact (%)	Parasitoid-Predator Contact (%)	Parasitoid Response to Contact (%)	Left patch by flight
<i>Chrysoperla carnea</i>	<i>A. colemani</i>	41.67 (5/12)	58.33 (7/12)	8.33 (1/12)	(1)
	<i>A. ervi</i>	0.00 (0/15)	100.00 (15/15)	13.33 (2/15)	(2)
<i>Episyrphus balteatus</i>	<i>A. colemani</i>	0.00 (0/17)	100.00 (17/17)	5.88 (1/17)	(1)
	<i>A. ervi</i>	6.25 (1/16)	93.75 (15/16)	6.25 (1/16)	(3)
<i>Coccinella septempunctata</i>	<i>A. colemani</i>	50.00 (8/16)	50.00 (8/16)	50.00 (8/16)	(2)
	<i>A. ervi</i>	77.78 (7/9)	22.22 (2/9)	66.67 (6/9)	2
<i>Myrmica rubra</i>	<i>A. colemani</i>	70.83 (17/24)	29.17 (7/24)	45.83 (11/24)	1
	<i>A. ervi</i>	87.50 (21/24)	12.50 (3/24)	62.50 (15/24)	7

In general, the frequency of and the time spent in the different behavioural states observed for foraging parasitoids was influenced by the presence of the predator. Overall, the impact of all predator species on the parasitoid species *A. colemani* and *A. ervi* was similar. For example, the parasitoids *A. colemani* and *A. ervi* spent significantly less time in the behavioural state “attack aphid” in the presence of the predator species *E. balteatus*, *C. septempunctata*, *C. carnea* and *M. rubra* compared to the control (Fig. 4c and 4d). In contrast, only the parasitoid species *A. colemani* reduced the time spent motionless in the presence of the predator species *E. balteatus* and *C. septempunctata* (Fig. 4d). Moreover, only the predator species *A. colemani* increased the frequency of the searching activity in presence of all predator species, compared to the control treatment without predator present (Fig. 4b).

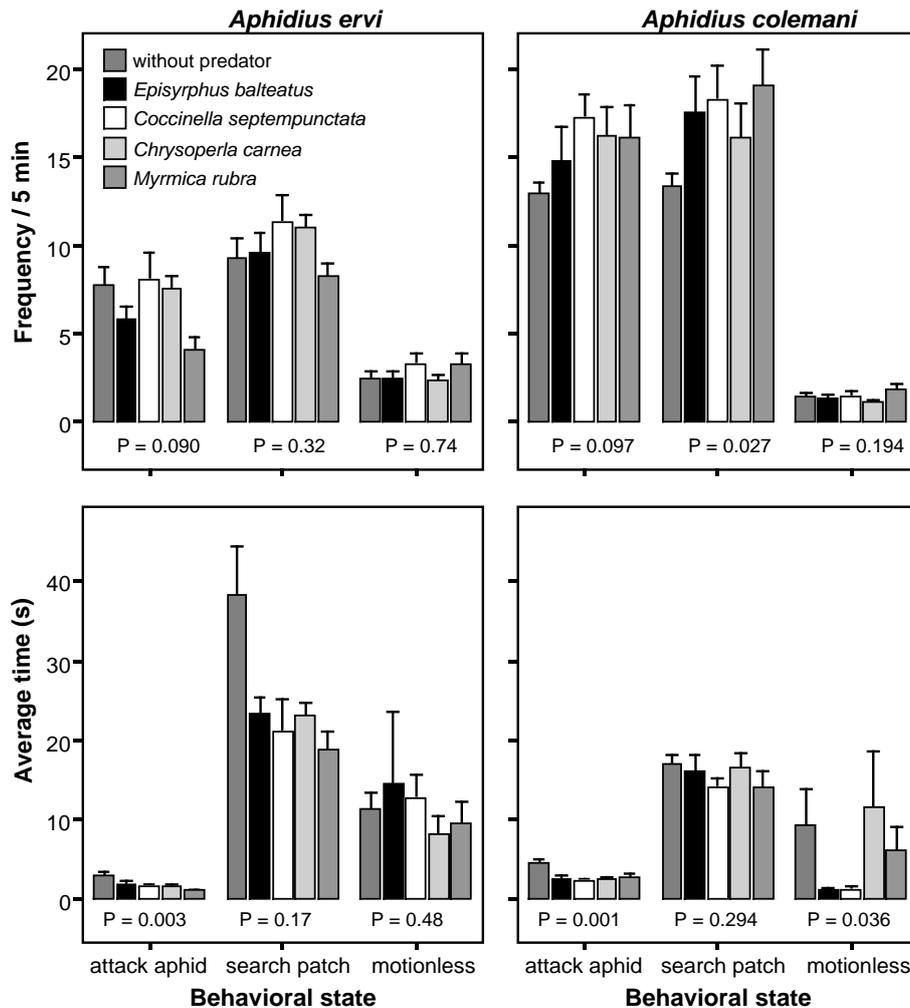


Figure 4. Average frequency ( $\pm$  SD) of, and average time ( $s \pm$  SD) spent in, different behavioural states by the aphid parasitoids *A. ervi* and *A. colemani*, in the presence and absence of different predator species on sweet pepper plants infested with the aphid *M. persicae*. In the standardized bioassay set-up aphids were fixed but predator moved freely on a single sweet pepper leaf. (\* indicate significant differences to the respective control treatment, Mann-Whitney U-Test,  $n=10$  for each group of data).

## Discussion

Optimal foraging theory predicts that prey individuals should avoid foraging in or near patches that are already exploited by natural enemies, to minimize the predation risk for themselves and their offspring (Lima & Dill, 1990). In general, behavioural decisions made by prey under the risk of predation include reduced feeding effort, increased anti-predator activity and/or activity shifts to less risky habitats. When parasitoid females, i.e. intraguild prey, encounter intraguild predators on a patch, they face a trade-off between local and travel mortality as well as offspring mortality risks (Weisser *et al.*, 1994). A few studies have so far indicated that adult aphid parasitoids may avoid patches with predators (Raymond *et al.*, 2000; Nakashima *et al.*, 2004; Shiojiri & Takabayashi, 2005) or at least reduce the patch residence time on plants where the predators are foraging (Taylor *et al.*, 1998). However, it remains still unclear whether

the predators affect parasitoid females directly, i.e. via physical contacts, visual and olfactory stimuli emanating from the predator, or indirectly, i.e. via disturbance and killing of aphids by the predator. Furthermore, our previous data (Meyhöfer & Klug, 2002) indicated that the aphid parasitoid *Lysiphlebus fabarum* is not affected at all by the presence of aphidophagous predators and was frequently killed in direct confrontations with the predator species *C. carnea*, *E. balteatus* and *C. septempunctata*. Although this result can be partly explained by the close relationship between *L. fabarum* and ant attendant aphid colonies (Liepert & Dettner, 1996; Völkl, 1994; Meyhöfer & Klug, 2002), it raised the question whether other parasitoid species might have evolved behavioural strategies to cope with predator aggression and if predators influence female parasitoids behavioural decisions when and where to lay their eggs.

In the following we first discuss behavioural responses of the two parasitoid species in the presence of *C. carnea* as intraguild-predator (IG-predator) with a focus on the impact of host and predator mobility. In the second part we discuss and compare the impact of different aphidophagous predators (IG-predator) on behavioural decisions made by the parasitoid species *A. ervi* and *A. colemani*. Finally, we interpret our data in the framework of optimal foraging behaviour and behavioural decisions made by parasitoids under the risk of predation.

### *Direct or indirect effects of predators on parasitoid foraging: what is more important?*

Our results show that both parasitoid species are affected by the presence *C. carnea* predatory larvae on the plant. In all predator treatments females left the plant in flight as a result of direct encounter with the predator. Therefore, patch residence times decreased for the parasitoid species *A. colemani* by 37 % and for *A. ervi* by 71 %, compared to treatments where predators were absent. Moreover, time allocation to different foraging activities shifted for *A. colemani* to more frequent but shorter searching activities, while time allocation was similar for *A. ervi* in presence and absence of *C. carnea*.

These results are similar to those in which coccinellids were the IG-predator (Taylor *et al.*, 1998). In their experiments, *A. ervi* females showed an approx. 50 % reduction in the patch residence time in the presence of *C. septempunctata*, regardless of whether only predator larval tracks, coccinellid larvae or adults were present. The followup

studies showed that this effect can be attributed to coccinellid larvae or adult footprints with an activity lasting for less than 24 h (Nakashima *et al.*, 2004).

Additionally, the results of the standardized bioassay set-up in the current study indicate that *A. ervi* and *A. colemani* were affected in a different way by physical or olfactory signals from the predator. While *A. colemani* only reduced the time spent performing oviposition attempts, *A. ervi* showed increased the frequency and time spent motionless, reduced frequency but prolonged searching behaviour and a constant number of oviposition attempts in presence of *C. carnea*. Since the number of hosts available, host mobility and frequency of predator contacts was constant in the standardized bioassay set-up, the observed behaviour can be attributed to the predator presence and contact, indicating that *A. ervi* was more sensitive to predator encounters than *A. colemani*. Hence, it is likely that the reduced patch residence time of the parasitoid *A. colemani* in the first experiment, i.e. without movement constraints of aphids (see above), was more affected by changes in host availability than predator activity. While the parasitoid *A. ervi* was directly affected by the predator activity and patch residence time decreased only slightly.

Behavioural strategies to escape from predator aggression were similar for both parasitoid species, but depended on the location where interference took place. If encounters between predator and parasitoid took place on the lower side of a leaf, female parasitoids left the plant immediately in flight. In contrast, the propensity to escape by flight was strongly reduced if encounters between predator and parasitoid took place while foraging on top of the leaves. Running away or short take offs from the leaf were the preferred strategy to increase the distance to the attacking *C. carnea* predator. These defensive behaviours were efficient enough that adults were, in most cases, not killed by the predator. Since reactive distance to aphids was estimated at 3-4 mm (Le Ralec *et al.*, 2005), it is likely that perception of predators was at similar distances. At least partly this short reactive distance would explain the frequent predator approaches by parasitoids.

Nevertheless, most females were not influenced by direct encounters at all and continued host foraging and oviposition activity, even in the close vicinity of predators. This unexpected result indicates that both studied parasitoid species, i.e. *A. colemani* and *A. ervi*, ignore the imminent risk of predation for their offspring. Since most parasitoid species are time limited, they usually die before they have laid all their eggs (Wajnberg, 2006). Moreover, motivation of female parasitoids to host foraging was high

during the experiments, because they were well fed and most likely had a high egg load. Therefore, it might be possible that a motivational conflict exists for adult parasitoids. In this situation female parasitoids might favour laying eggs, even if the predation risk for offspring is high, instead of leaving the encountered patch, missing opportunities of parasitizing hosts and searching for low risk patches. Over evolutionary time travel mortality between patches might be an additional factor that facilitates the reduced propensity to leave an aphid patch that is exploited by predators. Additional experiments are necessary that take different physiological states into account to completely understand parasitoid behaviour. But at least for *A. colemani* other studies support our results that host plant choice does not depend on predator presence (Bilu *et al.*, 2006)

### *Behavioural responses of adult parasitoids to different predator species*

Impacts of other mobile predator species on parasitoid behaviour were similar to the results obtained with standardized predator movement (see above). Both parasitoid species significantly reduced the time spent for oviposition attempts (and sometimes increased the frequency of oviposition attempts) but also show large differences in behavioural responses to the different aphidophagous predator species. The observed differences cannot simply be attributed to the mobility of the different predator species. Parasitoids normally attack aphids for oviposition, but behavioural responses to non-hosts, i.e. intraguild predators, might give some indication how parasitoids sense and classify aggressive opponents.

Although *E. balteatus* larvae are known to be aphidophagous predators with overall low activity level, they spent most of the experimental time searching for prey. Both parasitoid species encountered *E. balteatus* larvae frequently but did not show any defensive behaviour. In contrast, the most agile antagonist tested was the predatory ant species *M. rubra*. Primarily ants contacted the parasitoid species, which displayed defensive behavioural responses in 50 % of the confrontations. Mobility of *C. carnea* and *C. septempunctata* larvae was in-between these two extremes. The propensity to display defensive behaviour in direct confrontations with the predator *C. carnea* was low for both parasitoid species, although the parasitoid *A. colemani* and *C. carnea* contacted each other at equal proportions and the parasitoid *A. ervi* initiated all contacts to *C. carnea*. In contrast, defensive behaviour was identified in 50 % of all confrontations between parasitoid females and the predator species

*C. septempunctata*. Similarly, to experiments with *C. carnea* as IG-predator, *A. colemani* and *C. septempunctata* contacted each other at equal proportions, but confrontation between *A. ervi* and *C. septempunctata* were primarily initiated by *C. septempunctata*.

At the moment we can only speculate on how parasitoids might sense IG predators and vice versa when foraging in the same patch. Nevertheless, a few general patterns seem to emerge and will be investigated in future: (1) *E. balteatus* larvae are not perceived as threat but as potential host, indicated by frequent approaches by both parasitoid species; (2) *C. carnea* larvae are not perceived as threat but as host, indicated by frequent approaches by *A. ervi* and to a lesser extent by *A. colemani*; (3) *M. rubra* ant workers are perceived as potential host, indicated by frequent approaches, but at short distances parasitoids realise a threat and show defensive behaviour to increase the distance; (4) *C. septempunctata* are perceived as threat by both parasitoid species (frequent defensive behaviour), but only *A. ervi* avoids contacts with this predator species.

Although studies on behavioural response by parasitoids to predation risk are scarce the few available studies partly support our hypothesis. Takizawa *et al.* (2000) investigated the oviposition behaviour of *A. colemani* in the presence of three different coccinellid species and stated that females have the ability to recognize aphid patches which contained *C. septempunctata* larva or chemical tracks left by *C. septempunctata* larva. Taylor *et al.* (1998) showed similar results in a study with the aphid parasitoid *A. ervi*. In patches where the predator *C. septempunctata* was present or recently present, the female parasitoid reduced patch residence time and number of contacts with hosts. Finally, results from Bilu *et al.* (2006) showed that the coccinellid predator *C. undecimpunctata* did not influence host choice by *A. colemani*, even when predator free plants were offered nearby. Female parasitoids chose preferred host-plant combinations, regardless of predator presence. All of these studies do not explicitly show the nature of stimuli that are perceived by the parasitoids, but indicate that chemical cues most likely play a major role.

In contrast to the parasitoid *L. fabarum* (Meyhöfer & Klug, 2002), *A. colemani* and *A. ervi* females were able to defend themselves efficiently in direct confrontations with all tested predator species. Only in two confrontations with the predator was the female parasitoid killed by the predator. The defensive behaviours displayed included, on the

lower side of the leaf, primarily escape by flight, and on the upper side of the leaf, short take offs from the leaf and running away.

We hypothesize that population dynamics of the two aphid parasitoid species *A. colemani* and *A. ervi* are less affected by adults on patch foraging decisions in confrontations with predator species. Both species were able to successfully escape predatory aggressions from all tested aphidophagous predator species. The low propensity of female parasitoid species to leave a patch where host resources are exploited by predators was an unexpected result.

On the one hand this result might be attributed to high adult travel mortality risks and on the other hand to the unpredictability of finding host patches in the habitat not exploited by predators. In conclusion, female parasitoids continued to attack and parasitize aphids even in the presence of aggressive predator species. Parasitoid females underestimate the risk of predation for their offspring. Parasitoid larvae developing inside the aphid, have to completely rely on efficient defence strategies of its host in confrontation with intraguild predators. Additionally, they might manipulate the host behaviour for their own advantage and increase overall survival probability. Nevertheless, considering intraguild predation as one factor influencing population dynamics of aphid parasitoids it is likely that predation within the aphid antagonist guild predominantly acts on immature parasitoids, i.e. parasitized aphids and aphid mummies, which are readily exploited by different predators.

### **References**

- Abrams, P.A. (2000) The Evolution of Predator-Prey Interactions: Theory and Evidence. *Annual Review of Ecology and Systematics*, **31**, 79-105
- Bellows, T.S. & Fisher T.W. (1999) Handbook of biological control. San Diego, London, Academic Press.
- Bilu, E. & Coll, M. (2007) The importance of intraguild interactions to the combined effect of a parasitoid and a predator on aphid population suppression. *BioControl*, **52**,753–763.
- Bilu, E., Hopper, K.R., Coll, M. (2006) Host choice by *Aphidius colemani*: effects of plants, plant-aphid combinations and the presence of intra-guild predators. *Ecological Entomology*, **31**, 331-336.
- Brodeur, J. & Rosenheim, J.A. (2000) Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata*, **97**, 93-108.
- Colfer, R.G. & Rosenheim, J.A. (2001) Predation on immature parasitoids and its impact on aphid suppression. *Oecologia*, **126**, 292-304.
- Godfray, H.C.F. (1994) Parasitoids. Behavioural and Evolutionary Ecology. Princeton University Press, Chichester, West Sussex.
- Heimpel, G.E., Rosenheim, J.A. & Mangel, M. (1997) Predation on adult *Aphytis* parasitoids in the field. *Oecologia*, **110**, 346-352.
- Hübner, G. & Völkl, W. (1996) Behavioural strategies of aphid hyperparasitoids to escape aggression by honeydew-collecting ants. *Journal of Insect Behaviour*, **9**, 143-157.

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- Jervis, M.A. (2005) Insects as natural enemies: a practical perspective. Dordrecht, Springer.
- Liepert, C. & Dettner, K. (1996) Role of cuticular hydrocarbons of aphid parasitoids in their relationship to aphid-attending ants. *Journal of Chemical Ecology*, **22**, 695-707.
- Le Ralec, A., Curty, C. & Wajinberg, E. (2005) Inter-specific variation in the reactive distance of different aphid-parasitoid associations: analysis from automatic tracking of the walking path. *Applied Entomology and Zoology*, **40**, 413-420.
- Lima, S.L. & Dill, L.M. (1990) Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.
- Lima, S.L. (1998a) Non-lethal effects in ecology of predator-prey interactions. *BioScience*, **48**, 25-34.
- Lima, S.L. (1998b) Stress and decision-making under the risk of predation: recent developments from behavioural, reproductive, and ecological perspectives. *Advances in the Study of Behaviour*, **27**, 215-290.
- Mackauer, M. & Völkl, W. (1993) Regulation of aphid populations by aphid wasps: Does parasitoid foraging behaviour or hyperparasitism limit impact? *Oecologia*, **94**, 339-350.
- Meyhöfer, R. & Hindayana, D. (2000) Effects of intraguild predation on aphid parasitoid survival. *Entomologia Experimentalis et Applicata*, **97**, 115-122.
- Meyhöfer, R. (2001) Intraguild predation by aphidophagous predators on parasitised aphids: the use of multiple video cameras. *Entomologia Experimentalis et Applicata*, **100**, 77-87.
- Meyhöfer, R. & Klug, T. (2002) Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* Marshall. Hym., Aphidiidae.: Mortality risks and behavioural decisions made under the risk of predation. *Biological Control*, **25**, 239-248.
- Nakashima, Y., Birkett, M.A., Pye, B.J., Pickett, J.A. & Powell, W. (2004) The role of semiochemicals in the avoidance of the seven-spot ladybird, *Coccinella septempunctata*, by the aphid parasitoid, *Aphidius ervi*. *Journal of Chemical Ecology*, **306**, 1103-1116.
- Outreman, Y., Le Ralec, A., Wajinberg, E. & Pierre, J.S. (2005) Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. *Behavioural Ecology and Sociobiology*, **58**, 208-217.
- Polis, G.A., Myers, C.A. & Holt, R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review Entomology*, **20**, 297-330.
- Polis, G.A. & Holt, R.D. (1992) Intraguild predation: The dynamics of complex trophic interactions. *TREE*, **7**, 151-154.
- Price, P.W. (1997) Insect ecology. New York, John Wiley & Sons.
- Raymond, B., Darby, A.C. & Douglas, A.E. (2000) Intraguild predators and the spatial distribution of a parasitoid. *Oecologia*, **124**, 367-372.
- Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J. & Jaffee, B.A. (1995) Intraguild predation among biological-control agents: Theory and evidence. *Biological Control*, **5**, 303-335.
- Rosenheim, J.A. (1998) Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology*, **43**, 421-447
- Rosenheim, J.A. (2004) Top predators constrain the habitat selection games played by intermediate predators and their prey. *Israel Journal of Zoology*, **502**, 129-138.
- Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997) Behaviourally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, **78**, 1388-1399.
- Shiojiri, K. & Takabayashi, J. (2005) Parasitoid preference for host-infested plants is affected by the risk of intraguild predation. *Journal of Insect Behaviour*, **184**, 567-576.
- Steiner, U.K. & Pfeiffer, T. (2007) Optimizing time and resource allocation trade-offs for investment into morphological and behavioural defence. *American Naturalist*, **169**, 118-129.
- Stary, P. (1973) A review of the *Aphidius* species (Hymenoptera: Aphidiidae) of Europe. *Annales Zoologicae Botanicae*, **84**, 1-85.

## Chapter 05

- Takizawa, T., Yasuda, H. & Agarwala, B.K. (2000). Effect of three species of predatory ladybirds on oviposition of aphid parasitoids. *Entomological Science*, **3**, 465-469.
- Taylor, A.J., Müller, C.B. & Godfray, H.C.J. (1998) Effect of aphid predators on oviposition behaviour of aphid parasitoids. *Journal of Insect Behaviour*, **11**, 297-302.
- Van Steenis, M.J., El Khawass Kamh, Hemerik, L. & van Lenteren J.C. (1996) Time allocation of the parasitoid *Aphidius colemani* (Hymenoptera: Aphidiidae) foraging for *Aphis gossypii* (Homoptera: Aphididae) on cucumber leaves. *Journal of Insect Behaviour*, **9**, 283-295.
- Wajnberg, E. (2006) Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioural mechanisms. *Behavioural Ecology and Sociobiology*, **60**, 589-611.
- Werner, E.E. (1992) Individual Behaviour and Higher-Order Species Interactions. *American Naturalist*, **140** (Supplement),5-32.
- Van Alphen, J.J.M. & Jervis, M.A. (1996) Foraging behaviour. In: *Insect Natural Enemies* (Ed. By Jervis, M. A. & Kidd, N.), pp. 1-62. Chapman & Hall, London.
- Völkl, W. (1994) The Effect of Ant-Attendance on the Foraging Behaviour of the Aphid Parasitoid *Lysiphlebus cardui*. *Oikos*, **70**, 149-155.
- Völkl, W. & Kroupa, A.S. (1997) Effects of adult mortality risks on parasitoid foraging tactics. *Animal Behaviour*, **54**, 349-359.
- Völkl, W. & Mackauer, M. (2000) Oviposition behaviour of aphidiine wasps Hymenoptera: Braconidae, Aphidiinae.: morphological adaptations and evolutionary trends. *The Canadian Entomologist*, **132**, 197-212.
- Weisser, W.W., Houston, A.I. & Völkl, W. (1994) Foraging Strategies in Solitary Parasitoids: The Trade-Off Between Female and Offspring Mortality Risks. *Evolutionary Ecology*, **8**,587-597.
- Wissinger, S. & McGrady, Y.J. (1993) Intraguild predation and competition between larval dragonflies – direct and indirect effects on shared prey. *Ecology*, **74**, 207-218.

## Impact of aphid population density on parasitoid and predator intraguild predation

(based on Meyhöfer R., Klug T., unpublished)

### **Abstract**

In contrast to intraguild predation among predatory species, aphid parasitoids have as IG prey the disadvantage that they are inferior to any kind of aggression by IG predators. Besides morphological and behavioural adaptations parasitoids might profit from dilution effects among primary prey, also named alternative prey or extraguild prey. In the current study we investigated the impact of different aphid densities on survival of aphids parasitised by *Aphidius colemani* Viereck (Hymenoptera: Braconidae). Parasitised aphids and mummified aphids were exposed to predation by the aphidophagous predator *Chrysoperla carnea* Steph. (Neuroptera, Chrysopidae). Potted plants infested with *Myzus persicae* Sulzer (Homoptera, Aphididae) aphids served as experimental units. The results show that with an increasing aphid population density the survival probability of the parasitoid increased substantially. Compared to the low aphid density treatment average survival time was increased at least six fold at high aphid density. Only at high population density more than 50 % of the parasitoids were able to complete their developmental stage. Compared to parasitised aphids the average survival time of aphid mummies was increased 0.5 times at low and intermediate aphid densities. In contrast survival of parasitised aphids and mummified aphids was similar at high aphid densities. In general mummified aphids located in two different aggregations on the same plant were at similar risks of predation. Analysis of the data by Cox proportional hazard models with aphid density and parasitoid developmental stage as covariates shows significant impacts of single terms and interaction term on parasitoid survival. Increasing aphid densities reduced mortality by 4 % but aphid mummies were at a 49 % lower risk of predation than parasitised aphids. Natural selection should therefore favour fast larval development of parasitoids and pupation, i.e. mummification, in large aphid colonies.

## ***Introduction***

During foraging activities animals have to deal with predation risks and are expected to weigh the risk of predation against various benefits (Lima and Dill 1990). Extensive research exists on behavioural and evolutionary responses of primary prey or hosts to predators and parasites (Godfray 1994, Quicke 1997) but less is known about the relevance of predation risks to species on higher trophic levels (Rosenheim 1998). Although natural enemies belong to higher trophic levels they have to deal with similar mortality risks than individuals on lower trophic levels. For example in natural communities intraguild predation (IGP), which is defined as trophic interaction among antagonists competing for the same resource, was recently identified as important factor shaping population dynamics and foodweb structures (Polis and Holt 1992, Rosenheim 1998). On condition that competitors are frequently prey to IG-predators it is likely that natural selection favoured individuals which efficiently minimize predation risks. Behavioural strategies to do so include avoidance of predators, direct defence, and/or counterattack (Evans and Schmidt 1990). Additionally the outcome of IGP between two predatory species depends mainly on the size and the degree of feeding specificity of the protagonists (Werner and Gilliam 1984). In contrast in confrontations between parasitoid and predator the parasitoid is always inferior (Brodeur and Rosenheim 2000). Avoidance of predation is therefore of primary importance for adult female parasitoids to reduce mortality risks not only for themselves but also for its offspring. A few studies indicate that parasitoids avoid foraging for hosts in habitats where predators are already present (Taylor et al. 1998, Raymond et al. 2000, Takizawa et al. 2000). But if predators enter host patches that are at the same time exploited by parasitoids, female parasitoids rely on efficient escape strategies to be not victim to the predator but continue foraging for hosts (Meyhöfer and Klug, submitted). In consequence female parasitoids leave their own offspring in a host patch with extremely high mortality risk (Meyhöfer and Klug submitted).

Parasitoid offspring often develop as endoparasitoid inside the host. Species with a koinobiontic lifestyle allow the host to develop and grow. Immediately before pupation the parasitoid larvae kills the host. In most cases silky cocoons and/or shelters protect the pupa but nevertheless it has to remain immobile for a longer period of time at one place, i.e. developmental time pupa to adult emergence. Larval developmental stages of the parasitoid have to rely on host defence strategies in confrontation with predators and/or alter host behaviour to reduce predation risks (Brodeur and Rosenheim 2000).

Additionally the incidence of IGP between parasitoid and predator depends on the probability of encounter of the protagonists and whether parasitised individuals are detected as prey. This is especially important if the primary prey is gregarious and live in colonies (Meyhöfer and Hindayana 2000). Extra- and intraguild population densities are in the latter case important factors that influence the probability of IGP between parasitoid and predator (Lucas et al. 1998).

In the current study we investigated the effect of different extraguild prey densities on survival of different developmental stages of aphid parasitoids, i.e. mobile parasitised and immobile mummified aphids. Both developmental stages can be IG prey to different aphidophagous predator species (Meyhöfer 2001). Moreover several studies indicate that parasitised and mummified aphids are prey to most predators at equal proportions (Colfer and Rosenheim 2001) while other authors state that parasitised or mummified aphids are more frequently prey to coccinellid or chrysopid predators (Meyhöfer and Klug 2002). The entire study was done with a tritrophic system consisting of extreme polyphagous species. The predator *Chrysoperla carnea* preys on wide range of aphids and the aphid parasitoid *Aphidius colemani* accepts a wide range of aphid species as host. Moreover the aphid *Myzus persicae* attacks a broad range of host plants.

We hypothesize that extraguild prey will have a differential effect on survival of parasitised and mummified aphids: (1) at low and decreasing extraguild prey densities we expect that parasitoid survival is short and that both developmental stages are at similar predation risk; (2) at intermediate and more or less constant extraguild prey densities we expect that parasitoid survival is high and that mobile developmental stages are at lower predation risk than immobile; (3) at high and increasing population densities we expect that parasitoids face no risk of predation at all.

### **Materials and Methods**

The entire experiments were performed with the tritrophic system of sweet pepper, *Capsicum annuum* (c.v. Mazurka), as host plants, peach aphid, *M. persicae*, as herbivore, the parasitoid *A. colemani* as IG-prey and *C. carnea* as IG-predator. A stock colony of the parasitoid species was maintained under growth chamber conditions of 20 °C, 70% RH, and L:D (16:8) h with *M. persicae* as host. The aphidophagous predator *C. carnea* was supplied by a commercial breeder (Neudorff Ltd., Emmerthal, Germany). Predators were fed the peach aphid, *M. persicae* (Sulzer)

(Homoptera: Aphididae), until the L3 stage was reached and experiments were performed. Before experimental use, the predators were standardized by a 4h starving. For all experiments we used *M. persicae* aphids of the same age cohort. To obtain same age aphids, 20 adult aphids were allowed to settle on a sweet pepper leaf and reproduce for 24 h. To obtain three different initial aphid densities 20 offspring were transferred to each of 45 sweet pepper plants. For the low prey density treatment 15 plants were used immediately in an experiment, while for the intermediate prey density treatment the aphid population on 15 plants was allowed to grow for additional 5d (mean population density  $128 \pm 26$  aphids per plant). The remaining 15 plants were used for the high prey density treatment at day ten after infestation with an average aphid population density of  $455 \pm 40$  aphids per plant.

Parasitoid species were introduced as IG-prey to each plant of the three treatments as 10 parasitized (4 days after parasitism) and 10 mummified aphid (9 days after parasitism) individuals. Mobile parasitised aphids were marked 2h before the experiment started by a white colour dot on its abdomen (edding780 paint marker, 0.8 mm, Edding AG, Ahrensburg, Germany) and released randomly on the plant. Aphid mummies were attached to the lower side of two different leaves in colonies of five individuals with a water-based glue (Pentel, Roll'n Glue). Experiments started with the introduction of individual *Chrysopa carnea* L3 larva as IG-Predator.

The number of remaining prey (aphids, parasitized aphids, mummified aphids) was counted at time interval 4 (LD), 13, 24, 37, 48, 58, 66, 79, 96 (MD, HD), 128 (HD), 144 (HD), 168 (HD) hours. Experiments were terminated if all prey were killed or all parasitoids hatched from the mummies. Individual survival times for parasitized and mummified aphids were calculated and analysed by Kaplan-Meier survival curves and compared by Log-Rank tests (Kleinbaum, 1996). To analyse the impact of different covariates Cox proportional hazard models were used. Differences in aphid population density among treatments were analysed by repeated measurement ANOVA.

### **Results**

Survival of parasitized and mummified aphids in presence of the predator *C. carnea* was tested at three different densities of alternative prey. Population development of extraguild prey and individual survival times of ten parasitised aphids and ten mummified aphids was recorded and analysed by survival analysis. In all replicates

the predatory *C. carnea* larva was recovered at the end of the experiment and never was observed to pupate during the trials.

*Survival of parasitoids at low densities of alternative prey*

Start population for the low prey density treatment was 20 aphids per plant. Aphid population density decreased rapidly and reached 24h after introduction of the predator 4.7 ( $\pm 1.4$  SE) aphids per plant (Fig. 1).

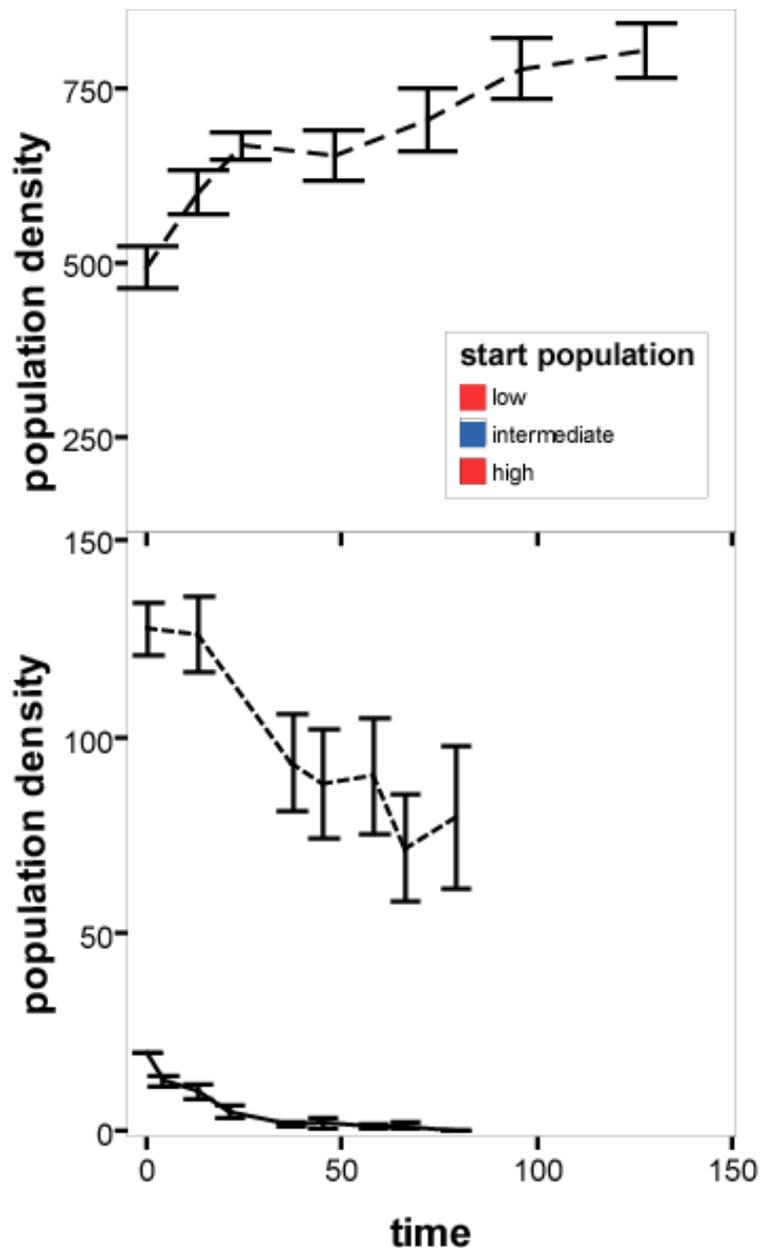


Fig. 1 Aphid population development in three different treatments tested in the current study. Start population for the low aphid density treatment was 20 aphids, intermediate density treatment 128 ( $\pm 26$  SD) aphids and for the high density treatment 494 ( $\pm 108$  SD) aphids. The figure shows average aphid densities ( $\pm$  SE) of 10 replicates per treatment.

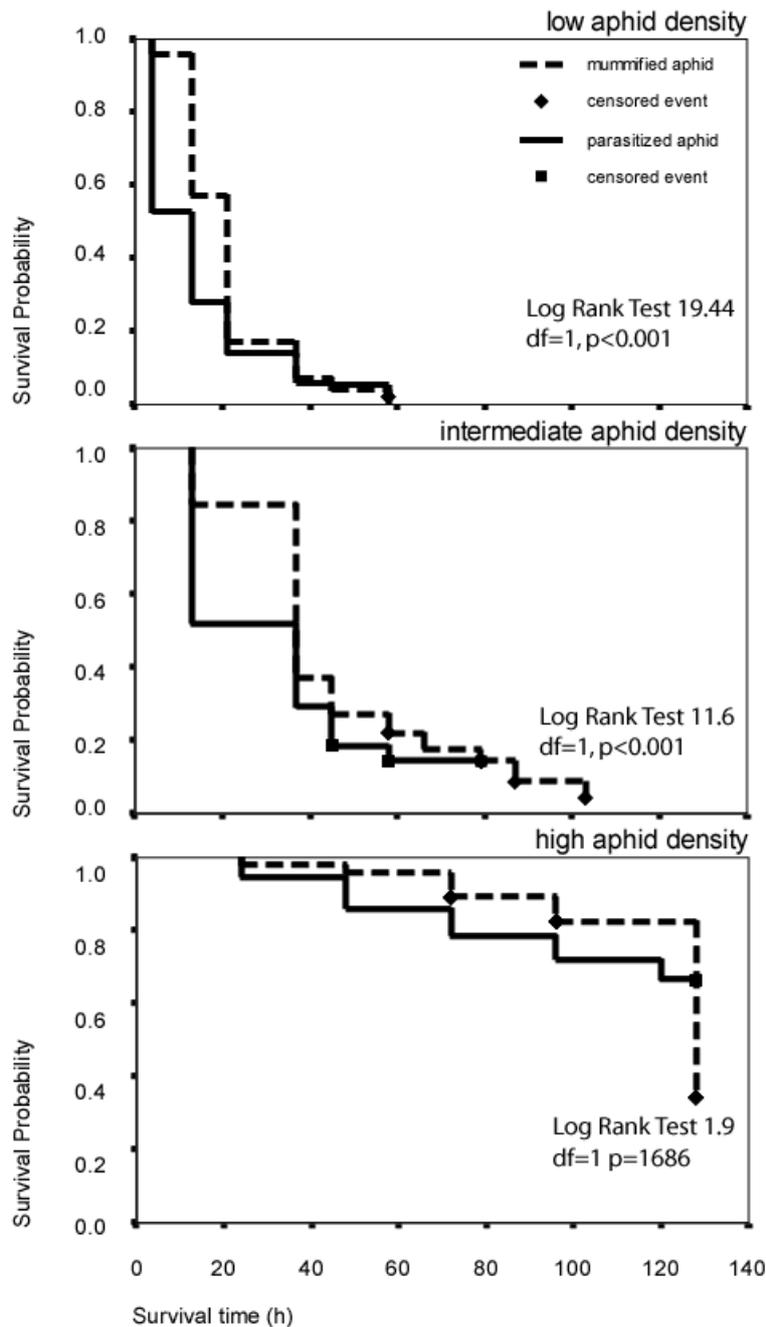


Fig. 2 Kaplan Meier estimates of survival probabilities ( $S(t)$ ) of parasitised aphids and mummified aphids in treatments with different densities of alternative prey, i.e. unparasitised aphids. *C. carnea* was introduced as IG predator into the microcosms. Experiments were replicated 15 times for each treatment. Survival probabilities were compared by log-rank tests.

The predator killed during the first experimental day more than 80 % of the introduced parasitized and mummified aphids (Fig. 2). None of the parasitized or mummified aphids survived more than 66h and only a single parasitoid emerged 1.9 from a mummy. Overall the 50 % survival probability of parasitized aphids was 14.39 h ( $\pm 1.18$  SD; 95 % CI 12.09 – 16.70 h) while the 50 % survival probability of mummified aphids was significantly prolonged to 21.11 h ( $\pm 0.95$  SD; 95 % CI 19.24 - 22,98 h) (Log-Rank-Test,  $\chi^2 = 19.44$ , FG = 1,  $p < 0.001$ ) (Fig. 3).

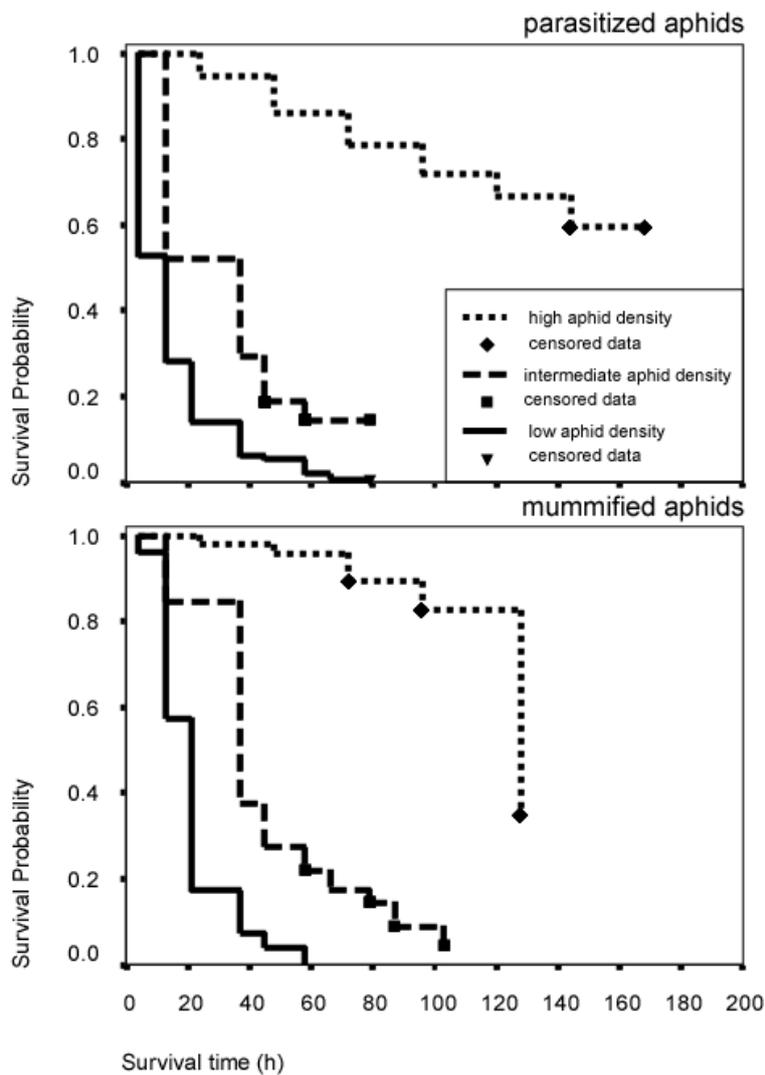


Fig. 3 Kaplan Meier estimates of survival probabilities ( $S(t)$ ) of parasitised aphids in treatments with different densities of alternative prey (upper graph) and mummified aphids in treatments with different of alternative prey (lower graph). *C. carnea* was introduced as IG predator into the microcosms. Experiments were replicated 15 times for each treatment.

#### *Survival of parasitoids at intermediate densities of alternative prey*

The *M. persicae* populations started in the intermediate density treatment with 128 ( $\pm 26$  SD) aphids per plant. The density of alternative prey decreased during the experiment only slightly to 78 ( $\pm 71$  SD) aphids per plant until the end. Within one day the chrysopid larvae killed on average 48 % ( $\pm 5.18$ ) of the parasitised aphids, but only 15.33 % ( $\pm 7.10$ ) of the mummified aphids. 48 h later the predator already killed more than 80 % of the introduced parasitised or mummified aphids. On average 16 % of the parasitised aphids per plant survived and reached the mummy stage and from 10 % of the mummified aphids adults emerged. Overall the 50 % survival probability was

33.30 h ( $\pm 1.92$  h; 95 % CI 29.54 – 37.06 h) for parasitised aphids. In contrast the survival probability for mummified aphids in the same experiment was significantly prolonged with 46.46 h ( $\pm 2.10$  h; 95 % CI 42.35 – 50.58 h) (Log-Rank-Test,  $\chi^2 = 11,60$ , FG = 1,  $p=0.0007$ ).

*Survival of parasitoids at high densities of alternative prey*

In the treatment with a high density of alternative prey experiments started with a population density of 494 ( $\pm 108$  SD) aphids per plant. Population density increased until the end of the first day to 507 ( $\pm 80$  SD), decreased slightly until the end of the second day and finally increased to 573 ( $\pm 118$  SD) aphids per plant in the end of the experiment. Approximately 2.5 times more parasitised aphids (14 %  $\pm 4$  SE) than mummified aphids (5.45 %  $\pm 3.12$  SE) were killed by the predator *C. carnea* during the first 48 h of the experiment. Moreover, 60 % of the introduced parasitised aphids mummified or emerged as adults until the end of the 5th day. The 50 % survival probability for parasitised aphids (108.85  $\pm 2.67$  h; 95 % CI 103.36 – 114.08 h) was similar to the survival probability of aphid mummies (118.30 h  $\pm 2.02$  h; 95 % CI 114.35 – 122.25 h) (Log-Rank-Test,  $\chi^2 = 1.90$ , FG = 1,  $p = 0.169$ ).

*Density dependent survival of parasitized aphids*

Cox proportional hazard models showed the quantitative impact of the different factors on the survival of parasitoids. Three different models were calculated including step by step the factors parasitoid developmental stage, density of alternative prey, and the interaction term. Table 3 compares the results of the three models.

The results show that in model one an increasing number of alternative prey, i.e. unparasitised aphids, reduced significantly the probability that parasitised or mummified aphids were killed. Moreover inclusion of the developmental stage of the parasitoid in model two and the interaction term in model three improved the model significantly (increasing chi-square values). The hazard of dying was therefore best explained by model three. The results of model three indicated that aphid density (coefficient B=-0.004) and the developmental stage of the parasitoid (coefficient B = -0.528) was negatively related to the hazard that parasitoids were IG prey to *C. carnea*.

## Chapter 06

Table 1 Summary table of survival data for parasitised and mummified aphids at the different treatments low, intermediate, and high aphid density. Events occurred if the aphidophagous predator *C. carnea* killed parasitised or mummified aphids. Individuals were censored if parasitised aphids developed into aphid mummies or if adult parasitoids emerged from aphid mummies. Survival probabilities were compared by log-rank tests.

treatment	low density		intermediate density		high density	
	parasitized aphid	mummified aphid	parasitized aphid	mummified aphid	parasitized aphid	mummified aphid
Number Events	147	150	135	126	50	48
Number Censored	3	0	15	24	100	92
Percent Censored	2.00	0.00	10.00	16.00	66.67	65.71
Average survival (h)	14.39	21.11	33.30	46.46	108.85	118.30
SE	1.18	0.95	1.92	2.10	2.67	2.02
Confidence interval	12.09	19.24	29.54	42.35	103.63	114.35
	-	-	-	-	-	-
	16.70	22.98	37.06	50.58	114.08	122.25
Log-Rank Test	A	a	B	b	C	C

Table 2 Summary table of survival data for mummified aphids located in two different colonies on the same plant at the different treatments low, intermediate, and high aphid density. Events occurred if the aphidophagous predator *C. carnea* killed mummified aphids. Individuals were censored if adult parasitoids emerged from aphid mummies. Survival probabilities were compared by log-rank tests.

Aphid density	low		intermediate		high	
	Patch I	Patch II	Patch I	Patch II	Patch I	Patch II
Number Events	75	75	67	68	27	21
Number Censored	0	0	8	7	43	49
Percent Censored	0	0	10.67	9.33	61.43	70
Average survival (h)	22.6	19.61	48.91	44.02	116.66	119.99
SE	1.47	1.21	2.97	2.95	3.23	2.46
Confidence interval	19.73	17.24	43.09	38.23	110.32	115.17
	-	-	-	-	-	-
	25.47	21.98	54.73	49.80	122.99	124.81
Log-Rank Test	a	a	a	a	a	a

Chapter 06

Table 3 Cox proportional hazard models including stepwise the variables aphid density, developmental stage of the parasitoid and interaction term. Dependent variable was survival time until predation by *C. carnea*. Aphid density was estimated at days parasitoids were killed. Censored values occurred when parasitised individuals mummified or adults emerged from mummified aphids.

<b>Model 1</b>			<b>-2 Log-Likelihood</b>	$\chi^2$	<b>df</b>	<b>P-Value</b>	
			8399.86	0.548	1	0.459	
	<b>Variables</b>	<b>B</b>	<b>SE</b>	<b>Wald</b>	<b>df</b>	<b>P-Value</b>	<b>Exp(B)</b>
	Developmental stage parasitoid	-0.058	0.078	0.55	1	0.459	0.940
<b>Model 1</b>			<b>-2 Log-Likelihood</b>	$\chi^2$	<b>df</b>	<b>P-Value</b>	
			7798.22	462.28	1	<0.001	
	<b>Variables</b>	<b>B</b>	<b>SE</b>	<b>Wald</b>	<b>df</b>	<b>P-Value</b>	<b>Exp(B)</b>
	Aphid density	-0.005	0.000	354.69	1	<0.001	0.995
<b>Model 2</b>			<b>-2 Log-Likelihood</b>	$\chi^2$	<b>df</b>	<b>P-Value</b>	
			7793.67	462.87	2	<0.001	
	<b>Variables</b>	<b>B</b>	<b>SE</b>	<b>Wald</b>	<b>df</b>	<b>P-Value</b>	<b>Exp(B)</b>
	Aphid density	-0.005	0.000	352.60	1	<0.001	0.995
	Developmental stage parasitoid	-0.171	0.080	4.56	1	0.033	0.843
<b>Model 3</b>			<b>-2 Log-Likelihood</b>	$\chi^2$	<b>df</b>	<b>P-Value</b>	
			7751.37	525.72	3	<0.001	
	<b>Variables</b>	<b>B</b>	<b>SE</b>	<b>Wald</b>	<b>df</b>	<b>P-Value</b>	<b>Exp(B)</b>
	Aphid density	-0.004	0.000	196.96	1	<0.001	0.991
	Developmental stage parasitoid	-0.528	0.096	30.26	1	<0.001	0.590
	Aphid density * Developmental stage parasitoid	0.003	0.000	41.90	1	<0.001	1.003

An increased aphid density reduced predation risk by 4 % while development of parasitised aphids to mummified aphids decreased predation risk by 41 % (Table 3 Model 3, risk ratio value = 0.59). Moreover the factor aphid density had a significant impact on the factor developmental stage of the parasitoid (Table 3 Model 3, interaction term). Aphid mummies profit more from increasing prey densities, i.e. unparasitised aphids, then parasitised aphids.

### ***Discussion***

We quantified the influence of extraguild prey on parasitoid survival in presence of the IG predator *C. carnea*. Either mobile parasitised aphids containing the parasitoid larvae or already mummified aphids containing the parasitoid pupa were exposed at three different scenarios to intraguild predation. Intraguild predation was observed in all tested extraguild prey densities. Both developmental stages of the parasitoid, parasitised and mummified aphids, were frequently IG prey to *C. carnea*. Nevertheless in all three scenarios the incidence of IGP was strongly related to the population development of extraguild prey. In the low aphid density treatment parasitised and unparasitised aphids were introduced initially at similar proportions, comprising each 50% of the parasitoid population. Extraguild prey density decreased rapidly during the first days after predator release leading to a short survival time of parasitised aphids in general. Although we expected that prey shortage leads to similar survival probabilities for parasitised and mummified aphids, the results show that survival times for mummified aphids were approximately 0.5 times prolonged compared to survival times for parasitised aphids. Most likely mobility of prey and the specific foraging behaviour of the predator contributed to the observed difference, but nevertheless only a single individual survived the experimental period.

In the second scenario prey population density was as expected more or less constant ranging between 128 aphids at day one and 62 aphids at the end of the experiment. Extraguild to intraguild prey ratio in the beginning of the experiment was approximately one to five and increased to the end of the experiment. Nevertheless only 13% of the parasitoids survived at intermediate prey density, i.e. reached the next developmental stage. Additionally, predation risk was not the same for parasitised and mummified aphids, indicating that mummified aphids had a larger profit from extraguild prey presence. In general increased vulnerability of parasitised aphids compared to extraguild prey can be explained by reduced defences of parasitised aphids.

Perception of an approaching predator and the following escape behaviour, i.e. running away or dropping off the plant, might be reduced due to the pathological effect of the developing parasitoid larva. Mummified aphids in contrast are not able to show any kind of defensive behaviour, but have to rely on their inconspicuousness and on the protection by the mummy shelter. The mummy shelter only provides a limited protection, at least when encountered by coccinellid or chrysopid predators (Meyhöfer 2001, Meyhöfer and Klug 2002). Therefore it is likely that initial encounter rates of mummified aphids by the predator were reduced in the second scenario with constant extraguild prey densities, leading to a twofold increase in survival probability compared to low extraguild prey density. Nevertheless if the first mummy of a colony was encountered often more than one mummy was destroyed, which can be attributed to an intensified local search behaviour of the predator (Meyhöfer and Hindayana 2000, Meyhöfer and Klug 2002).

In contrast to our initial hypothesis IGP was observed frequently even at high and increasing extraguild prey densities, i.e. IG prey to extraguild prey ratio larger than one to twenty. More than 30% of the parasitoids were killed by *C. carnea*. Nevertheless survival probability for mobile parasitised aphids and immobile mummified aphids increased approximately ten fold compared to low and three fold compared to intermediate extraguild prey densities. This unexpected result can be explained partly by the same mechanisms responsible for IGP at intermediate extraguild prey densities (see above). Additionally the availability of ample prey might reduce the aggressiveness and willingness to forage of the predator due to reduced starvation. But in contrast to the other scenarios similar survival probabilities were detected for parasitised aphids and mummified aphids. Hence the benefit of high extraguild prey densities for mobile parasitised aphids was larger than for mummified aphids.

Analysis of the data by Cox proportional hazard models allowed us to quantify the impact of extraguild prey and developmental stage of the parasitoid (IG prey) on parasitoid survival in presence of the IG predator *C. carnea*. As expected both, increasing extraguild prey densities and ongoing development of the parasitoid, decreased predation risk. Both factors interact with each other, with the effect that increasing aphid densities reduced mortality by 4 % but aphid mummies were at a 49 % lower risk of predation than parasitised aphids.

The three test scenarios show that the development of the aphid population on the one hand and the defensive behaviour of IG prey determined the incidence of IGP. In the

first scenario extraguild prey density decreased exponentially and at the same time the survival probability of parasitised aphids decreases exponentially. This scenario might be equivalent to the scenario - IGP increased steadily with decreased extraguild prey density - proposed by Lucas et al. (1998). In the second scenario extraguild prey density was adjusted at a constant level throughout the experimental period. But although the higher extraguild prey density led to a prolonged survival, the overall survival probability of parasitised aphids decreased again exponentially. In the third scenario extraguild prey density increased linear during the experimental period, while survival probability of parasitised aphids decreased slightly especially at the end of the experiment. These different outcomes clearly indicate that parasitoid survival depends not only on extraguild prey density (dilution effect), but also on unique behaviour of parasitised aphids. In consequence parasitised aphids are encountered at higher rates and are more susceptible prey to *C. carnea* than unparasitised aphids.

The incidence of IGP between parasitised aphids and predators depends not only on the foraging behaviour of the protagonists. The adult female parasitoid has to decide where to lay eggs and has to deal with different predation risks (Weisser et al. 1994). Our current knowledge on the behaviour of parasitoids under the threat of predation is limited and inconsistent. In contradiction to the assumption that female parasitoid should avoid the presence of predators to reduce mortality risks for themselves and their offspring the parasitoid species *A. colemani* and *A. ervi* continued foraging even in close neighbourhood of different predator species (Meyhöfer and Klug submitted) and *L. fabarum* did not even show successful escape behaviour (Meyhöfer and Klug 2002). In contrast predator presence seem to trigger either directly or indirectly via availability of prey that foraging parasitoid avoid predator presence (Taylor et al. 1998, Raymond et al. 2000). Nevertheless aphid parasitoids are not known to guard their offspring and once eggs are laid the offspring has to rely on its own. Parasitised aphids are always inferior in confrontations with aphidophagous predators and availability of extraguild prey may enhance survival sufficiently.

### References

- Brodeur, J., and J. A. Rosenheim. 2000. Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis et Applicata* 97:93-108.
- Colfer, R. G., and J. A. Rosenheim. 2001. Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* 126:292-304.
- Evans, D. L., and J. O. Schmidt. 1990. *Insect Defences*. Suny Press, Albany, NY.
- Godfray, H. C. F. 1994. *Parasitoids. Behavioural and Evolutionary Ecology*. Princeton University Press, Chichester, West Sussex.
- Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Lucas, E., D. Coderre, and J. Brodeur. 1998. Intraguild predation among aphid predators: Characterization and influence of extraguild prey density. *Ecology* 79:1084-1092.
- Meyhöfer, R. 2001. Natural enemies of aphids: a new video technique for monitoring field populations. *Entomologia Experimentalis et Applicata* 100:77-87.
- Meyhöfer, R., and D. Hindayana. 2000. Effects of intraguild predation on aphid parasitoid survival. *Entomologia Experimentalis et Applicata* 97:115-122.
- Meyhöfer, R., and T. Klug. 2002. Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hym., Aphidiidae): Mortality risks and behavioural decisions made under the risk of predation. *Biological Control* 25:239-248.
- Meyhöfer, R., and T. Klug. (submitted). Comparative study on the behaviour of *A. colemani* and *A. ervi* in confrontations with predators.
- Polis, G. A., and R. D. Holt. 1992. Intraguild predation: The dynamics of complex trophic interactions. *TREE* 7:151-154.
- Quicke, D. L. J. 1997. *Parasitic wasps*. Chapman & Hall, London.
- Raymond, B., A. C. Darby, and A. E. Douglas. 2000. Intraguild predators and the spatial distribution of a parasitoid. *Oecologia* 124:367-372.
- Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. *Annual Review of Entomology* 43:421-447.
- Takizawa, T., H. Yasuda, and B. K. Agarwala. 2000. Effect of three species of predatory ladybirds on oviposition of aphid parasitoids. *Entomological Science* 3:465-469.
- Taylor, A. J., C. B. Müller, and H. C. J. Godfray. 1998. Effect of aphid predators on oviposition behaviour of aphid parasitoids. *Journal of Insect Behaviour* 11:297-302.
- Weisser, W. W., A. I. Houston, and W. Volkl. 1994. Foraging Strategies in Solitary Parasitoids: The Trade-Off Between Female and Offspring Mortality Risks. *Evolutionary Ecology* 8:587-597.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*:393-425.

## Two protagonists on aphidophagous patches: effects of learning and intraguild predation

(based on Jazzar C., Meyhöfer R., Ebssa L., Poehling H.-M., 2007)

### **Abstract**

In aphidophagous systems, trophic interactions between parasitoids and predators, termed intraguild predation, are frequently asymmetric. To mitigate predation risk for themselves and their offspring, intraguild prey may exploit associative learning to gain accurate information about patch quality. Therefore, costs of unnecessary escape behaviour are avoided. We used sweet pepper patches (*Capsicum annuum* L., cv. "Mazurka") (Solanaceae), sustaining *Macrosiphum euphorbiae* (Thomas) or *Myzus persicae* (Sulzer) (Homoptera: Aphididae) aphids, as a model system to quantify the foraging behaviours of the parasitoid *Aphelinus abdominalis* (Dalman) (Hymenoptera: Aphelinidae), when confronted with predatory second larval instar *Chrysopa carnea* (Stephens) (Neuroptera: Chrysopidae).

The behaviour of predator-naïve or predator-experienced *A. abdominalis* foraging in a patch with or without *C. carnea* was recorded and analysed using a multiple video observation system. We investigated i) whether *A. abdominalis* could learn to detect the presence of a predator in a patch, ii) the impact of the predator presence on the learning and motor learning of the parasitoid, and iii) the effects of the aphid species on the guild interactions.

Results showed that the presence of, or experience with, the predator does not affect *A. abdominalis* learning or motor learning. We discuss the behavioural and ecological implications of our finding. Overall, predator-induced aphid mobility increased the frequency and allocation time of *Aphelinus* oviposition activities, especially when *Ma. euphorbiae* was the host. The predator imposed indirect fitness costs on the parasitoid. *Aphelinus* searched more often and longer, resulting in a tendency towards reduced *Ma. euphorbiae* parasitism rate in patches harbouring *C. carnea*.

## **Adding “personality” to biocontrol: characterization and suitability of microsatellites for sibship reconstruction of *Diaeretiella rapae***

(based on Eisele I., Meyhöfer R., 2015)

### **Abstract**

Efficiency of natural enemies in pest control in the field frequently shows high degree of variability, making it difficult to propose reliable biocontrol strategies. Due to the small size of many beneficials underlying mechanisms are difficult to evaluate. In the present study the potential of molecular markers to reconstruct individual foraging decisions of a small parasitoid species unsuitable for direct tracking, i.e. *Diaeretiella rapae* (M'Intosh) (Hymenoptera, Braconidae), a primary parasitoid of the cabbage aphid *Brevicoryne brassicae* (Linnaeus) (Hemiptera, Aphididae), was evaluated. Nine newly designed microsatellite primer pairs were tested for their reliability in parentage analysis. Therefore, several families of *D. rapae* with four to six daughters and high or low degree of inbreeding were established in the lab. Individuals were genotyped and parentage and sibship analysis was calculated with the software COLONY. The results indicated that 91 % of the 85 genotyped offspring from all families have been assigned to the correct family when all nine microsatellite loci have been used and 86 % when only six microsatellite loci have been used. Even in families with high degree of inbreeding up to 87 % of the offspring could be assigned correctly. In conclusion, the sibship analysis of *D. rapae* provides reliable results, especially with all nine selected microsatellite loci. Therefore it will be a valuable tool to reconstruct individual foraging decisions and characterize parasitoid “personality” in the field to improve biological control strategies.

## **Intraguild Predation among the Hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other Aphidophagous Predators**

(based on Hindayana D., Meyhöfer R., Dagmar Scholz D., Poehling H.-M., 2001, Biological Control 20, 236-246)

### **Abstract**

Aphidophagous predators compete for the same prey species. During their foraging activity they frequently encounter heterospecific aphid predators. These situations can lead to intraguild predation, and may disrupt biological control efforts against aphids where more than one predator species is present. We investigated the behaviour of larvae of the hoverfly *Episyrphus balteatus* de Geer and its interaction with three other aphid predators; the ladybird *Coccinella septempunctata* L., the lacewing *Chrysoperla carnea* Stephens, and the gall midge *Aphidoletes aphidimyza* (Rondani). Interspecific interactions between predators were examined in arenas of different sizes and in the presence of extraguild prey.

The outcome of interactions between *E. balteatus* larvae and the other predators depended predominantly on the relative body size of the competitors. Relatively large individuals acted as intraguild predators, while relatively smaller individuals became intraguild prey. Eggs and first as well as second instar larvae of *E. balteatus* were highly susceptible to predation by all other predators, whereas pupae of *E. balteatus* were only preyed upon by the larvae of *C. carnea*. Interactions between *A. aphidimyza* and *E. balteatus* were asymmetric and always favoured the latter. Eggs and first as well as second instar larvae of *E. balteatus* sustained IGP irrespective of the size of the arena or the presence of extraguild prey. However, the frequency of predation on third instar larvae of *E. balteatus* was significantly reduced. This study indicated that the same species can be both intraguild predator and intraguild prey. It is suggested that combinations of predators have to be carefully chosen for success in biological control of aphids.

## **Propensity towards cannibalism among *Hypoaspis aculeifer* and *H. miles*, two soil-dwelling predatory mite species.**

(based on Berndt O., Meyhöfer R., Poehling H.-M., 2003, Experimental and Applied Acarology, 31, 1-14)

### **Abstract**

In biological control programmes, the two predatory soil mites *Hypoaspis aculeifer* and *H. miles* are often applied against soil borne pests like mushroom flies, springtails and mites. Although the mites show high consumption rates on varying prey types in petri dish experiments and in greenhouses, their overall efficiency is sometimes limited. We hypothesized that intraspecific interactions, like cannibalism, could contribute to this decreased efficiency. Therefore, experiments were conducted to show the propensity of *H. aculeifer* and *H. miles* to cannibalise. Adult mites and nymphs were introduced as predators with conspecific eggs, larvae, nymphs, adult females or males as prey and number of killed individuals was recorded. Additionally the oviposition rate on conspecific prey was quantified and the correlation with the number of prey consumed was calculated to assess the influence of cannibalism on egg production. The results show that cannibalism occurs infrequently in both *Hypoaspis* spp., the only exception being *H. aculeifer* nymphs, which cannibalised one conspecific egg per day. Moreover, cannibalism never occurred in the presence of alternative prey. Oviposition rate decreased during the experiment in both species but it was positively correlated with the cannibalism rate only for *H. aculeifer*. The benefit of cannibalism for populations of *H. aculeifer* and *H. miles* is discussed.

## **Combining plant- and soil-dwelling predatory mites to optimise biological thrips control.**

(based on Wiethoff J., Poehling H.-M., Meyhöfer R., 2004)

### ***Abstract***

The efficiency of a natural enemy combination compared to single species release on control of western flower thrips (WFT) *Frankliniella occidentalis* (Pergande) on cucumber plants was investigated. Since soil passage seems to be obligatory for *F. occidentalis* a combined release of the plant-inhabiting predatory mite *Amblyseius cucumeris* (Oudemans) that feeds on thrips first instar larvae and the soil-dwelling predatory mite *Hypoaspis aculeifer* (Canestrini) that preys on thrips pupae on the ground might be a promising approach for a holistic control strategy. Therefore two sets of experiments were conducted in cooperation with a commercial vegetable grower. In both experiments plants in plots were infested with a defined number of larval and adult *F. occidentalis*. Two species of natural enemies were released in combination and alone and their efficacy was compared to control plots without antagonists. In both experiments predatory mites were released twice *A. cucumeris* in a density of 45.83 individuals/m<sup>2</sup>, *H. aculeifer* a density of 208.33 individuals/m<sup>2</sup> (low-density) in the first experiment and 520.83 individuals/m<sup>2</sup> (high-density) in the second experiment. Population growth of all arthropod species on plants and in the soil was quantified at regular intervals and included all soil-dwelling mites and alternative prey present in the substrate. The results show that *H. aculeifer* alone had a significant impact on thrips population development only when released at high-densities, but efficiency was lower compared to the other antagonist treatments. Impact of *A. cucumeris* alone and *A. cucumeris* & *H. aculeifer* treatments were similar. Thus, the combined use of natural enemies did not boost thrips control compared to the single species application of *A. cucumeris* (non-additive effect), which could be explained by indirect food competition between both predatory mite species. Species number and population size in the soil of the experimental plots both showed a high variability and probably interacted with released soil-dwelling predatory *H. aculeifer* mites. The impact of competition and presence of alternative prey on biological thrips control is discussed in detail.

## Chapter 11

The results of our study led to the conclusions that (1) the combined use of *H. aculeifer* and *A. cucumeris* cannot increase thrips control on cucumber compared to the release of *A. cucumeris* alone but the overall reliability of biological thrips control might be enhanced, (2) the availability of alternative prey seemed to affect the thrips predation rate of *H. aculeifer* and (3) the impact of naturally occurring predatory soil mite species on the control of WFT seemed to be limited.

## General discussion

In general, biological control relies on natural enemies to keep pests below a threshold in protected cultivation (greenhouse, polytunnels) and in the open field (O'Neil et al. 2003). Focal organisms to control pests come from different taxa and include entomopathogens (virus, fungi, nematodes) as well as parasitic and predatory arthropods (Bellows et al. 2008; Gurr, Wratten 2000). Many of them are commercially available to control mainly pests in greenhouses (see table 1, **chapter 01**), which comprises frequently a quite simple ecosystem with a limited spectrum of important pest species and more or less stable environmental conditions. For biocontrol in protected environments, most efficient natural enemies are selected, commercially mass reared and released in augmentative/inundative biocontrol (Gurr, Wratten 2000). Up to date more than 125 species are commercially available for augmentative control, i.e. inundative or inoculative release (van Lenteren 2000b). To control for example aphids in the greenhouse 6 parasitoid and 5 predator species are available (table 1, **chapter 01**). Combinations of natural enemies might be considered to optimise biocontrol, taking into account especially complementary life history traits of antagonists (figure 1, **chapter 01**). Beforehand promising combinations can be narrowed down based on environmental factors in the greenhouse environment, since temperature and or humidity as well as light conditions can be of major importance and define the boundaries of the application (van Lenteren 2007).

In contrast to the greenhouse, inundative release of natural enemies in the field is limited to species without or with very limited dispersal capabilities. Examples include the use of *Trichogramma* egg parasitoids against the cornborer *Ostrinia nubilalis* (Bigler 1994) or the application of entomopathogenic nematodes to control root feeding scarabid larva in the ground (Jackson et al. 2000). Alternative strategies focus on habitat manipulation and/or conservation biological control in the field to improve pest control (Gurr, Wratten 2000). Both options have in common that they aim at provision of key resources to natural enemies with low availability in the simple agricultural landscape. For the third trophic level, parasitoids and predators, provision of food resources and shelter as well as host plants for alternative prey and hosts for natural enemies is of high importance (Gurr et al. 2000). Establishment of flowering strips, overwintering and alternative habitats fill that gap and increase functional biodiversity (Wyckhuys et al. 2013; Rusch et al. 2017), with spill over effects into the crop field for

improved pest control (Tscharntke et al. 2005). At the landscape level increased complexity results also in increased abundance and biodiversity of natural enemies but compared to simple landscapes pest control is not necessarily improved (Chaplin-Kramer et al. 2011). Reasons behind are manifold, but recently natural enemy interaction, i.e. intraguild predation, was identified as major constrain for ecosystem services in complex agricultural landscapes (Martin et al. 2013). To increase reliability and open new options for manipulative strategies a better understanding of behavioural and trophic interactions among natural enemies seems to be mandatory. In the literature studies on trophic relationships in communities shifted from investigations of single trophic levels to omnivory of antagonists, covering several trophic levels (Rosenheim, Harmon 2006). For biological control two types of trophic interactions with major importance for pest control are now recognised, i.e. coincidental and omnivorous intraguild predation (Rosenheim, Harmon 2006). In both cases the IG predators preference for consuming the IG prey (predator/parasitoid) or the herbivore seems to be a key determinant whether biological control is disrupted or not. Therefore preference of the IG-predator for parasitized hosts (coincidental IGP) might lead to disruption when predator and parasitoid were released in combination, while high mortality on the intermediate predator (omnivorous IGP) leads to disruption in combined release of two predatory species (Snyder, Ives 2008; Snyder, Ives 2001). In contrast, preference of the IG-predator for unparasitized prey (instead of parasitized prey or IG-prey) might enhance the suppression of the targeted pest species (Heinz, Nelson 1996; Colfer, Rosenheim 2001).

Since most of the publications of this thesis deal with coincidental IGP I first discuss the results of the studies in the context of foraging behaviour, i.e. prey selection and risk perception as well as avoidance of IGP already during the process of habitat searching for egg laying (mother knows best principal). Then I continue considering chances to complete IG-prey larval development in the patch, potential defence strategies and IG-predator preferences for specific prey items. Finally, I conclude with the potential to improve biological control strategies based on the results so far.

### *Impact of intraguild predation on foraging adults*

Two aspects are known to influence prey specialisation process: the foraging decisions among available prey items, host species or different habitats made during oviposition by adult females, and the performance/preference of the predatory larvae on the food

sources (mobility, escape, nutritional quality) (Tauber & Tauber, 1987). Although adult females might also show feeding preferences for specific prey, the most important decision made is for the prospective habitat the offspring is born to and the prey items they will find in the environment. For phytophagous insects this is well documented in the preference-performance hypothesis or mother-knows-best-principle (Gripengberg et al. 2010; Jaenike 1978), which states that females will increase their fitness by laying eggs on hosts with best developmental conditions for their offspring.

In general, natural enemies are well directed to suitable habitats by a range of different cues including semiochemicals, visual and acoustic stimuli (Webster, Cardé 2017; Jervis 2007; Meyhöfer, Casas 1999). These cues can be directly or indirectly associated with the presence of prey or host organisms. Cues can originate directly from the organisms or can be induced via the feeding activity (herbivore-induced volatiles) (Kaplan 2012). In both cases, attractiveness of patches is frequently linked to the actual prey or host density (Vet 2001; Obrycki et al. 2009). But not only the primary prey will influence the actual host location process. Presence of competitors as well as antagonists from higher trophic levels, i.e. parasitoids of predatory species as well as hyperparasitoids of primary parasitoids, are well known to influence decisions taken by the foraging species (Kaneko 2003; Taylor et al. 1998; Pineda et al. 2007; Bucher et al. 2014). Multimodal integration of different cues is likely to play an important role also for natural enemies (Gilbert, Kuenen 2008)

For example the aphidophagous predator *Episyrphus balteatus* prefers to lay eggs on plants infested by aphids and egg laying increases with aphid density (Sutherland et al. 2001). Aphid honey dew plays an important role in the decision process and presence of conspecific eggs resulted in reduction of deposited eggs (Scholz, Poehling 2000). Most likely olfactory cues emitted by eggs play an important role.

Foraging decision of *E. balteatus* are not influenced by the fact that aphids are parasitised or not, but if aphid mummies or empty mummies are present on the patch the oviposition activity of females is strongly reduced (Almohamad et al. 2008; Pineda et al. 2007). If lower amounts of honeydew associated cues present on the patch are responsible, still has to be investigated. Besides competition for prey by other natural enemies the presence of superior IG-predatory species should influence foraging decisions of adult predators, e.g. *E. balteatus* (Frechette et al. 2007). But also presence of inferior competitors like aphid parasitoids might signal to foraging females that the patch is already overexploited by competitors (Pineda et al. 2007).

Presence of the coccinellid *H. axyridis* or syrphid *E. balteatus* larvae on aphid infested plants negatively influenced ovipositional behaviour of both and results in a lower number of eggs compared to the control (Alhmedi et al. 2010a). In direct confrontations on the patch larvae of *H. axyridis* were superior and preyed on *E. balteatus* eggs and L2-larvae, while L3-larvae were never killed and cannibalism was not observed for both species (Alhmedi et al. 2010a). The missing sensitivity of *E. balteatus* towards the competitive superior *H. axyridis* is surprising, but might be explained by its status as invasive species in Central Europe (Alhmedi et al. 2010b). A more detailed comparison of behavioural interactions in presence of native and invasive coccinellids will highlight the specifics of the adaptation process.

Other aphidophagous predators like the coccinellid *Adalia bipunctata* lay eggs in presence of different aphid species but also will reduced oviposition activity in presence of toxic aphids (Fréchette et al. 2006). In presence of the aggressive IG-predator *Harmonia axyridis* on a host plant, heterospecific coccinellids, i.e. *Hippodamia convergens*, shift egg laying activity to non-crop plants (Amaral et al. 2015).

In contrast *Chrysoperla* does not avoid to lay eggs even in presence of conspecific eggs, most likely an effect shaped by a weak selection pressure in the field (Fréchette et al. 2006). The stalk of lacewing eggs (Ruzicka 1997) as well as mechanical resistance of the egg shell (Canard 1970) lower the cannibalism risk in general. Other examples show, that the close mutualism between ants and many herbivorous insects negatively affects the attractiveness of prey patches, not only for parasitoids but also for predatory insects (Bilu et al. 2006; Eubanks et al. 2002; Shiojiri, Takabayashi 2005). These examples already indicate that predatory species searching for egg laying places are strongly affected by the presence of competitors on the patch. Although intraguild interactions among predatory species are in principle symmetric, i.e. preying on each other is possible, earlier developmental stages are frequently more vulnerable to intraguild predation, unless they are protected by physical or chemical defences. In contrast parasitic wasps are always inferior in aggressions with predatory species. Since they don't have the morphological adaptation for aggressive interactions the selection pressure on parasitic compared to predatory species should be even higher to evolve efficient avoidance/defence strategies to optimise the fitness. Patches already exploited by predatory species should be therefore avoided by foraging parasitoid female to maximise own survival and of course to maximise survival for their

own offspring. How strong the selection pressure is in the open field, is still an ongoing debate (Gillespie et al. 2016; Macfadyen et al. 2015; Chailleux et al. 2014; Fonseca et al. 2017; Guzman et al. 2016). Nevertheless the few field studies show that at least immature developmental stages can face an extraordinary high risk of predation, i.e. 50 % of exposed aphid mummies were rapidly destroyed by the natural population of predatory species in the field within a 5 day period (Meyhofer, Hindayana 2000) (**chapter 02**). Via video analysis damage caused by predators in the field could be attributed mainly to coccinellid, hemipteran predators as well as chrysopids (Meyhofer 2001) (**chapter 03**). In other field studies, analysis of predator gut content was used to identify on which species predators preyed upon. Although the technique has several limitations (Greenstone et al. 2014; Juen et al. 2012; Yang et al. 2017) it contributes valuable qualitative results. For example, remains of *A. colemani* were detected in the gut of *Harmonia axyridis* and *Chrysoperla carnea* (Chacon et al. 2008). Although more quantitative data are needed to identify the dimensions of the selection pressure of predatory species on foraging parasitoids, results at least highlight the potential role of predator groups and allows to focus on more detailed mechanistic studies in the laboratory and the field. The number of studies focussing on various aspects of behavioural adaptations of parasitoids in the laboratory is large but also shows a strong bias towards a few parasitoid species which can be easily reared under laboratory conditions. The ability to detect the presence of an intraguild predator was first shown for the aphid parasitoid *Aphidius ervi* (Taylor et al. 1998). Presence of either developmental stage of the coccinellid predator *Coccinella septempunctata* (larva, adult) and even traces left by foraging predators on the plant reduced patch residence time of *A. ervi* substantially (Taylor et al. 1998). In choice experiments *A. ervi* prefers plants without predator signs, where patch residence time is increased and resulted in higher parasitism. Similar results were obtained with other aphidophagous predators, i.e. *Harmonia axyridis*, *E. balteatus*, *C. carnea*, and *Myrmica rubra* (Almohamad, Hance 2014; Meyhöfer, Klug unpublished; Meisner et al. 2011; Takizawa et al. 2000) (**chapter 04 & 05**). But other parasitoid species do not follow the general trend. *A. colemani* for example foraging for *Myzus persicae* on radish plants only increases its activity instead of leaving plants already exploited by *C. undecimpunctata* (Bilu, Coll 2007). Even more extreme is the response of *Lysiphlebus* species foraging in ant protected aphid colonies, where the parasitoid is protected from ant aggression by chemical camouflage (Liepert, Dettner 1996). Without presence of ants the parasitoid

has to deal with other aphidophagous predators, but does not seem to show behavioural adaptations (Meyhofer, Klug 2002; Kaneko 2003) (**chapter 04**). Similar variability in parasitoid response can be found for other herbivorous species. While adult *Leptomastix dactylopii* parasitoids foraging for mealybugs reduce patch residence time in presence of *Cryptolaemus montrouzieri* (Chong, Oetting 2007), *Eretmocerus eremicus* foraging for *Trialeurodes vaporariorum* is not affected at all by the presence of the whitefly predator *Geocoris punctipes* (Hemiptera: Lygaeidae) (Concepcion Velasco-Hernandez et al. 2013). But not only predatory arthropods acting as IG-predator affect the foraging behaviour of parasitoids. The cabbage root fly parasitoid *Trybliographa rapae*, normally attracted to plants heavily infested by the cabbage root fly *Delia radicum*, avoids patches where entomopathogenic fungi (*Metarhizium brunneum*, which attacks also *T. rapae*) are present. However, parasitoids encountering high-density host patches may ignore fungal presence in the habitat (Cotes et al. 2015).

Behavioural plasticity of many insects is shaped by learning processes (Giunti et al. 2015). In the literature many examples show the capacity of natural enemies for associative learning while foraging for host or prey (Segura et al. 2007; Froissart et al. 2012; Giunti et al. 2015). But also host and prey species have capacities to detect danger, i.e. natural enemies (Dicke, Grostal 2001), and therefore associative learning can also play an important role at higher trophic levels. Although studied for many insect species (Giunti et al. 2015) the role of associative learning was rarely addressed in the context of intraguild predation. Nevertheless, the few studies show contradictory results. While the aphid parasitoid *Aphelinus abdominalis* was unable to adapt its foraging behaviour in the presence of the IG-predator *Chrysoperla carnea* (Jazzar et al. 2008) (**chapter 07**), several aphid parasitoids of the genus *Pauesia*, attacking conifer aphids, shift to reduced searching speed after repeated exposure to ant aggression (Völkl 2001).

Besides parasitoids also predatory mites show capacity for learning (Walzer, Schausberger 2011) where predation risk not only affects learning but experience also affects the anti-predator behaviour of the offspring, i.e. the protonymphs of the next generation show increased response to IG-predator traces (Seiter, Schausberger 2015). Further examples can be found for the risk avoidance behaviour in spider-ant interactions (Henaut et al. 2014) and among wolf spiders (Eiben, Persons 2007).

In conclusion, there are many indications that parasitoid species are able to react to risk of predation. The behavioural responses include preference for patches without predator, adjustment of the foraging activity, or reduction of the patch residence time. Whether or not this is an adaptation to reduce the own predation risk or the potential predation risk for its offspring is still an open question. Nevertheless several laboratory studies indicate that foraging adult parasitoids can be victim of predators foraging on the patch (Meyhofer, Klug 2002; Concepcion Velasco-Hernandez et al. 2013; Concepcion Velasco-Hernandez et al. 2015) (**chapter 04 & 05**), while others have evolved efficient escape strategies (Chong, Oetting 2007). Strong evidence of predation on adults comes also from a field study on *Aphytis aonidiae* and *A. vandenboschi*, minute parasitoids of the San Jose scale, *Quadraspidiotus perniciosus* (Comstock) (Homoptera: Diaspididae), with spiders, workers of the Argentine ant, *Linepithema humile*, and nymphs of the assassin bug *Zelus renardii* (Hemiptera: Reduviidae) being the most important IG-predators (Heimpel et al. 1997). Encounters between adult parasitoids and predator occurred every 3h of observations and every third encounter resulted in parasitoid death and authors underline impact on parasitoid fitness in the field (Heimpel et al. 1997).

### ***Intraguild prey vulnerability to intraguild predators***

The food preference of arthropod predators for prey items is important to understand the suppressive impact on pest populations as well as the trophic interactions among the guild members (Digel et al. 2014; Denno, Finke 2006). Especially in species rich food webs the preferences of predatory species for pests, i.e. herbivores, other guild members, i.e. predators or parasitoids, or alternative prey species is important to assess the overall impact of natural enemies. In general predatory arthropods can cover a broad (polyphagous, generalist omnivorous) or a narrow range (stenophagous) of prey species in their diet. For example syrphids, coccinellids, chrysopids, cecidomyiids and hemipterans show a preference for aphids but will also eat other small insects, while carabids, staphylinids, and ants cover a much wider range of prey species, i.e. arthropods, molluscs, and annelid worms (Symondson et al. 2002).

Two aspects are known to influence prey specialisation process: the foraging decisions made by females during oviposition among available prey items/habitats and the performance/preference of the predatory larvae on/for the food sources (mobility, escape, nutritional quality) (Tauber, Tauber 1987). Although predatory species might

also show feeding preferences for specific prey items (predatory adults are among coccinellids, carabids, heteropterans etc.) the most important decision is for the prospective habitat the offspring is born to and the prey items they will find in the environment (Gripenberg et al. 2010). The behavioural response of foraging females frequently is related to direct or indirect signals associated with prey presence (Hodek et al. 2012; Ballal, Singh 1999; Sutherland et al. 2001; Scholz, Poehling 2000). The higher specialised a predator is on a prey species the more careful the female should select oviposition places. Since most early larval stages of predatory species only have limited energy reserves and cover only small foraging distances, careful selection of prey patches is even more important to guarantee offspring survival. During foraging nutritional quality of the prey items frequently is not the main selection force, but escape potential (i.e. prey mobility and defence behaviour) may play a more important role (Eubanks, Denno 2000). This is also underlined by the fact that prey and predator face different costs, i.e. slight costs if the predator overlooks a prey (lost meal) but high costs (lost life) if the prey overlooks the predator (Cronin 2005). In consequence the sensory system should be more precise evolved for prey compared to predator species. Between predator and parasitoid the relationship is in general asymmetric, only the predator is able to feed on the parasitoid larva, which develop inside (endoparasitoid) or outside (ectoparasitoid) the host species. Since many of the ectoparasitoids attack concealed living host species, like miner or borer, the risk of attack by free foraging predators is reduced (Connor, Taverner 1997). Specific defence mechanisms might rely on inconspicuousness and/or perception of vibrational signals transmitted via the leaf substrate (Meyhöfer, Casas 1999; Bacher et al. 1997). In contrast, endoparasitic species deposit their eggs in still living host species and the developing larvae avoids feeding on important organs to keep the host alive as long as possible (Quicke 2015). In that case, the endoparasitoid at least partly can rely on the host specific defence system against natural enemies (Vinson 1999). For example, aphids use alarm pheromones, defensive secretions, defence kicking, walking or dropping from the host plant to escape from natural enemies (Gross 1993; Dixon 1998). Other hosts, like whiteflies are stationary and defend themselves by morphological characteristics (spines, hairs, wax-layer) (Bährmann 2002; Guershon, Gerling 2001, 1999), while mealybugs defend themselves efficiently by reflex bleeding and waxy secretions (Gullan, Kosztarab 1997).

Healthy as well as parasitized aphid individuals belong to the prey spectrum of all common predator groups, i.e. Coccinellids, Syrphids, Chrysopids, Heteropterans as well as Carabids (Dixon 1998; Brodeur, Rosenheim 2000; Brodeur, Boivin 2006; Meyhofer 2001) (**chapter 02**). Therefore, parasitoid-predator interactions clearly belong to the category of coincidental intraguild predation. In most cases IG predators do not show any specific preference for parasitised or unparasitised aphids (Brodeur, Boivin 2006). Predation rates on developing parasitoids vary largely and depend on the developmental stage of the IG-predator as well as on prey to IG-prey ratios. Nevertheless, few studies also highlight the fact that predators preferentially feed on parasitized aphids (Meisner et al. 2011; Meyhöfer, Klug unpublished) (**chapter 05 & 06**). In one case a coccinellid, *Harmonia axyridis*, preferred to feed on parasitized aphids, while in the second case the neuropteran species, *Chrysoperla carnea*, was involved. Most likely, the progressing development of the parasitoid inside the host affects the constitutive host defence system. The moribund host not only loses its physical defence capabilities, but also chemical, i.e. defensive secretions and pheromone production (Vandermoten et al. 2012; Moayeri et al. 2014). Reduced reactivity make them an easy victim for most predatory species. Reaching the mummy stage the sclerotized cuticle offers protection at least against aphid predators without sucking mouthparts, i.e. Coccinellids and Syrphids (Meyhofer, Klug 2002) (**chapter 04**). Both groups are apparently not able to open the mummy shelter with their rather short mandibulate mouthparts. In contrast predatory species with piercing sucking mouthparts, i.e. Chrysopids and Heteropterans, as well as those with rather strong mandibles, i.e. Carabids, even feed on aphid mummies of several parasitoid species. The immobility and attachment to the leaf offers an ideal counter bearing for sucking piercing mouthparts (Dolling 1991; Kullenberg 1944). To a certain degree morphological and physical construction of the mummy shelter provides protection, for example the power to penetrate *Sitobion avenae* mummies of the aphid parasitoid *Aphelinus abdominalis* has to be twice as high compared to *Aphis fabae* mummies of *Lysiphlebus fabarum* (Kießling 2007).

Most of the mentioned experiments were conducted as choice tests under laboratory conditions referring to worst case scenarios, with prey and predator confined in small arenas. Transfer of results to field or greenhouse situations has to be done carefully (Hindayana et al. 2001) (**chapter 09**). For example *Harmonia axyridis* preys frequently on parasitized aphids in the microcosm environment, but in the field disruption of

biological control was hardly observed (Snyder et al. 2004). Besides experimental conditions in the lab, biotic and abiotic factors have to be taken into account. For example, extraguild prey density (Meyhöfer, Klug unpublished) (**chapter 06**) as well as the IG predator identity (**chapter 02 & 03**) and diversity (Snyder, Ives 2001) will strongly influence the effect on parasitoid population dynamics and biological control in general. Additionally the impact on parasitoids over the entire season is highly dynamic (Meyhofer 2001) (**chapter 01**). Early in the season aphid population build up and extraguild prey density is rather low. During that phase, predation risk for IG prey (parasitized aphids) is rather high. In mid-season, peak population density of aphids is reached and the dilution effect lowers the predation risk for parasitoids. But with breakdown of aphid populations in autumn and aggregation of more and more IG predators in aphid patches the predation risk for parasitoids most likely reaches its seasonal maximum (Meyhofer, Hindayana 2000) (**chapter 02**). So far disruption of biological control in the field by intraguild predation was rarely observed. In the first documented example, disruption was attributed to small ground foraging Carabid beetles climbing up the plant canopy and feeding preferably on parasitoid mummies (Snyder, Ives 2001).

Although the literature on intraguild predation is dominated by studies on aphidophagous species, interactions among predator and parasitoid have been studied with other herbivores, e.g. whiteflies, mealybugs and scale insects, which are important pests in the greenhouse and in many field crops especially in tropical regions. Intraguild interactions are documented in many studies. For example, whitefly parasitoids, like the well-known biocontrol agents *Encarsia formosa* or *Encarsia pergandiella*, are frequently IG prey to coccinellids (Heinz, Nelson 1996) or heteropteran bugs (Concepcion Velasco-Hernandez et al. 2013). While the coccinellid *Delphastus* does not discriminate among parasitised and unparasitised whiteflies, the heteropteran predator *Geocoris punctipes* preferred to feed on unparasitised whitefly nymphs (Concepcion Velasco-Hernandez et al. 2013). A similar behaviour was also described for predators of mealybugs, among them several coccinellid species like *Nephus* or *Cryptolaemus* spp.. Both species avoid feeding on mummified mealybugs, the hard mummy shelter obviously provides sufficient protection (Chong, Oetting 2007; Hernandez-Moreno et al. 2012; Mustu, Kilincer 2014; Gkounti et al. 2014). But at least *Nephus* takes also advantage of reduced host defences like reflex bleeding, droplet secretion, or lowered mobility of parasitized but not jet mummified mealybugs (Mustu,

Kilincer 2014). Whether disruption of biological control of mealybugs in that case is likely was not clarified in that study.

But even if predators do not show specific feeding preferences for parasitized versus healthy prey items, nutritional quality can affect life history traits of IG predators. At least a few studies show that parasitism lowers nutritional quality of prey to IG predators (Takizawa et al. 2000; Bilu, Coll 2009). Prolonged developmental times and lowered weight are only a few consequences of exclusive feeding on parasitized prey items. This is true for L4 larvae of *C. undecimpunctata*, *H. axyridis*, and *P. japonica*, but at least for *C. septempunctata* it was also shown that larval survival is negatively affected. Whether prey selection behaviour of predatory species is affected by the nutritional quality on evolutionary time scales still has to be shown.

### ***The role of extraguild prey (in sensu primary resource for guild members)***

Susceptibility of parasitized host individuals or other intraguild prey not only depends on individual defence strategies or physical protection by for example sclerotized mummy shelters, but also on the availability and density of alternative prey items, i.e. extraguild prey. In general, the presence of extraguild prey decreases the incidence of intraguild predation due to a dilution process (Lucas et al. 2009; Ingels, Clercq 2011; Lucas et al. 1998). But other scenarios are also described in the literature, ranging from no effect at all to a linear or exponential decrease in IGP with increasing extraguild prey availability. For asymmetric intraguild predation on parasitized aphids, extraguild prey might offer protection as long as aphid colonies are growing rapidly. Extraguild prey and the fact that mummies normally form aggregations can be important determinants of IGP. Alternative prey for example reduced predation risk on mummies by 30 % while neighbourhood to conspecifics, i.e. other mummies, increased individual predation risk by 5 % (Meyhofer, Hindayana 2000) (**chapter 02**). Of course, these interactions are part of a highly dynamic process, due to the ephemeral nature of aphid outbreaks on host plants in the field. But in aphid colonies with increasing population densities the survival time for parasitized aphids can increase six-fold compared to aphid populations that decline. Additionally later developmental stages, i.e. aphid mummies, were at 50% lower risk compared to parasitized aphids. But in aphid colonies, the positive dilution effect for parasitized aphids is counteracted by the aggregation of predator species on patches with high prey densities (Chacon, Heimpel

2010). From an evolutionary point of view short larval developmental times should therefore be favoured to reduce the risk of intraguild predation (Meyhöfer, Klug unpublished) (**chapter 06**).

Even more subtle are the effects among predatory species, which engage in symmetric intraguild predation. While in absence of extraguild prey body size and mobility determines to a large extent the outcome of the interspecific interaction (Hindayana et al. 2001; Lucas et al. 1998) (**chapter 09**), i.e. larger individuals kill smaller ones, the presence of extraguild prey leads to a high diversity in outcome scenarios (Ingels, Clercq 2011; Lucas et al. 1998). For example the addition of extraguild prey to chrysopid/coccinellid or coccinellid/gall midge interactions, led in the first case to constant IGP and in the second case, to high IGP at low extraguild prey density and low IGP at very high extraguild prey densities (Lucas et al. 1998). Here, not only the extraguild prey availability but also other factors contribute to the different outcomes: (1) the specific risk perception, in which dominant competitors don't care about confrontations, (2) the preferred foraging path or the period of activity in the habitat, which increase or decrease the chance for direct confrontations among antagonists and finally (3) the specific preferences for extra- or intraguild prey items (Lucas et al. 1998). Although the mentioned factors are based on research with IGP among predatory species it is likely that they play an important role in parasitoids as well, besides the impact of extraguild prey density per se. For example, risk perception seems to be different for the two aphid parasitoids, *A. ervi* and *A. colemani*, when foraging in presence of *Chrysoperla carnea* larvae: both parasitoid species show efficient escape behaviour in direct confrontations, but continued egg laying and underestimate the predation risk for their offspring completely (Meyhöfer, Klug unpublished) (**chapter 04 & 05**).

But not only direct but also indirect effects could be important determinants for intraguild interactions. The parasitoid *Trybliographa rapae*, which prefers late developmental stages of *Delia radicum* for oviposition (Neveu et al. 2000), is not only influenced by the host density but also by the presence of the fungal IG-predator *Metarhizium brunneum* in the soil (Rannback et al. 2015). In both cases volatiles emitted by host larva and fungi most likely mediate the behavioural response of the parasitoid (Cotes et al. 2015). But since the entomopathogenic fungi also leads to rapid pathological effects the prey density is also reduced substantially with negative indirect effects for the foraging success of parasitoids (Cotes et al. 2015).

Finally, many predatory species are omnivorous and feed not only on prey but also as herbivores on plants, a kind of additional extraguild resource (Coll, Guershon 2002). Several mirid species are omnivorous and (Alomar et al. 2002). Although IGP among the two omnivorous mirid species *Dicyphus tamaninii* and *Macrolophus caliginosus*, followed largely the expected symmetric pattern in absence of extraguild resources, the addition of tomato fruits reduced IG predation significantly already in experimental setups and was not existent in microcosm studies including whole tomato plants (Lucas et al. 2009).

### ***Methodological approaches to IGP***

Studies on intraguild predation have been done mostly under laboratory conditions (e.g. Hindayana et al. 2001; Colfer, Rosenheim 2001; Taylor et al. 1998) (**chapter 09**) and to a lesser extent under field conditions (Chacon et al. 2012; Heimpel et al. 1997; Meyhofer 2001; Snyder, Ives 2001, 2003; Snyder et al. 2006). They mostly followed standardised bioassays focusing on individuals (Meyhofer, Klug 2002; Almohamad, Hance 2014) (**chapter 04**), population development (Schausberger, Walzer 2001) or complex interactions within the specific guild of natural enemies (Snyder et al. 2006). Most information comes from studies on the individual level, with the advantage that specific developmental stages can be selected and tested under standardised conditions within specific research questions. Arena setups are preferred setups to study the potential of IG-predators to feed on IG-prey, in presence or absence of extraguild prey (e.g. Hindayana et al. 2001) (**chapter 09**). Moreover, interest lies in the different sensory cues that are involved in behavioural reactions either directly or indirectly coming from the different player (Meisner et al. 2011; Pineda et al. 2007; Taylor et al. 1998; Cotes et al. 2015). With a strong general interest of research in chemical ecology, it is not surprising that many studies investigated IGP with a focus on chemical cues, either volatiles or traces left on the substrate. Experiments take frequently place in Petri-dishes, y-tube or four-arm olfactometers as well as in wind-tunnel. Other sensory modalities than olfactory cues, i.e. visual or mechanical cues, as well as the multimodal orientation remain largely unexplored and are open for further research (Libbrecht et al. 2007). The same is true for the direct and indirect defence of IG-prey as well as defence of extraguild prey against parasitoids or aggressive predatory species (Ikegawa et al. 2015; Janssen et al. 1998; Meyhofer, Klug 2002; Colfer, Rosenheim 2001) (**chapter 40**). On a higher level the impact of intraguild

predation on the population dynamics of the shared prey and natural enemies is studied. Frequently the focus is on pest species with high economic importance (aphids, whiteflies, mites, thrips etc.) with the aim to identify those antagonist combinations that perform best in biological control programs (Yano 2006; Brodeur, Boivin 2006; Brodeur, Rosenheim 2000; Rosenheim 2007). Since release of mass reared natural enemy species is common practice in many greenhouse crops, many studies concentrate on this system. Biological control strategies include mass or inundative release of antagonists. Therefore the initial conditions, i.e. number of released natural enemies, frequency etc. in studies focusing on population dynamics can vary largely. Micro- and mesocosms, i.e. single or numerous host plants infested with pests, are frequently used for population studies with the disadvantage that dispersal of organisms, and therefore risk avoidance, is restricted (Hindayana et al. 2001) **(chapter 09)**. In field studies, experimental techniques are complemented by the use of so-called exclusion cages, i.e. physical barriers to restrict the access of natural enemies entering the study area. Frequently these studies include effects along all trophic levels, considering also herbivore population dynamics (Karp, Daily 2014) and development of plant biomass (Cardinale et al. 2003).

Methods for the lab rely mostly on visual observations and counting's, but more sophisticated video observations, mark/recapture techniques, as well as molecular tools are explored as well in the lab and in the field. Video techniques have been used in several studies in the lab (Jazzar et al. 2008; Meyhofer, Klug 2002; Meyhöfer, Klug unpublished) **(chapter 04 - 07)** and two studies in the field (Meyhofer 2001; Merfield et al. 2004) **(chapter 02 - 03)**. They have the big advantage of continues recording of events over long periods of time. Depending on the number of video cameras, number of pictures taken per s and the storage capacities, recordings can be done from days to several month. Nevertheless observational area is restricted to display window and focus of the camera where behavioural events can be classified (Meyhofer 2001) **(chapter 03)**. The manual analysis of the video recording can be time consuming, but in the future automatic analysis by object recognition will be developed. But by video recordings individuals and intraguild interactions can only be tracked as long as they occur on the observational patch (Meyhofer 2001) **(chapter 03)**. Focusing on single individuals the analysis of the gut content allows conclusions about the recent food spectrum ingested. PCR is a powerful tool to detect DNA from target species in the gut. Similar results can be obtained also with ELISA or HPLC, but costs of the

techniques vary substantially (Aebi et al. 2011). But for molecular proofs the window of detection can be quite small, due to the fact that DNA degrades rapidly in the gut by digestion (Greenstone et al. 2014). To overcome these problems recently microsatellites were investigated to study the foraging behaviour of individual natural enemies, i.e. egg laying pattern in the natural environment (Eisele, Meyhoefer 2015) **(chapter 08)**. The method is based on the relatedness of individuals collected in the field and allows the analysis of reproductive activities of a species by sibship analysis. But even this procedure has some methodological disadvantages. First at all successful reproduction is mandatory otherwise relatedness cannot be estimated, which implies that all foraging activities that do not result in offspring production cannot be considered. For example total avoidance of patches or predation on developmental stage of the target species are impossible to track. To avoid these problems manipulative experiments should be preferred. On the one hand the genetic fingerprint of the parental generation can be taken if target species are released and on the other hand the time for foraging activities can be defined, e.g. allowing the development of one or maximum two generations before sampling. Finally, the depth of resolution of the sibship analysis depends strongly on the number of microsatellites investigated (Berger-Wolf et al. 2007). With 8-10 microsatellites relatedness can be tracked back very well over two generations, at least for the aphid parasitoid *Diaeretiella rapae* (Eisele, Meyhoefer 2015) **(chapter 08)**. Nevertheless sibship analysis will open the avenue for studying behaviour of small arthropods in the open field as well as in the greenhouse environment and by experimental variation in patch quality will give new insights in foraging behaviour of many natural enemies. Still most of the molecular methods are quite costly especially if larger numbers of individuals have to be considered, but most likely, these problems will be solved in the future. In conclusion, a complete picture on interactions in space and time will only emerge if several methods will be combined to study the various trophic and behavioural interactions among guild members.

### ***Conclusions: improving biological control strategies***

Many aspects of IGP have been explored already in detail (see above) and investigations are ongoing. In that context research is either interested in ultimate (fitness consequences) questions and stability of study systems or proximate (mechanisms) questions concerning the mechanism behind IGP. The timeline behind

differs substantially, since ultimate questions in population ecology require equilibrium conditions, while proximate questions focus on non-equilibrium conditions. Non-equilibrium states dominate in most cropping systems, at least at the time scale relevant for biological control and other pest-control tactics (Chacon, Heimpel 2010; Janssen et al. 2006; Murdoch et al. 1985).

A growing body of literature suggests that increasing natural enemy diversity may result in reduced herbivore suppression if this is associated with a larger number of antagonistic within-guild interactions (Letourneau et al. 2009). Although results vary largely, biological control was never completely disrupted by the release of multiple natural enemies so far (Muller, Brodeur 2002). Instead additive to synergistic effects on biological control of herbivores were frequently observed (Brodeur, Boivin 2006). Whether or not the release of multiple natural enemies is an economic strategy still has to be evaluated, but authors frequently highlight the general advantage of resilience (Rocca, Messelink 2017).

Without question, the use of multiple natural enemies improves biological control if the key pest colonies different habitats. A good example is the western flower thrips, which feed as herbivore in the plant canopy were also large parts of the larval development are completed (Berndt et al. 2004a). But since thrips pupation takes place primarily in the ground, biological control has to be targeted on both habitats (Berndt et al. 2004b) (**chapter 10**). Ground and plant dwelling natural enemies should be combined to maximise impact (Wiethoff et al. 2004; Premachandra et al. 2003) (**chapter 11**). Intraguild predation can be largely neglected, although it is known that predators also cross borders and forage frequently in the habitat, i.e. predatory mites on the soil, small carabid beetles on the plant (Snyder, Ives 2001).

But still there is a large gap between basic research and application of IGP knowledge in practice. Most likely growers are also reluctant to use several natural enemies if the overall advantage is not very clear. Single natural enemy species normally will do a good job because they were selected for specific traits, e.g. high searching efficiency, high intrinsic rate of increase, rapid numerical response/short generation time etc. With a focus on natural enemy combinations additional traits might be favourable and the selection procedure should be adapted. Nevertheless some general ideas can be develop from the studies reported in this thesis and the body of literature on intra guild predation: **(1)** Allelochemicals, i.e. kairomones, seem to play an important role also in behavioural interactions between parasitoids and predatory species (including

entomopathogenic fungi and nematodes) and result in avoidance of patches already occupied by others. Adults minimise the predation risk for themselves and their offspring. The compatibility of reactive natural enemy species for biological control is high and will improve pest control substantially if antagonists differ also in searching efficiency (high versus low pest density plots). Nevertheless, intraguild interactions still act during larval development with some negative impacts on population dynamics of involved natural enemies. In the future kairomones might be used as a tool to manipulate natural enemy populations in the field, if substances are characterised and commercially available. For example, reactive species might be directed towards certain parts of the cropping areas, e.g. borders, where pest are frequently concentrated. Outside the crop kairomones might also be used to push natural enemies from field boundaries, overwintering sites, or flowering strips into the crop. **(2)** Results so far indicated that different developmental stages of natural enemies are more or less vulnerable to intraguild predation. Nevertheless, if defensive behaviour or morphological defence are well developed, combined introduction of natural enemies should be feasible. Besides adapted release schedules, the number of species as well as the identity and the developmental stages to introduce can be crucial for success. **(3)** Introduction of superior IG-predators with a highly aggressive potential in any combination with other antagonists should be avoided, not only in field but also in the greenhouse. **(4)** Finally, taking into account the interactions between natural enemies so far, natural enemy breeding programs should consider the intraspecific variability in risk perception to maximise survival of inferior competitors.

Given that niches of antagonists overlaps only partially, the release of multiple natural enemies in practice will always add resilience to biological control. Difference in activity windows or complementary searching strategies are desirable. But whether or not the release of multiple natural enemies is of economic value to all fields of applications still has to be evaluated in the future in more detail.

## Publication bibliography

- Abrol, Dharam P. (Ed.) (2014): Integrated pest management. Current concepts and ecological perspective. Amsterdam: Elsevier/Academic Press. Available online at <http://www.loc.gov/catdir/enhancements/fy1606/2014395418-d.html>.
- Aebi, Alexandre; Brown, Peter M. J.; Clercq, Patrick de; Hautier, Louis; Howe, Andy; Ingels, Brecht et al. (2011): Detecting arthropod intraguild predation in the field. In *BIOCONTROL* 56 (4), pp. 429–440.
- Alhmedi, A.; Haubruge, E.; Francis, F. (2010a): Intraguild interactions and aphid predators: biological efficiency of *Harmonia axyridis* and *Episyrphus balteatus*. In *JOURNAL OF APPLIED ENTOMOLOGY* 134 (1), pp. 34–44.
- Alhmedi, Ammar; Haubruge, Eric; Francis, Frederic (2010b): Intraguild interactions implicating invasive species: *Harmonia axyridis* as a model species. In *BIOTECHNOLOGIE AGRONOMIE SOCIETE ET ENVIRONNEMENT* 14 (1), pp. 187–201.
- Almohamad, Raki; Hance, Thierry (2014): Encounters with aphid predators or their residues impede searching and oviposition by the aphid parasitoid *Aphidius ervi* (Hymenoptera: Aphidiinae). In *Insect Science* 21 (2), pp. 181–188.
- Almohamad, Raki; Verheggen, Francois J.; Francis, Frederic; Hance, Thierry; Haubruge, Eric (2008): Discrimination of parasitized aphids by a hoverfly predator: effects on larval performance, foraging, and oviposition behavior. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 128 (1), pp. 73–80. DOI: 10.1111/j.1570-7458.2007.00664.x.
- Alomar, O.; Goula, M.; Albajes, R. (2002): Colonisation of tomato fields by predatory mirid bugs (Hemiptera. Heteroptera) in northern Spain. In *AGRICULTURE ECOSYSTEMS & ENVIRONMENT* 89 (1-2), pp. 105–115.
- Amaral, Dany S.S.L.; Venzon, Madelaine; Perez, Andre L.; Schmidt, Jason M.; Harwood, James D. (2015): Coccinellid interactions mediated by vegetation heterogeneity. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 156 (2), pp. 160–169. DOI: 10.1111/eea.12319.
- Arim, M.; Marquet, P. A. (2004): Intraguild predation: a widespread interaction related to species biology. In *ECOLOGY LETTERS* 7 (7), pp. 557–564. DOI: 10.1111/j.1461-0248.2004.00613.x.
- Bacher, Sven; Casas, Jérôme; Wäckers, Felix; Dorn, Silvia (1997): Substrate vibrations elicit defensive behaviour in leafminer pupae. In *Journal of Insect Physiology* 43 (10), pp. 945–952. DOI: 10.1016/S0022-1910(97)00058-9.
- Bährmann, Rudolf (2002): Die Mottenschildläuse. Aleyrodina. 1. Aufl. Hohenwarsleben: Westarp Wiss (Die neue Brehm-Bücherei, 664).
- Bale, J. S.; van Lenteren, J. C.; Bigler, F. (2008): Biological control and sustainable food production. In *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 363 (1492), pp. 761–776. DOI: 10.1098/rstb.2007.2182.
- Ballal, C. R.; Singh, S. P. (1999): Host plant-mediated orientational and ovipositional behavior of three species of chrysopids (Neuroptera. Chrysopidae). In *BIOLOGICAL CONTROL* 16 (1), pp. 47–53.
- Bellows, Thomas S.; Fisher, T.W.; Caltagirone, L.E (2008): Handbook of biological control. Principles and applications of biological control. San Diego [etc.]: Academic Press.
- Berger-Wolf, Tanya Y.; Sheikh, Saad I.; DasGupta, Bhaskar; Ashley, Mary V.; Caballero, Isabel C.; Chaovalitwongse, Wanpracha; Putrevu, S. Lahari (2007): Reconstructing sibling relationships in wild populations. In *BIOINFORMATICS* 23 (13), 149-156. DOI: 10.1093/bioinformatics/btm219.
- Berndt, O.; Meyhofer, R.; Poehling, H. M. (2004a): The edaphic phase in the ontogenesis of *Frankliniella occidentalis* and comparison of *Hypoaspis miles* and *Hypoaspis aculeifer* as predators of soil-dwelling thrips stages. In *BIOLOGICAL CONTROL* 30 (1), pp. 17–24. DOI: 10.1016/j.biocontrol.2003.09.009.

## Chapter 13

- Berndt, O.; Poehling, H. M.; Meyhofer, R. (2004b): Predation capacity of two predatory laelapid mites on soil-dwelling thrips stages. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 112 (2), pp. 107–115.
- Bianchi, F. J. J. A.; Booij, C. J. H.; Tscharntke, T. (2006): Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. In *PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES* 273 (1595), pp. 1715–1727. DOI: 10.1098/rspb.2006.3530.
- Bigler, F. (1994): Quality control in Trichogramma production. In E. Wajnberg, S. A. Hassan (Eds.): Biological control with egg parasitoids. Wallingford, UK: CAB International on behalf of the International Organization for Biological Control of Noxious Animals and Plants.
- Bilu, Einat; Coll, Moshe (2007): The importance of intraguild interactions to the combined effect of a parasitoid and a predator on aphid population suppression. In *BIOCONTROL* 52 (6), pp. 753–763. DOI: 10.1007/s10526-007-9071-7.
- Bilu, Einat; Coll, Moshe (2009): Parasitized Aphids Are Inferior Prey for a Coccinellid Predator: Implications for Intraguild Predation. In *ENVIRONMENTAL ENTOMOLOGY* 38 (1), pp. 153–158. DOI: 10.1603/022.038.0119.
- Bilu, Einat; Hopper, Keith R.; Coll, Moshe (2006): Host choice by *Aphidius colemani*: effects of plants, plant-aphid combinations and the presence of intra-guild predators. In *ECOLOGICAL ENTOMOLOGY* 31 (4), pp. 331–336. DOI: 10.1111/j.1365-2311.2006.00786.x.
- Borer, Elizabeth T.; Briggs, Cheryl J.; Holt, Robert D. (2007): Predators, parasitoids, and pathogens: A cross-cutting examination of intraguild predation theory. In *ECOLOGY* 88 (11), pp. 2681–2688. DOI: 10.1890/06-1707.1.
- Brodeur, J.; Rosenheim, J. A. (2000): Intraguild interactions in aphid parasitoids. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 97 (1), pp. 93–108. DOI: 10.1046/j.1570-7458.2000.00720.x.
- Brodeur, Jacques; Boivin, Guy (2006): Trophic and Guild in Biological Interactions Control. Dordrecht: Springer (Progress in Biological Control, 3). Available online at <http://site.ebrary.com/lib/alltitles/docDetail.action?docID=10186872>.
- Bucher, Roman; Binz, Hellena; Menzel, Florian; Entling, Martin H. (2014): Effects of Spider Chemotactile Cues on Arthropod Behavior. In *JOURNAL OF INSECT BEHAVIOR* 27 (5), pp. 567–580. DOI: 10.1007/s10905-014-9449-1.
- Canard, M. (1970): Oophagy in first stage chrysopid larvae (Neuroptera, Chrysopidae). In *Entomol Exp Appl* 13 (1), 21–28.
- Cardinale, B. J.; Harvey, C. T.; Gross, K.; Ives, A. R. (2003): Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. In *ECOLOGY LETTERS* 6 (9), pp. 857–865.
- Chacon, J. M.; Landis, D. A.; Heimpel, G. E. (2008): Potential for biotic interference of a classical biological control agent of the soybean aphid. In *BIOLOGICAL CONTROL* 46 (2), pp. 216–225. DOI: 10.1016/j.biocontrol.2008.04.018.
- Chacon, Jeremy M.; Asplen, Mark K.; Heimpel, George E. (2012): Combined effects of host-plant resistance and intraguild predation on the soybean aphid parasitoid *Binodoxys communis* in the field. In *BIOLOGICAL CONTROL* 60 (1), pp. 16–25.
- Chacon, Jeremy Matthew; Heimpel, George Eugene (2010): Density-dependent intraguild predation of an aphid parasitoid. In *OECOLOGIA* 164 (1), pp. 213–220.
- Chailleux, Anaïs; Mohl, Emily K.; Teixeira Alves, Mickaël; Messelink, Gerben J.; Desneux, Nicolas (2014): Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. In *PEST MANAGEMENT SCIENCE* 70 (12), pp. 1769–1779. DOI: 10.1002/ps.3916.
- Chaplin-Kramer, Rebecca; O'Rourke, Megan E.; Blitzer, Eleanor J.; Kremen, Claire (2011): A meta-analysis of crop pest and natural enemy response to landscape complexity. In *ECOLOGY LETTERS* 14 (9), pp. 922–932. DOI: 10.1111/j.1461-0248.2011.01642.x.

## Chapter 13

- Chong, Juang-Horng; Oetting, Ronald D. (2007): Intraguild predation and interference by the mealybug predator *Cryptolalemus montrouzieri* on the parasitoid *Leptomastix dactylopii*. In *BIOCONTROL SCIENCE AND TECHNOLOGY* 17 (9-10), pp. 933–944. DOI: 10.1080/09583150701596305.
- Colfer, R. G.; Rosenheim, J. A. (2001): Predation on immature parasitoids and its impact on aphid suppression. In *OECOLOGIA* 126 (2), pp. 292–304. DOI: 10.1007/s004420000510.
- Coll, M.; Guershon, M. (2002): Omnivory in terrestrial arthropods: Mixing plant and prey diets. In *ANNUAL REVIEW OF ENTOMOLOGY, VOL 60* 47, pp. 267–297. DOI: 10.1146/annurev.ento.47.091201.145209.
- Concepcion Velasco-Hernandez, Maria; Ramirez-Romero, Ricardo; Cicero, Lizette; Michel-Rios, Claudia; Desneux, Nicolas (2013): Intraguild Predation on the Whitefly Parasitoid *Eretmocerus eremicus* by the Generalist Predator *Geocoris punctipes*: A Behavioral Approach. In *PLOS ONE* 8 (11).
- Concepcion Velasco-Hernandez, Maria; Ramirez-Romero, Ricardo; Sanchez-Hernandez, Carla; Biondi, Antonio; Munoz-Urias, Alejandro; Desneux, Nicolas (2015): Foraging behaviour of the parasitoid *Eretmocerus eremicus* under intraguild predation risk by *Macrolophus pygmaeus*. In *PEST MANAGEMENT SCIENCE* 71 (9), pp. 1346–1353. DOI: 10.1002/ps.3938.
- Connor, E. F.; Taverner, M. P. (1997): The evolution and adaptive significance of the leaf-mining habit. In *OIKOS* 79 (1), pp. 6–25.
- Cotes, Belen; Rannback, Linda-Marie; Bjorkman, Maria; Norli, Hans Ragnar; Meyling, Nicolai V.; Ramert, Birgitta; Anderson, Peter (2015): Habitat selection of a parasitoid mediated by volatiles informing on host and intraguild predator densities. In *OECOLOGIA* 179 (1), pp. 151–162.
- Cronin, Thomas W. (2005): The Visual Ecology of Predator-Prey Interactions. In Pedro Barbosa, Ignacio Castellanos (Eds.): *Ecology of predator-prey interactions*. Oxford: Oxford Univ. Press.
- Denno, Robert F.; Finke, Deborah L. (2006): Multiple predator interactions and food-web connectance: Implications for biological control. In *TROPHIC AND GUILD INTERACTIONS IN BIOLOGICAL CONTROL* 3, pp. 45–70.
- Dicke, Marcel; Grostal, Paul (2001): Chemical Detection of Natural Enemies by Arthropods. An Ecological Perspective. In *Annu. Rev. Ecol. Syst.* 32 (1), pp. 1–23. DOI: 10.1146/annurev.ecolsys.32.081501.113951.
- Digel, Christoph; Curtsdotter, Alva; Riede, Jens; Klärner, Bernhard; Brose, Ulrich (2014): Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. In *OIKOS* 123 (10), pp. 1157–1172. DOI: 10.1111/oik.00865.
- Dixon, Anthony Frederic George (1998): *Aphid ecology. An optimization approach*. 2. ed. London: Chapman & Hall.
- Dolling, W. R. (1991): *The Hemiptera*. London: Natural History Museum Publications.
- Eiben, Ben; Persons, Matthew (2007): The effect of prior exposure to predator cues on chemically-mediated defensive behavior and survival in the wolf spider *Rabidosa rabida* (Araneae: Lycosidae). In *BEHAVIOUR* 144 (8), pp. 889–906. DOI: 10.1163/156853907781492681.
- Eisele, Isabelle; Meyhoefer, Rainer (2015): Adding "personality" to biocontrol: characterization and suitability of microsatellites for sibship reconstruction in the aphid parasitoid *Diaeretiella rapae*. In *BIOCONTROL* 60 (2), pp. 189–197. DOI: 10.1007/s10526-014-9643-2.
- Eubanks, M. D.; Blackwell, S. A.; Parrish, C. J.; Delamar, Z. D.; Hull-Sanders, H. (2002): Intraguild predation of beneficial arthropods by red imported fire ants in cotton. In *ENVIRONMENTAL ENTOMOLOGY* 31 (6), pp. 1168–1174. DOI: 10.1603/0046-225X-31.6.1168.
- Eubanks, Micky D.; Denno, Robert F. (2000): Health food versus fast food. The effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. In *Ecol Entomol* 25 (2), pp. 140–146. DOI: 10.1046/j.1365-2311.2000.00243.x.
- Fonseca, Morgana Maria; Montserrat, Marta; Guzmán, Celeste; Torres-Campos, Inmaculada; Pallini, Angelo; Janssen, Arne (2017): How to evaluate the potential occurrence of intraguild predation. In *Experimental & applied acarology* 72 (2), pp. 103–114. DOI: 10.1007/s10493-017-0142-x.
- Frechette, B.; Dixon, A. F.G.; Alauzet, C.; Boughenou, N.; Hemptinne, J. L. (2006): Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey? In

## Chapter 13

- ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 118 (2), pp. 121–127. DOI: 10.1111/j.1570-7458.2006.00366.x.
- Fréchette, Bruno; Rojo, Santos; Alomar, Oscar; Lucas, Eric (2007): Intraguild predation between syrphids and mirids: who is the prey? Who is the predator? In *BIOCONTROL* 52 (2), pp. 175–191. DOI: 10.1007/s10526-006-9028-2.
- Fréchette, Bruno; Coderre, Daniel; Lucas, Éric (2006): *Chrysoperla rufilabris* (Neuroptera: Chrysopidae) females do not avoid ovipositing in the presence of conspecific eggs. In *BIOLOGICAL CONTROL* 37 (3), pp. 354–358. DOI: 10.1016/j.biocontrol.2005.12.012.
- Froissart, Lucie; Bernstein, Carlos; Humblot, Lionel; Amat, Isabelle; Desouhant, Emmanuel (2012): Facing multiple information sources while foraging on successive patches. How does a parasitoid deal with experience? In *ANIMAL BEHAVIOUR* 83 (1), pp. 189–199. DOI: 10.1016/j.anbehav.2011.10.025.
- Gabarra, R.; Alomar, O.; Castane, C.; Goula, M.; Albajes, R. (2004): Movement of greenhouse whitefly and its predators between in- and outside of Mediterranean greenhouses. In *AGRICULTURE ECOSYSTEMS & ENVIRONMENT* 102 (3), pp. 341–348. DOI: 10.1016/j.agee.2003.08.012.
- Gilbert, Cole; Kuenen, L. P. S. (2008): Multimodal integration: Visual cues help odor-seeking fruit flies. In *CURRENT BIOLOGY* 18 (7), R295–R297. DOI: 10.1016/j.cub.2008.02.020.
- Gillespie, Mark A.K.; Gurr, Geoff M.; Wratten, Steve D. (2016): Beyond nectar provision. The other resource requirements of parasitoid biological control agents. In *Entomol Exp Appl* 159 (2), pp. 207–221. DOI: 10.1111/eea.12424.
- Giunti, G.; Canale, A.; Messing, R. H.; Donati, E.; Stefanini, C.; Michaud, J. P.; Benelli, G. (2015): Parasitoid learning. Current knowledge and implications for biological control. In *BIOLOGICAL CONTROL* 90, pp. 208–219. DOI: 10.1016/j.biocontrol.2015.06.007.
- Gkounti, Vasiliki T.; Savopoulou-Soultani, Matilda; Milonas, Panagiotis G. (2014): Asymmetrical intraguild predation between natural enemies of the citrus mealybug. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 151 (2), pp. 122–127.
- Greenstone, Matthew H.; Payton, Mark E.; Weber, Donald C.; Simmons, Alvin M. (2014): The detectability half-life in arthropod predator-prey research: what it is, why we need it, how to measure it, and how to use it. In *MOLECULAR ECOLOGY* 23 (15), pp. 3799–3813. DOI: 10.1111/mec.12552.
- Gripenberg, Sofia; Mayhew, Peter J.; Parnell, Mark; Roslin, Tomas (2010): A meta-analysis of preference-performance relationships in phytophagous insects. In *ECOLOGY LETTERS* 13 (3), pp. 383–393. DOI: 10.1111/j.1461-0248.2009.01433.x.
- Gross, P. (1993): Insect Behavioral and Morphological Defenses Against Parasitoids. In *Annu. Rev. Entomol.* 38 (1), pp. 251–273. DOI: 10.1146/annurev.en.38.010193.001343.
- Guershon, Moshe; Gerling, Dan (1999): Predatory behavior of *Delphastus pusillus* in relation to the phenotypic plasticity of *Bemisia tabaci* nymphs. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 92 (3), pp. 239–248. DOI: 10.1046/j.1570-7458.1999.00543.x.
- Guershon, Moshe; Gerling, Dan (2001): Parental care in the whitefly *Aleyrodes singularis*. In *Ecol Entomol* 26 (5), pp. 467–472. DOI: 10.1046/j.1365-2311.2001.00345.x.
- Gullan, P. J.; Kosztarab, M. (1997): Adaptations in scale insects. In *ANNUAL REVIEW OF ENTOMOLOGY* 42, pp. 23–50.
- Gurr, G. M.; Wratten, S. D.; Barbosa, P. (2000): Success in Conservation Biological Control of Arthropods. In Geoff Gurr, Stephen D. Wratten (Eds.): *Biological control. Measures of success.* Dordrecht [Netherlands], Boston: Kluwer Academic Publishers.
- Gurr, Geoff; Wratten, Stephen D. (Eds.) (2000): *Biological control. Measures of success.* Dordrecht [Netherlands], Boston: Kluwer Academic Publishers.
- Guzman, C.; Sahun, R. M.; Montserrat, M. (2016): Intraguild predation between phytoseiid mite species might not be so common. In *EXPERIMENTAL AND APPLIED ACAROLOGY* 68 (4), pp. 441–453. DOI: 10.1007/s10493-015-9997-x.
- Heimpel, G. E.; Rosenheim, J. A.; Mangel, M. (1997): Predation on adult *Aphytis* parasitoids in the field. In *OECOLOGIA* 110 (3), pp. 346–352.

## Chapter 13

- Heinz, K. M.; Nelson, J. M. (1996): Interspecific interactions among natural enemies of Bemisia in an inundative biological control program. In *BIOLOGICAL CONTROL* 6 (3), pp. 384–393. DOI: 10.1006/bcon.1996.0049.
- Henaut, Yann; Machkour-M'Rabet, Salima; Lachaud, Jean-Paul (2014): The role of learning in risk-avoidance strategies during spider-ant interactions. In *ANIMAL COGNITION* 17 (2), pp. 185–195. DOI: 10.1007/s10071-013-0651-x.
- Hernandez-Moreno, SALVADOR; GONZÁLEZ-HERNÁNDEZ, HÉCTOR; LOMELI-FLORES, J. REFUGIO; RODRÍGUEZ LEYVA, ESTEBAN; ROBLES BERMÚDEZ, AGUSTÍN (2012): Effect of *Cryptolaemus montrouzieri* (Coleoptera: Coccinellidae) in the parasitoid activity of *Anagyrus kamali* (Hymenoptera: Encyrtidae) on *Maconellicoccus hirsutus* (Hemiptera: Pseudococcidae). In *Revista Colombiana de Entomología* 38 (1), pp. 64–69.
- Hindayana, D.; Meyhofer, R.; Scholz, D.; Poehling, H. M. (2001): Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera, Syrphidae) and other aphidophagous predators. In *BIOLOGICAL CONTROL* 20 (3), pp. 236–246. DOI: 10.1006/bcon.2000.0895.
- Hodek, Ivo; Honek, A.; van Emden, Helmut F. (2012): Ecology and Behaviour of the Ladybird Beetles (Coccinellidae). 2nd ed. Hoboken: John Wiley & Sons. Available online at <http://gbv.eblib.com/patron/FullRecord.aspx?p=896369>.
- Hooks, Cerruti R.R.; Johnson, Marshall W. (2003): Impact of agricultural diversification on the insect community of cruciferous crops. In *CROP PROTECTION* 22 (2), pp. 223–238. DOI: 10.1016/S0261-2194(02)00172-2.
- Ikegawa, Yusuke; Ezoe, Hideo; Namba, Toshiyuki (2015): Adaptive defense of pests and switching predation can improve biological control by multiple natural enemies. In *POPULATION ECOLOGY* 57 (2), pp. 381–395. DOI: 10.1007/s10144-014-0468-8.
- Ingels, Brecht; Clercq, Patrick de (2011): Effect of size, extraguild prey and habitat complexity on intraguild interactions: a case study with the invasive ladybird *Harmonia axyridis* and the hoverfly *Episyrphus balteatus*. In *BIOCONTROL* 56 (6), pp. 871–882. DOI: 10.1007/s10526-011-9363-9.
- Jackson, T. A.; Alves, S. B.; Pereira, R. M. (2000): Success in Biological Control of Above-ground Insects by Pathogens and Nematodes. In Geoff Gurr, Stephen D. Wratten (Eds.): *Biological control. Measures of success*. Dordrecht [Netherlands], Boston: Kluwer Academic Publishers.
- Jaenike, J. (1978): OPTIMAL OVIPOSITION BEHAVIOR IN PHYTOPHAGOUS INSECTS. In *THEORETICAL POPULATION BIOLOGY* 14 (3), pp. 350–356.
- Janssen, A.; Pallini, A.; Venzon, M.; Sabelis, M. W. (1998): Behaviour and indirect interactions in food webs of plant-inhabiting arthropods. In *EXPERIMENTAL AND APPLIED ACAROLGY* 22 (9), pp. 497–521. DOI: 10.1023/A:1006089924336.
- Janssen, Arne; Montserrat, Marta; HilleRisLambers, Reinter; de Roos, Andre M.; Pallini, Angelo; Sabelis, Maurice W. (2006): Intraguild predation usually does not disrupt biological control. In *TROPHIC AND GUILD INTERACTIONS IN BIOLOGICAL CONTROL* 3, pp. 21–44.
- Jazzar, Chantal; Meyhoefer, Rainer; Ebssa, Lemma; Poehling, Hans-Michael (2008): Two protagonists on aphidophagous patches: effects of learning and intraguild predation. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 127 (2), pp. 88–99.
- Jehle, Johannes A.; Herz, Annette; Keller, Brigitte; Kleespies, Regina G.; Koch, Eckhard; Larem, Andreas et al. (2014): Statusbericht Biologischer Pflanzenschutz 2013.
- Jervis, Mark A. (2007): *Insects as natural enemies. A practical perspective*. Dordrecht: Springer. Available online at [http://deposit.d-nb.de/cgi-bin/dokserv?id=2983897&prov=M&dok\\_var=1&dok\\_ext=htm](http://deposit.d-nb.de/cgi-bin/dokserv?id=2983897&prov=M&dok_var=1&dok_ext=htm).
- Juen, Anita; Hogendoorn, Katja; Ma, Gang; Schmidt, Otto; Keller, Michael A. (2012): Analysing the diets of invertebrate predators using terminal restriction fragments. In *JOURNAL OF PEST SCIENCE* 85 (1), pp. 89–100. DOI: 10.1007/s10340-011-0406-x.
- Kaneko, S. (2003): Different impacts of two species of aphid-attending ants with different aggressiveness on the number of emerging adults of the aphid's primary parasitoid and hyperparasitoids. In *ECOLOGICAL RESEARCH* 18 (2), pp. 199–212. DOI: 10.1046/j.1440-1703.2003.00547.x.

## Chapter 13

- Kaplan, Ian (2012): Trophic Complexity and the Adaptive Value of Damage-Induced Plant Volatiles. In *PLOS BIOLOGY* 10 (11). DOI: 10.1371/journal.pbio.1001437.
- Karp, Daniel S.; Daily, Gretchen C. (2014): Cascading effects of insectivorous birds and bats in tropical coffee plantations. In *ECOLOGY* 95 (4), pp. 1065–1074. DOI: 10.1890/13-1012.1.
- Kiessling, Dirk (2007): Untersuchungen zum Fraßverhalten von Blattlausantagonisten an Blattlausmumien. Examensarbeit. Leibniz Universität, Hannover. Institut für Pflanzenkrankheiten und Pflanzenschutz.
- Kullenberg, B. (1944): Studien über die Biologie der Capsiden. Uppsala (Zoologiska Bidrag Fran Uppsala, 23).
- Letourneau, Deborah K.; Jedlicka, Julie A.; Bothwell, Sara G.; Moreno, Carlo R. (2009): Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. In *ANNUAL REVIEW OF ECOLOGY EVOLUTION AND SYSTEMATICS* 40, pp. 573–592. DOI: 10.1146/annurev.ecolsys.110308.120320.
- Libbrecht, R.; Gwynn, D. M.; Fellowes, M. D. E. (2007): *Aphidius ervi* preferentially attacks the green morph of the pea aphid, *Acyrtosiphon pisum*. In *JOURNAL OF INSECT BEHAVIOR* 20 (1), pp. 25–32. DOI: 10.1007/s10905-006-9055-y.
- Liepert, C.; Dettner, K. (1996): Role of cuticular hydrocarbons of aphid parasitoids in their relationship to aphid-attending ants. In *JOURNAL OF CHEMICAL ECOLOGY* 22 (4), pp. 695–707. DOI: 10.1007/BF02033579.
- Lucas, E.; Coderre, D.; Brodeur, J. (1998): Intraguild predation among aphid predators: Characterization and influence of extraguild prey density. In *ECOLOGY* 79 (3), pp. 1084–1092.
- Lucas, Eric; Frechette, Bruno; Alomar, Oscar (2009): Resource quality, resource availability, and intraguild predation among omnivorous mirids. In *BIOCONTROL SCIENCE AND TECHNOLOGY* 19 (5-6), pp. 555–572.
- Ludwig, Martin; Schlinkert, Hella; Meyhöfer, Rainer (2017): Wind-modulated landscape effects on colonization of Brussels sprouts by insect pests and their syrphid antagonists. In *Agr Forest Entomol* 106, p. 954. DOI: 10.1111/afe.12237.
- Macfadyen, Sarina; Davies, Andrew P.; Zalucki, Myron P. (2015): Assessing the impact of arthropod natural enemies on crop pests at the field scale. In *Insect Science* 22 (1), pp. 20–34. DOI: 10.1111/1744-7917.12174.
- Martin, Emily A.; Reineking, Bjoern; Seo, Bumsuk; Steffan-Dewenter, Ingolf (2013): Natural enemy interactions constrain pest control in complex agricultural landscapes. In *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA* 110 (14), pp. 5534–5539. DOI: 10.1073/pnas.1215725110.
- Martinou, Angeliki F.; Raymond, Benjamin; Milonas, Panagiotis G.; Wright, Denis J. (2010): Impact of intraguild predation on parasitoid foraging behaviour. In *ECOLOGICAL ENTOMOLOGY* 35 (2), pp. 183–189. DOI: 10.1111/j.1365-2311.2009.01171.x.
- Meisner, Matthew; Harmon, Jason P.; Harvey, Chad T.; Ives, Anthony R. (2011): Intraguild predation on the parasitoid *Aphidius ervi* by the generalist predator *Harmonia axyridis*: the threat and its avoidance. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 138 (3), pp. 193–201.
- Merfield, C. N.; Wratten, S. D.; Navntoft, S. (2004): Video analysis of predation by polyphagous invertebrate predators in the laboratory and field. In *BIOLOGICAL CONTROL* 29 (1), pp. 5–13.
- Messelink, Gerben J.; Bennison, Jude; Alomar, Oscar; Ingegno, Barbara L.; Tavella, Luciana; Shipp, Les et al. (2014): Approaches to conserving natural enemy populations in greenhouse crops. Current methods and future prospects. In *BIOCONTROL* 59 (4), pp. 377–393. DOI: 10.1007/s10526-014-9579-6.
- Meyhofer, R. (2001): Intraguild predation by aphidophagous predators on parasitised aphids: the use of multiple video cameras. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 100 (1), pp. 77–87. DOI: 10.1046/j.1570-7458.2001.00850.x.
- Meyhofer, R.; Hindayana, D. (2000): Effects of intraguild predation on aphid parasitoid survival. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 97 (1), pp. 115–122. DOI: 10.1046/j.1570-7458.2000.00722.x.

## Chapter 13

- Meyhofer, R.; Klug, T. (2002): Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hymenoptera, Aphidiidae): mortality risks and behavioral decisions made under the threats of predation. In *BIOLOGICAL CONTROL* 25 (3), pp. 239–248. DOI: 10.1016/S1049-9644(02)00104-4.
- Meyhöfer, R.; Casas, J. (1999): Vibratory stimuli in host location by parasitic wasps. In *Journal of Insect Physiology* 45 (11), pp. 967–971. DOI: 10.1016/S0022-1910(99)00060-8.
- Meyhöfer, Rainer; Klug, Thomas (unpublished): Impact of aphid population density on parasitoid and predator intraguild predation.
- Moayeri, Hamid R. S.; Rasekh, Arash; Enkegaard, Annie (2014): Influence of cornicle droplet secretions of the cabbage aphid, *Brevicoryne brassicae*, on parasitism behavior of naïve and experienced *Diaeretiella rapae*. In *Insect Science* 21 (1), pp. 56–64. DOI: 10.1111/1744-7917.12022.
- Mouden, Sanae; Sarmiento, Kryss Facun; Klinkhamer, Peter GJ; Leiss, Kirsten A. (2017): Integrated pest management in western flower thrips: past, present and future. In *PEST MANAGEMENT SCIENCE* 73 (5), pp. 813–822. DOI: 10.1002/ps.4531.
- Muller, C. B.; Brodeur, J. (2002): Intraguild predation in biological control and conservation biology. In *BIOLOGICAL CONTROL* 25 (3), pp. 216–223. DOI: 10.1016/S1049-9644(02)00102-0.
- Murdoch, William W.; Chesson, Jean; Chesson, Peter L. (1985): Biological Control in Theory and Practice. In *The American Naturalist* 125 (3), pp. 344–366. DOI: 10.1086/284347.
- Mustu, Murat; Kilincer, Neset (2014): Intraguild predation of *Planococcus ficus* parasitoids *Anagyrus pseudococci* and *Leptomastix dactylopii* by *Nephus kreissli*. In *BIOCONTROL SCIENCE AND TECHNOLOGY* 24 (3), pp. 257–269. DOI: 10.1080/09583157.2013.856866.
- Neveu, N.; Krespi, L.; Kacem, N.; Nenon, J. P. (2000): Host-stage selection by *Trybliographa rapae*, a parasitoid of the cabbage root fly *Delia radicum*. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 96 (3), pp. 231–237.
- Obrycki, John J.; Harwood, James D.; Kring, Timothy J.; O'Neil, Robert J. (2009): Aphidophagy by Coccinellidae: Application of biological control in agroecosystems. In *BIOLOGICAL CONTROL* 51 (2), pp. 244–254. DOI: 10.1016/j.biocontrol.2009.05.009.
- O'Neil, Robert J.; Yaninek, J. Stephen; Landis, Douglas A.; Orr, David B. (2003): Biological control and integrated pest management. In Maria Palacios Lazo, Alfonso Lizarraga Travagliani, Ricardo Velasquez Ochoa, Enrique Carranza Hernandez, Isaias Segovia (Eds.): *Integrated pest management in Peru (Integrated Pest Management in the Global Arena)*, pp. 19–30.
- Pilkington, Leigh J.; Messelink, Gerben; van Lenteren, Joop C.; Le Mottee, Kristian (2010): "Protected Biological Control" - Biological pest management in the greenhouse industry. In *BIOLOGICAL CONTROL* 52 (3), pp. 216–220. DOI: 10.1016/j.biocontrol.2009.05.022.
- Pineda, A.; Morales, I.; Marcos-Garcia, M. A.; Fereres, A. (2007): Oviposition avoidance of parasitized aphid colonies by the syrphid predator *Episyrphus balteatus* mediated by different cues. In *BIOLOGICAL CONTROL* 42 (3), pp. 274–280. DOI: 10.1016/j.biocontrol.2007.05.017.
- Pineda, Ana; Marcos-Garcia, Ma Angeles (2008): Seasonal abundance of aphidophagous hoverflies (Diptera, Syrphidae) and their population levels in and outside Mediterranean sweet pepper greenhouses. In *ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA* 101 (2), pp. 384–391.
- Polis, G. A.; Myers, C. A.; Holt, R. D. (1989): The ecology and evolution of intraguild predation - potential competitors that eat each other. In *ANNUAL REVIEW OF ECOLOGY AND SYSTEMATICS* 20, pp. 297–330. DOI: 10.1146/annurev.es.20.110189.001501.
- Premachandra, WTSD; Borgemeister, C.; Berndt, O.; Ehlers, R. U.; Poehling, H. M. (2003): Combined releases of entomopathogenic nematodes and the predatory mite *Hypoaspis aculeifer* to control soil-dwelling stages of western flower thrips *Frankliniella occidentalis*. In *BIOCONTROL* 48 (5), pp. 529–541.
- Quicke, Donald L. J. (2015): *The Braconid and Ichneumonid parasitoid wasps. Biology, systematics, evolution and ecology.* Hoboken, NJ: John Wiley & Sons Inc.
- Rannback, Linda-Marie; Cotes, Belen; Anderson, Peter; Ramert, Birgitta; Meyling, Nicolai V. (2015): Mortality risk from entomopathogenic fungi affects oviposition behavior in the parasitoid wasp

## Chapter 13

- Trybliographa rapae. In *JOURNAL OF INVERTEBRATE PATHOLOGY* 124, pp. 78–86. DOI: 10.1016/j.jip.2014.11.003.
- Rocca, M.; Messelink, G. J. (2017): Combining lacewings and parasitoids for biological control of foxglove aphids in sweet pepper. In *J. Appl. Entomol.* 141 (5), pp. 402–410. DOI: 10.1111/jen.12355.
- Rosenheim, Jay A. (2007): Intraguild predation: New theoretical and empirical perspectives. In *ECOLOGY* 88 (11), pp. 2679–2680. DOI: 10.1890/07-0790.1.
- Rosenheim, Jay A.; Harmon, Jason P. (2006): The influence of intraguild predation on the suppression of a shared prey population: An empirical reassessment. In *TROPHIC AND GUILD INTERACTIONS IN BIOLOGICAL CONTROL* 3, pp. 1–20.
- Rusch, A.; Bommarco, R.; Ekbom, B. (2017): Conservation Biological Control in Agricultural Landscapes. In Nicolas Sauvion, Denis Thiéry, Paul-André Calatayud (Eds.): *Insect-plant interactions in a crop protection perspective*, vol. 81. First edition. London, Oxford, Cambridge, MA, San Diego, CA: Elsevier Academic Press (Advances in Botanical Research, volume 81), pp. 333–360.
- Rusch, Adrien; Valantin-Morison, Muriel; Sarthou, Jean-Pierre; Roger-Estrade, Jean (2010): BIOLOGICAL CONTROL OF INSECT PESTS IN AGROECOSYSTEMS: EFFECTS OF CROP MANAGEMENT, FARMING SYSTEMS, AND SEMINATURAL HABITATS AT THE LANDSCAPE SCALE: A REVIEW. In *ADVANCES IN AGRONOMY, VOL 109* 109, pp. 219–259. DOI: 10.1016/S0065-2113(10)09006-1.
- Ruzicka, Z. (1997): Protective role of the egg stalk in Chrysopidae (Neuroptera). In *EUROPEAN JOURNAL OF ENTOMOLOGY* 94 (1), pp. 111–114.
- Schausberger, P.; Walzer, A. (2001): Combined versus single species release of predaceous mites: Predator-predator interactions and pest suppression. In *BIOLOGICAL CONTROL* 20 (3), pp. 269–278. DOI: 10.1006/bcon.2000.0908.
- Schellhorn, Nancy A.; Parry, Hazel R.; Macfadyen, Sarina; Wang, Yongmo; Zalucki, Myron P. (2015): Connecting scales: achieving in-field pest control from areawide and landscape ecology studies. In *Insect Science* 22 (1), pp. 35–51. DOI: 10.1111/1744-7917.12161.
- Scholz, D.; Poehling, H.-M. (2000): Oviposition site selection of *Episyrphus balteatus*. In *ENTOMOLOGIA EXPERIMENTALIS ET APPLICATA* 94 (2), pp. 149–158. DOI: 10.1046/j.1570-7458.2000.00615.x.
- Segura, Diego F.; Viscarret, Mariana M.; Carabajal Paladino, Leonela Z.; Ovruski, Sergio M.; Cladera, Jorge L. (2007): Role of visual information and learning in habitat selection by a generalist parasitoid foraging for concealed hosts. In *ANIMAL BEHAVIOUR* 74 (1), pp. 131–142. DOI: 10.1016/j.anbehav.2006.12.005.
- Seiter, Michael; Schausberger, Peter (2015): Maternal intraguild predation risk affects offspring anti-predator behavior and learning in mites. In *SCIENTIFIC REPORTS* 5. DOI: 10.1038/srep15046.
- Shiojiri, K.; Takabayashi, J. (2005): Parasitoid preference for host-infested plants is affected by the risk of intraguild predation. In *JOURNAL OF INSECT BEHAVIOR* 18 (4), pp. 567–576. DOI: 10.1007/s10905-005-5613-y.
- Snyder, W. E.; Ballard, S. N.; Yang, S.; Clevenger, G. M.; Miller, T. D.; Ahn, J. J. et al. (2004): Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid *Aphelinus asychis* on greenhouse roses. In *BIOLOGICAL CONTROL* 30 (2), pp. 229–235. DOI: 10.1016/j.biocontrol.2004.01.012.
- Snyder, W. E.; Ives, A. R. (2001): Generalist predators disrupt biological control by a specialist parasitoid. In *ECOLOGY* 82 (3), pp. 705–716.
- Snyder, W. E.; Ives, A. R. (2003): Interactions between specialist and generalist natural enemies: Parasitoids, predators, and pea aphid biocontrol. In *ECOLOGY* 84 (1), pp. 91–107.
- Snyder, W. E.; Snyder, G. B.; Finke, D. L.; Straub, C. S. (2006): Predator biodiversity strengthens herbivore suppression. In *ECOLOGY LETTERS* 9 (7), pp. 789–796. DOI: 10.1111/j.1461-0248.2006.00922.x.

## Chapter 13

- Snyder, W.E.; Chang, G.C.; Prasad, R.P. (2005): Biodiversity and successful conservation biological control: is there a relationship? In Pedro Barbosa, Ignacio Castellanos (Eds.): Ecology of predator-prey interactions. Oxford: Oxford Univ. Press, pp. 324–343.
- Snyder, William E.; Ives, Anthony R. (2008): Behavior Influences Whether Intra-Guild Predation Disrupts Herbivore Suppression by Parasitoids. In : Behavioral Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications, pp. 71–91.
- Sohrabi, Fariba; Enkegaard, Annie; Shishehbor, Parviz; Saber, Moosa; Mosaddegh, Mohammad Said (2013): Intraguild predation by the generalist predator *Orius majusculus* on the parasitoid *Encarsia formosa*. In *BIOCONTROL* 58 (1), pp. 65–72. DOI: 10.1007/s10526-012-9468-9.
- Sutherland, J. P.; Sullivan, M. S.; Poppy, G. M. (2001): Oviposition behaviour and host colony size discrimination in *Episyrphus balteatus* (Diptera: Syrphidae). In *BULLETIN OF ENTOMOLOGICAL RESEARCH* 91 (05), pp. 411–417.
- Symondson, W. O. C.; Sunderland, K. D.; Greenstone, M. H. (2002): Can generalist predators be effective biocontrol agents? In *ANNUAL REVIEW OF ENTOMOLOGY* 47, pp. 561–594. DOI: 10.1146/annurev.ento.47.091201.145240.
- Takizawa, T.; Yasuda, H.; Agarwala, B. K. (2000): Effects of parasitized aphids (Homoptera. Aphididae) as food on larval performance of three predatory ladybirds (Coleoptera : Coccinellidae). In *APPLIED ENTOMOLOGY AND ZOOLOGY* 35 (4), pp. 467–472. DOI: 10.1303/aez.2000.467.
- Tauber, Catherine A.; Tauber, Maurice J. (1987): Food specificity in predacious insects: a comparative ecophysiological and genetic study. In *EVOLUTIONARY ECOLOGY* (1, Issue 2), pp. 175–186.
- Taylor, A. J.; Müller, C. B.; Godfray, H. C. J. (1998): Effect of aphid predators on oviposition behavior of aphid parasitoids. In *JOURNAL OF INSECT BEHAVIOR* 11 (2), pp. 297–302. DOI: 10.1023/A:1021056226037.
- Tscharntke, T.; Rand, T. A.; Bianchi, FJJA (2005): The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. In *ANNALES ZOOLOGICI FENNICI* 42 (4), pp. 421–432.
- van Lenteren, C. Joop (2000a): A greenhouse without pesticides. Fact or fantasy? In *CROP PROTECTION* 19 (6), pp. 375–384. DOI: 10.1016/S0261-2194(00)00038-7.
- van Lenteren, J. C. (2000b): Success in Biological Control of Arthropods by Augmentation of Natural Enemies. In Geoff Gurr, Stephen D. Wratten (Eds.): Biological control. Measures of success. Dordrecht [Netherlands], Boston: Kluwer Academic Publishers.
- van Lenteren, J. C. (2007): Internet Book of Biological Control. 4th Edition. Wageningen, The Netherlands. Available online at [www.IOBC-Global.org](http://www.IOBC-Global.org).
- Vandermoten, Sophie; Mescher, Mark C.; Francis, Frédéric; Haubruge, Eric; Verheggen, François J. (2012): Aphid alarm pheromone: an overview of current knowledge on biosynthesis and functions. In *Insect biochemistry and molecular biology* 42 (3), pp. 155–163. DOI: 10.1016/j.ibmb.2011.11.008.
- Vet, L. E.M. (2001): Parasitoid searching efficiency links behaviour to population processes. In *APPLIED ENTOMOLOGY AND ZOOLOGY* 36 (4), pp. 399–408.
- Vinson, S. B. (1999): Parasitoid manipulation as a plant defense strategy. In *ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA* 92 (6), pp. 812–828.
- Völkl, Wolfgang (2001): Parasitoid learning during interactions with ants. How to deal with an aggressive antagonist. In *BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY* 49 (2-3), pp. 135–144. DOI: 10.1007/s002650000285.
- Walzer, Andreas; Schausberger, Peter (2011): Threat-sensitive anti-intraguild predation behaviour: maternal strategies to reduce offspring predation risk in mites. In *ANIMAL BEHAVIOUR* 81 (1), pp. 177–184. DOI: 10.1016/j.anbehav.2010.09.031.
- Webster, Ben; Cardé, Ring T. (2017): Use of habitat odour by host-seeking insects. In *Biological reviews of the Cambridge Philosophical Society* 92 (2), pp. 1241–1249. DOI: 10.1111/brv.12281.
- Wiethoff, J.; Poehling, H. M.; Meyhofer, R. (2004): Combining plant- and soil-dwelling predatory mites to optimise biological control of thrips. In *EXPERIMENTAL AND APPLIED ACAROLOGY* 34 (3-4), pp. 239–261.

## Chapter 13

- Wyckhuys, Kris A.G.; Lu, Yanhui; Morales, Helda; Vazquez, Luis L.; Legaspi, Jesusa C.; Eliopoulos, Panagiotis A.; Hernandez, Luis M. (2013): Current status and potential of conservation biological control for agriculture in the developing world. In *BIOLOGICAL CONTROL* 65 (1), pp. 152–167. DOI: 10.1016/j.biocontrol.2012.11.010.
- Yang, Fan; Wang, Qian; Wang, Dongmei; Xu, Bin; Xu, Jianxiang; Lu, Yanhui; Harwood, James D. (2017): Intraguild Predation Among Three Common Coccinellids (Coleoptera: Coccinellidae) in China: Detection Using DNA-Based Gut-Content Analysis. In *ENVIRONMENTAL ENTOMOLOGY* 46 (1), pp. 1–10. DOI: 10.1093/ee/nvw154.
- Yano, Eizi (2006): Ecological considerations for biological control of aphids in protected culture. In *POPULATION ECOLOGY* 48 (4), pp. 333–339. DOI: 10.1007/s10144-006-0008-2.

## Summary (Zusammenfassung)

Der Einsatz von natürlichen Gegenspielern hat sich in den vergangenen Jahrzehnten zu einem bedeutendem Instrument im biologischen und integriertem Pflanzenschutz entwickelt. Zur Anwendung kommen dabei im geschützten Anbau und im Freiland verschiedene Nutzorganismen (Pilze, Viren, Bakterien, Nematoden, Räuber, Parasitoide), die gezielt eingesetzt oder aber im Freiland im Rahmen des konservierenden biologischen Pflanzenschutzes gefördert werden können. Um die Effizienz und Wirksamkeit von natürlichen Gegenspielern zu verbessern, wurde in der Vergangenheit verstärkt der kombinierte Einsatz von natürlichen Gegenspielern diskutiert (**Kapitel 01**). Daraus ergibt sich ebenfalls die Notwendigkeit, die Betrachtung von einfachen Räuber-Beute Beziehungen auf Wechselwirkungen über mehrere trophische Ebenen auszuweiten. Diese Wechselwirkungen haben den Begriff „Intraguild Predation“ (IGP) geprägt und kennzeichnen die Fraßbeziehung innerhalb der Gilde von Antagonisten, die an einer gemeinsamen Ressource, d.h. Schädlingen/Herbivoren, fressen. Vor allem Untersuchungen zur Populationsdynamik von Herbivoren haben die generelle Bedeutung der IGP für natürliche Gegenspieler unterstrichen und dazu geführt die Bedeutung von trophischen Ebenen zu verallgemeinern. Im Kontext von trophischen Wechselwirkungen wird deshalb von **omnivorer IGP** gesprochen, wenn räuberische Organismen neben Herbivoren auch andere räuberische Organismen angreifen, bzw. von **zufälliger IGP**, wenn räuberische Organismen bei ihrem Nahrungserwerb andere natürliche Gegenspieler (z.B. endoparasitische Schlupfwespen) zufällig mitfressen. Je nach Antagonisten Gruppe können diese Wechselwirkungen entweder symmetrisch bzw. bidirektional (Räuber – Räuber – Interaktionen) oder aber asymmetrisch bzw. unidirektional (Räuber – Parasitoid – Interaktionen) ausgeprägt sein. Im Rahmen der Untersuchungen der Habilitationsschrift wurden multitrophe Wechselwirkungen bei natürlichen Gegenspielern untersucht um die Auswirkungen von IGP auf die Populationsentwicklung von Schadinsekten im Freiland bzw. Gewächshaus zu charakterisieren.

In **Kapitel 02** wurde das Prädationsrisiko von mumifizierten *Aphis fabae* Blattläusen, parasitisiert durch die Schlupfwespe *Lysiphlebus fabarum* (Marshall 1896), im Freiland an Zuckerrüben untersucht um den potenziellen Selektionsdruck zu charakterisieren, der von Räufern auf Parasitoide wirkt. Ansammlungen von mehreren Mumien wurden

natürlich vorkommenden Räubern exponiert und ihr Überleben über einen 10 Tages Zeitraum erfasst. Zusätzlich wurde der Einfluss von Alternativbeute, d.h. unparasitierten Blattläusen, auf das Überleben der Blattlausmumien untersucht. Die Freilanddaten wurden mit Hilfe der Überlebensanalyse und „Cox proportional hazard“ Modellen ausgewertet. Die Ergebnisse zeigen, dass 50% der Mumien innerhalb von 4-5 Tagen nach Exposition von Räubern gefressen wurden. Dabei hatte sowohl die Anwesenheit von Alternativbeute als auch die Nachbarschaft zu weiteren Blattlausmumien einen signifikanten Einfluss auf das Überleben. Vor allem die Anwesenheit von Alternativbeute hat das Prädationsrisiko an Blattlausmumien um 29% gesenkt. Durch das hohe Prädationsrisiko von Mumien ist zu erwarten, dass natürliche Selektionsprozesse Suchstrategien von Schlupfwespen fördern sollten, die zur Vermeidung von Wechselwirkungen mit räuberischen Antagonisten führen.

Im **Kapitel 03** wird eine neuartige Videotechnik vorgestellt, die simultane Verhaltensbeobachtungen von zahlreichen Versuchsreplikaten unter Labor- oder Freilandbedingungen erlaubt. Die Videoanlage wurde eingesetzt um die Prädation an parasitierten Blattläusen in einem Zuckerrübenfeld zu überwachen. Videos von 16 schwarzweiß Videokameras wurden mit Hilfe eines Videomultiplexers und eines Zeitraffer-Videorekorders aufgezeichnet. Die Kameras waren mit Infrarot-Dioden ausgestattet um Nachtsicht zu ermöglichen. Beobachtet wurden einzelne Zuckerrübenblätter auf denen sich Kolonien von Blattlausmumien mit und ohne Alternativbeute, d.h. in Nachbarschaft zu unparasitierten Blattläusen, befanden. Die Kolonien wurden dem natürlich vorkommenden Räuberspektrum ausgesetzt. Die Ergebnisse zeigen, dass Kolonien aus Mumien und unparasitierten Blattläusen signifikant häufiger von Räubern besucht wurden als Kolonien ohne Alternativbeute. Bei Anwesenheit von Alternativbeute waren Marienkäfer und Wanzen für den Fraß an Mumien verantwortlich. Waren nur Mumien an den Blättern vorhanden konnten vor allem Florfliegen-Larven für den Schaden verantwortlich gemacht werden. In beiden Fällen war das Überleben der Schlupfwespen hauptsächlich von der Anzahl und Dauer der Räuberbesuche abhängig. Durch die kontinuierliche Videobeobachtung konnten zusätzliche Verhaltensparameter erhoben werden und die Identität der Gegenspieler den Schadenereignissen zugeordnet werden. Auch in anderen Forschungsbereichen könnte die Videoüberwachungstechnik zur Klärung funktioneller Zusammenhänge (Blütenbesucher, Aktivität von Laufkäfern auf dem Boden etc.) beitragen.

In **Kapitel 04** wird die asymmetrische Beziehung der IGP zwischen Parasitoid und Räuber untersucht, bei der nur der Parasitoid durch den Räuber bedroht wird. Durch den hohen Selektionsdruck ist zu erwarten, dass Schlupfwespen Strategien entwickelt haben um das Mortalitätsrisiko, das von Räufern ausgeht zu minimieren. In Laboruntersuchungen wurde das Mortalitätsrisiko von verschiedenen Entwicklungsstadien und von adulten Blattlausparasitoiden der Art *Lysiphlebus fabarum* (Marshall) in Konfrontationen mit verschiedenen Räufern ermittelt. Durch chemische Mimikry ist die Schlupfwespen-Art angepasst den feindfreien Raum in ameisenbelaufenen Blattlaus-Kolonien zu nutzen. Die Ergebnisse zeigen, dass ohne Ameisenschutz die meisten Entwicklungsstadien der Schlupfwespe einem hohen Prädationsrisiko aller getesteten Räuber ausgesetzt sind. Nur Blattlausmumien sind adulten und larvalen Coccinelliden sowie Schwebfliegenlarven in geringerem Masse zum Opfer gefallen als unparasitierte Blattläuse. Trotzdem haben adulte *L. fabarum* Weibchen weder die Anwesenheit von Räuber gemieden, noch ein effektives Abwehrverhalten gezeigt. Darüber hinaus waren Marienkäfer, Schwebfliegen und Florfliegen in der Lage erwachsene Schlupfwespen zu töten. Die Diskrepanz zwischen den beobachteten Prädationsrisiken und dem Fehlen von Verhaltensanpassungen deuten darauf hin, dass *L. fabarum* sich darauf verlässt durch chemische Mimikry gegenüber Angriffen von Ameisen geschützt zu sein, eine Anpassung die gegenüber anderen Blattlausräuber aber funktionslos ist. Sowohl im Freiland wie auch im biologischen Pflanzenschutz unter Glas kann diese fehlenden Verhaltensanpassung den Bekämpfungserfolg von Blattläusen negative beeinflussen.

In **Kapitel 05** wird das Verhalten von zwei weiteren Blattlausparasitoiden, *Aphidius colemani* und *A. ervi*, in direkten Konfrontationen mit verschiedenen Blattlausräubern unter standardisierten Versuchsbedingungen im Labor verglichen. Die Ergebnisse zeigen, dass beide Schlupfwespenarten in Anwesenheit von Florfliegenlarven die Aufenthaltszeit an der Pflanze reduzieren und weniger Zeit in Suchaktivitäten investieren, wobei *A. ervi* sich sensitiver zeigte als *A. colemani*. Die variablen Verhaltensreaktionen in direkten Konfrontationen mit verschiedenen Blattlausgegenspielern erlauben keine einfachen Schlussfolgerungen. Auf Basis der Ergebnisse wird die Hypothese aufgestellt, dass Marienkäfer als ein hohes Mortalitätsrisiko wahrgenommen werden, Ameisen und Florfliegen rangieren im Mittelfeld und Schwebfliegenlarven werden von den Schlupfwespen nur als geringes Risiko wahrgenommen. Obwohl adulte Schlupfwespen in direkten Konfrontationen nur

selten selbst erbeutet wurden, wird das Prädationsrisiko für die Nachkommen stark unterschätzt, da auch in Gegenwart von Räubern weiterhin Blattläuse angegriffen und parasitiert wurden. Es ist daher zu erwarten, dass der kombinierte Einsatz im biologischen Pflanzenschutz unter Glas zu nicht additiven Effekten führen könnte.

In **Kapitel 06** wurden die Auswirkungen von Alternativbeute auf IGP zwischen Schlupfwespe und Räuber bei verschiedenen Populationsdichten systematisch untersucht. Neben Anpassungen in Morphologie und Verhalten von parasitierten Blattläusen war zu erwarten, dass Schlupfwespen vor allem von einem Verdünnungseffekt durch hohe Alternativbeutedichten profitieren könnten. In Laborversuchen wurde der Einfluss verschiedener Blattlausdichten auf das Überleben von parasitierten Blattläusen und Blattlausmumien der Art *A. colemani* in Gegenwart von Florfliegenlarven untersucht. Die Ergebnisse zeigen, dass mit zunehmender Blattlaus-Populationsdichte die Überlebenswahrscheinlichkeit der Schlupfwespen zunimmt. Im Vergleich zur geringsten Blattlausdichte erhöhte sich die Überlebensrate bei hoher Blattlausdichte um den Faktor Sechs. Nur bei hoher Alternativbeutedichte konnten mehr als 50% der Schlupfwespen ihre Entwicklung vollenden. Darüber hinaus war nur bei geringen und mittleren Beutedichten die Überlebenszeit von Blattlausmumien gegenüber parasitierten Blattläusen erhöht. Zunehmende Blattlausdichten reduzieren das Mortalitätsrisiko um bis zu 4%, Blattlausmumien waren aber einem 49% geringeren Fraßrisiko ausgesetzt als parasitierte Blattläuse. Natürliche Selektionsprozesse sollten daher vor allem eine schnelle Larvalentwicklung und eine Verpuppung in großen Blattlauskolonien, d.h. auf dem Höhepunkt der Populationsentwicklung, begünstigen.

In **Kapitel 07** wird das Lernverhalten von Schlupfwespen im Kontext von IGP untersucht. Um das Prädationsrisiko für sich selbst und den Nachkommen zu minimieren sollten Schlupfwespen während der Wirtssuche assoziatives Lernverhalten nutzen um potenzielle Prädationsrisiken und somit die Patchqualität besser einschätzen zu können. Die Untersuchungen wurden mit der Blattlausschlupfwespe *Aphelinus abdominalis* (Dalman) (Hymenoptera: Aphelinidae), einer langlebigen und synovigenen Schlupfwespen-Art, sowie zwei verschiedenen Blattlausarten, *Macrosiphum euphorbiae* (Thomas) und *Myzus persicae* (Sulzer) (Homoptera: Aphididae) und L2-Larven der Florfliege *Chrysopa carnea* (Stephens) (Neuroptera: Chrysopidae) durchgeführt. Das Suchverhalten von naiven und erfahrenen Schlupfwespen wurde mit Hilfe einer Videoüberwachungsanlage

aufgezeichnet und ausgewertet um das Lernverhalten zu analysieren. Die Ergebnisse zeigen, dass weder die Erfahrungen mit, noch die Anwesenheit von Räubern in der Blattlauskolonie das Lernverhalten von *A. abdominalis* beeinflusst hat. Insgesamt scheinen indirekte Effekte auf die Blattlausmobilität, die durch das Fraßverhalten von Räubern verursacht werden, das Eiablageverhalten von *A. abdominalis* am stärksten zu beeinflussen. Blattlausräuber können somit indirekte Fitness Kosten für die Schlupfwespe verursachen, die negative Auswirkungen auf die Parasitierungsrate und somit den biologischen Pflanzenschutz haben können.

Da Schlupfwespen sich aufgrund ihrer geringen Körpergröße der direkten Beobachtung und somit der Analyse von Wechselwirkungen mit Räubern entziehen wurde im **Kapitel 08** die Eignung von molekulare Marker untersucht um den individuellen Suchpfad von Schlupfwespen unter natürlichen Bedingungen mit Hilfe der Verwandtschaftsanalyse zu charakterisieren. Zum Einsatz kamen 9 neu entwickelte Mikrosatelliten der Blattlausschlupfwespe *Diaeretiella rapae* (M'Intosh) (Hymenoptera, Braconidae), einem Primärparasitoiden der mehliges Kohlblattlaus *Brevicoryne brassicae* (Linnaeus) (Hemiptera, Aphididae). Die Verwandtschaftsbeziehungen auf der Ebene von 4-5 weiblichen Nachkommen unter verschiedenen Inzuchtbedingungen analysiert. Alle Individuen wurden genotypisiert um die Elternschaft bzw. den Geschwisterstatus mit Hilfe der Software COLONY zu bestimmen. Die Ergebnisse zeigen dass 91% der 85 genotypisierten Nachkommen der richtigen Familie zugeordnet werden können, wenn 9 Mikrosatelliten berücksichtigt werden. Sogar in Familien mit einem hohen Grad an Inzucht war es möglich bis zu 87% der Nachkommen eindeutig einem Elterntier zuzuordnen. Die Verwandtschaftsanalyse mit Hilfe von Mikrosatelliten hat sich deshalb als wertvolles Werkzeug erwiesen und wird in Zukunft die Rekonstruktion von individuellen Entscheidungen im Such- und Eiablageverhalten von Schlupfwespen unter komplexen Versuchs- und Freilandbedingungen ermöglichen um den biologischen Pflanzenschutz zu optimieren.

In **Kapitel 09** wird das Verhalten von aphidophagen Schwebfliegen in Konfrontationen mit verschiedenen anderen Blattlausräubern untersucht. Bei Wechselwirkungen zwischen zwei Räubern ist IGP symmetrisch bzw. bidirektional ausgeprägt, d.h. beide Kontrahenten haben das Potenzial sich gegenseitig zu fressen. In verschiedenen Laborversuchen wurde das Verhalten von Schwebfliegenlarven in Interaktion mit Marienkäfern, Florfliegen und Gallmücken quantifiziert. Dabei wurde auch die

Anwesenheit von Alternativbeute und die Dimension der Versuchsarena variiert. Die Ergebnisse zeigen, dass die Wechselwirkungen zwischen Schwebfliegenlarven und anderen Prädatoren hauptsächlich von der Körpergröße der Kontrahenten abhängen. Große Individuen haben als IG-Räuber agiert, während kleine Individuen in der Regel als IG-Beute fungierten. Eier und erste Larvenstadien der Schwebfliege waren besonders empfindlich und Puppen wurden nur von Larven der Florfliege erbeutet. Gallmückenlarven waren in allen Konfrontationen unterlegen. Unabhängig von der Arenagröße oder der Alternativbeutedichte fielen Junglarven der Schwebfliege allen Räubern zum Opfer, das Fraßrisiko für Altlarven war hingegen stark reduziert. Die Untersuchungen belegen das unterschiedliche Entwicklungsstadien einer räuberischen Art in Abhängigkeit des Kontrahenten als IG-Räuber oder IG-Beute fungieren können. Im biologischen Pflanzenschutz sollten Räuber – Kombinationen sorgfältig ausgewählt werden um den Bekämpfungserfolg nicht zu gefährden.

In **Kapitel 10** wurde das Bekämpfungspotenzial von Bodenraubmilben untersucht, die im biologischen Pflanzenschutz oftmals mit wechselndem Erfolg zur Bekämpfung von Milben, Collembolen oder Trauermücken eingesetzt werden. In Laborversuchen wurde die Hypothese untersucht ob kannibalistisches Verhalten der Raubmilben *Hypoaspis aculeifer* bzw. *H. miles* den Einsatzerfolg beeinträchtigen können. Deshalb wurde das Verhalten von Adulten und juvenilen Raubmilben in direkten Konfrontation mit Entwicklungsstadien der gleichen Art charakterisiert und der Entwicklungserfolg dokumentiert. Darüber hinaus wurde auch die Bedeutung von Alternativbeute untersucht. Die Ergebnisse zeigen, dass beide Arten gelegentlich zum Kannibalismus neigen. Nur bei *H. aculeifer* Nymphen konnte regelmäßig Kannibalismus an Eier der eigenen Art beobachtet werden. In Gegenwart von Alternativbeute zeigte keine der beiden Raubmilbenarten ein kannibalistisches Verhalten. Da beide Raubmilbenarten ihren Entwicklungszyklus bei ausschließlich kannibalistischer Ernährung nicht vollenden konnten, sind weder positive noch negative Auswirkungen auf die Raubmilbeneffizienz im biologischen Pflanzenschutz zu erwarten.

In **Kapitel 11** wird die Effizienz eines kombinierten Einsatzes von zwei Raubmilben-Arten bei der Bekämpfung von Thripsen im Gemüseanbau unter Glas untersucht. Weil der amerikanische Blüenthrisp *Frankliniella occidentalis* eine obligate Bodenpassage im Entwicklungszyklus durchläuft, wurde der Einsatz von Raubmilben an oberirdischen Pflanzenteilen mit dem Einsatz von Bodenraubmilben kombiniert. Zum Einsatz kam die Raubmilbe *Amblyseius cucumeris* (Oudemans) und die Boden-Raubmilbe

*Hypoaspis aculeifer* (Canestrini) in kontrollierten Versuchen unter praxisnahen Bedingungen. Der Einsatz erfolgte in zwei unterschiedlichen Dichten entweder als einzelne Art oder in Kombination. Das Populationswachstum wurde in regelmäßigen Abständen dokumentiert. Die Ergebnisse belegen, dass die Bodenraubmilbe *H. aculeifer* nur bei hohen Einsatzdichten einen signifikanten Einfluss auf das Thrips-Populationswachstum hatte, der Bekämpfungserfolg war aber geringer als bei allen anderen Varianten. Die Auswirkungen von einem alleinigen Einsatz von *A. cucumeris* auf das Thrips-Populationswachstum waren vergleichbar mit dem kombinierten Einsatz von *A. cucumeris* & *H. aculeifer*. Durch den kombinierten Einsatz der beiden Raubmilben Arten konnte somit keine Verbesserung der Thripsbekämpfung nachgewiesen werden. Der geringe Beitrag der eingesetzten Bodenbodenraubmilben wurde wahrscheinlich von der Verfügbarkeit an Alternativbeute im Boden beeinflusst. Bei der biologischen Bekämpfung von Thripsen mit Bodenraubmilben im gewachsenen Boden ist daher eine genaue Kenntnis der Biodiversität der Bodenfauna unabdingbar. Dabei können hohe Alternativbeutedichte genutzt werden um Bodenraubmilben rechtzeitig vor Kulturbeginn anzusiedeln und somit den biologischen Pflanzenschutz zu fördern.

In der abschließenden Betrachtung (**Kapitel 12**) wird die Bedeutung von Wechselwirkungen mit räuberischen Organismen für das Such- und Eiablageverhalten von Parasitoiden und Räubern verschiedener Schädlingsgruppen (Blattläuse, Weiße Fliege, Thripse, Schmierläuse, etc.) vergleichend diskutiert. Darüber hinaus wird die Gefährdung von larvalen Entwicklungsstadien (parasitierte Wirte, Mumien, larvale Entwicklungsstadien) verschiedener Gegenspielerarten betrachtet und die Bedeutung von morphologischen Abwehrstrategien sowie zugrundeliegende Verhaltensanpassungen diskutiert. Potenzielle Mortalitätsrisiken von allen Entwicklungsstadien hängen aber auch direkt von der Gesamtbeutedichte ab. Vor allem bei hoher Beutedichte profitieren natürliche Gegenspieler von einem Verdünnungseffekt, deshalb wird diese Beziehung gesondert diskutiert. Auf der methodischen Seite haben vor allem molekulare Methoden in den letzten Jahren viel zur Aufklärung von Fraßbeziehungen in Nahrungsnetzen beigetragen. Aber nur in Verbindung mit anderen innovativen Methoden (Langzeit-Videoüberwachung, Verwandtschaftsanalysen, etc.) wird es in Zukunft möglich sein Wechselwirkungen grundlegend aufzuklären. Trotzdem lassen sich auf Basis der vorliegenden Ergebnisse für den biologischen Pflanzenschutz einige generelle Schlussfolgerungen ziehen um den

kombinierten Einsatz von Nützlingen in Zukunft weiter zu optimieren: (1) Allelochemikalien, die Wechselwirkungen innerhalb der Gegenspielergerilde maßgeblich beeinflussen können, haben ein hohes Potential um die Ausbreitung und Verbreitung von Nützlingen im Agrarökosystem zu manipulieren, (2) Nützlinge mit speziellen Abwehrstrategien gegenüber Fraßfeinden weisen eine hohe Kompatibilität auf, vor allem wenn Einsatzpläne angepasst werden können, (3) auf den Einsatz von überlegenen Räubern sollte in Nützlingskombinationen verzichtet werden und (4) bei Massenzuchten von Nützlingen könnte die Reaktion auf Mortalitätsrisiken ein wichtiges Selektionskriterium darstellen um den Bekämpfungserfolg in der Praxis zu verbessern.

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## Curriculum vitae & Publications

### *Curriculum vitae*

- seit 2009 **Wissenschaftlicher Mitarbeiter/Dozent (100%)** am Institut für gartenbauliche Produktionssysteme, Abt. Phytomedizin, Leitung AG angewandte Entomologie (Geschäftsführung Prof. E. Maiss),
- 2009 **Wissenschaftlicher Mitarbeiter (100%)** Julius Kühn-Institut (JKI), Bundesforschungsinstitut für Kulturpflanzen, Institut für Pflanzenschutz in Ackerbau und Grünland (Geschäftsführung Prof. Dr. P. Zwerger), u.a. Zuständig für Pflanzenschutzmittelzulassung
- 2008 **Wissenschaftlicher Mitarbeiter (50%)** Julius Kühn-Institut (JKI), Bundesforschungsinstitut für Kulturpflanzen, Institut für Pflanzenschutz in Gartenbau und Forst (Leiter Prof. Dr. A. Wulf), u.a. Koordinator BLE-Verbundprojekt Bodenschädlinge
- 2006 – 2008 **Wissenschaftlicher Mitarbeiter (50%)** am Institut für Pflanzenkrankheiten und Pflanzenschutz der Universität Hannover (Leiter Prof. H.-M. Poehling), Leitung AG angewandte Entomologie
- 2003 – 2006 **Wissenschaftlicher Mitarbeiter (50 %)** am Institut für Pflanzenschutz im Gemüsebau der Biologischen Bundesanstalt Braunschweig (Leiter Dr. M. Hommes), u.a. Untersuchungen zur Biologie und Ökologie von invasiven Arten am Beispiel der Kastanien-Miniermotte.
- 1997 – 2002 **Wissenschaftlicher Mitarbeiter** am Institut für Pflanzenkrankheiten und Pflanzenschutz der Leibniz Universität Hannover unter Prof. H.-M. Poehling im DFG-Projekt „Interspezifische Wechselwirkungen zwischen Prädatoren und Parasitoiden und ihre Auswirkung auf die Effizienz als Blattlaus-Antagonisten“.
- 1992 – 1996 **Doktorarbeit an der Eidgenössischen Technischen Hochschule (ETH)** in Zürich (Schweiz) am Lehrstuhl für angewandte Entomologie von Prof. S. Dorn, betreut durch Prof. J. Casas und Dr. Felix Wäckers; Titel: „Die Bedeutung von

## Chapter 16

Substratvibrationen für die interspezifischen Wechselwirkungen zwischen Parasitoid und Blattminierer“.

Auszeichnung mit der Forschungsmedaille der ETH

- Sommer 1994 **Forschungsaufenthalt am Dept. of Biological Sciences, University of California**, Santa Barbara, USA, Modellierung von Verhaltenssequenzen mit Hilfe von Markov-Ketten; in Zusammenarbeit mit Prof. J. Casas und Prof. R. Nisbet.
- 1993 – 1994 **Nachdiplom-Studium** in angewandter Statistik an der ETH Zürich
- 1986 – 1992 **Studium der Biologie an der Christian-Albrechts-Universität Kiel**, Schwerpunkte in Zoologie, Mikrobiologie, Biochemie und Botanik; Diplomarbeit am Lehrstuhl für Terrestrische Tierökologie bei Prof. H. Pschorn-Walcher mit dem Titel: „Untersuchungen zur Biologie und Ökologie zweier Gallmücken aus der Gattung *Cystiphora* (Cecidomyiidae) und ihrer Parasitoide“.
- 1983 – 1985 **Ausbildung zum Technischen Assistenten an Naturkundemuseen und Forschungsinstituten am Forschungsinstitut Senckenberg**, Frankfurt.
- 1981 – 1982 Wehrdienst
- 1972 – 1981 **Meldorfer Gelehrtenschule**, Abitur

## **Buchkapitel**

1. Lehrbuch der Phytomedizin (Hrsg. Poehling/Verreet), Kapitel: Tierische Schädlinge und ihre natürlichen Gegenspieler (April 2013). Ulmer Verlag, Stuttgart.
2. Guideline Biological Control in Horticulture (Editors Richter/Berndt/ Hommes), Chapters: Biological Control in Gerbera; Biological Control in Botanical Gardens: A case study (2009). Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft.

## **Publikationen (nur peer reviewed)**

1. Casas, J. & **Meyhöfer**, R. (1994) A method for the continuous laboratory-rearing of the complex *Phyllonorycter blancardella* Fabr. (Lep., Gracillariidae) and its parasitoids. Journal of Applied Entomology 117, 530-532.
2. **Meyhöfer**, R.; Casas, J. & Dorn, S. (1994) Host location by a parasitoid using leafminer vibrations: Characterizing the vibrational signals produced by the leafmining host. Physiological Entomology 19, 349-359.
3. **Meyhöfer**, R., Casas, J. & Dorn, S. (1997) Vibration-mediated interactions in a host-parasitoid system. Proceedings of the Royal Society London: Biological Sciences 264, 261-266.
4. **Meyhöfer**, R., Casas, J. & Dorn, S. (1997) Mechano- and chemoreceptors and their possible role in host location behaviour of *Sympiesis sericeicornis* (Hymenoptera: Eulophidae). Annals of the Entomological Society of America 90 (2), 208-219.
5. Casas, J.; Bacher, S.; Tautz, J.; **Meyhöfer**, R. & Pierre D. (1998) Leaf vibrations and air movements in a leafminer-parasitoid system. Biological Control, Theory and Application in Pest Management 11, 147-153.
6. Dorn, S.; Schumacher, P.; Abivardi, C. & **Meyhöfer**, R. (1999) Global and regional pest insects and their antagonists in orchards: spatial dynamics. Agriculture, Ecosystems & Environment 73, 111-118.
7. **Meyhöfer**, R. & Casas, J. (1999) Vibratory stimuli in host location by parasitic wasps. Journal of Insect Physiology 45 (11), 967-971.
8. Djemai, I.; Casas, J. & **Meyhöfer**, R. (2000) Geometrical games between a host and a parasitoid. American Naturalist 156 (3), 257-265.
9. **Meyhöfer**, R. & Hindayana, D. (2000) Effects of intraguild predation on parasitoid survival. Entomologia Experimentalis et Applicata 97, 115-122.

10. Hindayana, D.; **Meyhöfer**, R.; Scholz, D. & Poehling, H.-M. (2001) Interspecific competition between the hoverfly *Episyrphus balteatus* de Geer and other aphidophagous predators. *Biological Control*, 20, 236-246.
11. **Meyhöfer**, R. (2001) Intraguild predation by aphidophagous predators on parasitised aphids: the use of multiple video cameras. *Entomologia Experimentalis et Applicata*, 100, 77-87.
12. **Meyhöfer**, R. & Klug, T. (2002) Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hym., Aphidiidae): Mortality risks and behavioural decisions made under the risk of predation. *Biological Control*, 25, 239-248.
13. Langhof, M.; Gathmann, A.; Poehling, H.-M. & **Meyhöfer**, R. (2003) Impact of insecticide drift on aphids and their parasitoids: residual toxicity, persistence and recolonisation. *Agriculture, Ecosystems & Environment*, 94, 249-265.
14. Berndt, O.; **Meyhöfer**, R. & Poehling, H.-M. (2003) Propensity towards cannibalism among *Hypoaspis aculeifer* and *H. miles*, two soil dwelling predatory mite species. *Experimental and Applied Acarology*, 31, 1-14
15. Klug T., Gathmann A., Poehling H.-M. & **Meyhöfer** R. (2003) Area-dependent effects of landscape structure on the colonisation of spinach cultures by the silver Y moth (*Autographa gamma* L., Lepidoptera: Noctuidae) in Western Germany. *Landscape Management for Functional Biodiversity IOBC wprs Bulletin*, 26, 77-82.
16. Berndt, O.; **Meyhöfer**, R. & Poehling, H.-M. (2004) The edaphic phase in the ontogenesis of *Frankliniella occidentalis* and comparison of *Hypoaspis miles* and *Hypoaspis aculeifer* as predators of soil-dwelling thrips stages. *Biological Control*, 30, 17-24.
17. Berndt, O.; Poehling, H.-M. & **Meyhöfer**, R. (2004) Predation capacity of two predatory laelapid mites on soil-dwelling thrips stages. *Entomologia Experimentalis et Applicata*, 112, 107-115.
18. Wiethoff J., Poehling H.-M. & **Meyhöfer** R. (2004) Combining plant- and soil-dwelling predatory mites to optimise biological thrips control. *Experimental and Applied Acarology*, 34, 239-261.
19. Langhof M., **Meyhöfer** R., Poehling H.-M. & Gathmann A. (2005) Measuring the field dispersal of *Aphidius colemani* Viereck (Hymenoptera: Braconidae). *Agriculture, Ecosystems & Environment*, 107, 137-143.

20. Jazzar, C., **Meyhöfer**, R., Ebssa, L. & Poehling, H.-M. (2008) Two protagonists on aphidophagous patches: effects of learning and intraguild predation. *Entomologia Experimentalis et Applicata*, 127, 88-99.
21. Klug, T., **Meyhöfer**, R., Kreye, M. & Hommes M. (2008) Native parasitoids and their potential to control the invasive leafminer *Cameraria ohridella* DESCH. & DIM. (Lep.: Gracillariidae). *Bulletin of Entomological Research*, 98 (4), 379-387.
22. Berndt, O., **Meyhöfer**, R. (2008) Is it possible to control the greenhouse whitefly *T. vaporariorum* on cut gerbera with the parasitoid *Encarsia formosa*? , *BioControl*, 53, 751-762
23. **Meyhöfer**, R., Klug, T., Poehling, H.-M. (2008) Are landscape structures important for the colonization of spinach fields by insects? *Landscape Management for Functional Biodiversity IOBC wprs Bulletin*, 34, 69-72.
24. Klug T., **Meyhöfer** R. (2009): Performance of two *Trichogramma brassicae* strains under greenhouse and field conditions for biocontrol of the silver Y moth in spinach cultures. *Journal of Pest Sciences*, 82 (1), 73-79..
25. Siekmann G., **Meyhöfer** R., Hommes M. (2009): Testing mating disruption of the horse chestnut leafminer *Cameraria ohridella* (Lepidoptera: Gracillariidae) in field tents. *Journal of Pest Sciences*, 82, 129-136.
26. Tuerke M., Andreas K., Gossner M.M., Kowalski E., Lange M., Boch S., Socher S., Müller J., Prati D., Fischer M., **Meyhöfer** R., Weisser W.W. (2012): Are gastropods, rather than ants, important dispersers of seeds of myrmecochorous forest herbs?, *American Naturalist* 179 (1)
27. Nyasani J. O., **Meyhöfer** R., Subramanian S., Poehling H.-M. (2012): Effect of intercrops on thrips species composition and population abundance on French beans in Kenya, *Entomologia Experimentalis et Applicata*, 142: 236–246
28. Nyasani J. O., **Meyhöfer** R., Subramanian S., Poehling H.-M. (2013): Feeding and oviposition preference of *Frankliniella occidentalis* for crops and weeds in Kenyan French bean fields, *Journal of Applied Entomology*, 137, 204–213
29. Nyasani J. O., **Meyhöfer** R., Subramanian S., Poehling H.-M. (2013): Seasonal abundance of western flower thrips and its natural enemies in different French bean agroecosystems in Kenya, *Journal of Pest Science* 86 (3), 515-523
30. Muvea A.M., **Meyhöfer** R., Subramanian S., Poehling H.-M., Ekesi S., Maniania N.K. (2014): Colonization of onions by endophytic fungi and their impacts on the biology of *Thrips tabaci*, *PLOS ONE*

31. Ludwig M., **Meyhöfer** R. (2014): Impact of landscape on cabbage pests and natural enemies: Launching a system oriented plant protection approach, IOBC-WPRS Bulletin 107: 113-114
32. Ludwig M., Schlinkert H., **Meyhöfer** R. (2014): Impact of oilseed rape on initial colonisation and pre-harvest infestation of Brussels sprouts by cabbage aphid, cabbage whitefly and whitefly parasitoids, IOBC-WPRS Bulletin 107: 163-169
33. Eisele I., **Meyhöfer** R. (2015): Adding "personality" to biocontrol: Characterization and suitability of microsatellites for sib ship reconstruction in the aphid parasitoid *Diaeretiella rapae*, BioControl, 60 (2): 189-197
34. Gebauer K., Hemerik L., **Meyhöfer** R. (2015): Effects of climate change on pest-parasitoid dynamics: Development of a simulation model and first results, Journal of Plant Diseases and Protection (JPDP), 122 (1): 28–35
35. Muvea A.M., **Meyhöfer** R., Maniania N.K., Poehling H.-M., Ekesi S., Subramanian S. (2015): Behavioural responses of Thrips tabaci Lindemann to endophyte inoculated onion plants, Journal of Pest Science, 88 (3): 555-562
36. Nyasani J.O., Subramanian S., Poehling H.-M., Maniania N.K., Ekesi S., **Meyhöfer** R. (2015): Optimizing western flower thrips management on French beans by combined use of beneficials and Imidacloprid, Insects - Special Issue "Integrated Pest Management", 6, 279-296
37. Böckmann E., Hommes M., **Meyhöfer** R. (2015): Yellow traps reloaded: What is the benefit for decision making in practice?, Journal of Pest Science, 88 (2): 439-449
38. Böckmann E., **Meyhöfer** R. (2017): Sticky trap monitoring of a pest-predator system in greenhouse tomato crop, are available trap colours sufficient? Journal of Applied Entomology 141 (5), 339-351
39. Hondelmann P., Nyasani J. O., Subramanian S., **Meyhöfer** R. (2017): The importance of alternative host plants as sources of Western Flower Thrips in Kenyan French bean production areas. International Journal of Tropical Insect Science, 37, 2 (Special Issue: Thrips and Tospovirus Management in East Africa), 71-78.
39. Mureithi DM, Fiaboe KKM, Ekesi S, **Meyhöfer** R. (accepted): Important arthropod pests on leafy Amaranth (*Amaranthus viridis*, *A. tricolour* and *A. blitum*) and broad-leafed African nightshade (*Solanum scabrum*) with a special focus on host-plant ranges. Afr. J. Hort. Sci. (March 2017) 11:1-17.

40. Ludwig M., Schlinkert H., **Meyhöfer** R. (accepted): Wind modulated landscape effects on colonisation of Brussels sprout by insect pests and their syrphid antagonists, *Agricultural and Forest Entomology* (early view)
41. Nyasani J.O., Subramanian S., Orindi B., Poehling H.-M., **Meyhöfer** R. (2017): Short range dispersal of western flower thrips in field-grown French beans in Kenya. *International Journal of Tropical Insect Science*, 37, 2 (Special Issue: Thrips and Tosspovirus Management in East Africa), 79-88.
42. Laurenz S., **Meyhöfer** R. (2017): Banker plants promote functional biodiversity in cabbage, *Landscape management for functional biodiversity IOBC-WPRS Bulletin* Vol. 122, 2017 pp. 16-20.
43. Laurenz S., **Meyhöfer** R. (2017): Overwintering of *Encarsia tricolour* on the cabbage whitefly, *Landscape management for functional biodiversity, IOBC-WPRS Bulletin* Vol. 122, pp. 156-159.
44. Mworira J.K., Murungi L.K., Turoop L., **Meyhöfer** R. (2017) Plant Nutrition Impacts Host Selection in Red Spider Mites: A Mini-Review. *Afr. J. Hort. Sci.* (March 2017) 11:35-46