# INTRAGUILD INTERACTIONS OF APHIDOPHAGOUS PREDATORS IN FIELDS: EFFECT OF *COCCINELLA SEPTEMPUNCTATA* AND *EPISYRPHUS BALTEATUS* OCCURRENCE ON APHID INFESTED PLANTS

# Ammar ALHMEDI<sup>1</sup>, Frédéric FRANCIS<sup>1</sup>, Bernard BODSON<sup>2</sup> & Eric HAUBRUGE<sup>1</sup>

<sup>1</sup> Functional & Evolutionary Entomology <sup>2</sup> Crop Production Gembloux Agricultural University Passage des Déportes 2, BE-5030 Gembloux, Belgium

## SUMMARY

Intraguild relations between beneficial insects have become a major research topic in biological pest control. In order to understand the intraguild competitions between aphidophagous populations in natural conditions, a field experiment was carried out in the experimental farm of the Gembloux Agricultural University. As biological control of pests involve a community of diverse natural enemies, this experiment firstly aimed to assess the aphidophagous predator diversity and abundance in green pea (Pisum sativum) field and secondly to investigate the impact of the large natural occurrence of *C. septempunctata* on the aphidophagous beneficial dispersion and efficiency as aphid biological control agents in pea field. Visual observations were weekly performed throughout the 2006 growing season. The pea aphids were attacked by several predatory groups, mainly ladybird beetles and hoverflies. Higher densities of ladybirds and hoverflies were recorded in the beginning of July, associated with an aphid occurrence peak. Using net cage system in the field, the particular intraguild relations between added C. septempunctata or E. balteatus and the natural beneficial arrivals and dispersion were observed. The E. balteatus (eggs and larvae) presence inhibited other aphidophagous predators presence on the aphid infested plants. Lower abundance of E. balteatus was observed on aphid infested plants already colonised by C. septempunctata. To explore more accurately the oviposition and predation behaviours of ladybirds and hoverflies and to determine the chemical factors that could influence these behaviours, current researches are performed in laboratory and will be discussed to promote efficient biological control of aphids by natural enemies.

Key words: Acyrthosiphon pisum, diversity, biological control, ladybirds, hoverflies, intraguild interactions.

# INTRODUCTION

The aphid *Acyrthosiphon pisum* (Harr.) (Homoptera: Aphidae) is a common pest on Fabaceae such as clover, lucerne, and peas (Djafaripour, 1976; Suter, 1977) in occidental Europe and on alfalfa in North America (Roitberg and Myers, 1979; Gutierrez *et al.* 1980; Losey and Denno, 1998a). In almost every habitat where aphids occur a whole range of aphid antagonists can be found (Brown, 1997; Groeger, 1993; Nunnenmacher, 1998) and interspecific interactions between natural enemies can be expected. Fuller knowledge of food web interactions in agricultural systems is often limited due to the complexity of tri-trophic relationships and the number of species involved (Bascompte and Melian, 2005).

Intraguild predation (IGP) is a common and important species interaction in many ecological systems (Polis and Holt, 1992; Arim and Marquet, 2004). Effective implementation of biological control must take IGP into consideration (Harmon and

Andow, 2004; Koss and Snyder, 2005). Studies of intraguild predation (IGP) have increased over the last two decades, especially with respect to the analysis of failures in biological control programs. In many cases, IGP was found to reduce the efficacy of biological control due to heterospecific competition between predator species. However, IGP is defined as the killing and eating of species that uses similar, often limited resources, and thus are potential competitors (Polis *et al.* 1989). It is likely that IGP increases if the predators not only belong to the same guild but also share the same foraging habitat (Rosenheim *et al.* 1995; Losey and Denno, 1999). Other factors that affect the occurrence of IGP are relative body size, prey specificity and mobility of predators (Lucas *et al.* 1998), as well as the availability of extraguild prey (Polis *et al.* 1989; Lucas *et al.* 1998).

Rosenheim *et al.* (1993) reported that survival of the green lacewing *Chrysoperla carnea* decreased by 90% due to interference from indigenous predators. Also, parasitoid mummies were reported to be preyed upon by different predators (Ferguson and Stiling, 1996; Rosenheim, 1998), and in a field study more than 50% of exposed *Lysiphlebus fabarum* Marshall (Hymenoptera: Braconidae) mummies were destroyed by aphidophagous predators within a four day period (Meyhöfer and Hindayana, 2000).

Cannibalism is one of intraguild interactions that defined as the feeding activity on conspecifics and occurs in various species of insects (Fox, 1975; New, 1991). This phenomenon mainly occurs when food resource is scarce (Agarwala and Dixon, 1992; Branquart *et al.* 1997), although some reports show that cannibalism can also be observed even when food is abundant (Hassan, 1975; Phoofolo and Obrycki, 1998; Chapman *et al.* 1999). Riechert (1981) suggests that cannibalistic tendencies are genetically determined. As these tendencies, those that were reported by Branquart *et al.* (1997) for *E. balteatus* and by Agarwala and Dixon (1992) for coccinellid, *Adalia bipunctata* and *C. septempunctata* (Coleoptera: Coccinellidae). In reality, the incidence of cannibalism in syrphids in the field has never been measured (Branquart *et al.* 1997). Without direct observation, the possibility of high encounter rates and crowding effects is extremely low. However, different studies performed by Chandler (1968a, b) and Scholz and Poehling (2000) showed that cannibalism in *E. balteatus* in the field is an uncommon phenomenon.

In aphidophagous communities, ladybirds are important because of their voracity and diversity. IGP and cannibalism in ladybirds in the field are associated with a decrease in aphid abundance and an asymmetry in the vulnerability of the ladybirds (Hirnori and Katsuhiro, 1997; Sato, 1997). Through intraguild predation, predators can exacerbate prey outbreaks (Rosenheim *et al.* 1993, Snyder and Ives 2001) and thus indirectly increase herbivore damage to plants (Snyder and Wise 2001). Despite these limitations, generalist predators such as ladybirds have been reported to be successful control agents in cropping systems as different as vegetable gardens (Riechert and Bishop 1990, Snyder and Wise 2001) and rice (Settle *et al.* 1996, Fagan *et al.* 1998).

The objectives of present study were firstly designed to realise a systematic observations of aphids and their aphidophagous predators in green pea field and secondly to study the relative impacts of intraguild interactions in aphidophagous predators' guild on aphid biological control as well on the structure of predatory natural enemies, especially in case of ladybird *C. septempunctata* and hoverfly *E. balteatus* presence using field cages.

#### MATERIALS AND METHODS

#### Field visual observation experiments

We conducted two experimental plots established at green pea field (4h) to determine the aphids and their predatory insects frequenting on pea crop through 2006 growing season. Our field experiments were carried out in the Research Farm located on Gembloux Agriculture University in south part of Belgium. Experimental plots were designed of 10 m wide x 20 m long, with distance of 100 m apart the one from the other.

Green pea field was without insecticide treatment; whereas, herbicides and fungicides were applied, at pea field, as standard practice: nitrogen solution 39 in 13<sup>th</sup> of April; Lexus Xpe (Mersulfuron-methyl and Flupyrsulfuro) and Platform (Carfentrazone and Mecoprop-P) in 18<sup>th</sup> of April; Cycofix 720 G (Chlormequat) in 4<sup>th</sup> of May; nitrogen solution 39 in 5<sup>th</sup> of May; Ammonitrate 27<sup>th</sup> in 1<sup>st</sup> of June and Bravo (Chlorothalonil) and Opus (Epoxiconazole) in 2<sup>nd</sup> of June.

Once weekly between May and August 2006, 10 plants were randomly selected in each plot to assess visually the aphid and aphidophagous predator densities on each plant. All insects observed were identified in the laboratory. The hoverfly and ladybird collected larvae were reared in laboratory to identify the emerged adults.

# Field cage experiments

Field cage experiments were conducted from the  $1^{st}$  to  $11^{th}$  of July 2006 at the same green pea field to evaluate the effect of intraguild interactions in aphidophagous predators' guild: (1) on aphidophagous predators' structure on the aphid infested plants already treated by *C. septempunctata* adults and *E. balteatus* adults and larvae(2) on aphid biological control. However, 10 aphid infested plants (10 replicates) were caged in each fine mesh ( $\pm 0.5$  mm) cage (100 aphids, *Acyrthsiphon pisum*, per plant). The plants were approximately the same height, but the number of leaves slightly varied between plants. The pea aphid, *A. pisum*, used in our experiments was collected from pea field.

Our experimental cages (100x100x120 cm) made of wood; a sliding door provided access; the sides were covered by fine mesh ( $\pm 0.5$  mm) screening. The field cages were installed at pea field with distance 5m apart the one from the other.

Three treatments as well the control were applied: (1) in two cages: 20 female adults of *E. balteatus* (10 females per cage) were released in the 1<sup>st</sup> of July, (2) in two cages: 20 female adults of *C. septempunctata* were introduced (10 females per cage) in the 1<sup>st</sup> of July, (3) in two cages: 100 larvae of *E. balteatus* were inserted in each cage at the 3<sup>rd</sup> of July (10 larvae per plant), (4) in two cages (control treatment): these cages were only consisted of 10 aphid infested plants in each cage (without aphidophagous insects) at the 3<sup>rd</sup> of July. The eggs laid in the treatments (1 and 2) were daily counted. All cages were removed at the same time in the 4<sup>th</sup> of July. Daily from 4<sup>th</sup> to 11<sup>th</sup> of July, aphid and their predatory natural enemy densities were visually assessed, so the collected hoverfly, ladybird and green lacewing larvae were reared in laboratory to identify the emerged adults.

Test Predators: the ladybird *Coccinella septempunctata* adults were collected from green pea field and reared in incubator device for two generations, at 22°C and photoperiod 16:8 L:D, and were provided with bee-collected pollen, crystalline sugar placed on a cover bottle lids on the floor of the culture box, and water on a soaked pad of cotton in a cover bottle lids. The pollen and water changed once per

week. We collect the batch of eggs regularly and with synchronous larva emergence to within 4-5 day. Adults were fed on *Megoura viciae* aphids on broad been and pollen in box of 10 x 30 x 10 cm. Larvae were also fed on *M. viciae* cultured on broad been in similar boxes.

The common hoverfly *Episyrphus balteatus* adults were reared in a culture room at 23±1°C and photoperiod 16:8 L:D. Larvae were fed on *M. viciae* cultured on broad been. The culturing system consist of adult cages (60x100x100 cm) made of wood; a sliding door provided access. Adults were provided with bee-collected pollen, crystalline sugar placed in Petri dish lids on the floor of the cage, and water on a yellow soaked sponge of cotton in a conical flask. The pollen and water changed every 2-4 days. To supply aphids as food for larvae, broad beans were sown densely (9 seeds) in small pots (6 pots per pack) in the culture room. To have enough flies when necessary, adult females in the mass culture were stimulated to oviposit by presenting out pots of broad bean infested with *M. viciae*.

# Data analysis

Minitab 14.2 software was used in statistical analyses of field cage data's. We firstly used one way ANOVA to analyse the variance between the different treatments. To analyze the effect of the previous introduction of *C. septempuncata* and *E. balteatus* on arrival aphidophagous predators, Dunnett test was used to compare the applied treatments with control (P<0.05). Prior to the analyses, data were checked for equal variances and normality, and were transformed if necessary. Student-Newman-Keuls test was used to compare the impact of intraguild interactions on aphid biological control.

#### RESULTS

## **Field visual observation**

# Diversity and abundance of aphid and related aphidophagous predators through growing season

Pea aphid, *A. pisum*, was the only species recorded infesting the pea crop in field. Whereas, several predatory aphidophagous groups were observed attacking pea aphid. In this area, ladybird beetles and hoverflies were the most abundant (respectively 55.6% and 35.6%). However, higher density of *C. septempunctata* was recorded with 84.0% of total ladybirds. Similarly in hoverfly group, *E. balteatus* was most abundant with 62.5% of total. Lower densities of both anthocorid and chrysop were found (6.7% and 2.2% respectively). These last groups were represented by only one species in each family, *Orius minutus* (anthocorid) and *Chrysoperla carnea* (chrysop), Table (1).

Table 1. Abundance (mean number/ $m^2$ /week) of aphids and related predators collected at green pea plots

		0/+	01++
	Mean number	%*	%**
Aphididae			
Acyrthosiphon pisum	591.67		
Aphidophagous predators			
Coccinellidae	8.33		55.57
Coccinella septempunctata	7.00	84.00	
Harmonia axyridis	1.00	12.00	
Propylea 14-punctata	0.33	4.00	
Syrphidae	5.33		35.56
Episyrphus balteatus	3.33	62.50	
Melanostoma mellinum	1.00	18.75	
Syrphus ribesii	0.33	6.25	
Ścaeva pyrastri	0.67	12.50	
Anthocoridae	1.00		6.67
Orius minutus	1.00	100.00	
Chrysopidae	0.33		2.20
Chrysonerla carnea	0 33	100.00	

\* Relative proportion of each studied specie in each family

\*\* Relative proportion of each aphidophagous family

### Field cage experiments

# *Effect of the previous introduction of C. septempuncata and E. balteatus on aphidophagous predators' arrival*

Dunnett test showed that the presence of *E. balteatus* larvae was significantly (P=0.003) inhibited other aphidophagous predators presence on the treated plants compared to control, while beneficial species numbers were significantly higher on the control plants.

In *C. septempunctata* adult, lower abundance of *E. balteatus* was observed on aphid infested plants already colonised by *C. septempunctata* (Table 2). However, no significant difference of arrival aphidophagous predator number was observed between both *C. septempunctata* and *E. balteatus* adult treatment compared to control (P=0.233 and P=0.079 respectively).

 Table 2. Abundance of aphidophagous predators (mean number/plant/day) observed according to different treatments from 05.07 to 11.07.2006

	Treatment			
	C. septempunctata (adult)	<i>E. balteatus</i> (adult)	<i>E. balteatus</i> (larva)	Control
Coccinellidae				
Ladybird eggs	0.00	0.00	0.00	0.00
Coccinella septempunctata	0.38	0.16	0.04	0.29
Harmonia axyridis	0.01	0.00	0.00	0.02
Syrphidae				
Hoverfly eggs	0.04	0.04	0.01	0.01
Episyrphus balteatus	0.01	0.05	0.34	0.04
Scaeva pyrasri	0.01	0.00	0.00	0.01
Sphaerophoria scripta	0.00	0.00	0.00	0.02
Melanostoma mellinum	0.02	0.00	0.00	0.01
Platycheirus scutatus	0.00	0.00	0.00	0.01
Chrysopidae				

	Treatment			
	C. septempunctata (adult)	E. balteatus (adult)	<i>E. balteatus</i> (larva)	Control
Green lacewing eggs	0.03	0.02	0.00	0.02
Chrysoperla carnea	0.00	0.01	0.00	0.00
Chrysopa perla	0.00	0.00	0.00	0.01
Anthocoridae				
Anthocoris nemorum	0.00	0.00	0.01	0.00
Aphidophagous species number	7	5	4	10

### Impact of the intraguild interactions on aphid biological control

Although lower number of arrival aphidophagous predators observed in *E. balteatus* adult and larva presence, aphid colonies were significantly controlled, mainly by *E. balteatus* larvae (F=44.28 and P<0.001) compared to both aphid infested plants already colonised by *C. septempunctata* and control. While, no significant difference of aphid biological control was found between *C. septempunctata* and control treatments (P>0.05).



Figure 1. Effect of intraguild interactions in aphidophagous predator guild on aphid biological control (mean number/plant/day)

386

# Impact of the intraguild interactions on eggs laid by *E. baltatus* and *C. septem-punctata* females

The ladybird larvae observed at green pea plots through cage experiments were in the 4<sup>th</sup> instars. Observation data's were showed that eggs laid were strongly reduced after one day of cages removed at 5<sup>th</sup> of July in both *C. septempunctata* and *E. balteatus* adulte treatments (Fig. 2). However, mean number of *C. septempunctata* eggs was reduced from 2.85 eggs per plant at 4<sup>th</sup> July to 0 egg after one day of cages removed, while the mean number of *E. balteatus* eggs was reduced from 2.45 to 0.3 eggs per plant.



Figure 2. Impact of intraguild interactions in aphidophagous guild on eggs laid by *C. septem-punctata* and *E. balteatus* females

### DISCUSSION

Field observation data's were showed only one aphid species, *A. pisum*, infesting green pea crop throughout growing season, whereas several aphidophagous predatory groups, mainly ladybird beetles and hoverflies, were observed attacking this aphid species. However, the native ladybird *C. septempunctata* and the common hoverfly *E. balteatus* were the most abundant among the aphidophagous predatory species recorded at green pea plots. The dominance of *C. septempunctata* and *E. balteatus* reported here was observed previously in the study by Francis *et al.* (2002) in carrot (*Daucus carota* L.) and broad bean fields (*Vicia fabae* L.) which was realised in South part of Belgium.

Higher densities of ladybirds and hoverflies were recorded in the beginning of July, associated with an aphid occurrence peak. These densities as well other aphido-phagous predators' guild caused an immediate decrease in the aphid population growth rate that remained constant at green pea plots. Consequently, despite evidence of intraguild interactions observed in field cage experiments, aphid biological control was slightly influenced, where aphid population numbers were almost remained constant throughout the cage experiment period. An additive effect is the result of two natural enemies that do not interact so that the total level of prey mortality is equivalent to their individual effects on the prey population (Ferguson and Stiling, 1996; Losey and Denno, 1998b). The effective control of aphid observed in *E. balteatus* larvae treatments, whereas the population density of *A*.

*pisum* in *C. septempunctata* presence was not significantly different from the control (Hindayana, 2001).

In our experimental cages, intraguild interactions in aphidophagous predators' guild were assessed by (1) the arrival beneficial numbers in each treatment after cage removed, (2) the impact of natural enemies after cage remove time on the egg number laying by C. septempunctata and E. balteatus females. Lesser species numbers were arrived towards aphid infested plants already colonised by E. balteatus larvae in comparison to both C. septempunctata adults and control treatments. The presence of natural enemies in a certain habitat not only reduces the prey population but also changes its distribution (Sih, 1987). According to Hindayana et al. (2001), E. balteatus L2 was the first developmental stage that was able to kill larvae of other aphidophagous predators such as C. septempunctata, Chrysoperla carnea and Aphidoletes aphidimyza. This ability was mainly due to well-developed mouthparts of L2, with the triangular sclerites already present (Tinkeu and Hance, 1998); Whereas, E. balteatus L3 produced considerably more repellent slime to other aphidophagous predators such C. carnea (Hindayana et al. 2001) than the younger instars (L2 > L1), and had a higher mobility. Slime is used by syrphid larvae as sticky salivary glue to capture prey and as a defensive secretion (Eisner, 1971). Consequently, they able to attack opponents or defend themselves better against attacks by other predators.

Since, coccinellid larvae, such *C. septempunctata*, excreted orally a black defense fluid containing alkaloids were previously found effective against larvae of *E. balteatus*. (Ceryngier and Hodek, 1996), lower abundance of *E. balteatus* was observed on aphid infested plants already colonised by *C. septempunctata*. In addition, *E. balteatus* and *C. carnea* larvae were previously found as IG prey in confrontations with L4 or adults of *C. septempunctata* (Hindayana *et al.* 2001).

Aphidophagous ladybird larvae visually observed at green pea field through cage remove time were in the 4th instar. Therefore, as the relationship between eggs laid, by both *C. septempunctata* and *E. balteatus* females, and the number of young larvae resulting from them in our cage experiments, it can be concluded that egg stage is particularly vulnerable to IGP. Similar observation in laboratory conditions was observed by Hindayana (2001).

We were evaluated intraguild interactions in aphidophagous predators' guild by field cage experiments' use (e.g. Rosenheim *et al.* 1993; Snyder and Ives 2001; Hoogendoorn and Heimpel, 2004). So to explore more accurately the intraguild interactions in real field conditions, molecular gut-content analyses are a very promising method for the quantification of IGP within the field. Therefore, application of PCR gut-content analyses to IGP research can provide biological control researchers with a better understanding of natural enemy interactions within a community.

# ACKNOWLEDGMENT

The authors are thankful to Prof. Bernard Bodson, Department of Crop Science (FuSaGx) for the experimentation field availability. We are most grateful to the undergraduate research technician Didier Conoir for their valuable help during experimentation.

# REFERENCES

AGARWALA B.K. & DIXON A.F.G. (1992). Laboratory study of cannibalism and interspecific predation in ladybirds. Ecological Entomology. **17**:303-309.

- ARIM M. & MARQUET P.A. (2004). Intraguild predation: A widespread interaction related to species biology. Ecology Letters. 7:557-564.
- BASCOMPTE J. & MELIAN C.J. (2005). Simple trophic modules for complex food webs. Ecology. 86:2868-2873.
- BRANQUART E., HEMPTINNE J.L., BAUFFE C. AND BENFEKIH L. (1997). Cannibalism in Episyrphus balteatus (Diptera: Syrphidae). Entomophaga. 42:145-152.
- BROWN M.W. (1997). Temporal changes in the aphid predator guild in eastern North America. Proc. Workshop on arthropod pest problems in pone fruits production. Einsiedeln, Switz.
- CERYNGIER P. & HODEK I. (1996). Enemies of Coccinellidae, pp. 319-350. In: I. Hodek and Honék, A. (eds.): Ecology of Coccinellidae. Kluwer Academic Publishers, The Netherlands.
- CHANDLER A.E.F. (1968a). Some factors influencing the occurrence and site of oviposition by aphidophagous Syrphidae (Diptera). Annals of Applied Biology. 61:435-446.
- CHANDLER A.E.F. (1968b). The relationship between aphid infestations ad oviposition by aphidophagous Syrphidae. Annals of Applied Biology. 61:425-434.
- CHAPMAN J.W., WILLIAMS T., ESCRIBANO A., CABALLERO P., CAVE R.D. & GOULSON D. (1999). Agerelated cannibalism and horizontal transmission of a nuclear polyhedrosis cirus in larval *Spodoptera frugiperda*. Ecological Entomology. 24:268-275.
- DJAFARIPOUR M. (1976). Wanderung-, Probe- und Seitenwechsel Verhatlen bei der Wirtswahl von zwei Aphiden-arten, *Acyrthosiphon pisum* (Harr.) *und Megoura viciae* (Buckt.), und einer Coccidae, Saissetia oleae (Bern.). Ph.D. thesis, University of Bonn, Germany.
- EISNER T. (1971). Chemical ecology: on arthropods and how they live as chemists. Verhandlungen der deutschen zoologischen Gesellschaft. 65:123-137.
- FAGAN W.F., HAKIM A.L., ARIAWAN H. & YULIYANTININGSIH S. (1998). Interactions between biological control efforts and insecticide applications in tropical rice agroecosystems: the potential role of intraguild predation. Biological Control. 13:121-126.
- FERGUSON K.I. & STILING P. (1996). Non-additive effects of multiple natural enemies on aphid populations. Oecologia. 108:375-379.
- Fox L.R. (1975). Cannibalism in natural population. Annual Review of Ecology and Systematics. 6:87-106.
- FRANCIS F., COLIGNON P., VANHAELEN N., GASPAR C. & HAUBRUGE E. (2002). A two year assessment of aphidophagous predator populations in Belgian vegetable crops. 8th International Symposium on Ecology of Aphidophaga, 1-6 septembre, SUMMARYs, Ponta Delgata: 76.
- GROEGER U. (1993). Untersuchungen zur Regulation von Getreideblatlauspopulationen unter dem Einfluss der Landschaftsstruktur. Agrarökologie. 6:1-169.
- GUTIERREZ A.P., SUMMERS C.G. & BAUMGAERTNER J. (1980). The phenology and distribution of aphids in California alfalfa as modified by ladybird beetle predation (Coleoptera: Coccinellidae). Canadian Entomologist. 112: 489-495.
- HARMON J.P. & ANDOW D.A. (2004). Indirect effects between shared prey: Predictions for biological control. Biological Control. 49: 605-626.
- HASSAN S.A. (1975). Über die Massenzucht von Chrysopha carnea. Zeitschrift Angewandte Entomologie. 7: 310-315.
- HINDAYANA D. (2001). Resource exploitation by *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) and intraguild predation. Ph.D. thesis, University of Hanover, Germany, 95p.
- 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. Biological Control. 20: 236-246.
- HIRONORI Y. & KATSUHIRO S. (1997). Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga. **42**: 155-165.
- HOOGENDOORN M. & HEIMPEL G.E. (2004). Competitive interactions between an exotic and a native ladybeetle: a field cage study. Entomologia Experimentalis et Applicata. 111: 19-28.
- Koss A.M. & SNYDER W.E. (2005). Alternative prey biocontrol by a guild of generalist predators. Biological Control. **32**: 243-251.
- LOSEY J.E. & DENNO R.F. (1998a). The escape response of pea aphids to foliar-foraging predators: factor affecting dropping behavior. Ecological Entomology. 23: 53-61.
- LOSEY J.E. & DENNO R.F. (1998b). Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology. **79** (6): 2143-2152.

- LOSEY J.E. & DENNO R.F. (1999). Factors facilitating synergistic predation: the central role of synchrony. Eccological Application. 9 (2): 378-386.
- LUCAS E., CODERRE D. & BRODEUR J. (1998). Intraguild predation among aphid predators: Characterization and influence of extraguild prey density. Ecology. **79** (3): 1084-1092.
- MEYHOFER R. & HINDAYANA D. (2000). Effects of intraguild predation on aphid parasitoid survival. Entomologia Experimentalis et Applicata. **97**: 115-122.
- New T.R. (1991). Insects as predators. The New South Wales Univ. Press., New South Wales, Australia.
- NUNNENMACHER L. (1998). Blattläuse auf Kopfsalat und deren Kontrolle durch gezielte Beeinflussung der Lebensgrundlagen ihrer Prädatoren. Ph.D. thesis, University of Bayreuth, Germany.
- PHOOFOLO M.W. & OBRYCKI J.J. (1998). Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. Entomologia Experimentalis et Applicata. 89: 47-55.
- POLIS G.A. & HOLT R.D. (1992). Intraguils predation: The dynamics of complex trophic interactions. Trends in Ecology and Evolution. 7: 151-154.
- 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 of Ecology and Systematics. 20: 297-330.
- RIECHERT S.E. (1981). The consequences of being territorial: spider, a case study. American Naturalist. 117: 871-892.
- RIECHERT S.E. & BISHOP L. (1990). Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology. **71**:1441-1450.
- ROITBERG B.D. & MYERS J.H. (1979). Behavioural and physiological adaptations of pea aphids (Homoptera: Aphididae) to high ground temperatures and predator disturbance. Canadian Entomologist. 111: 515-519.
- ROSENHEIM J.A. (1998). Higher-order predators and the regulation of insect herbivore populations. Annual Review of Entomology. 43:421-447.
- ROSENHEIM J.A., KAYA H.K., EHLER L.E., MAROIS J.J. & JAFFEE B.A. (1995). Intraguild predation among biological control agents: theory and practice. Biological Control. 5:303-335
- ROSENHEIM J.A., LAWRENCE R., WILHOIT R. & ARMER C.A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia. **96**:439-449.
- SATO S. (1997). Effects of cannibalism and intraguild predation on the ladybird assemblage. Ms Thesis, Yamagata University (in Japanese).
- SCHOLZ D. & POEHLING H.M. (2000). Oviposition site selection of Episyrphus balteatus. Entomologia Experimentalis et Applicata. 94:149-158.
- SETTLE W.H., ARIAWAN H., ASTUTI É.T., CAHYANA W., HAKIM A.L., HINDAYANA D., LESTARI A.S., PAJARN-INGSIH & SARTANTO (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology. **77**:1975-1988.
- SIH A. (1987). Predators and prey lifestyles: an evolutionary and ecological overview. pp. 203-224. In: Kerfoot, W. C. and Sih, A. (eds.). Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, London, UK.
- SNYDER W.E. & Ives A.R. (2001). Generalist predators disrupt biological control by a specialist parasitoid. Ecology. 82:705-716.
- SNYDER W.E. & WISE D.H. (2001). Contrasting trophic cascades generated by a community of generalist predators. Ecology. 82:1571-1583.
- SUTER H. (1977). Populationsdynamik der Erbsenblattlaus (Acyrthosiphon pisum Harr.) und Ihrer Antagonisten. Ph.D. thesis, University of Zürich, Switzerland.
- TINKEU L.N. & HANCE T. (1998). Functional morphology of the mandibles of the larvae of *Episyrphus balteatus* (De Geer, 1776) (Diptera: Syrphidae). Journal of Insect Morphology and Embryology. 27(2):135-142.