Resource exploitation by *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) and intraguild predation

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Zusammenfassung

Dadan Hindayana, 2001: "Ressourcennutzung von *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) und Intraguild predation"

Zur "Ressourcennutzung von *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) und Intraguild predation" wurden Untersuchungen im Labor durchgeführt. Ziel war es zu charakterisieren, (i) welcher Blattlaus-Wirtspflanze-Komplex eine optimale Entwicklung von *E. balteatus* gewährleistet, (ii) welche Faktoren zu Kannibalismus bei *E. balteatus*-Individuen führen, (iii) unter welchen Bedingungen es zu Intraguild predation zwischen *E. balteatus* und anderen aphidophagen Prädatoren kommt und (iv) inwiefern *E. balteatus* in Kombination mit anderen Blattlausprädatoren die Populationsentwicklung der Blattläuse und ihre Dispersionsdynamik beeinflusst.

Mit der Kartoffelblattlaus *Aulacorthum solani* Kaltenbach als Beute erhöhte sich die Überlebensrate von *E. balteatus* signifikant im Vergleich zu anderen Beutetieren. Darüber hinaus wurden eine erhöhte Fekundität und eine höhere Überlebensrate festgestellt, wenn die Wirtspflanzen (Gurke) der Blattlaus *A. solani* zusätzlich gedüngt wurden. Dabei zeigte sich, dass die erste trophische Ebene in der Nahrungskette einen indirekten Einfluss auf die Eignung von Beutetieren für *E. balteatus* hat. Im Fall der Blattläuse profitierten die Prädatoren vom optimalen Ernährungszustand der Herbivoren.

E. balteatus zeigte kein ausgeprägtes kannibalistisches Verhalten. Nur wenn keine Alternativnahrung vorhanden war bzw. wenn die Altersstruktur der Syrphidenlarven sehr heterogen war, fand Kannibalismus statt. Eier und das erste Larvenstadium wurden oft von älteren Larven gefressen.

Bei den Wechselwirkungen zwischen *E. balteatus*-Larven und anderen Blattlausprädatoren spielte vor allem die Größe der jeweiligen Gegner eine Rolle. In der Regel waren größere Entwicklungsstadien kleineren überlegen. Eier und Erstlarvenstadien (L$_1$) von *E. balteatus* wurden häufig von anderen Prädatoren gefressen. Puppen von *E. balteatus* wurden nur von *C. carnea*-Larven angegriffen. Die Interaktionen zwischen *E. balteatus* und *Aphidoletes aphidimyza* Rondani waren immer asymmetrisch. *E. balteatus* war *A. aphidimyza* in jedem Fall überlegen. Die Interaktionen waren in kleinen Arenen und bei Mangel an Alternativnahrung besonders ausgeprägt.

Die Blattlaus *Acyrthosiphon pisum* Harris reagierte in Gegenwart von *E. balteatus* und in Gegenwart einer Kombination aus zwei Räubern mit verstärkten Fluchtreaktionen. Als Folge veränderte sich die Verteilung der Blattläuse von stark geklumpt zu zufällig. Da *A. pisum* wie viele andere Blattläuse ein Vektor für Viruskrankheiten ist, könnte es bei der Schädlingsbekämpfung mithilfe von Prädatoren bei erhöhter Dispersion der Blattläuse zu verstärkten Virusinfektionen an den Pflanzen kommen.

Die Ergebnisse werden im Zusammenhang mit der Optimierung der biologischen Schädlingsbekämpfung diskutiert.

Keywords: *Episyrphus balteatus*, direct and indirect effects, prey suitability, efficiency of conversion ingested, intraguild predation, dispersal of prey, aggregation index, biological control, cannibalism.

Abstract

Dadan Hindayana, 2001: Resource exploitation by *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) and intraguild predation

All experiments on resource exploitation by *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) and intraguild predation between antagonists were conducted in the laboratory. The aim of this study was to investigate (i) the main factors that influence the suitability of prey for *E. balteatus*, (ii) the cannibalistic behavior of *E. balteatus*, (iii) the behavior of *E. balteatus* and its interaction with three other aphidophagous predators and (iv) the combined effect of *E. balteatus* and other aphidophagous predators on the population development and dispersal of aphids.

Episyrphus balteatus survival was enhanced and females laid numerous eggs when larvae were reared with *Aulacorthum solani* Kaltenbach as prey, especially when the host plants were fertilized cucumber plants. It seems that on the first trophic level the host plant has an indirect impact on the fitness of *E. balteatus*. An optimal nutritional condition of the herbivore had a positive effect on the predators.

Cannibalism in *E. balteatus* occurs only in the absence of prey and when the age structure among the syrphid larvae population was heterogeneous. Eggs and first instar larvae were extremely vulnerable in regard to larger conspecific larvae.

The outcome of interactions between *E. balteatus* larvae and the other predators mainly depends on the body size of the competitors. Large individuals behaved as intraguild predator while small individuals became intraguild prey. Eggs and young instars of *E. balteatus* were extremely vulnerable to predation by all other predators, while pupae of *E. balteatus* were only preyed upon by the larvae of *C. carnea*. Interactions between *Aphidoletes aphidimyza* Rondani and *E. balteatus* were asymmetric and always favored the latter. Neither the presence of aphids as extraguild prey nor a bigger arena prevented eggs and young instar larvae of *E. balteatus* from being affected by intraguild predation. However, the frequency of predation on older developmental stages of *E. balteatus* was significantly reduced.

Single *E. balteatus* larvae or combinations of *E. balteatus* with either *Chrysoperla carnea* Stephens or *Coccinella septempunctata* L. caused dispersion of the aphid *Acyrthosiphon pisum* Harris. Therefore *A. pisum* dispersed randomly within and among plants in the presence of any predator. Since *A. pisum* is a vector for the pea enation mosaic virus and easily drops from the host plant in the presence of predators, aphid control with natural enemies can have negative side effects on disease control.

In this thesis, the results are discussed further in the context of biological control efforts.

Key words: *Episyrphus balteatus*, direct and indirect effect, prey suitability, efficiency of conversion ingested, intraguild predation, dispersal of prey, aggregation index, biological control, cannibalism.

dedicated to:

my parents

my wife Nita Rosnita

my children Daffa and Farhan

my parents in-law

the whole family

Contents

1. Introduction

The hoverfly *Episyrphus balteatus* DeGeer (Diptera: Syrphidae) belongs to the subfamily of Syrphinae (Stubbs and Falk, 1983). The larvae of this species are predators on more than 100 species of aphids worldwide (Sadeghi and Gilbert, 2000b). *E. balteatus* is the most common hoverfly in central Europe (Tenhumberg and Poehling, 1991), in the UK (Stubbs and Falk, 1983; Gilbert, 1993) and in South Asia (Kalshoven, 1981). Predominance of *E. balteatus* in the natural habitat (Tenhumberg and Poehling, 1995) is due to the female oviposition behavior. Eggs are always laid near aphid colonies (Chandler, 1968a and 1968 b; Scholz and Poehling, 1999) and the emerging young larvae locate immediately the food sources (Scholz and Poehling, 1999). Therefore, *E. balteatus* has the potential to play an important role in the biological control of aphids in natural agroecosystems. Several examples show high efficacy of *E. balteatus* as predator, particularly in regard to cereal aphids (Dean, 1982; Ankersmith *et. al*., 1986; Chambers and Adams, 1986; Poehling, 1988; Entwistle and Dixon, 1989; Tenhumberg and Poehling, 1995), *Myzus persicae* Sulzer (Homoptera: Aphididae) in tobacco agroecosystems (Kalshoven, 1981) and *Brevicoryne brassicae* L. (Homoptera: Aphididae) on *Brasicca* plants (Pollard, 1971).

Apart from being an important group of naturally occurring aphid predators in field crops, syrphids can be used like any other natural enemy for biological control (Kreß, 1996; Schneller, 1997b). Recently *E. balteatus* was considered for aphid biological control of the black bean aphid, *Aphis fabae* Scopoli (Homoptera: Aphididae), the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae) (Ministerium für Ländlichen Raum, Ernährung, Landwirtschaft und Forsten Baden-Württemberg, 1995), or aphids on rose plants in greenhouses (Kreß, 1996). A prerequisite for the acceptance of natural enemies for inundative release in greenhouses is a high and constant quality (efficacy) of the biological control agent at a reasonable price (Van den Bosch *et al*., 1982; Krieg and Franz, 1989; Van Driesche, 1996; Flint and Dreistadt, 1998; Ehler, 1998). Therefore, mass rearing techniques must be developed which guarantee short developmental time, high survival rates and fecundity of *E. balteatus*. After

realizing that the mating behavior was a major obstacle in laboratory rearing of *E. balteatus* (Tanke, 1976), laboratory cultures were established in different working groups. However, no detailed studies were set up to optimize the rearing conditions by selecting suitable plant-aphid combinations although very often high mortality rates and low fecundity could be observed. This issue will be discussed in the first chapter. The experiments were divided into three parts. In the first set of experiments, five different aphid species representing three different herbivore feeding niches for *E. balteatus*, i. e. vegetables, cover crops, and cereal crops, were chosen. All aphid species were reared on their respective host plants without additional fertilizer. In a second set of experiments, the indirect effect of the host plant on syrphid fitness was estimated by comparison of the development of one aphid species, *Aulacorthum solani* Kaltenbach (Homoptera: Aphididae), on different host plants, i.e. potato and cucumber plants. Since it is documented that the nutritional value of herbivore for natural enemies can be influenced by the nutrient status of the host plants (Hodek, 1967 and 1993; Rüzicka, 1978; Ruberson *et al.*, 1989; Jørgensen and Lövi, 1999), a possible indirect effect of the host plants´ nutritional value on syrphid fitness was investigated in a third set of experiments.

Apart from prey effects, intra- and interspecific competition may be an important regulation factor in predator performance under rearing or application conditions. The most important intraspecific effect is cannibalism. Cannibalism occurs in various species of insects (Fox, 1975; New, 1991) and has twofold consequences (Fox, 1975). When food is plentiful, cannibalism is rare but if it occurs, it may result in death of individuals which would otherwise survive, and is then detrimental, particularly in mass rearing systems that can only be run economically with high output rates. However, under more natural conditions, especially when normal prey items are scarce, cannibalism can ensure the survival of a population which might otherwise become locally extinct, and in that case it has a positive adaptational value and is a stabilizing factor in the population dynamics (Taylor, 1984). Chapter 3 will deal with some aspects of cannibalism in *E. balteatus*.

The success of biological control efforts was initially determined by two major factors, i.e. host suitability and ecological requirements of the antagonist (Ehler, 1998; Greathead and Greathead 1992). However, over the last two decades many experts assumed that interspecific interactions among natural enemies (named intraguild predation [IGP]) play a critical role for the success of biological control efforts (Rosenheim, 1998; Janssen *et al*., 1998; Polis *et al*., 1989. Rosenheim *et al*., 1993 and 1995; Brodeur and Rosenheim, 2000). As a result the amount of studies of IGP increased constantly, and not only those of IGP between predatory insects (Sengonca and Frings, 1985; Polis *et al*., 1989; Rosenheim *et al*., 1993; Lucas *et al*., 1998; Phoofolo and Obrycki, 1998; Snyder and Wise, 1999), but also those of IGP between parasitoids and predators (Ferguson and Stiling, 1996; Rosenheim, 1998; Meyhöfer and Hindayana, 2000; Brodeur and Rosenheim, 2000). On the other hand the behavior of *E. balteatus* in interspecific relationships with other predators and their combined effect on the population growth of aphids has been neglected so far. For this reason chapter 4 will discuss intraguild predation between *E. balteatus* and other aphidophagous predators in the laboratory. The outcome of IGP was studied both in the presence and in the absence of the extraguild prey *Acyrtosiphon pisum* Harris (Homoptera: Aphididae).

Finally, intraguild predation among natural enemies can influence biological control efforts. Theoretically the combined release of two predators can result in three different effects on the pest population, i.e. synergistic, additive or non-additive effects (Ferguson and Stiling, 1996). However, the presence of natural enemies does not only reduce the prey population (direct effect), but can also change the distribution of the prey in the natural habitat (Sih, 1987). As a result, the spread of plant viruses transmitted by the prey can be influenced by intraguild predation. So chapter 5 will deal with the effect of the combined release of *E. balteatus* with *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) or with *Chrysoperla carnea* Stephens (Neuroptera: Crysophidae) on the population growth of the aphid, *A. pisum*, and the changes in prey distribution. As each chapter of this thesis can be used as a paper for publication, certain overlaps, especially in the introduction and discussion, were inevitable.

2. Host plants - aphids - predator: tritrophic effects on the life history of the hoverfly *Episyrphus balteatus* DeGeer (Diptera: Syrphidae)

2.1. Introduction

Episyrphus balteatus DeGeer (Diptera: Syrphidae) is a primary predator and occupies the third trophic level in the food chain hierarchy. On this level prey suitability depends on more complex factors than the host plant choice by herbivores (Hodek, 1993). Food suitability can be affected not only by the prey itself (direct effects), but also by the condition of the host plants (indirect effects). The direct effects can reduce the suitability of prey to predator due to a bitter taste produced by the prey itself as a defense strategy against predators (Berenbaum, 1995). The indirect effects obtained from the host plants and their influence on predators depend on substance ingested by the herbivore (secondary plant compounds). Some studies show that indirect effects play an important role for the prey suitability. *Metasyrphus corrolae* Fabricius (Diptera: Syrphidae) larvae cannot complete their development on *Aphis sambuci* Linnaeus (Homoptera: Aphididae) which contains the glucosid sambunigrin of its host plant *Sambucus nigra* (Rüzicka, 1978). Hodek (1967 and 1993) reports similar effects of *A. sambuci* on the development of coccinellidae. Both the longevity and effectiveness of the parasitoid *Edovum puttleri* Grissell (Hymenoptera: Eulophidae) are reduced when fed on eggs of Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) which were reared on potato plants resistant against aphids (Ruberson et al., 1989). Consumption rates of the carabid *Harpalus affinis* (Schrank) (Coleoptera: Carabidae) decrease if the predator was reared on caterpillars *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) that fed on proteinase inhibitor-containing diets (Jørgensen and Lövi, 1999). Hilbeck *et al.* (1998) also show that the mortality rate of *C. carnea* larvae fed on European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), reared on transgenic Bt corn is much higher than that of lepidopteran larvae reared on normal cultivar. Such secondary plant substances like alcaloids or induced enzym inhibitors often

caused detrimental effects on predators or parasitoids of herbivores. On the other hand the plant´s nutritional status can improve food quality of prey items particularly with nitrogen fertilization. On bean plants enhanced fecundity and faster development of the parasitoid *Chrysocharis oscinidis* Ashmead (Hymenoptera: Eulophidae) attacking the leafminer *Liriomyza trifolii* Burgess (Diptera: Agromyzidae) can be induced by nitrogen supply (Kaneshiro and Johnson, 1996). Moreover, Loader and Damman (1991) report that *Pieris rapae* L. (Lepidoptera: Pieridae) larvae reared on nitrogen-rich plants are preferred by natural enemies due to both better nutritional quality of host as well as more vigorous and green host plants.

Two non-exclusive mechanisms can influence indirectly the suitability of prey for predators (Hodek, 1993; Jørgensen and Lövi, 1999): (i) metabolism of herbivores changes to bad or unfavorable conditions when feeding on unsuitable host plants and (ii) herbivores sequester plant secondary compounds that are toxic or at least unsuitable for predators or parasitoids. In the first case, it is well known that food quality affects the performance, behavior and survival of insects (Mattson, Jr., 1980; Scriber and Slansky, Jr., 1981; Fajer *et al.*, 1989). The nitrogen supply of food plants is a critical factor for the nutritional physiology of insects and mainly results in low or imbalanced contents of amino acids or proteins. Such poor diets often cause sub-lethal effects like reduced growth or reproduction or delayed development (Scriber and Slansky, Jr., 1981; Mattson and Scriber, 1987; Fajer et al., 1989; Loader and Damman, 1991). Fajer *et al.* (1989) show that herbivores reared on poor diets ingest more plant tissue to compensate for their nutritional needs. In spite of this full compensation cannot often be achieved due to the unfavorable energy loss during food consumption including searching activities and food assimilation (Begon *et al.*, 1996). In the second case, sequestration of plant secondary compounds is directly related to the defense of herbivores against natural enemies (Romoser and Stoffolano, Jr., 1998). I.e. the aphid *A. sambuci* uses the glucosid sambunigrin produced by its host plant *Sambucus niger* to reduce its suitability as prey for syrphid and coccinellid larvae (Hodek, 1967 and 1993; Rüzicka, 1978).

A series of experiments to determine the major factors that influence prey suitability for *E. balteatus* was conducted. In the first experiment, five different aphid species were taken representing four different herbivore feeding niches, i. e. broad bean for vegetable and cover crops with *A. pisum* and *A. fabae*, wheat for cereal crops with *Sitobion avenae* Fabricius, potato for a field vegetable crop with *Aulacorthum solani* Kaltenbach as well as cucumber with *A. gossypii* and *A. solani* for vegetables under protected cultivation. All aphids are important pests in the agricultural and horticultural ecosystem. *A. pisum* is a common pest on Fabaceae such as clover, lucerne and peas (Djafaripour, 1976; Suter, 1977) in central Europe and on alfalfa in North America (Roitberg and Myers, 1979; Gutierrez *et al*., 1980; Losey and Denno, 1998b). *A. fabae*, *A. solani* and *A. gossypii* are the most frequent aphid species that infest plants in greenhouses in Germany (Schneller, 1997a), while *S. avenae* is the cereal aphid species with the largest damage potential particularly in winter wheat (Watt, 1979). The aphids were reared on host plants without additional fertilizer. The aim of this experiment was to determine whether particular aphid species and aphid-plant combinations affect the fitness of *E. balteatus* (i.e. efficiency of conversion of ingested food to body substance, the duration of development, survival of larvae, longevity and fecundity of adults). In the second experiment, the indirect effect of the host plant on syrphid fitness was estimated by comparing the prey suitability of *A. solani* reared on different host plants for the development of *E. balteatus*, while in the third experiment effects of the host plants´ nutritional state on *E. balteatus* was investigated.

2.2. Materials and Methods

2.2.1. Rearing of insects and host plants

Episyrphus balteatus specimens were collected from a field site near the Institute of Plant Diseases and Plant Protection in Hannover, Northern Germany. Hoverflies were reared in the laboratory following the protocol of Bargen (1998). Adult flies were fed with bee pollen (Melzer's Bienenfarm, Bonn, Germany) and crystalline sugar. This combination of carbohydrates and proteins was sufficient to induce egg production. Females readily laid their eggs on broad bean plants (*Vicia faba* L. var. Hang down) infested with the pea aphid, *A. pisum*. Immediately after hatching, larvae were transferred to rearing cages (18 x 13.5 x 6.5 cm) and pea aphids were provided as food on leaf cuttings of broad beans until pupation. Rearing conditions were 20 $\pm$ 1 ^{o}C, 50 $\pm$ 10% relative humidity, 16 h of daylight and artificial lighting of 5000 lux (cd/m2).

Pea aphid (*A. pisum*) and black bean aphid (*A. fabae*) were reared on the broad bean *(V. faba)* variety "Hang down, Grünkernige", grain aphid (*S. avenae*) on the wheat (*Triticum avenae*) variety "Tinos", glasshouse potato aphid (*A. solani*) on the potato (*Solanum tuberosum*) variety "Mirabel" and cotton aphid (*A. gossypii*) on the cucumber (*Cucumis sativus* L.) variety "chinesische Schlangengurken". None of the host plants received additional fertilizer.

2.2.2. Experimental set-up

2.2.2.1. Effects of different prey species on the life history parameters of *E. balteatus*

All experiments were conducted in a climate chamber at 20 $\pm$ 1 ^{o}C, 50 $\pm$ 10% relative humidity, 16 h of daylight and a light intensity of approximately 5000 lux. Petri dishes (5.5 cm diameter and 1.5 cm high) were used as experimental arenas in all experiments. A 1.5 cm wide hole was made in the center of each petri dish lid and covered with a gauze for ventilation purpose. Only synchronized aphids with a uniform age structure were used in these

experiments. Approximately 20 adult aphids were placed on a host plant. After 24 h the adults were removed and the offspring had reached the desired age. The aphids were transferred directly into the experimental arena. Single *E. balteatus* larvae were placed into the experimental arena immediately after hatching. As prey a surplus of the different aphid species was provided. Every 24 h the number of consumed aphids was recorded, the remaining aphids were removed, and new aphids were introduced into the petri dish. Until the second day of the development *E. balteatus* larvae were fed with up to 3-day-old aphids (L_2) while later developmental stages were fed with 7-day-old aphids (L_4). To quantify the effect of the different aphids on the fitness of *E. balteatus*, the following parameters were recorded during the experiment:

(i) biomass and number of consumed aphids per day

(ii) fresh weight of pupae

(iii) survival of larvae, pupae and adults of *E. balteatus*

(iv) pre-oviposition period and lifetime fecundity of females

The biomass ingested was calculated as the difference between the introduced and the remaining biomass (left-overs) in the experimental arenas after 24 h. The introduced biomass was therefore estimated as a product of the number of introduced aphids and the average biomass of an introduced aphid. The remaining biomass was weighed directly and the consumption rate was calculated. The pupae biomass was estimated 12 - 18 h before hatching. At this time the pupa changed its color from light yellow to dark brown and changes in biomass ceased. The efficiency of conversion of ingested food to body substance (E.C.I) was calculated to compare the nutritional value of the different aphid species *for E. balteatus* according to the formula of Waldbauer (1968):

$$E.C.I \ = \ \frac{weight\ gained}{weight\ food\ ingested} \ \times \ 100$$

Weight gain was calculated as the difference between pupal weight and initial weight of the first larval stage. Since the L_1 weight was on average only 0.003 ± 0.00001 mg (SE), the initial weight was neglected. Weight of pupae in our experiments therefore meant the weight gained during the larval development. All biomasses were weighed with a Sartorius micro balance scale (Model MC 5). The E.C.I.s of *E. balteatus* reared with the five different aphid species were analyzed by using ANOVA. In case of significant F-values, pairwise comparison was performed with a bonferroni posthoc test, while T-test was used for comparison of two different treatments (Sokal and Rohlf, 1995). To confirm that the pupal weight of *E. balteatus* represents a parameter for adult size, the correlation between adult thorax width and pupal biomass was calculated as well. The relationship between weight of pupae and thorax width of adults was analyzed by using Regression Model II test (Sokal and Rohlf, 1995). For investigations concerning the longevity and fecundity of adults a male and a female were transferred into a plexiglas tube arena (15 cm diameter and 40 cm height) after hatching. In each experimental arena, water, sugar and bee pollen were provided separately as food on small petri dishes. Cuttings of broad bean plants with aphids were put into small bottles with water and placed into the arena six days after the hatching of the adults. The cuttings were replaced and checked daily for eggs laid and survival of adults.

2.2.2.2. Effects of host plants on the life history parameters of *E. balteatus*

a. The same prey species reared on different host plants

The first experiments showed that *E. balteatus* reached the highest E.C.I with *A. solani* as prey reared on potato plants (see results Table 2.1). For the comparison of host plant effects only the development of *E. balteatus* was studied by offering *A. solani* as prey on both potato and cucumber. Consumption rates as well as longevity and fecundity of *E. balteatus* served to quantify host plant effects. Since *A. solani* is a very polyphagous herbivore (Dixon, 1998), it was possible to rear the aphid on potato (variety "Mirabel") as well as on cucumber (variety "chinesische Schlangengurken". The experimental

set-up for the measurement of prey consumption, fecundity and longevity of adults was the same as described before.

b. The same prey species reared on the same host plant but with different fertilizer regimes

Since *E. balteatus* showed the highest efficiency of conversion on *A. solani* reared on cucumber plants (see results Table 2.2), these plants were chosen to test the indirect effect of plant fertilization on hoverfly development. The cucumber plants were treated twice with 20 ml of 2% fluid fertilizer (Euflor flory Hydrodünger N-P-K-Mg 15-7-22-6) in the 3rd and 4th week after planting. The following week *A. solani* aphids were transferred to the host plants. The aphids were reared 8 days on the cucumber plants before they were offered to the hoverfly larvae. The experimental set-up for the provision of prey and the tests for fecundity and longevity of adults were the same as described before.

2.3. Results

2.3.1. Effects of different prey species on the life history parameters of *E. balteatus*

As expected the result showed that the average number of aphids consumed *by E. balteatus* during larval development depended on the body size of the different prey species. The smaller the body size of an aphid species the more prey was consumed until the end of larval development. Among the different aphid species the individual weight of L_4 ranged from 0.26 mg for *A. gossypii* to 1.49 mg *for A. pisum*. On average *E. balteatus* larvae consumed 246.5 ± 6.7 (SE) specimens of *A. gossypii* and only 61.5 ± 2.7 (SE) specimens of the five times larger *A. pisum* (Table 2.1). When the amount of biomass of aphids consumed was considered, *A. solani* was the lowest (55.9 ± 2.2 mg, SE), while *A. pisum* was the highest (91.9 ± 2.8 mg, SE). However, the overall nutritional value of the different aphid species could be best explained with the E.C.I. parameter, i.e. the efficiency of conversion of the ingested food into body biomass. The highest E.C.I. was obtained with *A. solani* as prey (37.9%) while

the lowest efficiency was calculated for *A. pisum* as prey (31.9%). All other aphid species showed intermediate ECIs which were not significantly different (Table 2.1).

The developmental time of *E. balteatus* larvae until pupation significantly depends on the aphid prey species (F = 25.25, df = 4; 74, P < 0.0001) (Fig. 2.1). The bonferroni post hoc test showed that *E. balteatus* preying on *A. fabae* developed significantly faster (7.20 ± 0.11 days, SE) than *E. balteatus* specimens preying on *A. solani* (9.00 ± 0.18, SE) (p < 0.0001) or *S. avenae* (8.42 ± 0.12, SE) (p < 0.0001). However, the difference between the larvae fed on *A. fabae* and *A. pisum* (7.62 ± 0.15 days, SE) or *A. gossypii* (7.62 days ± 0.14 days, SE) was not significant (p = 0.373 and p = 0.648).

Table 2.1. Consumption rates (biomass ingested), pupal weight and efficiency of food conversion (E.C.I.) of *E. balteatus* larvae preying on five different aphid species. Average values ± SE. Different letters (column) indicate a significant difference (p < 0.05, ANOVA followed by a bonferroni post hoc test). N = 22 for *A. pisum*, N = 20 for *A. solani*, N = 18 for *A. fabae*, N = 19 for *S. avenae*, N = 13 for *A. gossypii*.

Prey species	Host plant	Mean no. aphids eaten (total)	Mean biomass of L_4 aphids (mg)	Mean biomass ingested (mg)	Mean weight gained (pupae) (mg)	Efficiency of food conversion (E.C.I)
A. pisum	Bean	61.5 ± 2.7	1.49 ± 0.06	91.9 ± 4.0	28.2 ± 0.8	31.9 ± 1.64 **a**
A. solani	Potato	83.1 ± 3.2	0.59 ± 0.03	55.9 ± 2.2	21.3 ± 0.6	37.9 ± 2.27 **b**
A. fabae	Bean	147.5 ± 5.6	0.50 ± 0.01	73.6 ± 2.8	25.5 ± 1.1	35.7 ± 1.47 **ab**
S. avenae	Wheat	148.8 ± 3.6	0.45 ± 0.01	67.5 ± 1.6	24.8 ± 0.8	36.9 ± 0.97 **ab**
A. gossypii	Cucumber	246.5 ± 6.7	0.26 ± 0.01	65.1 ± 1.8	21.3 ± 0.4	33.0 ± 0.93 **ab**

The feeding activity of *E. balteatus* larvae reached its peak generally three to four days before pupation. About 90% of the larvae molted or changed to the pupal stage and 73% of the pupae hatched. However, only few adults reached the reproductive stage and started laying eggs. In experiments where *E. balteatus* larvae were fed with *A. pisum*, 84% of the larvae reached the adult stage (21 adults; 13 males, 8 females) but only one female reached the

reproductive stage and laid 1112 eggs in total. Similar results were obtained with the other prey species: 16 larvae (73 %) fed with *A. solani* reached the adult stage (7 males, 9 females) and only two females started laying eggs (613 and 2373 eggs/specimen), 15 larvae (75%) fed with *A. fabae* reached the adult stage (9 males, 6 females) and only one female laid eggs (531 eggs/specimen), and 17 larvae (85%) fed with *S. avenae* reached the adult stage (11 males, 6 females) but none of the females survived. When larvae were reared with *A. gossypii* as prey 73% (3 males and 8 females) survived and five females reached the reproductive stage. On average they laid 28.07 ± 5.35 (SE) eggs/specimen (range 31 – 302 eggs/specimen).

2.3.2. Effects of host plants on the life history parameters of *E. balteatus*

a. Effect of host plant species

To investigate the effect of the first trophic level (host plant) on the third trophic level (predator) *A. solani* was reared on two different host plants, potato and cucumber. In general, *A. solani* aphids reared on cucumber were approximately 1.3 times larger than aphids reared on potato plants. *E. balteatus* larvae consumed on average 10 aphids more per day when the prey was reared on potato rather than on cucumber (Table 2.2). However, predator larvae still ingested more biomass if aphids were reared on cucumber (T-test, $t = -1.77$; $df = 36$; $p = 0.086$) and pupae reached a significantly higher biomass (Table 2.2; T-test, $t = -4.86$; $df = 27$; $p < 0.0001$). The efficiency of conversion of ingested aphid biomass (E.C.I) was slightly higher for prey reared on cucumber although the differences were not significant (Table 2.2; T-test, $t = -1.33$; $df = 27$; $p = 0.195$).
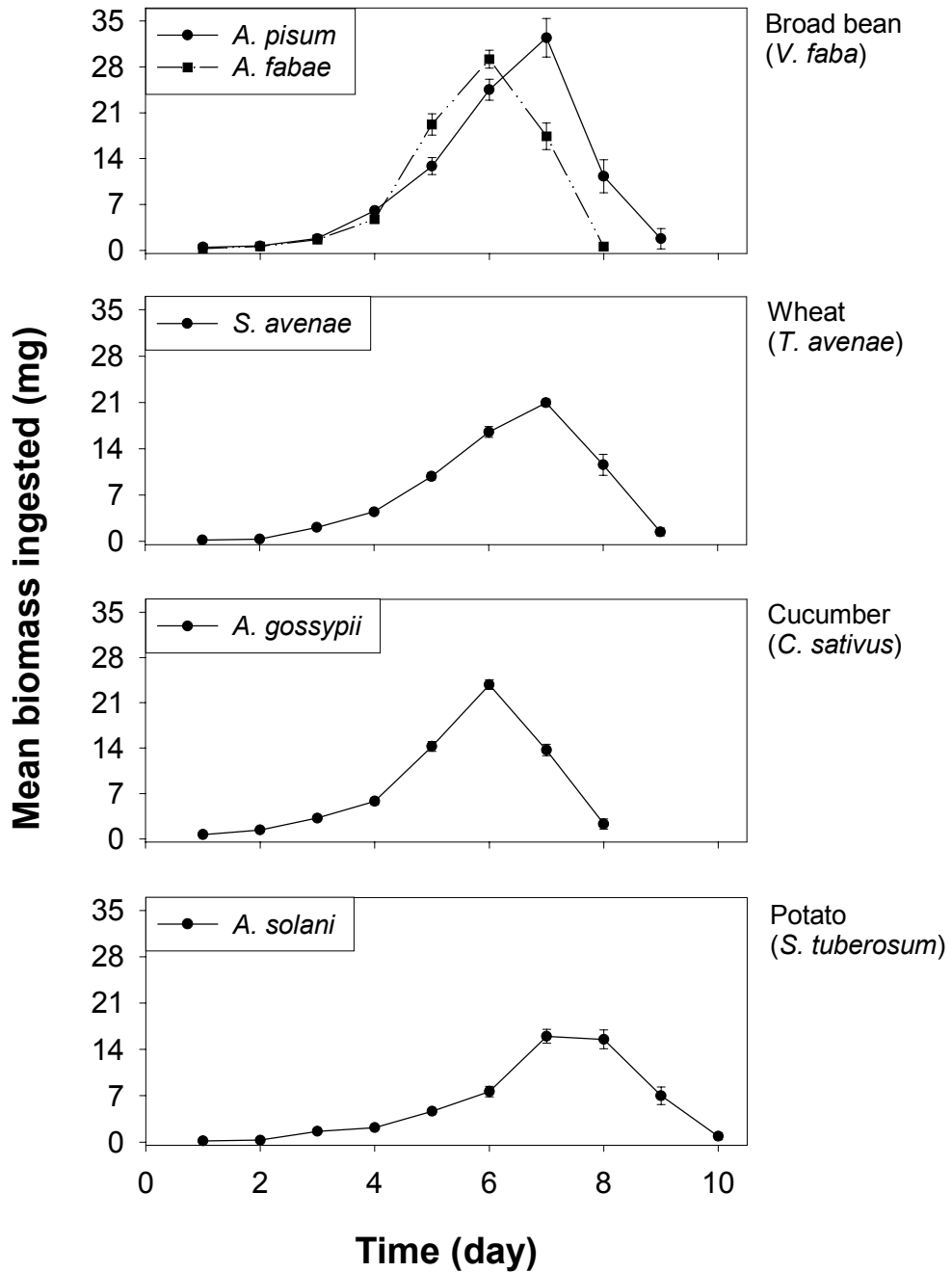
Fig. 2.1. Average daily consumption rates of *E. balteatus* larvae preying on five different aphid species. N = 22 for *A. pisum*, N = 20 for *A. solani*, N = 18 for *A. fabae*, N = 19 for *S. avenae*, N = 13 for *A. gossypii*, average values ± SE). The experiment ends with the pupation of the larvae.

Table 2.2. Consumption rates (biomass ingested), pupal weight and efficiency of food conversion (E.C.I.) of *E. balteatus* larvae preying on *A. solani* reared on two different host plants. Average values ± SE. Different letters (column) indicate a significant difference (p < 0.05, T-test). N = 18 for cucumber and N = 20 for potato. NS = not significant.

Host plant	Mean no. aphids eaten (total)	Mean biomass of L_4 aphids (mg)	Mean biomass ingested (mg)	Mean weight gained (Pupae) (mg)	Efficiency of food conversion (E.C.I)
Cucumber	72.8 ± 3.0	0.85 ± 0.02	61.8 **ns** ± 2.5	26.2 **b** ± 0.9	41.8 **ns** ± 1.70
Potato	83.1 ± 3.2	0.59 ± 0.03	55.9 **ns** ± 2.2	21.3 **a** ± 0.6	37.9 **ns** ± 2.27

The developmental time of *E. balteatus* larvae fed on *A. solani* reared on cucumber was significantly shorter (7.62 ± 0.14 days, SE) (T-test, t = 5.79; df = 27; p < 0.0001) than that for larvae fed with *A. solani* reared on potato plants. With *A. solani* prey reared on cucumber, 15 individuals (75%) completed their lifecycle and hatched from the pupae (7 males and 8 females). 5 females finally reached the reproductive stage and laid on average 516 ± 180.8 (SE) eggs/specimen (range 217 - 1215). With *A. solani* prey reared on potato, 16 larvae (73%) reached the adult stage (7 males, 9 females) and only two females started laying eggs (613 and 2373 eggs/specimen). Despite the better overall performance *of E. balteatus* larvae on aphids reared on cucumber compared to potato, the fecundity of the females was still quite low and showed a high variability.

b. Effects of the nutritional value of the host plant

Host plant nutrition has a direct impact on herbivore performance and in turn might influence herbivore suitability for predators. As *E. balteatus´* larval efficiency of conversion was the highest with *A. solani* on cucumber (Table 2.2), *A. solani* was reared on fertilized cucumber and on plants that had not been supplied with additional fertilizer. These aphids were offered to *E. balteaus* larvae. *E. balteatus* larvae were fed on equal numbers of prey reared in the different treatments, but ingested a significantly higher biomass if prey was

reared on plants without additional fertilizer (T-test, t = -2.36; df = 35; p = 0.024). Despite the reduced biomass ingested from prey reared on fertilized plants the pupae showed a significant higher biomass (T-test, t = 2.08; df = 29; p = 0.047). As a consequence the E.C.I of *E. balteatus* larvae preying on *A. solani* reared on fertilized cucumber was on average 10% higher than on prey reared on unfertilized cucumber plants (Table 2.3, T-test, t = 5.87; df = 30; p < 0.0001). Moreover, the average developmental time of larvae fed with aphids reared on fertilized plants (7.26 ± 0.10 days, SE, N = 19) was significantly shorter compared to larvae fed with aphids from unfertilized plants (7.62 ± 0.14 days, SE); (T-test, t = -2.06; df = 30; p = 0.048). The fertilization of host plants also had a positive impact on the survival of adults as well as on longevity and fecundity (Table 2.3 and 2.4). 95% of the individuals reached the adult stage and seven out of eight females entered the reproductive stage. Females fed with aphids reared on fertilized plants laid on average three times more eggs than females fed with *A. solani* reared on plants without additional fertilizer (Table 2.4, T-test, t = 3.20; df = 10; p = 0.009).

Table 2.3. Consumption rates (biomass ingested), pupal weight and efficiency of food conversion (E.C.I.) of *E. balteatus* larvae preying on *A. solani* reared on cucumber plants with different fertilizer regimes. Average values ± SE. Different letters (column) indicate a significant difference (p < 0.05, T-test). N = 18 for unfertilized plants and N = 19 for fertilized plants.

Treatment	Mean no. aphids eaten (total)	Mean biomass of L_4 aphids (mg)	Mean biomass ingested (mg)	Mean weight gained (Pupae) (mg)	Efficiency of food conversion (E.C.I)
Unfertilized plants	72.8 ± 3.0	0.85 ± 0.02	61.8 ± 2.5**b**	26.2 ± 0.9**a**	41.8 ± 1.70**a**
Fertilized plants	71.9 ± 2.1	0.76 ± 0.02	54.9 ± 1.6**a**	28.8 ± 0.8**b**	52.7 ± 1.00**b**

Table 2.4. Comparison of larval to adult development of *E. balteatus* larvae preying on *A. solani* reared on fertilized and not fertilized host plants. For egg laying, cucumber plants with *A. solani* were offered. Average values ± SE. Different letters (column) indicate a significant difference (p < 0.05, T-test).

Treatment	N	No. of larvae reaching adult stage (%)	Sex ratio Male : Female	No. females reaching reproductive stage	Mean no. of eggs laid (± SE) (range)
Unfertilized plants	20	15 (75)	7 : 8	5	561.0 ± 180.8**a** (217 – 1215)
Fertilized plants	20	19 (95)	11 : 8	7	1396.6 ± 178.1**b** (683 – 1998)

2.3.3. Feeding behavior of *E. balteatus* larvae and impact on female and male body size

In all experiments, male larvae of *E. balteatus* constantly consumed more aphid biomass than female larvae, although the differences in most cases were not significant (ANOVA, F = 0.302; df = 5, 85; p = 0.910). Significant differences could only be found when larvae were fed on *A. solani* reared on fertilized cucumber plants (Fig. 2.2a, T-test, t = 5.03; df = 17; p < 0.0001). The slight differences in biomass ingested in most cases led to a higher individual weight of male pupae of males (Fig. 2.2b) indicating a higher conversion efficiency in male than in females, although the differences were not significant (Fig. 2.2c, ANOVA, F = 1.43; df = 6, 102; p = 0.211). Per mg ingested aphid biomass males reached 1.05 – 1.15 times higher pupal weights. A reliable parameter of adult body size was the thorax width of males, which was significantly larger than the thorax width of females (Fig. 2.3a). In addition, for both sexes pupal weight correlated with the thorax width of the adults (Fig. 2.3b and 2.3c).
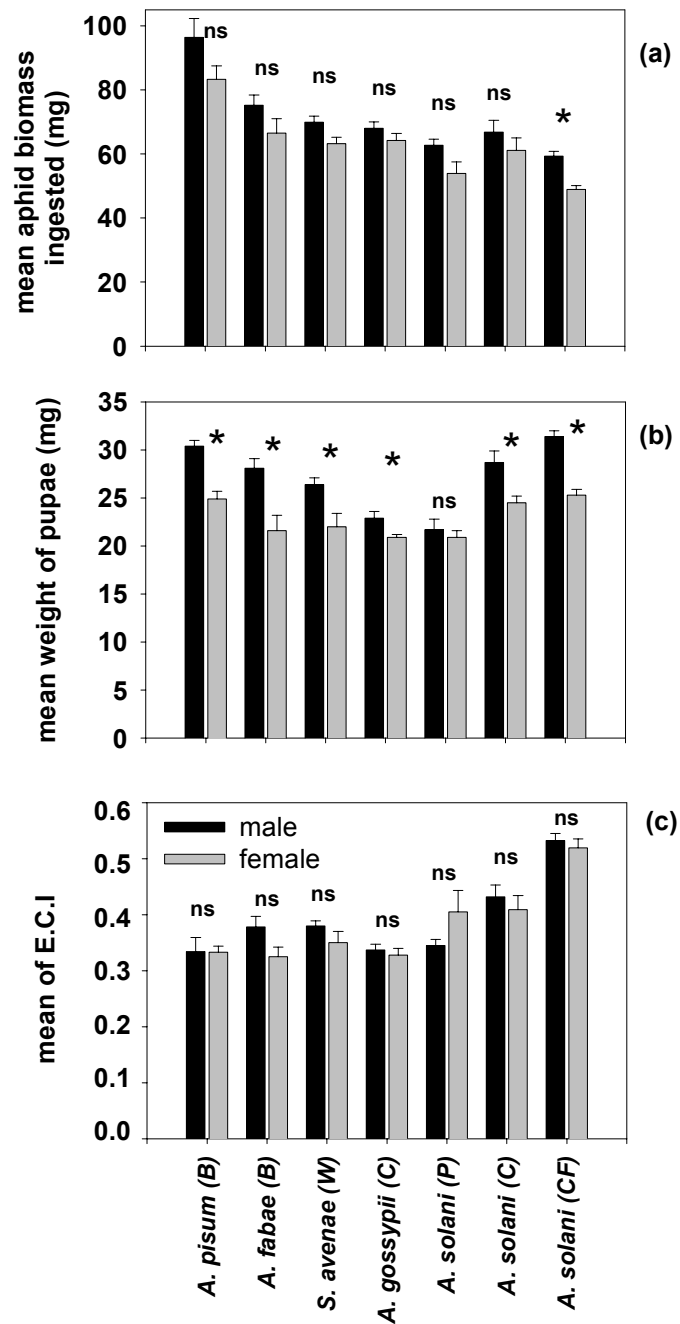
Fig. 2.2. Differences in larval consumption rates between male and female *E. balteatus*. (a) aphid biomass ingested, (b) weight of pupae and (c) efficiency of food conversion (T-test, * = 0.001 > p < 0.05, ns = not significant, B = broad bean, W = wheat, P = potato, C = cucumber, CF = fertilized cucumber).
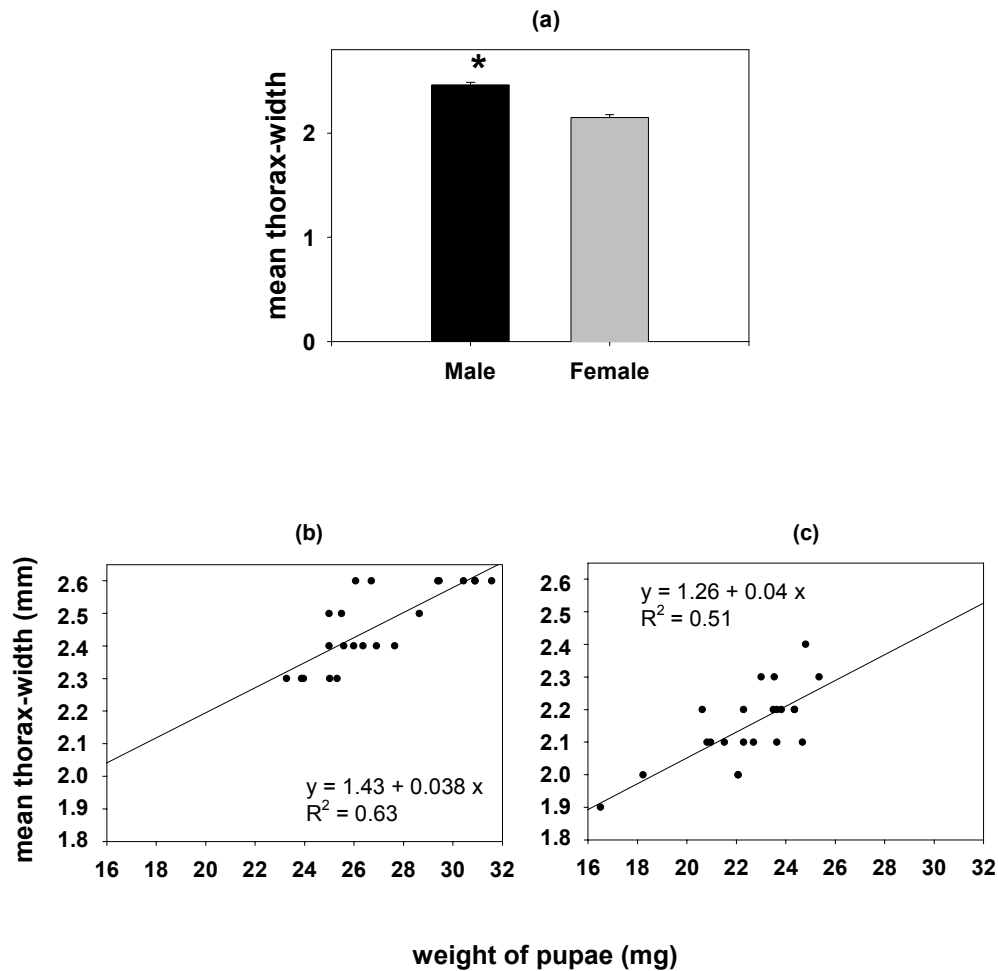
Fig 2.3. Differences in the thorax width between male and female specimens of
        E. balteatus (a) (N = 23 for male and N = 22 for female; T-test, t = -8.75;
        df = 43; p < 0.0001). The correlation between the thorax width and the
        pupal weight was estimated for male (b) (N = 23; F = 33.79; df = 1, 20;
        p < 0.0001) and female (c) (N = 22; F = 20.77; df = 1, 20; p < 0.0001)
        specimens separately.

2.3.4. Temporal pattern in reproduction of *E. balteatus* females and fertility of eggs

E. balteatus specimens fed with *A. solani* reared on cucumber were used for the
analysis of temporal patterns in the reproduction of *E. balteatus* females and the
fertility of eggs, since this was the only plant-prey system which produced a
reasonable number of *E. balteatus* specimens reaching the reproductive stage.
Female *E. balteatus* had a pre-reproductive phase of about 9 days (Fig. 2.4)
before mating took place. Females started egg laying 10 days after hatching.
During the first two days, on average, 40 eggs were laid. During the following

days the number of eggs laid increased steadily until day 18. Two more cycles of egg laying occurred thereafter, each with a period of 4 days. Ten random samples of 762 eggs from different specimens showed that 67.6 ± 1.8% (SE) of the eggs were fertile and developed into first larval stage.
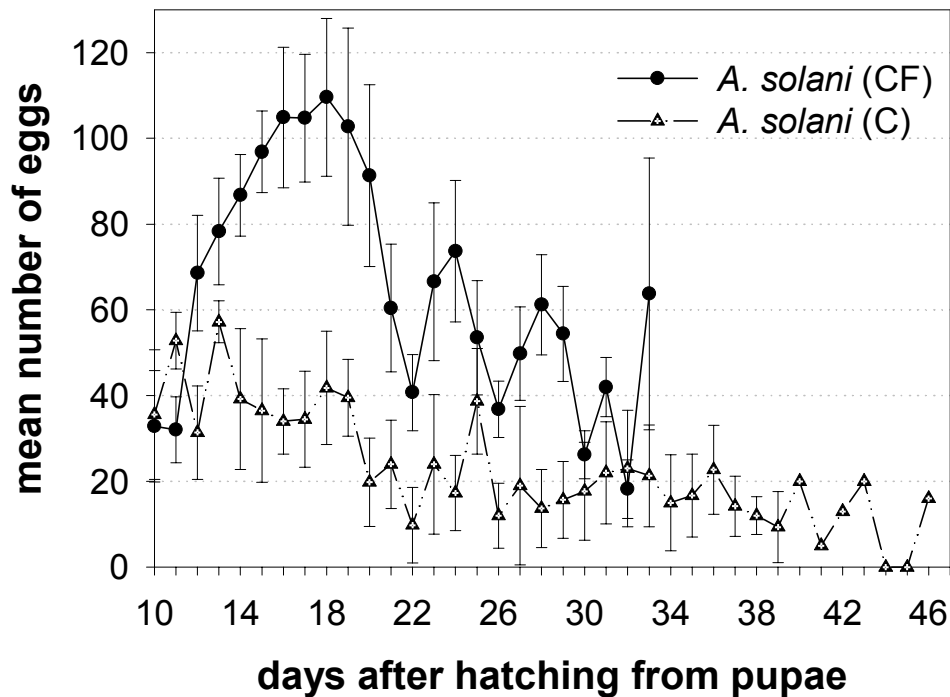
Fig. 2.4. Temporal pattern in the number of eggs laid per day by female *E. balteatus*. Specimen either fed on *A. solani* reared on fertilized cucumber plants (CF) (N = 7 from day 10 – 24, N = 6 from 25 – 27, N = 5 from 28 – 32 and N = 4 on 33 day after hatching from the pupae) or on *A. solani* reared on not fertilized cucumber plants (C) (N = 5 from day 10 – 14, N = 4 from 15 – 24, N = 3 from 25 – 39 and N = 1 from day 40 – 46 after hatching from pupae). Bars indicate the standard error.

2.4. Discussion

2.4.1. Suitability of different aphid species

New (1991) suggested that food resources ingested by predators could be defined as either "essential" or "alternative". Essential food sources ensure

completion of the larval development and subsequent adult reproduction, whereas alternative food sources merely serve as energy source and guarantee survival without providing sufficient nutrients for development or reproduction. Estimates of larval development are therefore an unreliable parameter to classify the suitability of different prey species for predators (Hodek, 1993). Moreover, estimates of survival, longevity as well as fecundity of adults are of primary importance in judging the relative value of different prey species. During the experiments the suitability of five different aphid prey species, *A. pisum*, *A. fabae*, *S. avenae*, *A. gossypii* and *A. solani, was* estimated. Four of the aphid prey species turned out to be only more or less alternative prey for *E. balteatus*. Female specimens rarely reached the reproductive developmental stage, except for *E. balteatus* feeding on *A. gossypii*, their fecundity, however, was very low (28.07 ± 5.35, SE). Of the tested aphid species only *A. solani* and only when reared on cucumber as host plant could be classified as essential prey. Syrphid survival increased and females laid numerous eggs. Fecundity was even higher and reached as much as 1396.6 ± 178.1 (SE) eggs per female (683 - 1998 eggs) when *A. solani* aphids were reared on fertilized cucumber plants. Compared to the results of Tenhumberg (1993) with the aphid species *Metopolophium dirhodum* (Walk.) as prey the fecundity of *E. balteatus* in these experiments was more than four times higher. Moreover, fertilization of the host plant significantly enhanced the conversion efficiency of ingested biomass. The enrichment of the nutritional contents of the food plant in the first trophic level influenced the third trophic level indirectly via the nutritional value of the aphid prey. The important nutritional element might be nitrogen. It induces enhanced health, growth, reproduction and survival in many organisms (Mattson, Jr., 1980) and therefore is of major importance for the feeding physiology of insects (Loader and Damman, 1991; Fajer *et al.*, 1989; Scriber and Slansky, Jr., 1981; Mattson, Jr. and Scriber, 1987; Mattson, Jr., 1980). The evidence of the role of nitrogen in regard to the nutrition of insects was studied by Slansky and Feeny (1977) who reported that the E.C.I. and growth rate of *Pieres rapae* L. (Lepidoptera: Pieridae) increases and their consumption rate decreases when the larvae are fed on collards heavily fertilized with ammonium nitrate. Almost the same effects of nitrogen supply were observed for the parasitoid *C. oscinidis* attacking the leafminer *L. trifolii* on fertilized bean plants. Parasitoid

fecundity was enhanced and the larval developmental time was shorter on hosts feeding on plants with nitrogen treatment (Kaneshiro and Johnson, 1996). Since the specific nutritional requirements of entomophagous insects are still little known (Thompson, 1999), these facts and the results of this study more or less indicate that the requirements of *E. balteatus* are not much different from those of herbivores and of parasitoids. However, the effect of fertilization of host plants was not tested with all aphid host-plant combinations, therefore it cannot generally be concluded that nitrogen supply of host plants improves prey suitability. Secondary plant compounds acting via the food chain can also have a negative effect on the development of predators like *E. balteatus*. To compensate for a low quality of food insects often ingest higher quantities (Fajer *et al.* 1989). In a similar manner *E. balteatus* larvae ingested more biomass when feeding on alternative prey, especially when host plants were unfertilized. But nevertheless the increased voracity does not guarantee that *E. balteatus* can compensate deficiencies in food conversion and reach sufficient larval and pupal size, the reproductive stage or even successful reproduction. Voracity of predators is therefore an insufficient parameter to estimate the suitability of different prey species (Rüzicka, 1978; New, 1991; Hodek, 1993).

Hagen (1987) explained that prey suitability can influence the behavior of a predator in different ways: (i) the predator may reject the prey immediately after "tasting" it, (ii) it may be killed by toxins in the prey, (iii) the predator may consume an individual prey at a slower rate, (iv) develop at a slower rate, and/or (v) might be less fecund as adult and live a shorter life. *E. balteatus* readily preyed on all aphid species in this study. None of the prey species was rejected or caused a premature death of specimens which might have indicated strong toxins delivered via the food chain. The observed reactions of *E. balteatus* in the here tested treatments cannot explain in detail the underlying mechanism. Since different prey species lead to more or less typical gradual sublethal effects like retarding the velocity of development, reduced body weight or reproduction capacities, the hypothesis of nutritional value as key factor seems to be more logical than strong intoxication effects of secondary plant compounds acting via the food chain. Only the experiments with *A. solani* on different host plants may allow some speculations about the role of secondary

plant compounds. Syrphid larva in our study reached the highest E.C.I. with *A. solani* reared on potato as prey while the developmental time was slightly extended. An important secondary compound of potatoes that is known to influence survival are *Solanum* glycoalkaloids such as solanin and chanonine (Soule *et al.*, 1999). This secondary metabolites had a negative effect upon the survival of the Colorado potato beetle, *Leptinotarsa decemlineata* insect (Say) (Coleoptera: Chrysomelidae) and the potato leafhopper, *Empoasca fabae* (Harris) (Homoptera: Cicadellidae) (Tingey, 1984) and moderately influenced the metabolism of *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae) (Günther *et al.*, 1997). Similar effects may to a certain degree be responsible for the lower suitability of *A. solani* reared on potato plants and the better adaptation of *E. balteatus* to the prey reared on cucumber plants.

On the other hand, deficiencies of nutritional value as a result of lacking or imbalanced primary compounds like amino acids and proteins may act in combination with "soft" toxins influencing the efficiency of food conversion mechanism. The low food conversion efficiency even on prey with high feeding rates may support this hypothesis as well as the observation. When *A. solani* from cucumber under different fertilizer regimes served as prey item, the higher nutritional value caused by conversion of nitrogen to essential primary compounds at low or lacking toxin levels in cucumbers could be responsible for the higher assimilation efficiency. This hypothesis is supported by qualitative observations on the amount of feces excreted, which indicates the amount of nutrient loss. The higher the nutrient loss the lower the assimilation efficiency (New, 1991). In this study the amount of feces excreted was not quantified, the frequency of feces excretions that occurred at the third larval stage immediately before pupation, however, was noted. Frequency of feces excretions varied between prey species. For example, feces excretions occurred 2-3 times with *A. pisum* and *A. fabae*, 1-2 times with *S. avenae* and *A. gossypii* as prey and only once with *A. solani* reared on potato as prey. This indicates that *E. balteatus* might reach higher assimilation efficiency with *A. solani* as prey.

2.4.2. Thorax width as a parameter for body size of adult *E. balteatus*

Many morphological parameters were used in previous studies to distinguish between female and male specimens of syrphids (Gilbert, 1985a, 1985b and 1985c), i.e. wing length, wing width, head width, thorax width, tibia length, proboscis length, fulcrum length, labrum-epipharynx, prementum length, labellum length, tergite 2 width, tergite 3 width and tergite 4 width. Among all of these parameters there is no morphological parameter which can be used to characterize the body size of female and male specimens (Gilbert, 1985c). Most of these parameters are difficult to measure and might change with the age of the specimen (i.e. damaged wings). In this study, the thorax width of the adult as a parameter to characterize the body size of adult *E. balteatus* was chosen for two reasons: (i) it is easier to measure than to apply other parameters, (ii) it is a fixed parameter regardless of the age of the adult. The results show that the thorax width was a good parameter to distinguish between male and female *E. balteatus*. Males always showed a larger thorax than females. Moreover, the thorax width was positively correlated with the pupal weight. It is therefore suggested that either the weight of pupae or the thorax width should be used as a standard parameter to represent the body size of adult syrphids.

In general females are heavier and larger than males in the world of insects (Scriber and Slansky, 1981) because of the female need to accumulate more energy reserves for reproduction. This generalization, however, does not apply to syrphids. There are at least two species where males are to be known larger than females, i.e. *Heringia heringi* Zettrstedt and *Xylota sylvarum* L. (Stubbs and Falk, 1996). Both of them belong to the subfamily Milesiinae. The results show that *E. balteatus* males are also larger than females (Fig. 2.2b and 2.3a) and that male larvae are more voracious than female larvae (Fig. 2.2a). Gilbert (1984) speculated that the foraging and mating behavior of *S. ribesii* was related to thermoregulatory abilities, which are dependent on the body size. A larger female has the advantage of regulating the body temperature more efficiently than a smaller one (Heinrich, 1999). Therefore it arrives at the mating place earlier in the morning and is able to occupy the best sites. As a consequence females might "choose" larger males as mating partners because

they have better thermoregulatory abilities. In a similar way, this might also explain the different sizes of male and female *E. balteatus*, but there is still no literature dealing with behavioral observations during mating.

2.4.3. Temporal patterns of egg laying and the survival of eggs

Since *E. balteatus* specimens fed with *A. solani* reared on fertilized cucumber plants were the only plant-prey system which resulted in a reasonable number of *E. balteatus* specimens reaching the reproductive stage, the discussion on temporal reproduction patterns of *E. balteatus* females and the fertility of eggs is limited (Fig. 2.4). From literature, it is known that *E. balteatus* has a well-defined temporal pattern in egg production and egg laying behavior. Every second day the number of eggs laid reaches its maximum (Volk, 1964; Bargen, 1998). On the other hand, the experiments showed that *E. balteatus* females needed a nine day premature period and then started to lay eggs almost continuously. The number of eggs laid per day increased steadily until the 18th day after hatching. Only in the end of the reproductive phase a time period of two days between the peaks in egg production could be identified. The contradiction between the various studies can partly be explained because of the differences in the experimental set-ups. Bargen and Volk assumed that females needed two days to regenerate their ovaries and therefore they offered females plants with aphids for egg laying every second day. In our experiments broad bean plants were offered each day.

Large numbers of the eggs laid by *E. balteatus* were fertile. An average hatching rate of the first larvae of 67.6 ± 1.8% (SE) was observed. This was slightly higher than the average hatching rate of 53.6 ± 12.6% observed by Geusen-Pfister (1987). Food quality and/or experimental set-up seemed to be crucial for maintaining high survival rates of *E. balteatus* offspring in rearing. During the experiments *E. balteatus* were fed exclusively with *A. solani* which were reared on fertilized cucumber plants, whereas Geusen-Pfister offered *E. balteatus* a mixture of *Aphis craccivora* (Koch) and *A. pisum* aphids reared on broad bean plants. Apart from that it remains unclear whether the host plants were fertilized or not. Moreover, only single pairs of male and female were kept

together in one cage, whereas in the previous study with *E. balteatus* adults were kept in groups of 16 males and 14 females. While storing groups of males and females the probability of successful mating attempts might be reduced. It is expected that food quality enhances the fitness of males as well as the number of fertile eggs.

2.5. Conclusion

The first trophic level, the host plant, has an indirect impact on the fitness of *E. balteatus*. The importance of the nutritional value of a prey was investigated in the experiment with fertilized host plants. Supply of nitrogen can improve suitability of prey. Survival, longevity and fecundity of *E. balteatus* were enhanced, especially when the host plant had an optimal nutritional value for the herbivore. Therefore, future studies on suitability of prey/host for predators/parasitoids should take into account the condition of host plants for prey/hosts. Additionally, for mass rearing of *E. balteatus*, although there are still many other aspects to be studied, fertilization can be applied to enhance the nutritional value of aphids for further increase of the fitness of *E. balteatus*. This study shows that *A. solani* reared on fertilized cucumber plants should be used to optimize mass rearing of *E. balteatus*.

3. Cannibalism in *Episyrphus balteatus* de Geer (Diptera: Syrphidae)

3.1. Introduction

Cannibalism is defined as the feeding activity on conspecifics and occurs in various species of insects (Fox, 1975; New, 1991). Cannibalism is not restricted to insects which normally are predatory, but also appears to be widespread among herbivores, e.g. the cotton leafworm, *Spodoptera littoralis* (Abdel-Salam, 1973), the corn earworm *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) (Fox, 1975; Kalshoven, 1981) and the fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) (Chapman *et al.,* 1999). Cannibalism 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 (Fox, 1975; Hassan, 1975; Branquart *et al*., 1997; Phoofolo and Obrycki, 1998; Chapman *et al*., 1999). Riechert (1981) suggests that cannibalistic tendencies are genetically determined.

In the laboratory, the larvae of *E. balteatus* fed on conspecific eggs both in the presence and in the absence of aphids (Chandler, 1969; Branquart *et al*., 1997). Especially in regard to the third instar larvae (L_3), Branquart *et al.* (1997) observed that cannibalism on conspecific eggs was in inverse proportion to the amount of aphids present in the petri dishes. They further discovered that cannibalism of L_3 decreased with increasing body size of conspecific larvae. However, the information whether cannibalism does occur between the same instar or not is not yet available. Since cannibalism was observed among similar stages of *C. carnea* and *Coleomegilla maculata* (DeGeer) (Coleoptera: Conccinellidae) (Phoofolo and Obrycki, 1998), cannibalism studies with *E. balteatus* were set up. This study was carried out both in the presence and in the absence of aphids to observe the effect of availability of food. Cannibalism is also density-dependent (Fox, 1975), such as in *S. frugiperda* (Chapman *et al.,* 1999), therefore different numbers of larvae were kept together to

investigate whether the density factor plays a role in inducing cannibalism in *E. balteatus*.

3.2. Materials and methods

Cannibalism experiments were carried out at 20 ± 1° C, $50 \pm 10\%$ relative humidity, 16 h of daylight and a light intensity of approximately 5000 lux (cd/ m^2). The rearing procedure for *E. balteatus* is described in chapter 2. In the first experiment (food availability), cannibalism was tested by keeping two larvae of *E. balteatus* together in petri dishes (5.5 cm diameter and 1.5 cm height). *E. balteatus* eggs were offered in small groups of 7.4 ± 0.1 (SE) as well as of 13.3 ± 0.3 (SE) eggs per leaf to first instar larvae (L_1) and third instar larvae (L_3). All experiments were carried out both in the presence and in the absence of aphids. Aphids were provided on leaf cuttings. Approximately 20 aphids were used for the combination between L_1, 50 aphids for second instar larvae (L_2) and 100 aphids for L_3. The latter amount was also used for experiments between eggs and L_3, L_1 and L_3 as well as L_2 and L_3 combinations. The larvae were selected one, three and five days after hatching for L_1, L_2 and L_3. Each combination was replicated 15 times and the experiments lasted for 24 h. The frequency of cannibalism was compared using χ^2 tests with *Yate's correction for continuity* recommended for small sample sizes. Eggs consumed by the conspecific larvae in the presence and in the absence of aphids were compared using T-tests. The data were transformed using arc-sin before analysis (Sokal and Rohlf, 1995). In the second experiment, densities of 2, 5 and 10 larvae *E. balteatus* were kept together in similar petri dishes. Since cannibalism between L_3 was observed neither in the presence nor in the absence of aphids (see Table 1), the density experiments were only conducted in the absence of aphids. The experiments were replicated 10 times, except for density of 2 larvae (N = 15). The incidence of cannibalism was calculated by using a method of Chapman *et al*. (1999) and was defined as the proportion of potential victims consumed with a maximum of the total amount of larvae per petri dish minus one.

3.3. Results

Cannibalism on *E. balteatus* eggs. In the absence of aphid, *E. balteatus* eggs were heavily cannibalized by the conspecific larvae, especially by L_3, which consumed approximately 87.1% of the eggs offered (Fig. 1). Even in the presence of aphid, cannibalism on eggs was still observed. However, the consumption of eggs by L_1 (T-test, t = -4.89; df = 28; p < 0.0001) as well as by L_3 (T-test, t = -5.44; df = 28; p < 0.0001) (Fig. 1) decreased significantly.
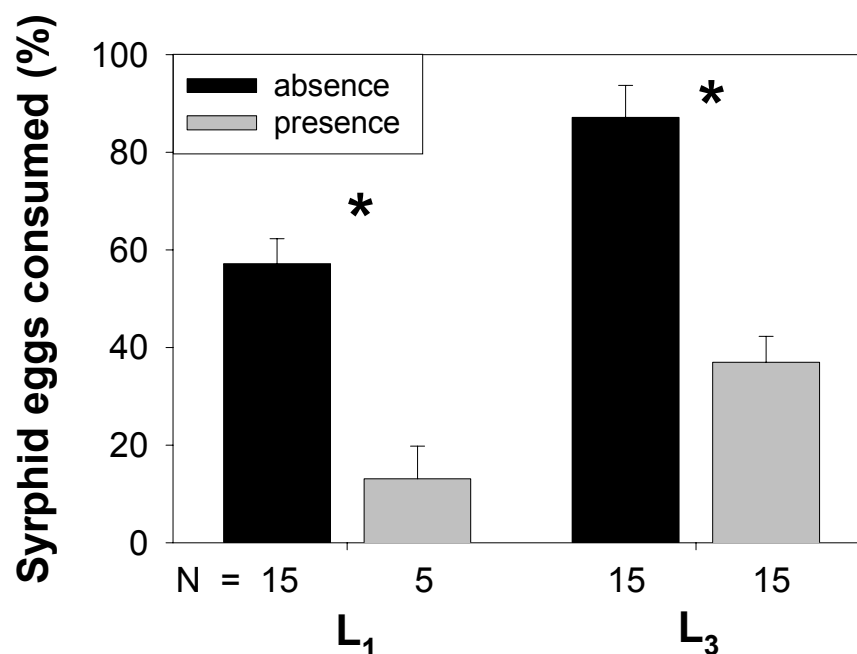

Fig. 3.1. Cannibalism on *E. balteatus* eggs by conspecific larvae (L_1 and L_3). Bars represent the mean percentage ($\pm$ SE) of *E. balteatus* eggs consumed during a 24 h interval. * indicate significant differences between treatments with and without aphids at p < 0.05 tested with a T-test. The number (N) of replicates with cannibalism is given below each bar (in total N = 15).

Cannibalism on L_1 *E. balteatus*. In the absence of aphids, L_1 was vulnerable to both L_2 and L_3. However, the frequency in cannibalism between the different treatments was not statistically significant (χ^2 test, value = 0.14; df = 1; p = 0.713; N = 30). There was no cannibalism when L_1 was confronted with the same instar. In the presence of aphids, there was no cannibalism at all (Table 3.1).

In general, the cannibalism on L_1 decreased significantly in the presence of aphids (Table 3.1, χ^2 test, value = 12.95; df = 1; p < 0.0001; N = 90).

Cannibalism on L_2 *E. balteatus*. In the absence of aphids, there were two replicates with cannibalism on L_2 by L_3 (Table 3.1). Cannibalism did not occur when L_2 was confronted with L_2. In the presence of aphids, there was no cannibalism.

Cannibalism on L_3 *E. balteatus*. Cannibalism among L_3 did not occur, neither in the absence nor in the presence of aphids (Table 3.1).

The density of cannibalism. In serial density tests of 2, 5 and 10 larvae per petri dish in the absence of aphids, cannibalism among L_3 occurred very rarely, only 1.1 % of the replicates with the density of 10 specimen per petri dish (Table 3.2).

Table 3.1. Cannibalism between different developmental stages of *E. balteatus* in petri dishes in the absence and presence of aphids. N = 15.

Superior developmental stage of *E. balteatus*	Number of victims					
	Absence of aphids			Presence of aphids		
	L_1	L_2	L_3	L_1	L_2	L_3
L_1	0	0	0	0	0	0
L_2	6	0	0	0	0	0
L_3	7	2	0	0	0	0

Table 3.2. Cannibalism of *E. balteatus* in different densities of larvae in the absence of aphids as alternative prey. The amount of cannibalism was calculated by using the method of Chapman *et al.* (1999).

Density of *E. balteatus* larvae	No. of replications (no. of larvae in total)	Amount of cannibalism % ± SE (no. of larvae in total)
2	15 (30)	0.0 ± 0.0 (0)
5	10 (50)	0.0 ± 0.0 (0)
10	10 (100)	1.1 ± 1.1 (1)

3. 4. Discussion

The factors that can induce cannibalism in many species are natural food availability, population density, behavior of victims (defense mechanism) and susceptibility (e.g. size relations, nutritional value), stress and encounter rate (Fox, 1975). From the mentioned factors, only "alternative" food, population density and susceptibility of potential victims were discussed in this study. Cannibalism mainly occurs when prey is scarce (Fox, 1975; New, 1991; Agarwala and Dixon, 1992; Branquart *et al.*, 1997; Schellhorn and Andow, 1999). The experiments with *E. balteatus* showed that indeed natural food supply (aphids) influenced cannibalism rates, but even with extremely low availability of food (in the absence of aphids) and with high population density (Table 3.1 and 3.2), cannibalism rarely occurs when specimens of similar age (size) (L_3) of *E. balteatus* interacted. On the other hand, cannibalism in chrysopid, *Chrysoperla carnea* (Neuroptera: Chrysopidae) (Ridgway *et al.*, 1970; Hassan, 1975; Phoofolo and Obrycki, 1998), *H. armigera* (Kalshoven, 1981) and *S. frugiperda* (Chapman *et al.*, 1999) frequently occurred and was high even when food was abundant and population density low. In *S. frugiperda* kept in plastic pot arenas (9 cm diameter and 4 cm height), cannibalism increased from 40% in density of 2 to 53% in density of 4 larvae per pot in the presence of 400 cm^2 of maize leaves (Chapman *et al.*, 1999). This study shows that there is no evidence that food scarcity and density-dependence play a role in cannibalism of *E. balteatus* larvae when the size is equal. In our department in Hannover, approximately 100 – 150 larvae were kept in Plexiglas boxes (18 x 13.5 x 6.5 cm) and cannibalism was hardly observed. The larvae would rather starve to death than eat the conspecific larvae (Hindayana, unpublished data).

The extent of cannibalism is strongly dependent on the size and therefore influenced by the degree of habitat segregation among size classes or the defense mechanisms of smaller larvae (New, 1991). New´s statement could be confirmed in this experiment. When L_3 were confronted with smaller specimens (L_2), cannibalism only occurred in 2 cases (13.3%). A stronger asymmetry in the body size of the interacting specimens, however, induced a higher amount of cannibalism, a finding which is supported by observation on egg predation,

since eggs were attacked by all instar larvae (Fig. 3.1) even in the presence of aphids. The same tendencies were reported by Branquart *et al.* (1997) for *E. balteatus* and by Agarwala and Dixon (1992) for coccinellid, *Adalia bipunctata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae). These developmental stages can easily be found and only have few possibilities to defend themselves (New, 1991). However, in Coccinellid (Agarwala and Dixon, 1992; Phoofolo and Obrycki, 1998), chrysopid, *C. carnea* (Phoofolo and Obrycki, 1998), *H. armigera* (Kalshoven, 1981) and *S. frugiperda* (Chapman *et al.*, 1999) the extent of cannibalism even in the same size (same instar larvae) was still high.

The low cannibalism rates observed under experimental conditions in this study suggest that cannibalism in *E. balteatus* can only be expected in mass rearing when extremely different age groups of larvae are kept together in small cages with low food supply, conditions which are more or less unusual. Also under field or greenhouse conditions, cannibalism should be not important. In reality, the incidence of cannibalism in syrphids in the field has never been measured (Branquart *et al.*, 1997). But also without direct observation, the possibility of high encounter rates and crowding effects is extremely low. Different studies showed that females always laid eggs near aphid colonies (Chandler, 1968a and 1968 b; Scholz and Poehling, 1999) and only in a very limited number in small patches. Females were not only able to adapt their egg deposition in regard to aphid density but also to perceive the presence of conspecific eggs and therefore oviposited less often in small aphid colonies or if conspecific eggs were already present (Scholz and Poehling, 1999). It could be speculated that cannibalism in *E. balteatus* in the field is an uncommon phenomenon.

The question whether *E. balteatus* is able to use cannibalism to prevent starvation when aphid densities are extremely low under certain circumstances cannot be answered in these experiments. Therefore more detailed studies particularly on the nutritional value of eggs or first instar larvae may be necessary. Branquart *et al.* (1997), however, observed that larvae feeding on conspecific eggs could complete their development, although their growth rate was not as fast as that of larvae that fed on aphids. In terms of larval growth

and survival, conspecific eggs of coccinellids serve as better food than aphids (Agarwala and Dixon, 1992; Yasoda and Ohnuma, 1999). It is still unclear whether this suitability of conspecifics on larval growth and survival is positively correlated with fecundity of adults, although the study of Walzer and Schausberger (1999) with predatory mite, *Neoseiulus californicus* McGregor (Acari: Phytoseiidae), showed that the suitability of conspecifics on larval growth and survival is not positively correlated with fecundity of adults. Immature stages of *N. californicus* feeding on conspecific larvae could reach adulthood, but their female did not lay eggs. In relation to food suitability, conspecifics probably could only be used as alternative food rather than as essential food.

3.5. Conclusions

Cannibalistic tendencies in *E. balteatus* are very low. As long as the larvae are fed continuously and, even more important, are homogenous in size, cannibalism occurs very rarely. Cannibalism only occurs when eggs or young instar larvae are kept together with larger larvae, especially L_3, in the absence of aphids. Considering these facts, there may be no need to change the conditions for mass rearing of *E. balteatus* in our department in Hannover.

4. Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators *

4.1. Introduction

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. Snyder and Wise (1999) reported that carabid beetles and lycosid spiders reduced the number of non-lycosid spiders and foliar-foraging predators, mainly nabid bugs, in Cucurbits experimental plots by 50%. Survival of *C. carnea* decreased by 90% due to interference from indigenous predators (Rosenheim *et al.*, 1993). 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). Under the same conditions, we observed in a preliminary experiment that on average 20% of exposed syrphids eggs were consumed by predators (Hindayana, unpubl. data). Therefore, it is likely that IGP has a strong impact on the population dynamics of many beneficial and pest insect species.

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). The likelihood of 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 (Sengonca and Frings, 1985; Polis *et al*., 1989; Lucas *et al*., 1998).

In this study, the interspecific interactions of *E. balteatus* with three other aphidophagous predators, with the ladybird *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), the lacewing *C. carnea* and the gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) were investigated. Interactions between predators were studied in arenas of different sizes and in the presence or absence of the pea aphid *A. pisum* as extraguild prey. In central Europe, *E. balteatus* is the most common hoverfly and a voracious aphid predator in different crops. Particularly in cereals, this hoverfly is often an effective aphid predator (Ankersmith *et al*., 1986; Chambers and Adams, 1986; Poehling, 1988; Tenhumberg and Poehling, 1995). Strong effects on aphid populations were observed whenever high levels of syrphid oviposition occurred early and high numbers of larvae hatched before aphid populations achieved high growth rates (Tenhumberg and Poehling, 1995). Abundant immigration of adult female syrphids into crops depends on the local availability of suitable hibernation sites and spring habitats or long distance migration (Salveter, 1996; Krause, 1997; Hart *et al*., 1998). But even if immigration rates are high, the efficacy of aphid control by hoverflies shows considerable variability that cannot be explained simply by abiotic conditions (Poehling *et al*., 1991; Tenhumberg and Poehling, 1995). As the relationship between eggs laid and the number of young larvae resulting from them is the most variable factor influencing the population size of *E. balteatus*, it is hypothesized that biotic interactions with other predators might be an influence on the survival of these highly vulnerable life stages. In almost every habitat with aphids, a whole range of different aphid antagonists is also present (Groeger, 1993; Tenhumberg, 1993; Hindayana and Meyhöfer, unpubl. data; Brown, 1997; Nunnenmacher, 1998) and IGP can be expected. In both conservation of biological agents in outdoor crops and in greenhouses, such mixed predator communities are encouraged for biological control of aphids (Krieg and Franz, 1989; Schneller, 1997b; Flint and Dreistadt, 1998). However, the possible effects of intraguild predation are often neglected.

The objectives of this study were to elucidate the role of *E. balteatus* within its predator guild. As an aphidophagous predator, immature *E. balteatus* should show specific defense behaviors against other aphid predators. In a series of laboratory experiments, range intensities of predatory interference were elaborated. Conditions producing a high probability of interference among predators were simulated by using small arenas without extraguild prey. This setup mimicked situations in which an extraguild prey population rapidly decreases while predator densities are still high. An intermediate level of interference among predators was simulated in both small arenas with extraguild prey or large arenas without extraguild prey. Finally, low probability of interference among predators was expected in large arenas with whole plants and extraguild prey. Such conditions might occur in field situations with high extraguild prey populations. The potential role of all immature stages of *E. balteatus* as well as the effects of arena size and the availability of extraguild prey were also examined.

4.2. Materials and Methods

4.2.1. Rearing of the insects

Laboratory cultures were started with *C. septempunctata* and *E. balteatus* that were collected from a field near the Institute of Plant Diseases and Plant Protection in Hannover, northern Germany, and with *C. carnea* and *A. aphidimyza* obtained from a commercial supplier of biological control agents (Neudorff Ltd., Emmerthal, Germany). For all predator species, continuous laboratory cultures were established. Pea aphids, *A. pisum* on broad bean plants were offered to all predator species during their development. All rearing and experiments were conducted 20 $\pm$ 1 $^{\circ}$ C, 50 $\pm$ 10% relative humidity, 16 h of daylight and a light intensity of approximately 5000 lux (cd/m2).

E. balteatus was reared in accordance to the protocol of Bargen (1998) with slight modifications for the rearing of the larvae, which were kept in Plexiglas boxes (18 x 13.5 x 6.5 cm). Bee pollen (Melzer's Bienenfarm, Bonn, Germany), and crystalline sugar were fed to promote egg production of adult females.

Adult *C. septempunctata* were kept in groups of 20 to 30 in Plexiglas boxes (30 x 25 x 13 cm). Eggs laid were transferred to a smaller Plexiglas box which similar manner as *E. balteatus* larvae and kept there until pupation.

Adult *C. carnea* were kept in plastic tubes (10 cm in diameter, 20 cm in height) and reared on a diet previously described by Hassan (1975). Larvae were maintained in the same tubes as the adults until pupation. The pupae were transferred to petri dishes (5.5 cm diameter and 1.5 cm height) to avoid cannibalism by conspecific larvae.

Adult gall midges were kept in plexiglas boxes (40 x 30 x 20 cm) with a gauze window on one site. Broad bean plants, infested with *A. pisum*, were introduces into the boxes to stimulate egg laying. The larvae were kept in a similar manner as *C. carnea*.

4.2.2. Consumption rate and development time of aphidophagous predators

For experiments on intraguild predation, test insects need to be synchronized and voracious in confrontations. Therefore, before running IGP experiments, the developmental times and daily consumption rates of each predator species were investigated.

Only synchronized groups of pea aphids with a uniform age structure were used in these experiments as prey. Immediately after hatching, predator larvae were placed individually in petri dishes (5.5 cm diameter and 1.5 cm height) with a defined number of aphids. After 24 h, the number of aphids consumed was recorded, the remaining aphids were removed, and new aphids were introduced into the petri dish. Predator larvae of up to three days old were fed with 2-day-old aphids (L_2 stage). Older predator larvae were fed with 7-day-old aphids (L_4 stage). Aphids were provided on excised bean leaves. Experiments were replicated 22 times with *E. balteatus* and *C. septempunctata* and 17 times with *C. carnea*. Results of the experiment conducted with *A. aphidimyza* are not reported because very few individuals completed their development on this diet.

All experiments were conducted at 20 ± 1 $^{\circ}$ C, 50 ± 10% relative humidity, 16 h of daylight and a light intensity of approximately 5000 lux (cd/m^2). The total biomass of aphids consumed by predators in the experiments was compared using ANOVA, and in case of significant F-values, followed by a least significant different test (LSD) (Sokal and Rohlf, 1995).

4.2.3. Intraguild predation

The experiments on IGP were conducted at 20 ± 1 $^{\circ}$ C, 50 ± 10% relative humidity, 16 h of daylight and a light intensity of approximately 5000 lux (cd/ m^2). In the experimental set-up, different spatial dimensions of the foraging arena as well as the role of extraguild prey were considered. Except for gall midges, which were only tested in petri dishes (5.5 cm diameter and 1.5 cm height), two different types of arenas were used. Petri dishes served as small arenas, while broad bean plants in plexiglas tubes (15 cm diameter and 40 cm height) served as large arenas. The volume in large arenas was therefore 223 times greater than in small arenas. In small as well as in large arenas, IGP was investigated in the absence and presence of extraguild prey, i.e., aphids. In small arenas aphids were provided excised bean leaves and in large arenas on whole plants. The number of aphids offered varied in the different predator combinations, and was adjusted according to the specific consumption rates of the predators. Approximately 20 aphids were used for experiments in small arenas with early developmental stages, while 100 aphids were used in experiments in small arenas with late developmental stages, and 60 aphids for all experiments in large experimental arenas. In all treatments, aphids were always provided in surplus to predator consumption.

Larval stages of predators used in treatments were defined based on their consumption rates and developmental stages (see results; Fig. 4.1). First (L$_1$) and second (L$_2$) instar larvae of *E. balteatus*, *C. septempunctata* and *C. carnea* as well as third (L$_3$) instar larvae of *C. septempunctata* were tested one day after hatching or molting, respectively. Third instar of *E. balteatus* and fourth (L$_4$) instar larvae of *C. septempunctata* were collected 48 h after molting. Third instar larvae of *C. carnea* could be collected from the third until the eighth day

after molting (see Fig. 4.1). Old larvae (L_3) of *A. aphidimyza* used in the experiment were 120 h old.

The outcome of predatory interference between larvae was tested by confining individual *E. balteatus* larvae with one of the other species of predators. If an instar of *E. balteatus* acted as an IG predator, the next developmental stage of the opponent was tested. If *E. balteatus* turned out to be inferior, it was assumed that in confrontation with the next developmental stage of the opponent it would remain inferior. Therefore, these combinations were not tested. Eggs of *E. balteatus* were offered to *C. septempunctata* and *C. carnea* in all experiments in small groups of 12.1 ± 0.5 (SE) eggs per leaf as laid by female *E. balteatus*. In small arenas, leaf cuttings with eggs were introduced. The number of eggs consumed per egg mass was recorded. In the small arena, pupae were introduced individually, whereas in the large arenas, old L_4 *E. balteatus* were transferred into the arenas to allow pupation directly on the plants. Each combination was replicated 15 times. Each experiment lasted for 24 h. During the first two hours of each experiment in the small arena, all confrontations between the antagonists were observed directly to characterize the attack, counterattack and defense behavior of the opponents. Based on these characterizations the evidence of IGP was evaluated at the end of the 24h period under a stereo microscope and the outcome was classified.

The outcome of IGP was treated as a nominal variable (Köhler et al., 1996). The frequency of IGP in these experiments was compared using χ^2 tests with *Yate's correction for continuity* recommended for small sample sizes (Sokal and Rohlf, 1995). Percentages of syrphid eggs consumed by a predator in the absence and in the presence of aphids were tested using ANOVA. Data were arcsine transformed before analyses (Sokal and Rohlf, 1995).

4.3. Results

4.3.1. Consumption rate and developmental time of aphidophagous predators

At $20 \pm 1\ ^{\circ}$C, larval development of *C. septempunctata* and *C. carnea* took twice as long as that of *E. balteatus* (Fig. 4.1). Larvae of *C. septempunctata* consumed more prey biomass (154.4 ± 9.5 mg, SE) than did those of *C. carnea* (112.8 ± 4.6 mg, SE) or *E. balteatus* (91.9 ± 4.0 mg, SE) ($F = 24.6$; df = 2, 56; $p < 0.0001$). Late instars of all predators were more voracious than younger instars (Fig. 4.1). The molting and associated periods without feeding by larvae of *E. balteatus* were extremely short. Hence, molting could only be detected by direct observation. In contrast, molting in *C. septempunctata* and *C. carnea* could easily be detected by the shape of the aphid consumption curve. For both L_1 and L_2 of *E. balteatus,* development took an average of two days. Developmental time of both L_3 *C. carnea* and L_4 *C. septempunctata* were particularly long, lasting approximately seven days.

The choice of individuals for use in IGP experiments depended on species-specific behaviors. Directly after molting, larval instars of *C. septempunctata* and *C. carnea* were not very voracious. Thus, young instar larvae (L_1 and L_2 as well as L_3 *C. septempunctata*) and old instar larvae (L_4 *C. septempunctata* and L_3 *C. carnea*) of both predators were collected 24 h and 48 h after molting, respectively, to standardize the voracity of the predators. Extended starvation periods prior to the onset of IGP tests were not necessary. Thus, all predator larvae were starved only for 3 h before the beginning of an experiment.
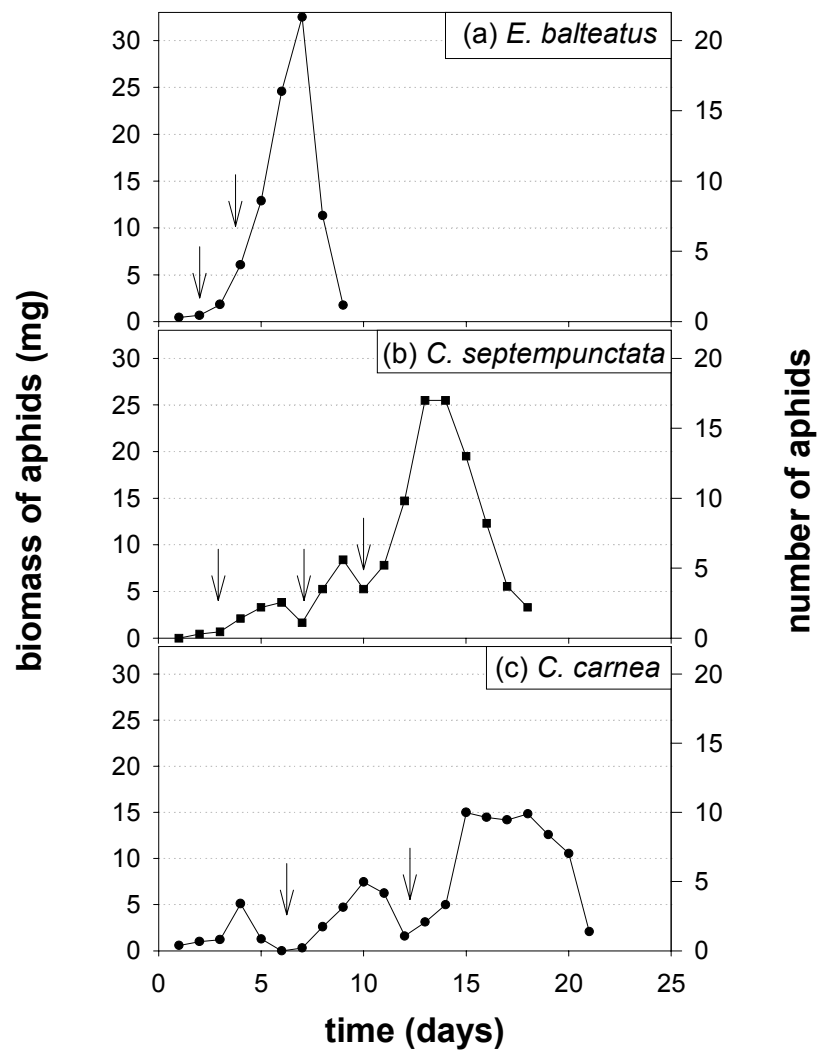
Fig. 4.1. Consumption rates (means) of *E. balteatus* (a), *C. septempunctata* (b) and *C. carnea* (c) during larval development (pea aphid *A. pisum* as prey). The amount of prey biomass eaten (in mg) was estimated as difference between prey input and remaining prey on a daily basis. The number of L_4 aphids (given on the second y-axis) was calculated taking into account the consumed biomass (in mg) and the average weight *of* L_4 *A. pisum*. Arrows indicate the moulting periods for the different larval stages of the predators. N = 22 for *E. balteatus* and *C. septempunctata* and N = 17 for *C. carnea*.

4.3.2. Intraguild predation

Behavioral characterization of intraguild predation. During the first two hours of each experiment, interspecific interactions between predators were observed. First instar larvae of *E. balteatus* did not show defense reactions or counterattack behavior in confrontations, while older larval stages (L_2 and L_3) of *E. balteatus* used oral secretions (slime) to defend themselves against the opponent or to attack it. Counterattacks by *E. balteatus* were seldom observed. When *E. balteatus* larvae were superior in confrontations, the remaining body parts of the intraguild (IG) prey showed a rather large circular hole as a result from repeated mouthhook insertions and slime secretions on the whole body surface. *C. carnea* larvae could often be observed to recoil repeatedly from the opponent during confrontations, which increased the distance to the aggressor. When *C. carnea* was IG predator, species-specific puncture holes from the mandible insertion could be observed in the remaining body parts of the IG prey. Moreover, the color of *E. balteatus* pupae turned from light yellow to black when destroyed by *C. carnea*. In contrast, larvae of *C. septempunctata* did not recoil but showed the ability to orally secret a black defense fluid that caused the opponent to recoil. In these experiments, *C. septempunctata* were never observed to show reflex bleeding. When acting as an IG predator, *C. septempunctata* larvae used then mandibles to tear large irregular holes in prey.

Based on these species-specific signs likely to be found on the remaining body parts of the IG prey, the behavioral interactions at the end of each experiment could be classified as (1) opponent dead and eaten by the IG predator, species-specific signs were present on the remaining parts, (2) the opponent dead but not eaten by the IG predator, species-specific signs indicated aggressions, (3) the opponent alive but was engaged in counterattacks or defensive behaviors, indicated by species-specific signs on its body, or (4) the opponents were both alive and showed no obvious signs of aggressions. A classification of confrontations is summarized in Table 4.1. In experiments where *E. balteatus* larvae were IG prey, both IG predator species, *C. septempunctata* and *C. carnea* larvae, consumed their prey items. In those

cases where *E. balteatus* larvae behaved as IG predator, a large proportion of *C. septempunctata* larvae survived an aggression, i.e., were not consumed by *E. balteatus* (Table 4.1). In contrast, *C. carnea* larvae were consumed, killed or survived an attack of *E. balteatus* in equal proportions, depending on the relative body size of IG prey (*C. carnea*) and IG predator (*E. balteatus*). There were very few contacts between *E. balteatus* and *A. aphidimyza*. In those cases where *E. balteatus* and *A. aphidimyza* did come into contact, *A. aphidimyza* was killed and its body fluids sucked out by *E. balteatus*.

Intraguild predation on eggs of *E. balteatus*. In all experiments, *C. septempunctata* and *C. carnea* larvae preyed on *E. balteatus* eggs. Particularly in the absence of aphids, the percentage of *E. balteatus* eggs consumed was related to the developmental stage of the predatory larvae. The larger the larvae, the more eggs of *E. balteatus* they consumed, leading in many cases to more than 70% egg mortality in small arenas (Fig. 4.2a and 4.3a) and 40% egg mortality in large arenas (Fig. 4.2b and 4.3b). In the presence of aphids in small arenas, young instars (L_1) of both predators and older instars of *C. septempunctata* consumed less than 20% of the eggs (Fig. 4.2 and 4.3), while old *C. carnea* larvae killed approximately 50% of *E. balteatus* eggs (Fig. 4.3a). In general, the presence of extraguild prey both in small and large arenas significantly reduced predation on *E. balteatus* eggs by *C. septempunctata* ($F = 114.14$; $df = 1, 58$; $p < 0.0001$ and $F = 6.89$; $df = 1, 28$; $p = 0.014$, respectively) and *C. carnea* larvae ($F = 12.70$; $df = 1, 88$; $p < 0.0001$ and $F = 16.75$; $df = 1, 28$; $p < 0.0001$, respectively). Increasing the foraging arena reduced predation on *E. balteatus* eggs by L_3 *C. carnea* both in the absence and presence of extraguild prey ($F = 24.29$; $df = 1, 28$; $p < 0.0001$ and $F = 11.80$; $df = 1, 28$; $p = 0.002$, respectively). However, the reduction in predation by L_4 *C. septempunctata* was only significant in the absence of aphids ($F = 30.90$; $df = 1, 28$; $p < 0.0001$ and $F = 0.34$; $df = 1, 28$; $p = 0.566$, respectively)

Table 1. Behavioral interactions between IG prey and IG predator (larvae) in relation to *E. balteatus*. Based on direct observations of predatory interference the outcome of all experiments was classified according to (1) opponent was dead and eaten by the IG predator, species specific marks were present, (2) the opponent was dead but not eaten by the IG predator, species specific marks indicated aggressions, (3) the opponent was alive but was engaged in counterattacks or defensive behaviors, indicated by species specific marks on its body, respectively and (4) the opponents were both alive and showed no obvious signs of aggressions. Values are given in percent of the total number of observations.

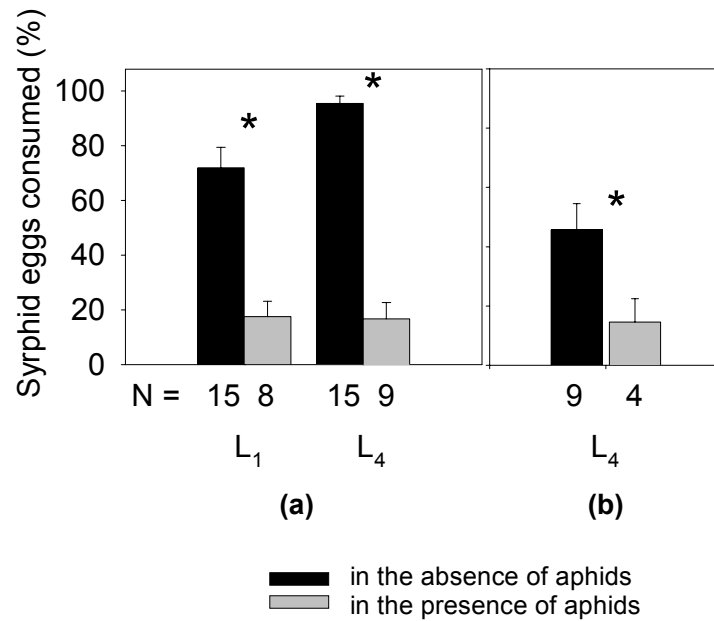| %	*C. septempunctata*		*C. carnea*		*A. aphidimyza*	
	as IG prey	as IG predator	as IG prey	as IG predator	as IG prey	as IG predator
(1) Eaten/Ingested	1.1 (3/270)	26.3 (71/270)	6.1 (11/180)	17.8 (32/180)	15.0 (18/120)	0.0 (0/120)
(2) Contact-dead	7.4 (20/270)	0.0 (0/270)	6.7 (12/180)	0.0 (0/180)	0.0 (0/120)	0.0 (0/120)
(3) Contact-survival	16.3 (44/270)		5.0 (9/180)		0.0 (0/120)	
(4) No contact-survival	48.9 (132/270)		64.4 (116/180)		85.0 (102/120)	

Fig. 4.2. Intraguild predation on syrphid eggs by *C. septempunctata*. The frequency of IGP was determined in small (a) and in large arenas (b). Bars represent the mean percentage (± SE) of syrphid eggs consumed during a 24h interval in small (a) and in large arenas (b). * indicate significant differences between treatments with and without aphids (p < 0.05, ANOVA), ns = not significantly different. The number (N) of replicates with IGP is given below each bar (in total N = 15).

Intraguild predation on L_1 *E. balteatus*. In the absence of aphids, L_1 *E. balteatus* turned out to be highly vulnerable to IGP, even when confronted with the same larval developmental stages of the two other predators *C. septempunctata* and *C. carnea* (Fig. 4.4a and 4.5a). No IGP was recorded when L_1 *E. balteatus* were exposed to *A. aphidimyza* larvae (Fig. 4.6). In experiments with *C. septempunctata* and *C. carnea*, the presence of aphids significantly decreased the frequency of IGP (x^2, value = 42.1; df = 1; p < 0.0001; N = 60) (Figs. 4.4 and 4.5). In large arenas, IGP on L_1 *E. balteatus* could not be verified. Because of their small body size, surviving larvae could not be located. Remains of dead L_1 also could not be found on the plants. Therefore, IGP on L_1 *E. balteatus* in large arenas could not be evaluated.
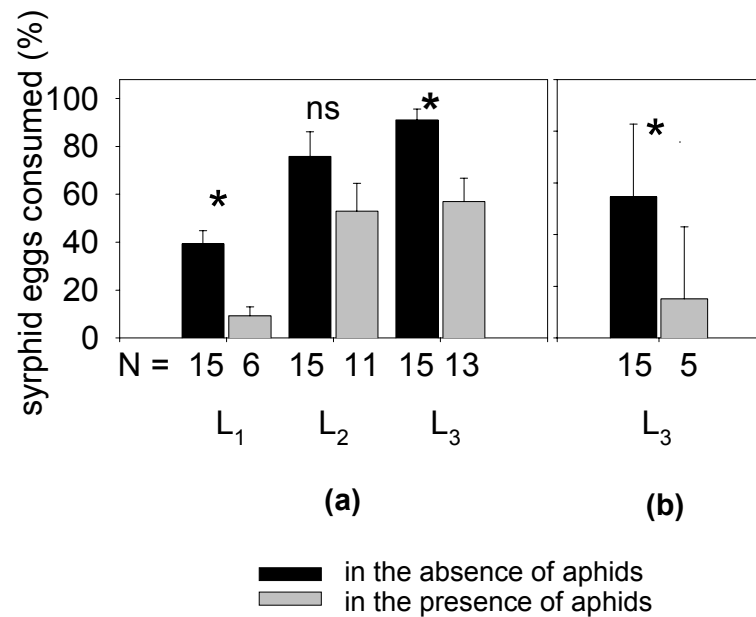
Fig. 4.3. Intraguild predation on syrphid eggs by *C. carnea*. The frequency of IGP was determined in small (a) and in large arenas (b). Bars represent the mean percentage ($\pm$ SE) of syrphid eggs consumed during a 24 h interval in small (a) and in large arenas (b). * indicate significant differences between treatments with and without aphids ($p < 0.05$, ANOVA), ns = not significantly different. The number (N) of replicates with IGP is given below each bar (in total N=15).

Intraguild predation on L_2 *E. balteatus*. In small arenas and in the absence of aphids, L_2 of *E. balteatus* was only vulnerable to late instars and adults of *C. septempunctata* (Fig. 4.4a) and to late instar larvae of *C. carnea* (Fig. 4.5a). When exposed to L_3 *C. septempunctata* or L_2 *C. carnea*, the predatory interference was symmetrical: L_2 *E. balteatus* fed on other predators and vice versa. When L_2 *E. balteatus* were confronted with younger instars of *C. septempunctata*, *C. carnea* or with late instars of *A. aphidimyza*, *E. balteatus* larvae were able to kill other predators (Figs. 4.4, 4.5 and 4.6). In the presence of extraguild prey, IGP on L_2 *E. balteatus* by *C. septempunctata* and *C. carnea* decreased in small arenas significantly (χ^2, value = 40.24; df = 1; p < 0001; N = 180) (Figs. 4.4a and 4.5a), while in large arenas IGP remained constant in presence and absence of extraguild prey (χ^2, value = 0.32; df = 1; p = 0.57; N = 90) (Fig. 4.4b and 4.5b).

Intraguild predation on L_3 *E. balteatus*. Compared to L_2, a reduced frequency of IGP was recorded between L_3 *E. balteatus* larvae and L_3 *C. septempunctata*

and L$_4$ *C. carnea*, respectively. However, in small arenas and in the absence of aphids, in most cases *E. balteatus* larvae were killed by adult as well as by L$_4$ *C. septempunctata* and IGP was reduced significantly in the presence of aphids (χ^2, value = 21.01; df = 1; p < 0.0001; N = 30) (Fig. 4.4a). In large arenas, hardly any L$_3$ *E. balteatus* were killed by adult or L$_4$ *C. septempunctata* and there was no significant difference between the treatments with and without aphids (χ^2, value = 0.00; df = 1; p = 1; N = 30) (Fig. 4.4b). In contrast, L$_3$ *E. balteatus* were superior in confrontations with L$_2$ and L$_3$ of *C. carnea* (Fig. 4.5). When interacting with earlier larval instars of the other predators as well as with all stages of *A. aphidimyza* (Fig. 4.6), L$_3$ *E. balteatus* behaved as an intraguild predator.

Intraguild predation on *E. balteatus* pupae. Neither larvae nor adults of *C. septempunctata* preyed on *E. balteatus* pupae (Fig. 4.4). L$_3$ *C. carnea* but not L$_1$ or L$_2$ were able to feed on *E. balteatus* pupae. In the absence of aphids and in small arenas, the mortality risk for pupae of *E. balteatus* was about 33%. Increasing the foraging arena did not affect the mortality risk for *E. balteatus* by *C. carnea* larvae neither in the absence nor in the presence of aphids (χ^2, value = 1.08; df = 1; p = 0.30; n = 30 and χ^2, value = 0.54; df = 1; p = 0.46; N = 30; respectively) (Fig. 4.5).
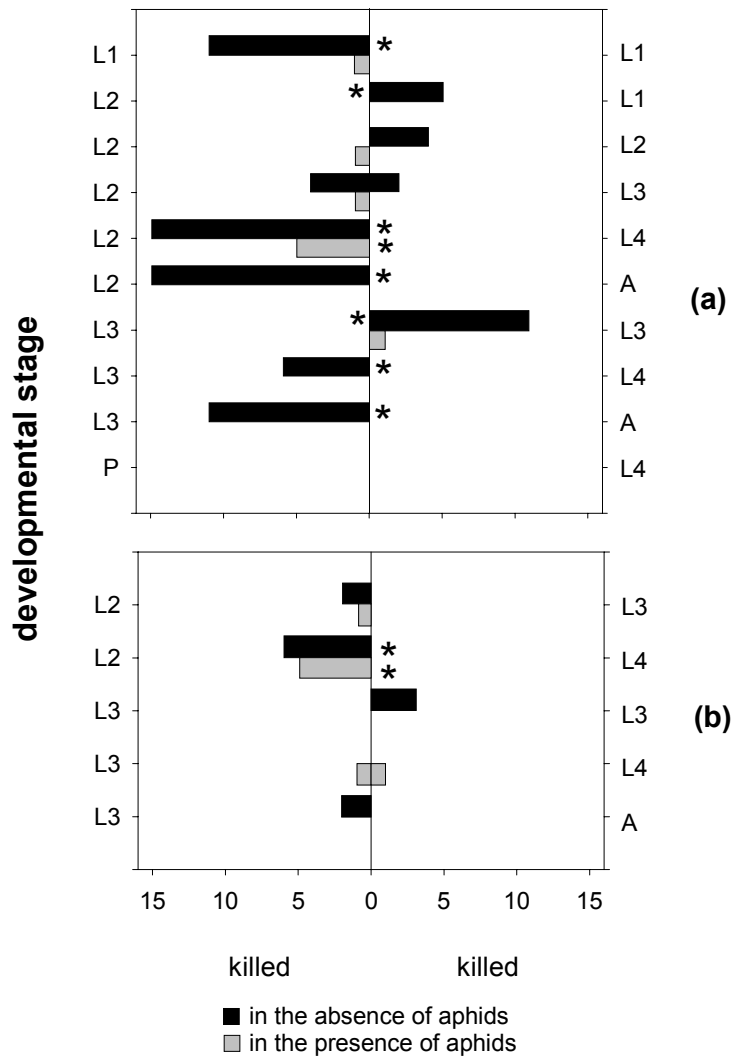
Fig. 4.4.   Intraguild predation between different developmental stages of *E. balteatus and C. septempunctata* in small arenas (a) and in large arenas (b). Bars represent the number of replicates (in total N = 15) where the opponent was IG prey. Significant differences in the number of predator aggressions are indicated with * (p < 0.05, χ^2 tests with *Yate's correction for continuity*). L_1-L_4 = larval developmental stages 1 – 4, P = pupae, A = Adult.

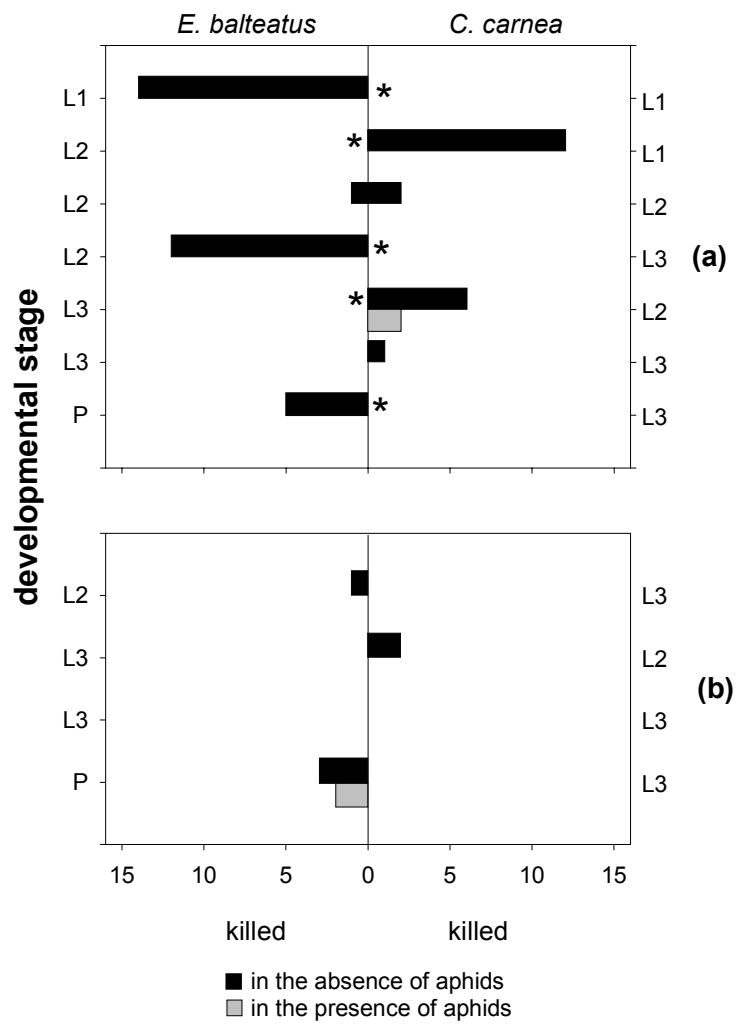Fig. 4.5. Intraguild predation between different developmental stages of *E. balteatus and C. carnea* in small arenas (a) and in large arenas (b). Bars represent the number of replicates (in total N=15) where the opponent was IG prey. Significant differences in the number of predator aggressions are indicated with * (p < 0.05, χ^2 tests with *Yate's correction for continuity*). L_1-L_3 = larval developmental stages 1 – 3, P = pupae.
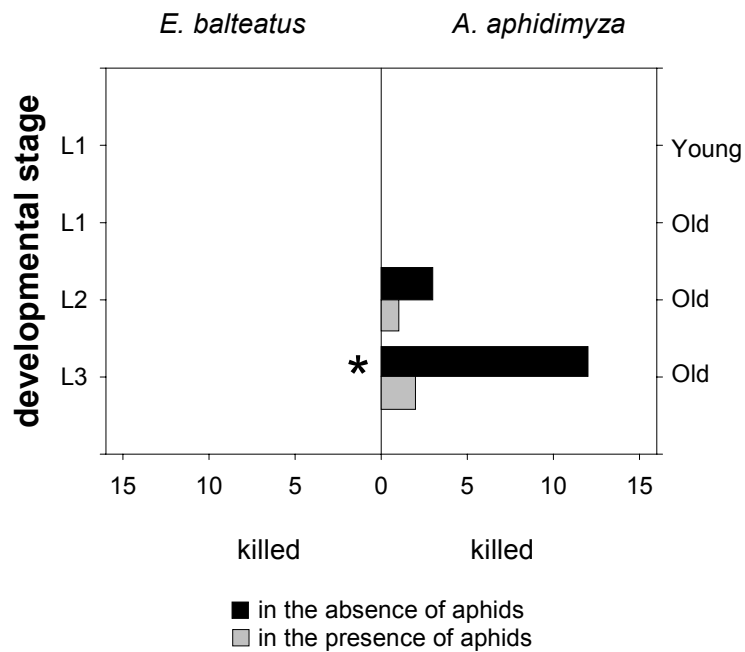
Fig. 4.6.   Intraguild predation between different developmental stages of *E. balteatus and A. aphidimyza* in small arenas in the absence and presence of extraguild prey. Bars represent the number of replicates (in total N =15) where the opponent was IG prey. Significant differences in the number of predator aggressions are indicated with * (p < 0.05, χ^2 tests with *Yate's correction for continuity*). L_1 - L_3 = larval developmental stages 1 – 3, young = 48 h old larvae, old = 120 h old larvae.

Influence of extraguild prey (aphids) and different assay arenas on IGP.
The outcome of interspecific interactions between the different predators was significantly influenced by both the availability of extraguild prey and by the size of the arena. In all but one experiment, the presence of aphids as extraguild prey significantly reduced the frequency of IGP (Table 4.2). In all treatments, the total number of IGP events decreased by half in the presence of aphids. The same trend of interspecific relationships was observed for *E. balteatus* and *C. septempunctata* and for *E. balteatus* and *C. carnea*. In the absence of extraguild prey, a significantly higher level of IGP was recorded in small compared to large arenas (Table 4.3).

Table 4.2. The effect of extraguild prey (aphids) on IGP between *E. balteatus* (eggs, larvae and pupae) and other aphidophagous predators. Numbers represent the sum of predatory interference between the opponents either in presence or absence of extraguild prey. Significance level was estimated by χ^2 tests with *Yate's correction for continuity*.

Predator species	Arena type	N	Occurrence of IGP		p
			No-aphids	Aphids	
C. septempunctata	Small arena	360	115	26	0.001
	Large arena	180	22	12	0.087
C. carnea	Small arena	300	98	32	0.001
	Large arena	150	21	7	0.006
A. aphidimyza	Small arena	120	15	3	0.005

Table 4.3. The effect of arena size on IGP between *E. balteatus* (eggs and larvae and pupae) and other aphidophagous predators. Numbers represent the sum of predatory interference between the opponents either in small arenas or in large arenas. Significance level was estimated by χ^2 tests with *Yate's correction for continuity*.

Predator species	Aphids	N	Occurrence of IGP		p
			Small arena	Large arena	
C. septempunctata	Absence	180	64	22	0.001
	Presence	180	16	12	0.537
C. carnea	Absence	150	39	21	0.005
	Presence	150	15	7	0.106

4.4. Discussion

Under laboratory conditions, the role of immature developmental stages of *E. balteatus* within the guild of aphidophagous predators was characterized. Direct and indirect interactions between predators are one of the most recently identified factors that determine the abundance and densities of predators (Janssen *et al.*, 1998). The focus of this study was on direct interactions between *E. balteatus* and other aphidophagous predators. These interactions may include defense behavior of *E. balteatus* larvae and tropic interaction, e.g. IGP. The results with *E. balteatus* confirm that the size of the respective predator determines the outcome of the interaction, with larger individuals behaving as IG predators and smaller individuals becoming IG prey (Sengonca and Frings, 1985; Polis *et al.* 1989; Lucas et al, 1998; Snyder and Wise, 1999). Confrontations between predators of similar size often resulted in symmetric interactions where neither species consistently took on the role of the IG predator. The importance of body size for the outcome of interspecific interaction reflects the sum of species-specific behavioral and morphological attributes: (i) weapons and attack behavior, (ii) body strength of the opponents, (iii) defense mechanisms and (iv) escape mechanisms. Each of these factors will be discussed separately and finally the role of extraguild prey and size of foraging arenas are considered to explain the mortality risk for *E. balteatus* by intraguild predation.

4.4.1. Role of attack, strength and defense mechanisms for the hierarchy of IGP

Large individuals are able to fight longer than small individuals because of proportionally larger energy reserves (Peter, 1983; Griffiths, 1991). Additionally, they have larger mandibles (Griffiths, 1992). Therefore, they could usually overcome the adversary. In *E. balteatus,* the L_2 was the first developmental stage that was able to kill larvae of *C. septempunctata*, *C. carnea* and *A. aphidimyza*. This ability was mainly due to well-developed mouthparts of L_2, with the triangular sclerites already present (Tinkeu and Hance, 1998) and an increased slime production in L_2 compared to L_1 *E. balteatus* (D. Hindayana,

pers. observation). Slime is used by syrphid larvae as sticky salivary glue to capture prey and as a defensive secretion (Eisner, 1971). L_3 produced considerably more slime than the younger instars, and had a higher mobility. Consequently, they able to attack opponents or defend themselves better against attacks by other predators. Adversaries that came into close contact with the defensive slime secretions of *E. balteatus* larvae but were not killed sometimes until to 16 %recovered (Table 1).

Coccinellid larvae excreted orally a black defense fluid, containing alkaloids (Ceryngier and Hodek, 1996). Oral secretions of L_4 *C. septempunctata* were effective against larvae of *E. balteatus.* After contact with the defensive fluid of coccinellids, L_3 *E. balteatus* were immobilized, but recovered after a few minutes and started crawling again. Additionally, spikes on the dorsal integument of *C. septempunctata* larvae prevent successful attacks of *E. balteatus* larvae. L_3 *C. carnea* possess powerful mandibles (Romoser and Stoffolano, 1998) and were able to pierce *E. balteatus* pupae. However, *C. carnea* larvae were repelled by the slime secreted by larval *E. balteatus*. In general, defense mechanisms were less pronounced in less sessile stages like eggs, L_1 and pupae. These developmental stages have few possibilities to defend themselves against a predator's attack (New, 1991). All instars of the rather small, immobile and defenseless *A. aphidimyza* larvae were always IG prey to *E. balteatus* larvae. Lucas *et al.* (1998) also showed that *A. aphidimyza* was an easy IG prey of the coccinellid *Coleomegilla maculata lengi* Timberlake and the chrysopid *Chrysoperla rufilabris* (Burmeister).

Certain predators usually have low predation rates on inactive prey (Englund, 1997; Eubank and Denno, 2000). The observations indicated that *E. balteatus* belongs to this category. *E. balteatus* larvae were more mobile in the presence of actively foraging predators (D. Hindayana, unpubl. data) and the encounter risk between *E. balteatus* and *C. carnea* was lower than between *E. balteatus* and *C. septempunctata*. The high mobility of *C. septempunctata* larvae caused the high activity of *E. balteatus* larvae, thus increasing the probability of IGP. By contrast, in both small and large arenas, *C. carnea* larvae were less active. Chang (1996) observed that the lacewing *Chrysoperla plorabunda* Fitch often

hides in the leaf-axil when inactive. Hiding in a shelter could reduce the number of contacts with other predators, and thereby minimizes the risk of IGP. In addition, we observed that most often L_3 *C. carnea* avoided counterattacks and tried to escape from *E. balteatus* larvae.

Lucas *et al.* (1998) concluded that highly-specialized aphid predators like *A. aphidimyza* are completely ineffective in conflicts with more generalist predators like *C. maculata lengi* and *C. rufilabris*. According to the results here, this does not necessarily apply to all specialist predators in the same way. Larvae of *E. balteatus*, a specialist predator of aphids, were able to defend themselves and could kill more generalist coccinellid and chrysopid predators. In interspecific confrontations, predator size and defense behavior seems to be more important than prey specificity.

The experiments showed that the potential for predatory interference between larvae of *E. balteatus* and other aphidophagous predators depends on the body size, foraging activity and defense behavior, with large individuals usually behaving as intraguild predators, and small individuals prey. In confrontations between *E. balteatus* and *C. septempunctata* or *C. carnea*, for example, there is a dynamic shift in the behavior of *E. balteatus* from that of an IG predator to an IG prey as the relative size of the life stages of two confronting species change. *E. balteatus* L_2 as an IG predator in confrontations with *C. septempunctata* L_1 and L_2, while symmetric IGP could be observed with L_3 larvae. The role of *E. balteatus*, however, shifted to that of IG prey in confrontations with L_4 or adults of *C. septempunctata*. Similar shifts in the behavior could be observed in confrontations with *C. carnea*. Figure 4.7 summarizes the changes in the hierarchy of the different developmental stages of *E. balteatus* within the guild of synchronized aphid antagonists in relation to larval development of each species. Such situations can occur when several antagonists are released in a greenhouse at the same time.
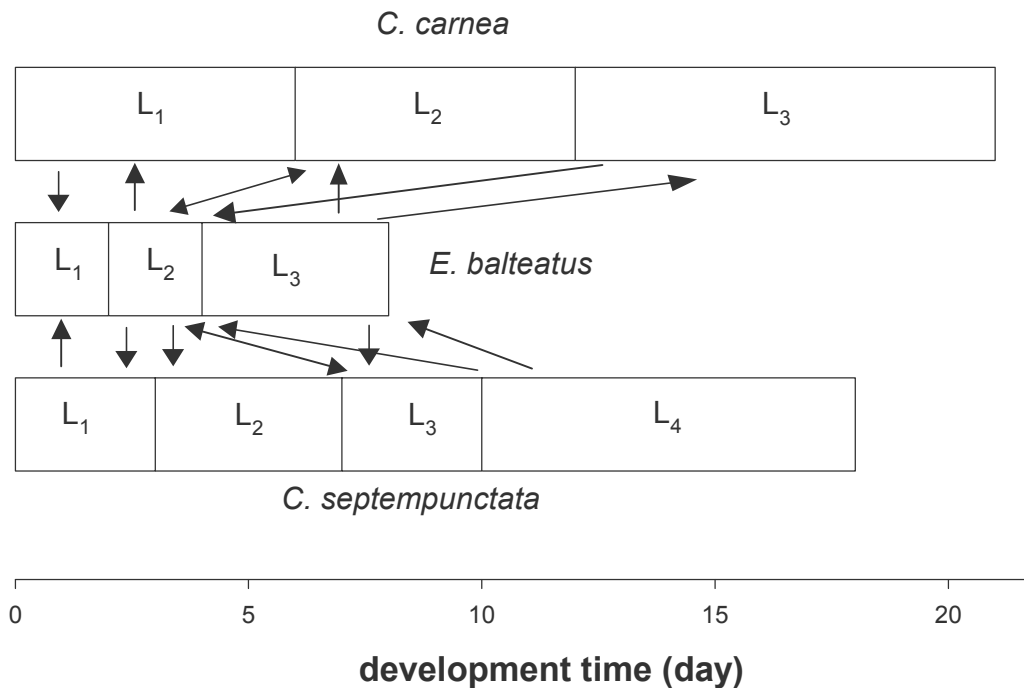
Fig. 7 Linkage between the developmental time of larval instars and the occurrence of IGP between *E. balteatus* and *C. carnea* as well as *C. septempunctata* in a perfectly synchronized antagonist community. Arrows indicate the direction of IGP, pointing towards IG prey. The graph is based on the results obtained in small arenas and absence of extraguild prey. L_1-L_4 = larval developmental stages 1 – 4.

Moreover, the figure shows that *E. balteatus* larvae develop twice as fast as *C. septempunctata* and *C. carnea*. Molting phases during which predators might be extremely vulnerable were not observed during larval development of *E. balteatus*. Fast larval development in general is interpreted as an adaptation to limited resource availability (Mattson, 1980; Scriber and Slansky, 1981). Additionally, the experiments showed that short developmental times could be interpreted as adaptation to minimize exposure times of vulnerable stages to high predation risks. The rapid larval development of *E. balteatus* without reduced mobility during molting periods minimizes the exposure times of susceptible young larval stages. *E. balteatus* grows rapidly and L_2 change in the hierarchy within the antagonist guild quickly from IG prey to IG predator (Fig. 4.7).

4.4.2. Influence of extraguild prey and assay arenas on IGP

The presence of extraguild prey could either increase or decrease the probability of IGP or could have no effect (Lucas *et al.*, 1998). A decrease could be due to a dilution effect by the extraguild prey, while an increase could be the result of predator aggregation in prey colonies. Meyhöfer and Hindayana (2000) observed that IGP on parasitoid mummies was similar in the presence and absence of extraguild prey. This indicates that aggregation of predators in aphid colonies and the dilution effect might offset each other. Lucas *et al*. (1998) proposed four different scenarios to characterize the role of extraguild prey in IGP.

1). IGP might decrease steadily with increased extraguild prey densities (e.g., predation of the phytoseiid *Amblyseius cucumeris* Oudemans by the predatory bug *Orius tristicolor* [White]).

2). IGP might decrease exponentially as extraguild prey is introduced (e.g., confrontation between L_1 *C. rufilabris* and L_1 *C. maculata*).

3). IGP might be constant regardless of extraguild prey density (e.g., confrontation between L_3 *C. rufilabris* and L_1 *C. maculata*).

4). IGP might remain constant and high at low extraguild prey densities but decrease at very high densities (e.g., confrontation between L_3 *C. rufilabris* and old larvae of *A. aphidimyza*).

The results show that the presence of extraguild prey reduced predatory interference between *E. balteatus* and *C. septempunctata*, *C. carnea*, or *A. aphidimyza*, irrespective of the size of the arena, and led to a threefold decrease in IGP (Tab. 4.2). Since different densities of extraguild prey were not tested, it is impossible to distinguish between a linear or exponential decrease in IGP. However, the impact of extraguild prey on the role of *E. balteatus* within predator guild seems to be best explained by the scenario of Lucas *et al*. (1998) in which IGP decreases with increased the extraguild prey density.

The presence or absence of extraguild prey may not only influence the direction and outcome of IGP, but also the foraging behavior of the predators. The size of the experimental arenas has an important effect on IGP (Chang, 1996). Depending on the different assay arenas and the availability of extraguild prey,

the results reflect different levels of IGP, i.e., strong, intermediate and moderate levels of IGP. Strong IGP, when more than 50% of the confrontations end with predatory interference was found only in small arenas in the absence of extraguild prey. These experiments in small arenas show the potential outcome of predatory interference between two antagonists and allowed to estimate the effectiveness of attack and defense mechanisms (Diamond, 1986; Wiens, 1989; Levin, 1992) prior to more complex situations (Diamond, 1986; Kareiva, 1990). However, strong IGP with 50% predatory interference are also frequently observed in the field in extreme situations, i.e., when extraguild prey populations rapidly decrease and predator densities are still high (Rosenheim *et al.*, 1993; Snyder and Wise, 1999; Meyhöfer and Hindayana, 2000). Intermediate levels of IGP, with predatory interference between 20-50%, were observed either in small foraging arenas in the presence of aphids, or in larger arenas without extraguild prey (Table 4.3). Occurrence of symmetry and probability of IGP was similar in both situations. In the presence of aphids, IGP most likely was reduced because of the dilution effect, which increases the chances of survival for the competing predators (Taylor, 1984; Turchin and Kareiva, 1989; Lucas *et al.*, 1998; D. Hindayana, unpub. data). In larger foraging arenas, the predators were able to stay in refuge patches (Englund, 1997). However, a larger searching arena and the presence of extraguild prey did not completely prevent IGP, although the occurrence of IGP was reduced approximately fivefold compared to small arenas (moderate IGP**,** less than 20% predatory interference). It is believed that the incidence of IGP in large arenas and in the presence of extraguild prey is related to the defense mechanism of aphids and the searching activity of predators. *C. septempunctata* can dislodge nearly 60% *of A. pisum* from the plant (Losey and Denno, 1998a). In consequence, two predators forage for prey on the same plant and on similar foraging paths and extraguild prey gets scarce, while the chances of IGP increase.

4.5. Conclusion

In carnivore guilds, IGP is the result of a cascade of foraging decisions leading to various degrees of interference between predators. The oviposition decisions

of adults, whether eggs are laid singly or in batches, the foraging behaviors of young and old larvae, larval defensive abilities, the phenology and developmental times of predators, and the effect of extraguild prey density, all influence the extent of IGP. Because of these factors, the current knowledge is insufficient to predict the importance of IGP at the community level. For *E. balteatus*, it can be concluded that the egg stage and young developmental stages are particularly vulnerable to IGP. Intraguild predation as a possible mortality risk for antagonists should not be neglected when explaining pest population dynamics in the field or in IPM projects. Especially in greenhouses where a diverse guild of predators is often employed, IGP might be of primary importance.

5. The effect of predator combination on population dynamics and dispersal of aphids

5.1. Introduction

Studies on predator-predator interactions and their consequences for prey population dynamics are relatively new (Kareiva, 1994; Losey and Denno, 1998b). Traditional research on pest population regulation emphasizes chemical input, resistant plant varieties or specific natural enemies (Letourneau and Andow, 1999) with focus on individual pairwise interactions at any time (Kareiva, 1994). In nature, however, things are far more complex. Interactions among predators, for instance, can have a substantial effect on the total impact of an antagonist guild on the pest population dynamics. The term intraguild predation (IGP) (Polis et al., 1989) is nowadays most commonly used for trophic interference among natural enemies.

In theory intraguild predation can lead to three different effects on pest population regulation, i.e. synergistic, additive or non-additive effects (Ferguson and Stiling, 1996). Synergistic effects of two natural enemies on the pest population can be found when their impact is higher than the expected value, i.e. the sum of the impact of each antagonist on its own. This effect can occur when the foraging activity of one predator species alters the behavior or feeding niche of the prey, making it more susceptible to another predator (Losey and Denno, 1998b and 1999; Soluk, 1993). An additive effect might occur when natural enemies do not interact, so that the total level of prey mortality is equal to the individual mortality rates (additive mortality) (Ferguson and Stiling, 1996; Losey and Denno, 1998b). A non-additive effect can be observed when one natural enemy kills or interferes with another natural enemy (Losey and Denno, 1998b). In case of non-additive effects the impact of the antagonists on the pest population is less than the additive effects or the mortality caused by one natural enemy alone (Ferguson and Stiling, 1996). Synergistic or at least additive effects should be favored in all biological control efforts.

The presence of natural enemies in a certain habitat not only reduces the prey population but also changes its distribution (Sih, 1987). Predators are responsible for proximate and also for olfactory cues (Bargen, 1998) and prey directly respond with defense behaviors against natural enemies. Defensive responses such as kicking, walking away and especially dropping off from the plant are known to be the most common escape behaviors of aphids for increasing individual survival (Klingauf, 1967; Niku, 1971; Roitberg and Myers, 1977 and 1979; New, 1991; Losey and Denno, 1998). In a similar fashion the alteration of prey activity in the presence of predators was observed for caterpillars (Stamp and Bowers, 1992). Moreover, sucking pests (Homoptera, Heteroptera) can function as vectors for various diseases. As a consequence predator induced dispersal of the prey might have an indirect impact on the spread of certain plant diseases within a crop (Niku, 1971). On the other hand, alteration in the distribution of prey could also be of advantage for some predators, since some of them cannot perceive preys at a great distance and rely on random searching movement to locate the prey (Gutierrez *et al.*, 1980; New, 1991; Berenbaum, 1995). The more prey disperses the higher is the possibility for predators to encounter them.

In central Europe, *E. balteatus* is the most common hoverfly and a voracious aphid predator in different crops. The aphid *Acyrthosiphon pisum* (Harr.) (Homoptera: Aphidae) is a common pest on leguminoceae such as clover, lucerne, and peas (Djafaripour, 1976; Suter, 1977) in central Europe and on alfalfa in North America (Roitberg and Myers, 1979; Gutierrez *et al.*, 1980; Losey and Denno, 1998). In almost every habitat where aphids occur a whole range of aphid antagonists can be found (Brown, 1977; Groeger, 1993; Hindayana & Meyhöfer, unpub. data; Nunnenmacher, 1998; Tenhumberg, 1993) and interspecific interactions between natural enemies can be expected. Moreover, the pea aphid *A. pisum* can cause not only direct damage on the plant by causing leaf yellowing, stunting and even plant death (Guiterez et al., 1980), but also indirect damage as a virus vector for the pea enation mosaic virus (Farah, 1968; Adam, 1976). Since *A. pisum* is known to escape from predator attacks by use of alarm pheromones and dropping from the plants

(Klingauf, 1967; Niku, 1971; Losey and Denno, 1998a), it might speed up the spread of a virus disease.

In this study the specific interactions of *E. balteatus* with two other aphidophagous predators, i.e. the ladybird *C. septempunctata* and the lacewing *C. carnea,* were investigated. The aim was to quantify the effect of predator combinations on the population dynamics and the distribution of the pea aphid *A. pisum* in the habitat.

5.2. Materials and Methods

5.2.1. Rearing of the insects

Laboratory cultures were started with *C. septempunctata* and *E. balteatus* that were collected from a field near the Institute of Plant Diseases and Plant Protection in Hannover, Northern Germany, and with *C. carnea* obtained from a commercial supplier of biological control agents (Neudorff Ltd., Emmerthal, Germany). For all predator species, continuous laboratory cultures were established. *E. balteatus* was reared in accordance with the protocol of Bargen (1998). Bee pollen (Melzer's Bienenfarm, Bonn, Germany) and crystalline sugar were fed to promote egg production of adult females. Adult *C. carnea* were reared on an artificial diet (Hassan, 1975). Broad bean plants (cv. Hang down "Grünkernige") with pea aphids were offered to both predator species for egg laying. Pea aphids on cut sections of broad beans were provided as prey for all developmental stages of the predatory species until pupation. Rearing conditions were $20 \pm 1\ ^{\circ}C$, $50 \pm 10\%$ relative humidity, 16 h of daylight and a light intensity of approximately 5000 lux (cd/m^2). A more detailed description of the rearing procedures is given in chapter 4.

5.2.2. Experimental set-up

The experiments to evaluate the effect of single and combined predator impact on the population and distribution of aphids were conducted in a greenhouse at $24 \pm 2\ ^{0}C$, $50 - 60\ \%$ relative humidity and 16 h of daylight. Two different arena

types with different spatial dimensions were used. A single broad bean with 4 leaves in a plexiglas tube (15 cm diameter and 40 cm height) served as small arena, while 9 broad bean plants in a cage (75 x 56 x 52 cm) served as a large arena. The volume of the large arenas was approximately 30.9 times bigger than in the small arenas. In the large arenas nine broad bean plants were planted on a tray (48 x 30 x 7 cm). The distance between the individual plants was approximately 13 cm. At this distance plants do not touch each other and aphids as well as predators have to cross the soil to change plants. In both arenas, 30 synchronized L_4 aphids were introduced as a starting population. Specimens were placed on the stem of the host plant close to the ground 3 h before the release of the predator larvae. Second instar larvae (L_2, three days old) of *E. balteatus*, fourth instar larvae (L_4, directly after molting) of *C. septempunctata* and third instar larvae (L_3, two days after molting) of *C. carnea* were used in the experiments. Single and combined release of *E. balteatus* with either *C. carnea* or *C. septempunctata* was tested. *E. balteatus* larvae were released on the upper leaves of the broad bean plant, while *C. septempunctata* or *C. carnea* were released on the stem of the broad bean plant near the ground. In the cage, aphids and predators were released on the plant in the center of the tray (no. 5). Experiments were replicated 15 times in the plexiglas tubes and 10 times in the cages.

The number of aphids per plant was counted every 24 h over a period of 5 days. The average number of aphids per day in the presence of different predator species was compared with repeated measures ANOVA, and in case of significant differences, followed by a bonferroni posthoc test (Sokal and Rohlf, 1995). The data of the proportions of aphids in the various plant locations, i.e. canopy, first leaf (Leaf-1), second leaf (Leaf-2), third leaf (Leaf-3), stem and off-plant, were arc-sin transformed. The distribution of aphids within and among plants was analyzed using a method developed by Lloyd (1967). He named the distribution parameter as "patchiness" of a given distribution. Changes in population density have little impact on this parameter.

Patchiness is defined as:

$$\text{mean crowding } (X^*) \, / \, \text{mean } (X)$$

where mean crowding (X^*) is defined as

$$X^* \; = \; X + (S^2/X - 1)$$

with S^2 being the population variance. Values of patchiness less than, equal to, or bigger than 1 indicate uniform, random and aggregated distribution. The patchiness index was rank transformed for the comparison between different treatments and analyzed with a nonparametic ANOVA, i. e. the Kruskal-Wallis test for measure differences in location and in case of significant differences, followed by the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1995).

5.3. Results

5.3.1. Impact of predators on population growth and dispersal of aphids within plants

Aphid populations. All experiments were carried out in plexiglas arenas covering a single plant. Therefore neither aphids nor predators had the possibility to spatially escape from predation. The growth of the aphid populations under different treatments and the aphid distributions within a single plant were analyzed. The repeated measures ANOVA showed a statistically significant TREATMENT x TIME effect ($p<0.001$) that indicates that the population growth was different under the tested treatments (Fig. 5.1, Table 5.1). The presence of either a single predator or a combination of two predator species significantly reduced the population growth of the pea aphid compared to the control (Table 5.2). Most of the single predator species treatments had a similar impact on the aphid population growth and were not significantly different from each other or from the predator combination treatment of *E. balteatus* and *C. septempunctata* (Fig. 5.1a, Table 5.2). On the contrary the simultaneous treatments of *E. balteatus* with *C. carnea* had a significantly higher impact on the aphid population in comparison with the single predator treatments (Fig. 5.1b, Table 5.2). Predator combination treatments were not significantly different from each other.
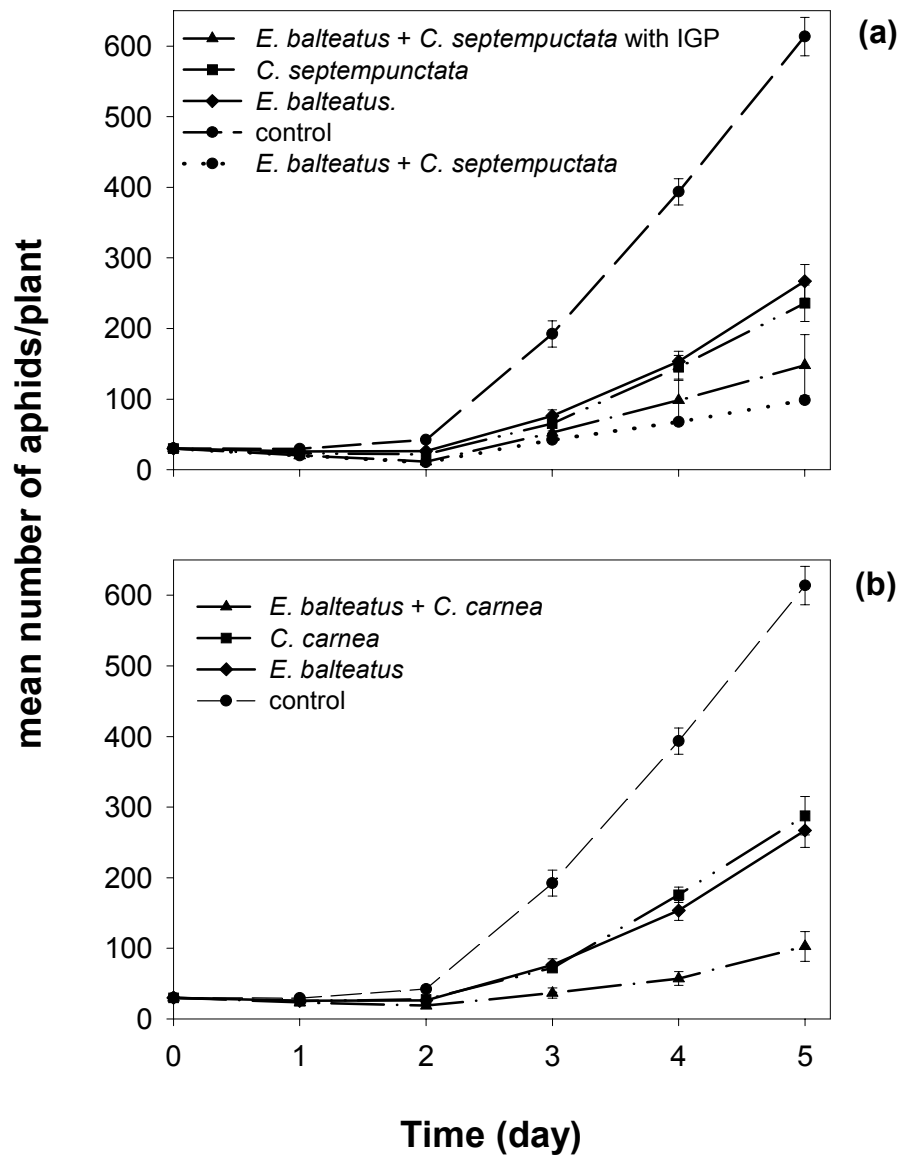
Fig. 5.1. Effects of predator combination on the aphid population growth of *A. pisum* on single plants in plexiglas arenas. *E. balteatus* was tested simultaneously with *C. septempunctata* (a) or *C. carnea* (b). N = 12 for *C. carnea*, all other treatments N = 15, mean number of aphids ± SE.

At the end of the experiments, the mean number of aphids in the presence of *E. balteatus*, *C. septempunctata* and *C. carnea* was approximately 2 times less than in the control (613.9 ± 23.9 (SE) aphids/plant) (p < 0.0001, p < 0.0001 and p < 0.0001). When two predators were combined the mean number of aphids was 4.2 times less for *E. balteatus* and *C. septempunctata* (147.9 ± 43.3, SE) and 6.0 times less for *E. balteatus* and *C. carnea* (102.7 ± 21.1, SE) compared to the control. In the combined treatment with *E. balteatus* and *C. septempunctata* intraguild predation was observed in 5 replicates. The syphid

larvae were killed by the coccinellid larvae in all cases. Compared to the replicates without IGP the effectiveness of the predators in the presence of IGP was slightly reduced (see Fig. 1a), although the reduction was not significant (t-test, $t = -0.804$; $df = 23$; $p = 0.429$). Intraguild predation in a predator combination of *E. balteatus* and *C. carnea* was not observed.

Table 5.1. Repeated measures ANOVA of the population growth (plexiglas cylinders) for a period of five days. Six treatments were considered: control, single predator treatments (*E. balteatus*, *C. septempunctata*, *C. carnea*), combined predator treatments (*E. balteatus* + *C. septempunctata*, *E. balteatus* + *C. carnea*). N = 12 for *C. carnea*, all other treatments N = 15.

Between subjects Source	df	MS	F	P>F
Treatment	5	399272.4	43.64	< 0.001
Error	81	9150.0		

Within subject Source	df	MS	F	P>F
Time	4	1000513.4	401.76	< 0.001
Treatment x Time	20	85432.3	34.31	< 0.001
Error (time)	324	2490.4		

Aphid dispersal. The distribution of aphids was analyzed at two different times: (1) immediately after the release of the predator to estimate initial dispersal and (2) at the end of the experiment (day 5) when aphid dispersal to refuge patches had been more or less established. The within plant distribution of aphids varied between the different treatments and days (ANOVA, $F = 2.97$; $df = 25, 486$; $p < 0.0001$ for the second day and $F = 3.69$; $df = 25, 486$; $p < 0.0001$ for the fifth day). In general, aphids preferred young leaves in or near the top of a plant.

Table 5.2. Significant differences in the aphid population growth between different treatments (plexiglas cylinders) (Bonferoni posthoc test). Six treatments were considered: control, single predator treatments (*E. balteatus*, *C. septempunctata*, *C. carnea*), combined predator treatments (*E. balteatus* + *C. septempunctata*, *E. balteatus* + *C. carnea*). N = 12 for *C. carnea*, all other treatments N = 15

	Control	*E. balteatus* (*E. b.*)	*C. septempunctata* (*C. s.*)	*C. carnea* (*C. c.*)	*E. b.* + *C. s.*	*E. b.* + *C. c.*
Control	-					
E. balteatus	< 0.001	-				
C. septempunctata	< 0.001	n.s.	-			
C. carnea	< 0.001	n.s.	n.s.	-		
E. b. + *C. s.*	< 0.001	n.s.	n.s.	0.038	-	
E. b. + *C. c.*	< 0.001	0.002	0.026	0.001	n.s.	-

Approximately 60% of the aphid population could be found on Leaf-3 and the canopy of the broad bean plant, while equal proportions (approximately 15%) were located on the other leaf pairs (Fig. 5.2). In the presence of most of the tested predators aphids still preferred the canopy as feeding habitat, but leaves near the canopy (leaf-3) were more attractive than in the control (Fig. 5.2, Table 5.3). The only exception was found in experiments with *C. carnea* as predator. On the fifth days less then 20% of the aphid population were found in the canopy while on the other leaf pairs similar proportions of approximately 25% were located and a fraction of less than 3% was found off plant (Fig. 5.2, Table 5.3).

The evidence of patchiness was significantly different between treatments on the second day (Kruskal-Wallis test, value = 17.1; df = 5; p = 0.004) and on the fifth day (Kruskal-Wallis test, value = 29.4; df = 5; p < 0.0001). Immediately after the release of the predators the aggregation index of the aphids was significantly reduced in the single predator treatments *C. carnea* and *C. septempunctata* and the predator combination treatment of *E. balteatus* and *C. septempunctata* compared to the control. Until the fifth day, the distribution of aphids within the plant slightly changed (Fig. 5.3). Only in the presence of *C. carnea* as single predator aphids tended to a more uniform distribution within a plant than in the presence of other predators (Fig. 5.3). The aphid populations in all other treatments had a similar aggregation index and were not significantly

different from each other or from the control, except in the combination *of E. balteatus* with *C. carnea* from control.

Table 5.3. Proportion of aphids on different parts of broad bean plants (± SE) in the presence of various predators on the second and the fifth day after the release of predators. Different letters (row) indicate a significant difference (p < 0.05, ANOVA followed by Bonferroni post hoc test). *E. b.* = *E. balteatus*, *C. s.* = *C. septempunctata*, *C. c.* = *C. carnea*, *E. b.* + *C. s.* and *E. b.* + *C. c.* = *E. balteatus* in combination with *C. septempunctata* as well as with *C. carnea*. N = 12 for *C. carnea*, all other treatments N = 15. Data were arc-sin transformed before analysis.

| Plant part	Day	Control	*E. b.*	*C. s.*	*C. c.*	*E. b.* + *C. s.*	*E. b.* + *C. c.*
Off-plant	2nd	0.0 ± 0.0 a	4.2 ± 1.8 ab	2.5 ± 1.0 ab	2.3 ± 1.2 ab	7.9 ± 2.4 b	0.4 ± 0.4 a
	5th	0.1 ± 0.1 ab	0.1 ± 0.1 ab	0.0 ± 0.0 a	0.8 ± 0.4 b	0.3 ± 0.3 ab	0.1 ± 0.1 ab
Stem	2nd	0.9 ± 0.6 n.s.	3.2 ± 2.0 n.s.	0.0 ± 0.0 n.s.	1.4 ± 0.9 n.s.	0.8 ± 0.5 n.s.	0.7 ± 0.4 n.s.
	5th	3.0 ± 1.1 bc	0.8 ± 0.5 ab	0.1 ± 0.1 a	5.6 ± 1.6 c	0.0 ± 0.0 a	1.3 ± 0.6 ab
Leaf-1	2nd	31.0 ± 0.6 n.s.	22.9 ± 6.3 n.s.	14.3 ± 3.0 n.s.	28.3 ± 4.7 n.s.	14.7 ± 4.0 n.s.	29.5 ± 5.8 n.s.
	5th	22.9 ± 5.7 ab	12.2 ± 3.5 ab	11.6 ± 3.5 a	28.3 ± 3.6 b	13.4 ± 6.2 ab	20.4 ± 4.1 ab
Leaf-2	2nd	10.9 ± 2.7 n.s.	20.7 ± 2.4 n.s.	24.9 ± 4.2 n.s.	19.5 ± 3.2 n.s.	20.9 ± 4.7 n.s.	25.4 ± 4.7 n.s.
	5th	7.1 ± 2.2 a	14.6 ± 2.2 ab	18.6 ± 3.3 ab	24.5 ± 2.7 b	18.4 ± 5.8 ab	23.5 ± 3.8 b
Leaf-3	2nd	16.3 ± 4.2 n.s.	14.3 ± 2.1 n.s.	28.9 ± 4.7 n.s.	21.9 ± 3.1 n.s.	27.9 ± 6.2 n.s.	30.3 ± 5.1 n.s.
	5th	10.5 ± 3.1 n.s.	17.2 ± 3.1 n.s.	23.5 ± 6.0 n.s.	24.4 ± 4.1 n.s.	25.5 ± 4.1 n.s.	21.9 ± 3.8 n.s.
Canopy	2nd	40.8 ± 7.0 b	34.7 ± 5.5 ab	29.3 ± 5.5 ab	26.7 ± 5.2 ab	27.8 ± 6.2 ab	13.8 ± 4.7 a
	5th	56.5 ± 7.1 b	55.3 ± 5.5 b	46.2 ± 8.0 ab	18.1 ± 1.9 a	42.4 ± 8.3 ab	30.8 ± 5.6 ab
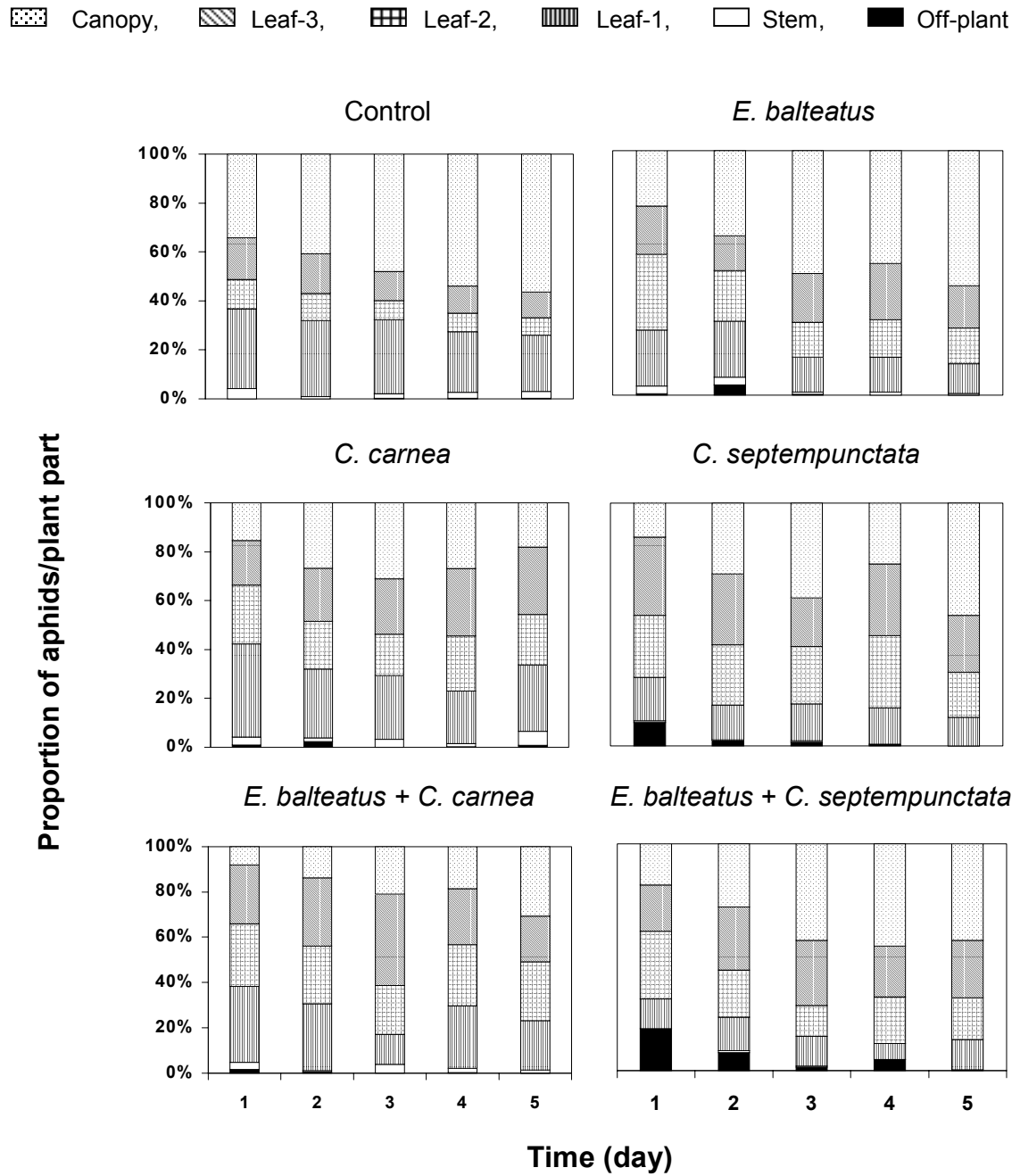
Fig. 5.2. Variation in the distribution of the aphid, *A. pisum*, on different parts of broad bean plants in the absence and in the presence of predators on five successive days. Bars indicate the proportion of the aphid population in the various plant parts. N = 12 for *C. carnea*, all other treatments N = 15.
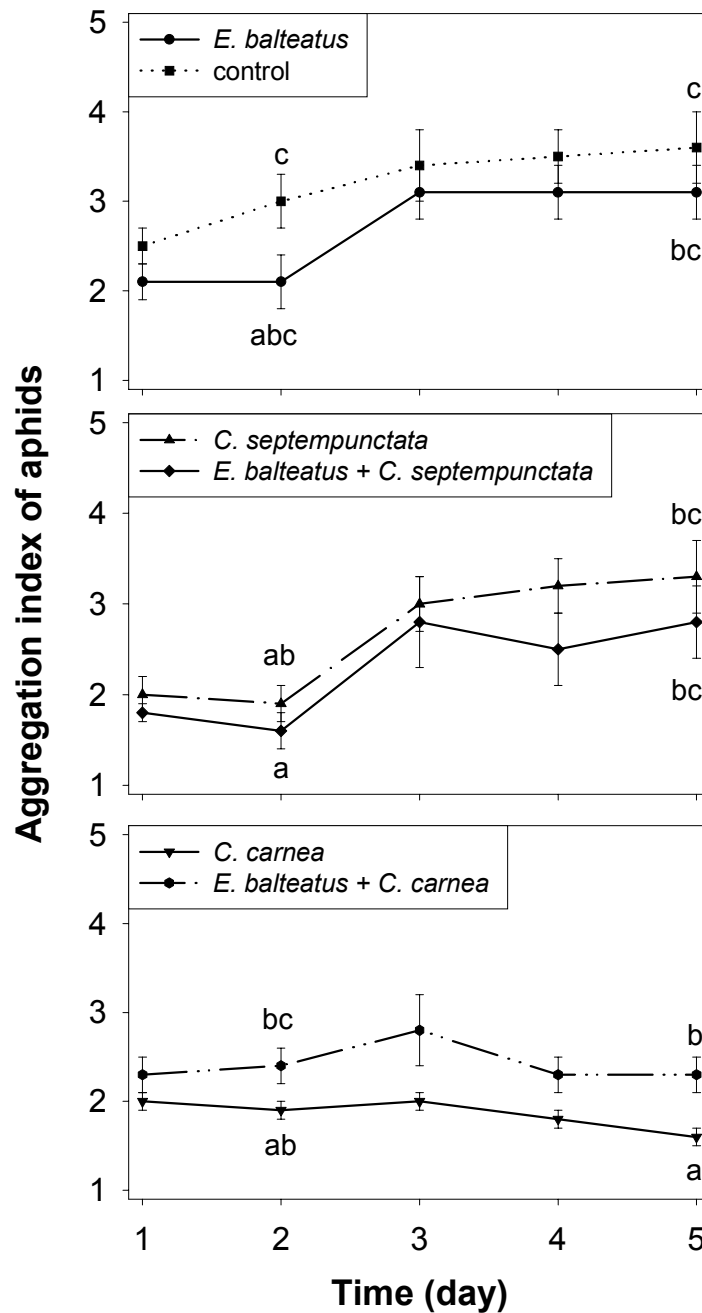
Fig. 5.3. Variations in the mean (± SE) of the aggregation index of the aphid, *A. pisum*, within a single broad bean plant (plexiglas tubes) in the absence and in the presence of predators on five successive days. The "patchiness" method developed by Lloyd (1967) was used to calculate the aggregation index. Calculations were based on the number of aphids in six different plant parts: canopy, Leaf-1, Leaf-2, Leaf-3, stem and off-plant. Letters indicate significant differences ($p <$ 0.05, Kruskal-Wallis test and Kolmogorov-Smirnov two-sample test). N = 12 for *C. carnea*, all other treatments N = 15. Data were rank transformed before analysis.

5.3.2. Impact of predators on population growth and dispersal of aphids between plants

Aphid populations. These experiments were carried out in an arena consisting of 9 broad been plants. Prey and predators were released on the plant in the center of the arena from which they started to disperse. Prey as well as predators (i.e. in the combination treatment) were able to stay in refuge patches and hence were able to escape predation. The presence of predators significantly reduced the population growth of the pea aphid. The repeated measures ANOVA showed a statistically significant TREATMENT x TIME effect ($p < 0.001$), which indicates that the population growth was different in the tested treatments (Fig. 5.4, Table 5.4). In comparison with the control, the presence of the ladybird larvae as aphid predator was the only treatment that did not influence the population growth of the aphid (Fig. 5.4a, Table 5.5). All other single predator treatments and treatments with predator combinations significantly reduced the aphid population density (Fig. 5.4, Table 5.5).

Table 5.4. Repeated measures ANOVA of aphid population growth (cages, large arena) for five days. Six treatments were considered: control, single predator treatments (*E. balteatus*, *C. septempunctata*, *C. carnea*), combined predator treatments (*E. balteatus* & *C. septempunctata*, *E. balteatus* & *C. carnea*). N = 6 for *C. carnea* and *E. balteatus* + *C. carnea*, all other treatments N = 10.

Between subjects Source	Df	MS	F	P>F
Treatment	5	399272.4	43.64	< 0.001
Error	81	9150.0		

Within subject Source	Df	MS	F	P>F
Time	4	1000513.4	401.76	< 0.001
Treatment x Time	20	85432.3	34.31	< 0.001
Error (time)	324	2490.4		

Table 5.5. Significant differences in aphid population growth between the different treatments in cages (Bonferroni posthoc test). Six treatments were considered: control, single predator treatments (*E. balteatus*, *C. septempunctata*, *C. carnea*), combined predator treatments (*E. balteatus* & *C. septempunctata*, *E. balteatus* & *C. carnea*). N = 6 for *C. carnea* and *E. balteatus* + *C. carnea*, all other treatments N = 10.

	Control	*E. balteatus* (*E. b.*	*C. septempunctata* (*C. s.*)	*C. carnea* (*C. c.*)	*E. b.* & *C. s.*	*E. b.* & *C. c.*
Control	-					
E. balteatus	0.013	-				
C. septempunctata	n.s.	n.s.	-			
C. carnea	0.049	n.s.	n.s.	-		
E. balteatus & *C. septempunctata*	< 0.001	n.s.	0.001	n.s.	-	
E. balteatus & *C. carnea*	0.001	n.s.	0.013	n.s.	n.s.	-

To the contrary, only a few predator treatments were found not to be significantly different from each other, i.e. a single predator treatment with *E. balteatus* or *C. carnea*. The treatments with predator combinations, however, turned out to be more efficient than the single predator treatment with *C. septempunctata* (Table 5.5). At the end of the fifth day the mean number of aphids in the single predator treatments *E. balteatus* and *C. carnea* was approximately two times less than in the control (489.8 $\pm$ 25.3 SE). On the other hand *C. septempunctata* was not able to reduce the population density (426.7 $\pm$ 20.6, SE; p = 1.00). The combined effect of two different predator species led to a further reduction in the population density of the aphid compared to single predator treatments. In the presence of *E. balteatus* with either *C. carnea* (193.7 $\pm$ 45.8, SE) or *C. septempunctata* (184.3 $\pm$ 29.1, SE) the aphid population density was approximately 2.5 times less than in the control (489.8 $\pm$ 25.3, SE). In none of the treatments with predator combinations intraguild predation was observed (Fig. 5.4).
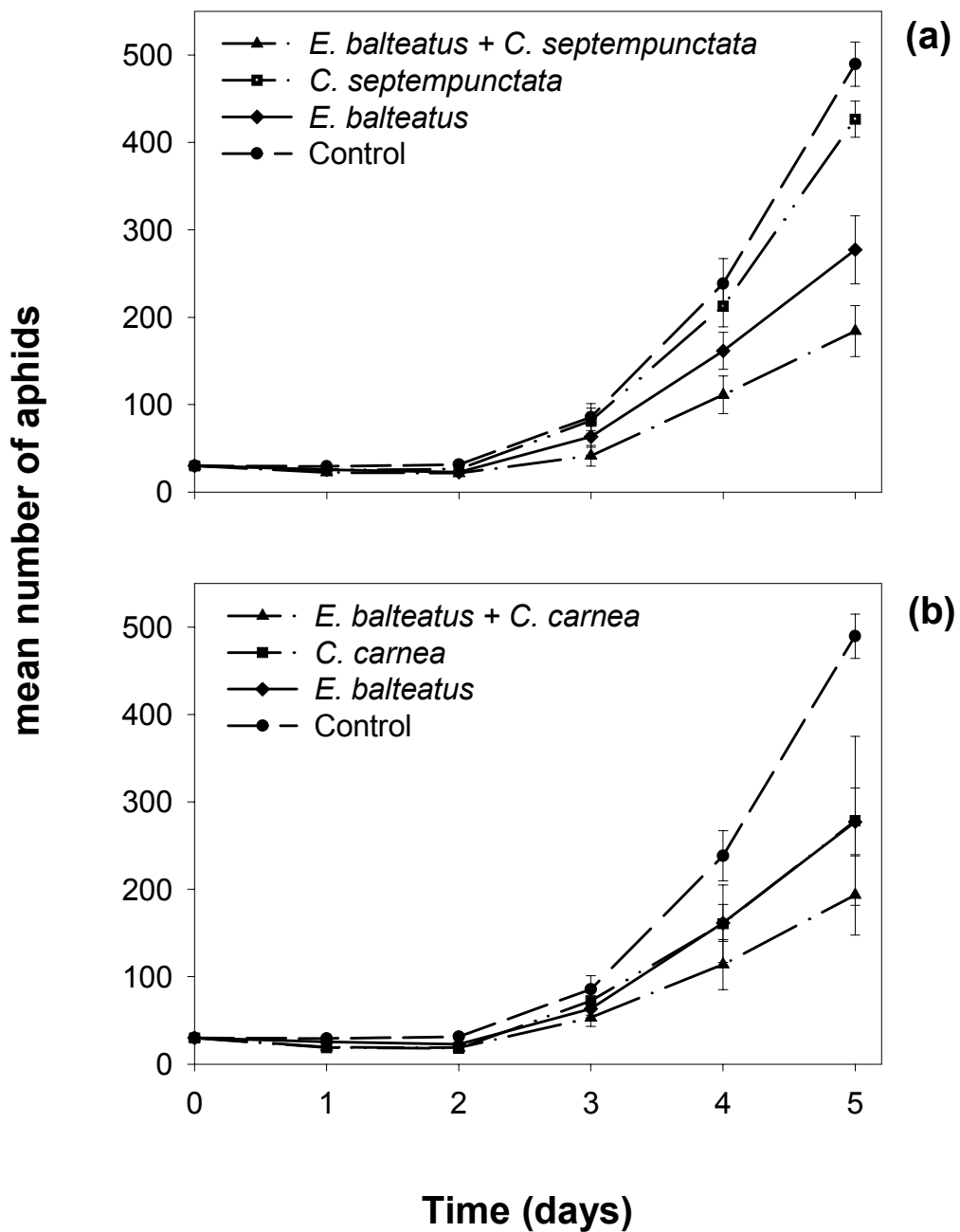
Fig. 5.4. Effects of predator combination on the aphid population growth of *A. pisum* on 9 broad bean plants in cages. *E. balteatus* was tested simultaneously with *C. septempunctata* (a) or *C. carnea* (b). N = 6 for *C. carnea* and *E. balteatus* + *C. carnea*, all other treatments N = 10.

Aphid dispersal. The distribution of aphids was analyzed at two different times: (1) immediately after the release of the predator to estimate initial dispersal and (2) at the end of the experiment (day 5) when aphid dispersal to refuge patches had been more or less established. In the predator treatments, aphids started to

disperse immediately after the release of the predators from the center plant to neighboring plants (Fig. 5.5), while in the control treatment on the second day after release 99% of the aphids could still be found on the release site. The presence of predators forced 21% (*E. balteatus* and *C. septempunctata*) to 68% (*C. carnea*) of the aphids to leave the release site (center plant). The evidence of patchiness was significantly different between the treatments of the second day (Kruskal-Wallis test, value = 23.56; df = 5; p < 0.0001) and those of the fifth day (Kruskal-Wallis test, value = 29.19; df = 5; p < 0.0001). The presence of *E. balteatus*, *C. carnea* or a combination of both predators resulted in a significantly reduced aggregation compared to the control (Fig. 5.5 and 5.6), i.e. a more uniform distribution. To the contrary the presence of *C. septempunctata* alone or in combination with *E. balteatus* had no immediate impact on the aggregation of aphids on the second day (Fig. 5.5 and 5.6). Until the fifth day, the distribution of aphids on the plants generally developed into a uniform distribution in the presence of predators. All predator treatments showed a significant lower aggregation index than the control (Fig. 5.6). In the presence of *E. balteatus*, *C. carnea* or in the presence of a combination of *E. balteatus* and *C. septempunctata* a significant lower aggregation index could be determined than in treatment with *C. septempunctata*. The aggregation of aphids in all other treatments did not differ from each other (Fig. 5.6).

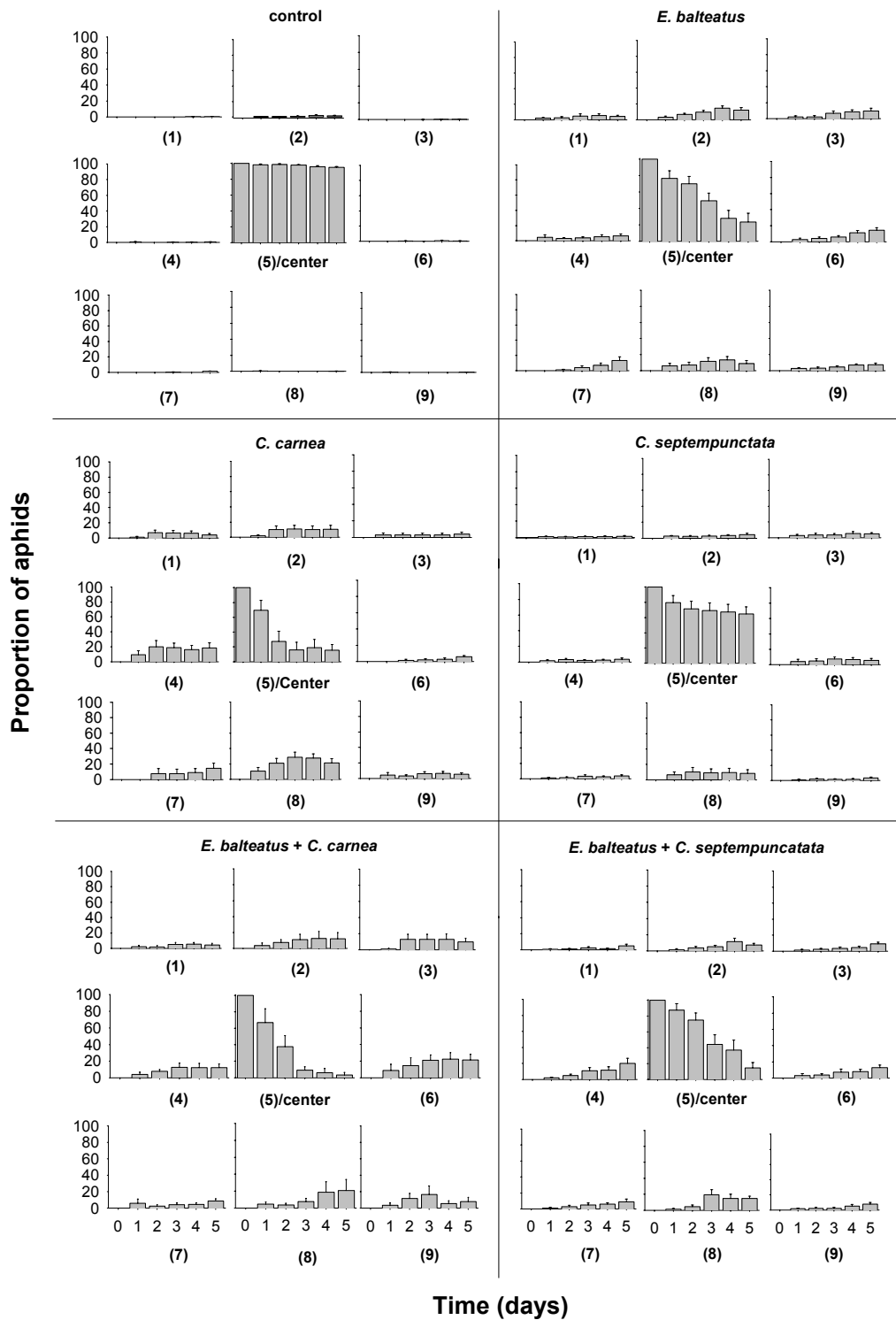**Proportion of aphids**

Time (days)

Fig. 5.5. Variations in the distribution of *A. pisum* populations on 9 broad bean plants in the absence and in the presence of predators on five successive days. Bars indicate the average proportion of the aphid population on the different plants. Numbers in brackets [(1) – (9)] indicate the position of the plant in the experimental arena. Aphids and predators were released on the plant (5) in the center of the arena. N = 6, for *C. carnea* and *E. balteatus* + *C. carnea*, all other treatments N = 10.
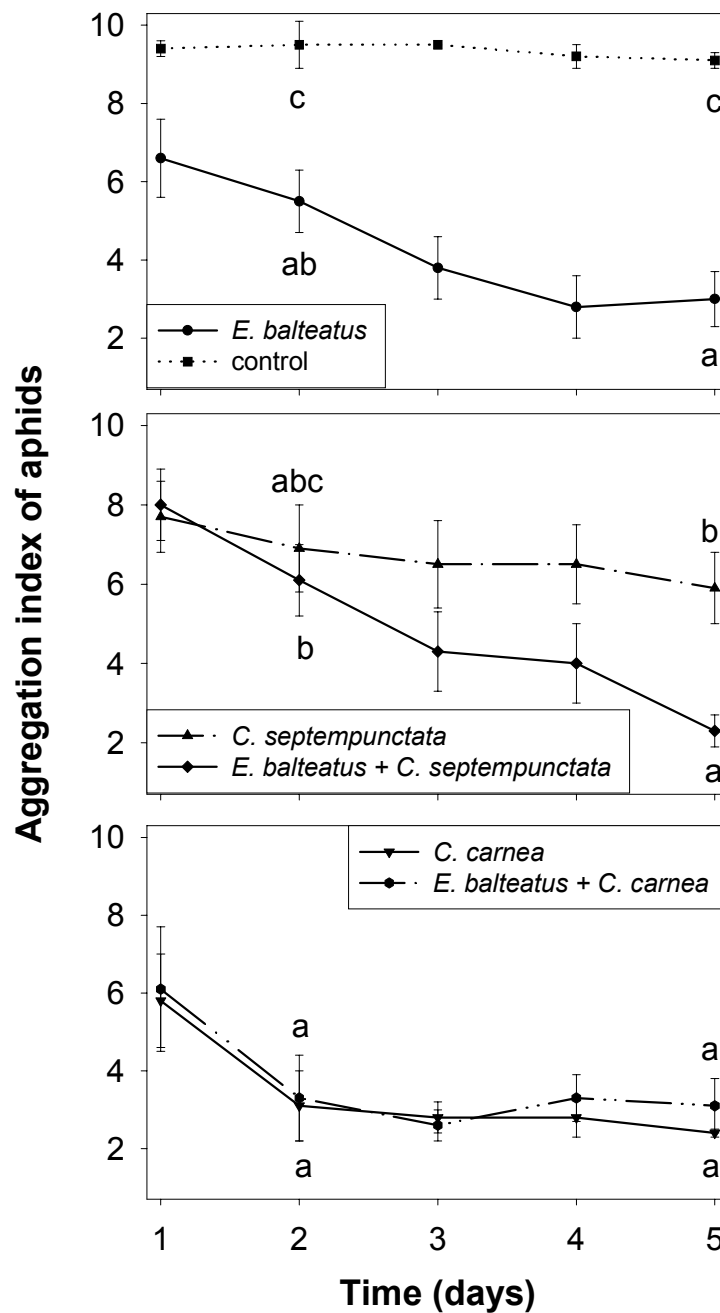
Fig. 5.6. Variations in the mean (± SE) of the aggregation index of the aphid, *A. pisum*, on 9 broad bean plants (cages) in the absence and in the presence of predators on five successive days. The "patchiness" method developed by Lloyd (1967) was used to calculate the aggregation index. Calculations were based on the number of aphids in 9 different plants. Letters indicate significant differences (p < 0.05, Kruskal-Wallis test and Kolmogorov-Smirnov two-sample test). N = 6, for *C. carnea* and *E. balteatus* + *C. carnea*, all other treatments N = 10. Data were rank transformed before analysis.

5.4. Discussion

5.4.1. Effect of predators on the population growth of *A. pisum*

The presence of predator species reduced the population growth of the aphid *A. pisum* significantly. The impact of predators (in all treatments) on the aphid population in large arenas was lower compared to the impact on small ones. This can be explained by the different spatial dimensions of the arenas. While in the small arenas the movement of aphids was focused on one plant ensuring a small patch size with high prey density, aphids in the large arenas dispersed in enlarged patch sizes with low prey density and settled on plant parts which are less efficiently foraged by predators (refuges) (Englund, 1997). Apart from reduced efficiency, this situation increases energy loss of the predator. When single predator species, i.e. *E. balteatus*, *C. carnea* or *C. septempunctata*, were introduced into the arena the reduction in the aphid population density was similar in all cases, especially in small arenas. In large arenas, the population density of *A. pisum* in the presence of *C. septempunctata* was not significantly different from the control. The ladybird larvae seemed to have a low impact on the population development. This means that the consumption rate of *C. septempunctata* in the cages is much lower than the potential consumption rate observed in petri dishes (see Fig. 4.1, chapter 4). The consumption rate of the last instar larvae (L_4) in petri dishes was approximately 76.1 ± 6.6 (SE) L_4 *A. pisum* or 2/3 of the feeding capacity of *C. septempunctata* larvae during their development (100.3 ± 7.5, SE). The decreasing consumption rate in cages can partially be explained by the individual behavior since the larvae were rarely found in the prey colony. Similar patterns were also observed in the experiment in plexiglas arenas where the larvae were very often found on the cylinder surface. The principles underlying this phenomenon of larvae staying away from aphid colonies hasn't been very well researched yet. However, possible explanations could be: (i) fitness of larvae which have not adapted yet to a large system, or (ii) unsuitability of prey and host plant, since the mobility of prey (Schneller, 1997) and the color (Lorenzetti *et al.*, 1997) as well as the structure of plants (Carter *et al.,* 1984) affected the preferences of predators, or (iii) the loss of orientation towards the aphid colonies due to intense pressure in the

rearing cage. In regard to the preferences of larvae to the host plant, Lorenzetti *et al.* (1997) observed that coccinellid, *Harmonia axyridis* Pallas were significantly more abundant on yellow than on green maize plants. It might as well be that broad bean plants were not attracted to *C. septempunctata*. In the field, Obrycki and Kring (1998) observed that populations of coccinellids were abundant in refuge habitats and only seasonally occurred in large numbers. In relation with the biological control program, ladybird beetles have been used successfully to control coccid pests (Hodek and Honek, 1996), however, their role as biological control agents of aphids has been disappointing so far (Hemptinne *et al.*, 1992). Additionally, we still have no experience in using *C. septempunctata* to control aphids in greenhouses (Schneller, 1997), although these predators are taken as one of the important natural enemies against aphids (Krieg and Franz, 1989; Ministerium für Ländlichen Raum, Ernährung, Landwirtschaft und Forsten Baden-Württemberg, 1995; Schneller, 1997b; Flint and Dreistadt, 1998; Obrycki and Kring,1998).

The combined effect of two predator species (*E. balteatus* & *C. septempunctata* and *E. balteatus* & *C. carnea*) reduced the population density of the aphid *A. pisum* in small as well as in large arenas more efficiently than a single predator. However, in most treatments the impact of two predators was lower than the sum of the impact observed in single predator species. The semi-natural conditions of the cage experiments revealed two different effects for the combined release of two predators. *E. balteatus* in combination with *C. septempunctata* had an additive effect on the aphid mortality, while *E. balteatus* in combination with *C. carnea* showed a non-additive effect. 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). It could be suggested that additive or synergistic effects are difficult to obtain when the two predator species each have a high impact on the prey population and even more when they share the same foraging habitat. On the contrary a nice example of synergistic effects was shown by Losey and Denno (1998b and 1999), i.e. the combined effect of *C. septempunctata* as foliar-foraging predator and *Harpalus pennsylvanicus* (Colepotera: Carabeidae) as ground-foraging predator. Without

any foliar-foraging predators, *H. pennsylvanicus* had very little impact on the aphid population. Thus *H. pennsylvanicus* took advantage of facilitation mechanisms, i.e. when the foraging activity of one predator species alters the feeding behavior of the prey, making it more susceptible to attacks by another predator species (Soluk, 1993; Losey and Denno, 1998b and 1999).

5.4.2. Aphid dispersal

The biology and ecology of aphids suggests that aggregations occur in the absence of predators, since most aphid species are relatively immobile, reproduce parthenogenetically and form colonies (Gutierrez *et al.*, 1980). However, Gutierrez *et al.*, (1980) observed in their experiments that predation of the ladybird *Hippodamia convergens* (G.-M.) (Coleoptera: Coccinellidae) on aphids caused aphids to aggregate even more. The explanation for this contradiction was that predation by beetles tends to destroy the colony by consuming the aphids or causing them to flee to the stem. An increase of predation will not only lead to a lower average density but also to a smaller proportion of the stem being colonized – i.e. increasing the distance between the colonies. To the contrary, our experiments showed that the presence of any predator decreased the aggregation of aphids, both within plants and among plants (Fig. 2-3 and 5-6). The presence of foliar-foraging predators significantly increased the number of aphids that drop off the plant (Klingauf, 1967; Niku, 1971; Losey and Denno, 1998a, see also Table 3 and Fig 2-8). Vibration of the predators during foraging induced the anti-predator response of the aphids (Klingauf, 1967; Niku 1971; Brodsky and Barlow, 1986; Losey and Denno, 1998a). Aphids produce alarm pheromones as a warning to conspecifics to avoid areas with predator activity (Berenbaum, 1995; van Emden and Peakall, 1996; Janssen *et al.*, 1998).

Brodsky and Barlow (1986) concluded that aphids have a flexible behavioral repertoire, which enables them to develop a case specific escape response to different predator species. Aphids dropped off a plant in response to the approach of a coccinellid beetle or started kicking with the hind legs when confronted with a foraging syrphid larvae, *Metasyrphus corollae* (Fab.). Nearly

6 % of the aphids dropped off the plant when the ladybird beetle, *C. septempunctata*, was present (Losey and Denno, 1998a), and *Syrphus corrolae* Fabr. has a strong effect on the dropping behavior of *A. pisum* (Niku, 1971). The defense behavior of kicking with the legs is a successful way to escape when the predator reacts slowly. However, if the predator reacts faster, it may still capture the aphid even if it starts kicking. Therefore, when a fast reacting predator approaches (i.e., with a high foraging rate), kicking with the hind leg is likely to be unsuccessful. The anti-predator mechanisms of *A. pisum* were not quantified. However, the results suggested that dropping behavior was the most common strategy of *A. pisum* to escape from predator attacks. This behavior causes aphids to disperse rapidly and to aggregate again in smaller colonies in refuge patches.

The position of aphids within a plant is related to the searching behavior of the different predator species. *E. balteatus* was able to search on all parts of the broad bean plant and therefore there was no specific plant part that could serve as refuge patch. *C. septempunctata* preferred to move along leaf edges and stems (Chang, 1996). Therefore in the presence of *C. septempunctata*, we observed hardly any aphid on the stem of the plant (Table 5.3). On the other hand, chrysopid larvae were able to search directly on the leaf surface (Chang, 1996) and preferred to rest in the leaf axils of the broad bean plants (Chang, 1996) and within the leafs of the canopy. Moreover, the results show that the *A. pisum* population was almost uniformly distributed on the plant in the presence of *C. carnea* (Table 5.3). In the absence of predators, *A. pisum* tended to colonize the canopy of the broad bean plant and dispersal only occurred when population densities were rather high (Losey and Denno, 1998a; Fig. 5.5). Without the activity of predators, aphids showed no need to drop off the host plant, especially if the host plant still was in a good condition. In this regard, Dill *et al.* (1990) hypothesized that aphids are able to make an economical decision to "select" a type of behavior which gives the "best" (pay-off situation) response to prevailing conditions.

5. 5. Conclusion and implication of the dispersal of plant viruses

Predators, singly or simultaneously introduced, could reduce aphid population growth significantly compared to the control, except for *C. septempunctata* in large arenas. These facts show the important role of predators in biological control efforts. However, in particular circumstances, aphid control with natural enemies can have negative side effects, since *A. pisum* is a vector for the pea enation mosaic virus and easily drops off from the host plant and disperses in the presence of predators. Not every developmental stage of an aphid is equally suited for virus transmission. Ossiannilsson (1966) stated that alate aphids play a most important role for virus transmission, but on the other hand, Farah (1968) showed that immature and apterae-virgin adults of *A. pisum* can transmit the pea enation mosaic virus better than alate-virgin adults. The remaining question is, whether it might be more reliable to use spot treatments with e.g. botanical insecticides to control insects that serve as virus vectors instead of the release of natural enemies, or whether the natural enemies themselves could completely avoid the risk of spreading plant pathogenic virus by reducing vector population. An answer to these questions requires more research. The results indicate that predators could heavily trigger *A. pisum* dispersal to new host plants. Nevertheless, the correlation between *A. pisum* dispersal and the spread of viruses should be investigated.

6. General Discussion

To promote *E. balteatus* as biological control agent for innundative or innoculative release, it is of primary importance that the biology and ecology of adults and predatory larvae are well known. Furthermore this knowledge is necessary for an efficient mass production and for the evaluation of the conditions when and where *E. balteatus* should be used as antagonist. Since hoverflies are not the only antagonists that can be used e.g. in greenhouses it is also important to consider intraguild predation among antagonists. This PhD study deals with of the questions relevant for the optimization of biological control efforts with the hoverfly *E. balteatus*.

Chapter 2, "Host plants - aphids - predator: tritrophic effects on the life history of *E. balteatus*", offers several suggestions for the mass rearing of hoverflies. The potato aphid *A. solani* reared on cucumber as host plant could be classified as essential prey for *E. balteatus*, i.e. food which ensures the completion of larval development and subsequent adult reproduction (New, 1991). In general syrphid survival was enhanced and females laid numerous eggs when larvae were reared with *A. solani* as prey, especially when the host plants were fertilized cucumber plants. It can be concluded that the first trophic level, the host plant, has an indirect impact on the fitness of *E. balteatus*. Survival, longevity and fecundity of *E. balteatus* were enhanced especially when the host plant had an optimal nutritional value for the herbivore and in consequence for the predator. This dependence of *E. balteatus* larvae on the nutritional value of food is relevant in regard to the foraging theory which focuses on caloric consumption or the selection of prey after its nutrient availability (Waldbauer and Friedman, 1991). Therefore, for mass rearing of *E. balteatus* these results should be taken into account in order to enhance the production of insects and optimize the fitness of adult syrphids at the release site i.e. in the greenhouse. However, the effect of fertilization of the host plants was tested only with a single aphid host plant combination. Generalizing the assumption that nitrogen is an important essential nutrient not only in combination with *A. solani* and cucumber as host plant, the effect of host plant fertilization should also be studied in other aphid host plant associations. In nature, however, the prey

selection of *E. balteatus* highly depends on the capability of the females to select aphid species and respective host plants that can provide the larvae with qualified food. Unfortunately, the information that the prey selection of *E. balteatus* is related to optimal foraging and based on caloric consumption, hasn´t spread yet. From field sampling and oviposition preference experiments Sadeghi and Gilbert (2000a) observed that the nettle aphid, *Microlophium carnosum* (Buckton), is rarely selected for oviposition by gravid females, although this aphid is highly suitable for the development of *E. balteatus* larvae in the laboratory (Sadeghi and Gilbert, 2000b). As the preferences of the *E. balteatus* females were not tested in this study, it cannot be guaranteed that *A. solani* on fertilized cucumber plants would be selected by *E. balteatus* females. Additionally, there are still many other factors that could determine prey selection, such as the color (Lorenzetti *et al.*, 1997) and structure of a plant as a habitat for the larvae (Carter *et al.*, 1984; Schneller, 1997), size (Sadeghi and Gilbert, 2000) and mobility of prey (Eubanks and Denno, 2000), intraspecific interaction (Scholz and Poehling, 1999) and, very important, also interspecific interaction. Schneller (1997b) suggested that cucumber might not be suitable for *E. balteatus* larvae due to leaf morphology. Eubanks and Denno (2000) gave another example of the low significance of nutrient ability in regard to the decision process of predators. In experiments with the big-eyed bug *Geocoris punctipes* (Heteroptera: Geocoridae) they observed that the predator preferred attacking pea aphids, *A. pisum*. Compared to the nutritional value of *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) eggs, the nutritional value of aphids was quite low. The authors suggest that prey mobility is the primary motive for prey selection by the big-eyed bug.

The experiments on the cannibalistic behavior of *E. balteatus* larvae (chapter 3) showed that cannibalism only occurs in the absence of prey and when the age structure among the syrphid larvae population was heterogeneous. Cannibalism very rarely occurs even when population densities of similar larvae are high in the absence of alternative prey. Cannibalism therefore isn´t very likely to be a limitation factor for the mass rearing of *E. balteatus*. In nature, cannibalism in *E. balteatus* is an uncommon phenomenon, because females where able to perceive the presence of conspecific eggs and oviposited less often in aphid

colonies in which eggs were already present (Scholz and Poehling, 1999). This phenomenon is seldom found in other insects, neither in predatory insects nor in herbivores, for example the chrysopid, *C. carnea* (Ridgway, 1970; Hassan,1975; Phoofolo and Obrycki, 1998), *C. septempunctata* (Agarwala and Dixon, 1992; Phoofolo and Obrycki, 1998), *H. armigera* (Kalshoven, 1981) and *S. frugiperda* (Chapman *et al*., 1999), which shows that cannibalism occurs even when plenty of alternative food is available and the population densities of insects are low. The factors that determine these differences are little known, Riechert (1981), however, suggested that cannibalistic tendencies might be genetically determined. The already mentioned genetic variation was also observed in *H. axyridis* (Wagner *et al*., 1999). Why does *E. balteatus* show low cannibalistic tendencies? This question remains open to investigation.

The experiments on intraguild predation (chapter 4) showed that the egg stage and the young developmental stages are particularly vulnerable to IGP. This result could be confirmed in a preliminary field experiment in sugar beets where on average 20% of the exposed syrphid eggs were consumed by predators. Moreover, it is likely that 60% of exposed young larval stages were killed by predators, although the amount of aphids was approximately 200 aphids per plant (Hindayana, unpubl. data). These results show how important interspecific interaction, i.e. intraguild predation, can be for the survival of *E. balteatus* in the field. However, in practical application in Germany, young developmental stages of *E. balteatus* are preferred to be released (Kreß, 1996; Schneller, 1997b). The attempt of releasing *E. balteatus* adults was reported to have failed because the adults always moved away from the greenhouse (Kreß, 1996). The results of the introduction of *E. balteatus* in greenhouse and field were contradictory. Kreß (1996) reported a successful control of *E. balteatus* against aphids on rose plants (such as *Macrosiphum euphorbiae* Thomas). To the contrary, Briem and Timm (1999) reported a control failure of *E. balteatus* against *Nasonovia nibisnigri* (Mosley) *and M. euphorbiae* on lettuce (*Lactuva sativa* L.). To explain those results there are many factors to be taken into account. Some of the factors are temperature (Tenhumberg, 1993), type of plant in relation with leaf morphology as well as type of aphid species in relation with size and mobility (Schneller, 1997b; Sadeghi and Gilbert, 2000), and the

fitness of *E. balteatus* (Chapter 2) and intraguild predation (Chapter 4). The explanation of a link between the developmental time of larval instar and the occurrence of IGP between *E. balteatus* and *C. carnea* as well as *C. septempunctata* (Fig. 4.7) could help reducing the predators´ interference, especially when *E. balteatus* is being released together with other aphidophagous predators. Considering the current level of knowledge it can be concluded that *E. balteatus* should better be released in combination with *C. carnea* instead of with *C. septempunctata*. There was less interference between these two predators, as *C. carnea* always avoided the counterattack and moved away from a confrontation with *E. balteatus*, and therefore the impact on the aphid population was higher (see chapter 5, "The effect of predatory interaction on aphid population and distribution"). However, to verify this conclusion further studies in greenhouses and in natural communities are necessary.

Finally, *E. balteatus* alone or in combination with other predators induces dispersal in aphid populations (chapter 5). As several aphids also serve as vector for plant pathogenic viruses, the introduction of natural enemies is not necessarily an advantage for disease control. However, the results in this study might not be extensive enough to be generalized, as different aphid species show a different behavior in mobility from very mobile (example, *A. solani* and *A. pisum*) to almost sedentary aphids (example, *A. gossypii* and *M. persicae*) (Schneller, 1997b). Additionally, the periods of observation were also too short to evaluate the roles of predators in the dispersion of aphids. Therefore, intense research is necessary to understand the importance of *E. balteatus* and other aphidophagous predators for the secondary spread of plant diseases.

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- **Hindayana, D**., Meyhöfer R., Scholz, D. & Poehling, H.-M. (**in press**).
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Eidesstattliche Erklärung

Hiermit versichere ich an Eides Statt, die vorliegende Arbeit selbstständig angefertigt und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt zu haben, sowie die Arbeit noch nicht als Dissertation oder andere Prüfungsarbeit vorgelegt zu haben.

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