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Intraguild predation by the generalist predator *Orius majusculus* on the parasitoid *Encarsia formosa*

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Abstract Intraguild predation of *Orius majusculus* (Reuter) (Heteroptera: Anthocoridae) on *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae), both natural enemies of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), was studied under laboratory conditions. The experiments quantified prey consumption by 5th instar nymphs and adults of *O. majusculus* offered unparasitised 3rd, early 4th or 4th instar *B. tabaci* nymphs or parasitised nymphs containing 2nd or 3rd larval instar or pupal parasitoids. In addition, prey preference of the two stages of *O. majusculus* for parasitised or unparasitised whitefly nymphs was studied using nine different prey combinations. Both predator stages readily preyed upon on both unparasitised and parasitised *B. tabaci*. In no-choice experiments, predation on 3rd instar *E. formosa* by adult predators was the highest, while predator nymphs preyed most on unparasitised 3rd instar *B. tabaci* and 2nd instar parasitoids. Predation of predator stages was lowest on 4th instar *B. tabaci* and *E. formosa* pupae. In all prey combinations, both stages of *O. majusculus* showed a significant preference for parasitised over unparasitised whitefly nymphs except for the combination of 5th instars of *O. majusculus* with early 4th instar whiteflies and *E. formosa* pupae. The results indicate that intraguild interactions between *O. majusculus* and *E. formosa* may have negative effects on biological control of *B. tabaci*.

Keywords Anthocoridae · Aphelinidae · *Bemisia tabaci* · Biological control · Prey preference

Introduction

Intraguild predation (IGP) where species that compete for a shared (extraguild) prey also engage in predator–prey interactions (Polis et al. 1989; Holt and Polis 1997) is common in food webs both in natural systems and in managed systems of pests and natural enemies (Polis and Holt 1992; Rosenheim et al. 1995; Janssen et al. 2006). IGP may have a negative effect on the outcome of biological control (e.g. Rees and Onsager 1982; Snyder and Ives 2001; Rosenheim 2005) although some authors

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have found that the presence of intraguild predators could have a positive effect on pest biocontrol (e.g. Schausberger and Walzer 2001; Snyder et al. 2004; Gardiner and Landis 2007). In biocontrol programmes of greenhouse crops, several species of natural enemies are often used concurrently to combat the pest complex. When polyphagous predators are part of such programmes, the possibility arises that IGP occurs and affects biological control. Optimal combinations of beneficial species for simultaneous use in biocontrol should therefore be based on knowledge on the potential for and intensity of IGP among the various biocontrol agents (Meyling et al. 2004).

Biological control of the sweet potato whitefly, *Bemisia tabaci* (Gennadius) Biotype B (*B. argentifolii* Bellows and Perring) (Homoptera: Aleyrodidae) (Oliveira et al. 2001), an economically important pest, is frequently based on the use of aphelinid parasitoids, especially of the genera *Encarsia* and *Eretmocerus* (Hymenoptera: Aphelinidae) (Gerling et al. 2001; Naranjo and Ellsworth 2005; Asiimwe et al. 2007), with *Encarsia formosa* (Gahan) being among the best studied biological control agents of whiteflies. In greenhouse crops, whiteflies often occur alongside thrips, which can be controlled using predatory mites (Riudavets 1995; Zhang 2003) and polyphagous minute pirate bugs of the genus *Orius* (Heteroptera: Anthocoridae) (e.g. Trottin-Caudal et al. 1991; Tommasini et al. 2004). Among the minute pirate bugs, the species *Orius majusculus* (Reuter) also has a potential for control of whiteflies (Arno et al. 2008). In spite of the fact that the recently marketed predatory mite *Amblyseius swirski* (Athais-Henriot) (Acari: Phytoseiidae) has the ability to control both whiteflies and thrips, also in cases of dual infestations (Messelink et al. 2008), other natural enemies of both whiteflies and thrips will likely still be needed for adequate control in some greenhouse crops or under some greenhouse conditions. A combined used of *E. formosa* and *O. majusculus* is therefore expected to take place also in the time to come.

Several studies have documented IGP by generalist predators on the specialist parasitoids in the form of parasitised hosts (coincidental IGP, Polis et al. 1989) (Meyling et al. 2004; McGregor and Gillespie 2005; Shiojiri and Takabayashi 2005). The occurrence of IGP by the oligophagous predator *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae) on aphelind parasitoids has been documented in several studies (Heinz et al. 1994; Hoelmer et al. 1994; Zang and Liu 2007), with the predator preferring unparasitised whiteflies. Naranjo (2007) similarly reported IGP by three generalist predators, *Geocoris punctipes* (Say) (Heteroptera: Lygaeidae), *Orius insidiosus* (Say) (Heteroptera: Anthocoridae), and *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae), on *Eretmocerus* sp. nr. *emiratus*, a parasitoid of *B. tabaci*. However, these predators either preferred parasitised whiteflies or were non-discriminative (Naranjo 2007).

Studies on the predation of *O. majusculus* on other predators are scarce (Christensen et al. 2002; Jakobsen et al. 2004; Brødsgaard and Enkegaard 2005) and no information regarding IGP by *O. majusculus* on *E. formosa* or other parasitoid species has previously been published. With the overall objective to determine whether the combination of these two biological control agents could result in better control of *B. tabaci*, we tested the discrimination of predators feeding on parasitised and non-parasitised whitefly nymphs and measured predation on various types of prey.

Materials and methods

Plants and insects

Cucumber plants (*Cucumis sativus* L., cv. Cordoba RZ) were grown in 9 cm plastic pots filled with peat substrate (Mosebrug A/S, Denmark). The pots were placed in insect-proof net-covered cages (68 × 75 × 82 cm) in a climate-controlled greenhouse compartment at 25 °C, 70 % RH, 16:8 L:D. Plants with two fully extended true leaves were used for experiments.

The sweet potato whitefly, originally supplied by Nina Svae Johansen, BioForsk, Norway, was reared on cucumber plants in similar cages and at similar conditions as above. *O. majusculus* and *E. formosa* were supplied by EWH BioProduction, Tappernøje, Denmark. All experiments were conducted in climate cabinets at 25 ± 1 °C, 70 ± 5 % RH, 16:8 L:D.

Production of parasitised whiteflies

To obtain parasitised whitefly nymphs, groups of approximately 20–30 adult whiteflies were introduced into clip cages (2 cm diameter) exposed to the lower surface of a cucumber leaf (1–3 clip cages per leaf) on a potted plant. The whiteflies were allowed to oviposit for 24 h and subsequently removed. The plants with whitefly eggs were incubated in a climate-controlled greenhouse compartment at 25 °C, 70 % RH, 16:8 L:D to allow development to the early 4th nymphal stage. Subsequently, groups of 5–6 adult parasitoids were confined in clip cages (4 cm diameter) placed over the leaf areas where the whitefly nymphs were situated. The parasitoids were allowed to parasitise for 24 h. The plants, now harbouring parasitised nymphs, were incubated under similar conditions as above until parasitoid development had progressed to the desired stage (2nd instar, 3rd instar, or pupal parasitoid stage) (Agekyan 1982).

No-choice tests

IGP of *O. majusculus* on *E. formosa* was examined separately for 5th instar predator nymphs and adult females. Each predator stage was offered parasitised whitefly nymphs containing parasitoids of either the 2nd, 3rd or pupal stage. Leaves with parasitised whiteflies were taken from the plants described above. For each leaf area with parasitised whiteflies, fifteen whitefly nymphs containing the desired larval or pupal stage of *E. formosa* were then identified under a binocular stereoscopic microscope and marked by encircling them with a felt pen. Excess whitefly nymphs were removed using an insect pin. Leaf discs harbouring parasitised whitefly nymphs were cut from the leaves and placed in experimental arenas consisting of organdy-vented Petri dishes (5 cm diameter) with a thin layer (2–3 mm) of 1 % agar on the bottom as a substrate to keep the leaf discs fresh. Since *O. majusculus* could not walk easily on the agar substrate, any agar surface not occupied by leaf discs was covered by pieces of moistened filter paper. Controls consisted of leaf discs with unparasitised 3rd, early 4th and 4th instar whitefly nymphs. These leaf discs were cut from the leaves taken from the whitefly rearing after identifying 15 whitefly nymphs in the desired stage and removing excess nymphs.

One newly moulted 5th instar nymph or one adult female of *O. majusculus* was individually placed on each leaf disc. The predators were starved for 24 h prior to the experiment by confining them in small boxes (70 cm^3) kept in the laboratory (approx. 22 °C). After 24 h, predator nymphs or adults were removed, and numbers of consumed prey were estimated by subtracting the number of undamaged individuals from the total numbers offered. The number of replicates per treatment varied from 15 to 30.

Choice tests

The results from the no-choice tests demonstrated that *O. majusculus* was able to prey on both parasitised and unparasitised whitefly nymphs in different developmental stages. We were consequently interested in investigating the prey preference of *O. majusculus* using all possible combinations of the prey items offered in the no-choice experiment. The following prey combinations were used:

(a) 15 2nd instar parasitoids and 15 unparasitised 3rd instar whiteflies
(b) 15 3rd instar parasitoids and 15 unparasitised 3rd instar whiteflies
(c) 15 parasitoid pupae and 15 unparasitised 3rd instar whiteflies
(d) 15 2nd instar parasitoids and 15 unparasitised early 4th instar whiteflies
(e) 15 3rd instar parasitoids and 15 unparasitised early 4th instar whiteflies
(f) 15 parasitoid pupae and 15 unparasitised early 4th instar whiteflies
(g) 15 2nd instar parasitoids and 15 unparasitised 4th instar whiteflies
(h) 15 3rd instar parasitoids and 15 unparasitised 4th instar whiteflies
(i) 15 parasitoid pupae and 15 unparasitised 4th instar whiteflies

The experimental procedures, experimental conditions, and experimental arenas were as described above except that two different kinds of leaf discs were added to each Petri dish—one harbouring parasitised nymphs and one harbouring unparasitised whitefly nymphs in the desired stage. Prey preference was examined separately for 5th instar predator nymphs and adult females. The predators were individually introduced to each Petri dish and the number of prey consumed was recorded as described above. Each combination was replicated 15–17 times.

Data analysis

The data were analysed with generalised linear models. For the no-choice experiments the effect of prey and predator stage together with their interaction was included as fixed effects. It was assumed that the number of individuals were Poisson distributed with an unknown overdispersion, which had to be estimated. The natural logarithm was used as link function. For the choice experiments the effect of prey combination and predator stage together with their interaction was included as fixed effects. It was assumed that the number of individuals chosen was binomially distributed with an unknown overdispersion, which had to be estimated. The logit function was used as link. All analyses were performed using the procedure Glimmix of SAS (SAS Institute Inc 2010).

For analysis of prey preference, Manly's preference index (Manly 1974) was calculated for each predator stage and each prey combination:

$$\beta_1 = \frac{\log(e_1/A_1)}{\log(e_1/A_1) + \log(e_2/A_2)}$$

where β_1 is the preference for prey type 1, A_1 and A_2 are the number of prey types 1 and 2 offered, and e_1 and e_2 are the numbers of prey type 1 and 2 remaining after the experiment, respectively. The preference index (β) can attain values between 0 and 1, with a β-value higher than 0.5 indicating a preference for prey type 1. In the present study, parasitised *B. tabaci* was chosen as prey type 1. Manly's index applies to data originating from experiments where killed prey items are not replaced (Cock 1978; Sherratt and Harvey 1993). Five replicates (out of a total of 277) in which neither of the two prey types offered had been predated were excluded from the analysis of prey preference. Differences between prey preference indices were analysed using two-way ANOVA and the means were separated using Duncan's multiple range test at $P = 0.05$ where applicable (SAS Institute Inc 2010). Each preference index was tested for significance (i.e. difference from a value of 0.5) with a one-sample t test with SAS 9.0 (SAS Institute Inc 2010).

Results

No-choice tests

Both adults and 5th instar nymphs of *O. majusculus* preyed on different unparasitised and parasitised *B. tabaci* nymphal stages (Table 1). The predation rate was significantly affected by prey stage ($F = 16.32$, df = 5, 248, $P < 0.0001$), predator stage ($F = 17.57$, df = 1, 248, $P < 0.0001$) and the interaction between prey and predator stage ($F = 4.44$, df = 5, 248, $P = 0.007$). Predation of unparasitised as well as parasitised 4th instar *B. tabaci* nymphs containing 3rd larval instars and pupae of *E. formosa* by adult predators was significantly higher than predation by 5th instar predator nymphs ($P = 0.0023$, $P < 0.0001$ and $P = 0.0040$, respectively). Adult *O. majusculus* showed the highest predation on parasitised whitefly nymphs containing 3rd larval instars of *E. formosa*, while the 5th instars had the highest predation on unparasitised 3rd instar and parasitised *B. tabaci* nymphs containing 2nd instar parasitoids. Both adults and 5th instar *O. majusculus* consumed significantly fewer unparasitised 4th instar *B. tabaci* nymphs than other prey types ($P = 0.0003$ and $P = 0.0205$ for adults and 5th instar predators, respectively).

Table 1 Mean number ± SE of different types of prey consumed by adults and 5th instars *O. majusculus*

Prey stage	Adult	5th instar nymph
3rd instar *B. tabaci* nymph	6.07 ± 0.87 (15) Ab	5.60 ± 0.62 (17) Aa
Early 4th instar *B. tabaci* nymph	5.30 ± 0.80 (20) Ab	3.86 ± 0.59 (28) Ab
4th instar *B. tabaci* nymph	0.73 ± 0.16 (30) Ad	0.12 ± 0.09 (25) Bd
2nd instar *E. formosa* larva	5.80 ± 0.70 (30) Ab	6.00 ± 0.72 (15) Aa
3rd instar *E. formosa* larva	9.47 ± 0.99 (15) Aa	3.33 ± 0.71 (15) Bb
Pupa of *E. formosa*	3.70 ± 0.50 (30) Ac	1.75 ± 0.23 (20) Bc

Means in a column followed by different lower case letters or in a row by different upper case letters are significantly different (Duncan's multiple range test; $P < 0.05$)

The number of replicates is shown in parentheses

Choice tests

In the choice tests, predation rates were significantly affected by the prey combination ($F = 2.97$, df = 8, 254, $P = 0.0034$) but not by the predator stage ($F = 0.00$, df = 1, 254, $P = 0.98$) or by the interaction between prey combination and predator stage ($F = 0.63$, df = 8, 254, $P = 0.75$). Both adults and 5th instars of *O. majusculus* had a clear preference for parasitised over unparasitised whitefly nymphs (Table 2), with all preference indices being significantly different from 0.5 ($P < 0.003$ and $P < 0.0001$ for adults and 5th instar predators, respectively), except for the case of 5th instar predators choosing between unparasitised early 4th instar whiteflies and whiteflies containing *E. formosa* pupae ($P = 0.0725$). The mean preference indices of adult *O. majusculus* did not differ significantly among prey combinations, whereas significant differences were apparent for 5th instar predators, with the lowest and highest preference index being observed in the combination of unparasitised early 4th instar *B. tabaci* and *E. formosa* pupae and unparasitised 4th instar *B. tabaci* and 3rd instar *E. formosa*, respectively. The preferences exhibited by the two stages of the predator in the different prey combinations were not significantly different except in the prey combination with unparasitised 4th instar whiteflies and 2nd instar parasitoids where 5th instar *O. majusculus* had a slightly higher preference index for *E. formosa* ($P = 0.0294$).

Discussion

The present results confirm that both adults and large nymphs of *O. majusculus* are able to prey upon unparasitised *B. tabaci* with consumption rates comparable to those reported by Arno et al. (2008). In the

Table 2 Mean ± SE number of prey eaten as well as mean preference indices ± SE of *O. majusculus* for *E. formosa* (β_1) when offered various prey combinations

Predator stage	Prey combination		Bt eaten	Ef eaten	Comparison* Bt eaten	Preference index	*n*
	Bt	Ef					
Adult	3rd	2nd	0.75 ± 0.36	10.5 ± 0.89	A, abh	0.96 ± 0.03 Aa	14
	3rd	3rd	0.59 ± 0.29	6.77 ± 0.61	A, abk	0.95 ± 0.03 Aa	17
	3rd	Pupa	0.73 ± 0.38	4.07 ± 0.68	A, bce	0.88 ± 0.07 Aa	15
	E4th	2nd	0.94 ± 0.26	6.71 ± 0.84	A, bcdg	0.92 ± 0.03 Aa	17
	E4th	3rd	1.2 ± 0.45	8.07 ± 1.05	A, cfhik	0.82 ± 0.09 Aa	15
	E4th	Pupa	1.06 ± 0.35	4.63 ± 0.83	A, egik	0.81 ± 0.07 Aa	16
	4th	2nd	0.6 ± 0.19	6.4 ± 0.84	A, acfgi	0.90 ± 0.04 Aa	15
	4th	3rd	0.13 ± 0.09	8.53 ± 0.94	A, a	0.99 ± 0.01 Aa	15
	4th	Pupa	0.67 ± 0.19	5.2 ± 0.71	A, be	0.82 ± 0.09 Aa	15
5th instar	3rd	2nd	0.4 ± 0.19	6.87 ± 0.8	A, ab	0.97 ± 0.01 Aab	14
	3rd	3rd	0.87 ± 0.6	7.33 ± 0.72	A, ag	0.93 ± 0.04 Aab	14
	3rd	Pupa	1.67 ± 0.53	5.8 ± 0.58	A, eghk	0.82 ± 0.06 Abc	14
	E4th	2nd	1.07 ± 0.42	5.8 ± 0.86	A, bgi	0.90 ± 0.04 Aab	15
	E4th	3rd	1.38 ± 0.42	7.81 ± 0.82	A, bdghk	0.84 ± 0.06 Aabc	16
	E4th	Pupa	1.2 ± 0.53	2.93 ± 0.48	A, chi	0.71 ± 0.11 Ac	15
	4th	2nd	0.07 ± 0.07	5.87 ± 0.73	A, a	0.99 ± 0.01 Ba	14
	4th	3rd	0 ± 0	4.87 ± 0.67	A, aik	1.00 ± 0.00 Aa	15
	4th	Pupa	0.07 ± 0.07	2.13 ± 0.34	A, aik	0.98 ± 0.02 Aab	15

Means in a column followed by different lower case letters are significantly different between prey combinations within each predator stage. Upper case letters are used to compare predation by different predator stages when offered the same prey combination (Duncan's multiple range test; $P < 0.05$)

Bt *Bemisia tabaci*, Ef *Encarsia formosa*, *n* number of replicates, *E4th* early 4th instar

* The statistics for comparison of number of *E. formosa* eaten is the same as for the comparison of number of *B. tabaci* eaten

no-choice tests with unparasitised whiteflies both stages of *O. majusculus* showed very low predation on 4th instar *B. tabaci* in comparison to predation on 3rd and early 4th instars. This difference might be explained by differences in cuticle thickness and/or cuticular lipids composition among whitefly stages, which is a known physical defence mechanism against predators in *B. tabaci* as well as in the greenhouse whitefly *Trialeurodes vaporariorum* Westwood (Neal et al. 1994), making penetration of the whitefly nymph cuticle increasingly difficult for *O. majusculus* with increasing host age (Gerling 1990).

Orius majusculus did not only prey upon unparasitised whiteflies but also on *B. tabaci* nymphs parasitised by *E. formosa*. The intraguild predator characteristics of *O. majusculus* towards a range of different beneficials (Christensen et al. 2002; Jakobsen et al. 2004; Brødsgaard and Enkegaard 2005; Sanderson et al. 2005) has herewith been documented to pertain also to parasitoids. IGP on immature stages of parasitoids has been reported for a number of other predators (Hoelmer et al. 1994; Heinz et al. 1994; Heinz and Nelson 1996; Colfer and Rosenheim 2001; Snyder and Ives 2001; Zang and Liu 2007; Naranjo 2007).

In the no-choice tests with parasitised whiteflies both adults and 5th instars of *O. majusculus* had a lower predation on *E. formosa* pupae compared with parasitoids in the larval stages. The same pattern has been found for other predators (e.g. Hoelmer et al. 1994; Heinz and Nelson 1996; Al-Zyoud and Sengonca 2004; Fazal and Xiang 2004; Zang and Liu 2007; Kutuk et al. 2011). This phenomenon could be due to changes in chemical and physical characteristics during the pupal phase of parasitoid development (Hoelmer et al. 1994). In addition, parasitism-induced hardening of the whitefly cuticle and formation of air spaces around the developing parasitoid hinders the predator in attacking the parasitoid (Hoelmer et al. 1994; Kutuk et al. 2011). In other parasitoid-predator systems, however, the predation rate is independent of the parasitoid development, or may be highest on parasitoid pupal stages (Naranjo 2007).

In the present study, *O. majusculus* exhibited a clear preference for parasitised over unparasitised prey, except when 5th instar predators were offered a choice between early 4th instar whiteflies and *E. formosa* pupae. Similar preferences have been reported for several other predator species (Naranjo 2007). The same author speculated that this preferential predation is related to prey appearance, differential distribution of parasitised and non-parasitised prey or nutritional aspects (Naranjo 2007). Based on our observations, parasitoid development causes the otherwise flat and translucent whitefly nymphs to swell and become opaque (Gelman et al. 2002). This may render the parasitised hosts more apparent to searching *O. majusculus*.

The ability of *O. majusculus* to prey upon parasitised *B. tabaci* and its preference for parasitised hosts may have detrimental effects on *E. formosa*-based biological control of *B. tabaci* and, most likely, other whiteflies. Disruption of parasitoid-based biological control by inclusion of an intraguild predator has been documented by several authors (e.g. Rees and Onsager 1982; Raymond et al. 2000; Snyder and Ives 2001). In contrast, Heinz and Nelson (1996) and Colfer and Rosenheim (2001) found that the level of suppression of pest populations was increased despite the occurrence of IGP.

In view of the possible detrimental effects of *O. majuscules* on *E. formosa*, the consequences of using *O. majusculus* against whiteflies (Arno et al. 2008) concurrently with the use of *E. formosa* should be evaluated based on studies of biocontrol with combinations of these two species. In situations in which *O. majusculus* is applied for control of other pest species, typically thrips, predation on whiteflies is likely to occur to some extent (Montserrat et al. 2000). Studies on the prey preference of *O. majusculus* for its target pest and parasitised and unparasitised whiteflies will be needed, as will larger-scale studies in multi-species biocontrol systems under semi-field or field conditions on the degree of IGP on *E. formosa* and its effect on biocontrol of whiteflies and other pests.

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References

Agekyan NG (1982) Biological features of *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae). Entomol Obozr (Entomol News) 60:90–94

Al-Zyoud F, Sengonca C (2004) Prey consumption preferences of *Serangium parcesetosum* Sicard (Col., Coccinellidae) for different prey stages, species and parasitized prey. J Pest Sci 77:197–204

Arno J, Roig J, Riudavets J (2008) Evaluation of *Orius majusculus* and *O. laevigatus* as predators of *Bemisa tabaci* and estimation of their prey preference. Biol Control 44:1–6

Asiimwe P, Ecaat JS, Otim M, Gerling D, Kyamanywa S, Legg JP (2007) Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. Ent Exp Appl 122:37–44

Brødsgaard HF, Enkegaard A (2005) Intraguild predation between *Orius majusculus* (Reuter) (Hemiptera: Anthocoridae) and *Iphiseius degenerans* Berlese (Acarina: Phytoseiidae). Bull OILB/SROP 28(1):19–22

Christensen RK, Enkegaard A, Brødsgaard HF (2002) Intraspecific interactions among the predators *Orius majusculus* and *Aphidoletes aphidimyza*. Bull OILB/SROP 25(1):57–60

Cock MJW (1978) The assessment of preference. J Anim Ecol 47:805–816

Colfer RG, Rosenheim JA (2001) Predation on immature parasitoids and its impact on prey suppression. Oecologia 126:292–304

Fazal S, Xiang RS (2004) Interaction of *Serangium japonicum* (Coleoptera: Coccinellidae), an obligate predator of whitefly with immature stages of *Eretmocerus* sp. (Hymenoptera: Aphelinidae) within whitefly host (Homoptera: Aleyrodidae). Asian J Plant Sci 3:243–246

Gardiner MM, Landis DA (2007) Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. Biol Control 40:386–395

Gelman DB, Blackburn MB, Hu JS, Gerling D (2002) The nymphal-adult molt of the silverleaf whitefly (*Bemisia argentifolii*): timing, regulation, and progress. Arch Insect Biochem Physiol 51:67–79

Gerling D (1990) Natural enemies of whiteflies: predators and parasitoids. In: Gerling D (ed) Whiteflies: their bionomics, pest status and management. Intercept, Andover, UK, pp 147–185

Gerling D, Alomar O, Arno J (2001) Biological control of *Bemisia tabaci* using predators and parasitoids. Crop Prot 20:779–799

Heinz KM, Nelson JM (1996) Interspecific interactions among natural enemies of *Bemisia* in an inundative biological control program. Biol Control 6:384–393

Heinz KM, Brazzle JR, Pickett CH, Natwick ET, Nelson JM, Parrella MP (1994) Predatory beetle may suppress silverleaf whitefly. Calif Agric 48:35–40

Hoelmer KA, Osborne LS, Yokomi RK (1994) Interactions of the whitefly predator *Delphastus pusillus* (Coleoptera: Coccinellidae) with parasitized sweet potato whitefly (Homoptera: Aleyrodidae). Environ Entomol 23:136–139

Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. Am Nat 149:745–764

Jakobsen L, Enkegaard A, Brødsgaard HF (2004) Interactions between two polyphagous predators, *Orius majusculus* (Hemiptera: Anthocoridae) and *Macrolophus caliginosus* (Heteroptera: Miridae). Biocontrol Sci Technol 14(1):17–24

Janssen A, Montserrat M, HilleRisLambers R, de Roos AM, Pallini A, Sabelis MW (2006) Intraguild predation usually does not disrupt biological control. In: Brodeur J, Boivin G (eds) Trophic and guild interactions in biological control. Springer, Dordrecht, The Netherlands, pp 21–44

Kutuk H, Yigit A, Alaoglu O (2011) Intraguild predation of *Serangium parcesetosum* Sicard (Coleoptera: Coccinellidae), on whitefly *Bemisia tabaci* (Homoptera: Aleyrodidae) parasitized by *Eretmocerus mundus* (Hymenoptera: Aphelinidae). Biocontrol Sci Technol 21(8):985–989

Manly BFJ (1974) A model for certain types of selection experiments. Biometrics 30:281–294

McGregor RR, Gillespie DR (2005) Intraguild predation by the generalist predator *Dicyphus hesperus* on the parasitoid *Encarsia formosa*. Biocontrol Sci Technol 15(3):219–227

Messelink GJ, van Maanen R, van Steenpal SEF, Janssen A (2008) Biological control of thrips and whiteflies by a shared predator: two pests are better than one. Biol Control 44(3):372–379

Meyling NV, Enkegaard A, Brødsgaard HF (2004) Intraguild predation by *Anthocoris nemorum* (Heteroptera: Anthocoridae) on the aphid parasitoid *Aphidius colemani* (Hymenoptera: Braconidae). Biocontrol Sci Technol 14(6): 627–630

Montserrat M, Albajes R, Castane C (2000) Functional response of four Heteropteran predators preying on greenhouse whitefly (Homoptera: Aleyrodidae) and western flower thrips (Thysanoptera: Thripidae). Environ Entomol 29: 1075–1082

Naranjo SE (2007) Intraguild predation on *Eretmocerus* sp. nr. *emiratus*, a parasitoid of *Bemisia tabaci*, by three generalist predators with implications for estimating the level and impact of parasitism. Biocontrol Sci Technol 17(5/6): 605–622

Naranjo SE, Ellsworth PC (2005) Mortality dynamics and population regulation in *Bemisia tabaci*. Entomol Exp Appl 116:93–108

Neal JW Jr, Leonhardt BA, Brown JK, Bentz JA, Devilbiss ED (1994) Cuticular lipids of greenhouse whitefly and sweet potato whitefly type A and B (Homoptera: Aleyrodidae) pupal exuviae on the same hosts. Ann Entomol Soc Am 87:609–618

Oliveira MRV, Henneberry TJ, Anderson P (2001) History, current status, and collaborative research projects for *Bemisia tabaci*. Crop Prot 20:709–723

Polis GA, Holt RD (1992) Intraguild predation: the dynamics of complex trophic interactions. Trends Ecol Evol 7:151–154

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

Raymond B, Darby AC, Douglas AE (2000) Intraguild predators and the spatial distribution of a parasitoid. Oecologia 124:367–372

Rees NE, Onsager JA (1982) Influence of predators on the efficiency of the *Blaesoxipha* spp. parasites of the migratory grasshopper. Environ Entomol 11:426–428

Riudavets J (1995) Predators of *Frankliniella occidentalis* (Perg.) and *Thrips tabaci* Lind.: a review. In: van Lenteren JC, Loomans AJM (eds) Biological control of thrips pests. Wageningen Agricultural University, Wageningen, The Netherlands, pp 46–78

Rosenheim JA (2005) Intraguild predation of *Orius tristicolor* by *Geocoris* spp. and the paradox of irruptive spider mite dynamics in California cotton. Biol Control 32:172–179

Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological control agents: theory and evidence. Biol Control 5:303–335

Sanderson J, Brødsgaard HF, Enkegaard A (2005) Preference assessment of two *Orius* spp. for *Neoseiulus cucumeris* vs. *Frankliniella occidentalis.* IOBC/WPRS Bull 28(1): 221–224

SAS Institute Inc. (2010) SAS/STAT® 9.22 user's guide. SAS Institute Inc., Cary, USA

Schausberger P, Walzer A (2001) Combined versus single species release of predaceous mites: predator–predator interactions and pest suppression. Biol Control 20:269–278

Sherratt TS, Harvey I (1993) Frequency-dependent food selection by arthropods: a review. Biol J Linn Soc 48:167–186

Shiojiri K, Takabayashi J (2005) Parasitoid preference for host-infested plants is affected by the risk of intraguild predation. J Insect Behav 18(4):567–576

Snyder WE, Ives AR (2001) Generalist predators disrupt biological control by a specialist parasitoid. Ecology 82: 705–716

Snyder WE, Ballard SN, Yang S, Clevenger GM, Miller TD, Ahn JJ, Hatten TD, Berryman AA (2004) Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid *Aphelinus asychis* on greenhouse roses. Biol Control 30:229–235

Tommasini MG, van Lenteren JC, Burgio G (2004) Biological traits and predation capacity of four *Orius* species on two prey species. Bull Insectol 57(2):79–93

Trottin-Caudal Y, Grasselly D, Trapateau M, Dobelin H, Millot P (1991) Biological control of *Frankliniella occidentalis* with *Orius majusculus* on cucumber. Bull OILB/SROP 14(5):50–56

Zang LS, Liu TX (2007) Intraguild interactions between an oligophagous predator, *Delphastus catalinae* (Coleoptera: Coccinellidae), and a parasitoid, *Encarsia sophia* (Hymenoptera: Aphelinidae), of *Bemisia tabaci* (Homoptera: Aleyrodidae). Biol Control 41:142–150

Zhang ZQ (2003) Mites of greenhouses. Identification, biology and control. CABI Publishing, Cambridge, UK