CANNIBALISM AND INTRAGUILD PREDATION IN THE PHYTOSEIID MITES *TYPHLODROMIPS SWIRSKII, EUSEIUS SCUTALIS* AND *TYPHLODROMUS ATHIASAE* (ACARI: PHYTOSEIIDAE)

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ABSTRACT: The intraguild predation and cannibalism on eggs and immatures by the adult females of *Euseius scutalis*, *Typhlodromus athiasae* and *Typhlodromips swirskii* were examined under laboratory conditions. Adult females of all three species exhibited higher predation rates on larvae than on protonymphs. *Typhlodromips swirskii* had higher predation rates on heterospecific than on conspecific prey and all females failed to predate on eggs and protonymphs of its own. Also, *T. swirskii* females were able to sustain oviposition when preying upon eggs and immatures of *T. athiasae* and *E. scutalis*, whereas cannibalizing *T. swirskii* females did not lay eggs and all died in a short time (6.0–7.3 days), respectively. *Typhlodromus athiasae* failed to predate on eggs as well as immatures of *T. swirskii* and females suffered a higher mortality than vice versa. *Euseius scutalis* females ate 6.0 larvae or 5.2 protonymphs of *T. athiasae* and 0.7 eggs or 0.4 larvae of *T. swirskii* per female per day. Females of *E. scutalis* were hardly able to sustain oviposition irrespective of con- or heterospecific prey, so reproduction was very low. The present study indicates that phytoseiid immatures are suitable prey for surviving and reproduction of polyphagous phytoseiids.

KEY WORDS: Acari, cannibalism, generalist predators, intraguild predation, Phytoseiidae

INTRODUCTION

Predatory mites of the family Phytoseiidae are of economic importance because they efficiently control pest mites in many crops around the world (Sabelis 1985). *Euseius scutalis* (Athias-Henriot), *Typhlodromips swirskii* (Athias-Henriot) and *Typhlodromus athiasae* Porath and Swirski are known to play important roles in the natural control of tetranychid and eriophyid mites on vegetables, vineyards, orchards and strawberry fields (Swirski et al. 1967 a, b; Bounfour and McMurtry 1987; Momen and El-Sawi 1993; Abou-Awad et al. 2000; Momen and Abdel-Khalek 2008; Momen 2009). *Typhlodromips swirskii* and *T. athiasae* are reported as generalist type III predators while *E. scutalis* as type IV predators which are generalist of phytophagous mites, but specialist feeders on pollen (McMurtry and Croft 1997). Predation among various life stages may take place between different species within a guild (intraguild predation) as well as within each species (cannibalism). Cannibalism and intraguild predation are expected to occur mainly when the preferred prey are low (Polis 1981; Polis et al. 1989). Intraguild predation (IGP) is defined as predation between potential competitors that share the same food / prey (Polis et al. 1989). Such predation can involve one species being the intraguild predator and the other intraguild prey or each species can prey upon the other (Rosenheim et al. 1995; Janssen et al. 1998). Numerous studies have reported that intraguild predation and cannibalism is common among phytoseiid mites (Croft and Croft 1996; Schausberger 1997; Walzer and Schausberger 1999 a, b; Castag-

noli et al. 2002). Palvesky et al. (1999) have addressed cannibalism and predation of *T. athiasae* but never in comparison to *T. swirskii* and *E. scutalis*, while Rasmy et al. (2004) compared intraguild predation by *T. swirskii* on *E. scutalis* and cannibalism by *T. swirskii*. Most studies on intraguild interaction between predators have been done in relatively small-scale laboratory experiments. However, intraguild interactions at this small spatial scale may differ from that in the field. For example, habitat structure may increase persistence of the intraguild prey by decreasing the strength of the interaction between intraguild predator and intraguild prey (Janssen et al. 2007). Also, predators may induce antipredator behaviour in prey, such as escaping and this behaviour may have positive or negative effects on the risk of predation by other predators (Vance-Chalcraft et al. 2007). The above factors as well as the spatial heterogeneity and differences in food web complexity suggest that the IGP effects on pest population might not be so relevant in the field. Since the three phytoseiid species inhabit the same plant and share the same food resources, the risk of competition for space and food resources increases and so does the potential for negative interactions, with significant consequences for their population dynamics and biological control of their shared prey *Tetranychus urticae* Koch (Acari: Tetranychidae).

This paper aims to characterize the cannibalism and intraguild predation by adult females when preying upon either con- or heterospecific

immature stages of *E. scutalis*, *T. athiasae* and *T. swirskii* under laboratory conditions. In this study, comparisons of prey consumption and fecundity of each mite species were made to help in predicting of their possible interaction in the field.

MATERIALS AND METHODS
Mite rearing

Cohorts of the three phytoseiid predators used in this study originated from colonies initiated with forty individuals of each species. *Typhlodromus athiasae* and *T. swirskii* were collected in 2006 from mango orchards in Faywam Province, and *E. scutalis* was collected in 2007 from apple and mango orchards in Tanta Province, Egypt. The predatory mites, *T. swirskii* and *T. athiasae,* were reared at 26ºC on detached bean leaves (*Phaseolus vulgaris* L.) infested with two-spotted spider mites, *T. urticae*, while *E. scutalis* was fed on pollen *Ricinus communis* L (Euphorbiaceae). These leaves were surrounded by water-saturated tissue paper folded over the edges of leaves and arenas (foam arenas) preventing the mites from escaping. Some 2–3 leaves from the spider mite culture were added to the predacious cultures bi-weekly and pollen was brushed onto arenas and leaves for *E. scutalis* twice a week. Preliminary tests showed that a supply of either seven eggs or eight larvae or protonymphs per day is sufficient for females of all predators to survive and reproduce. Rearing unites and experimental arenas were held in environmental chambers at 28 ± 1ºC and 70 ± 5% RH and 16 h photoperiod.

Experimental set-up

Adult females preying upon con- and hetero-specific eggs, larvae and protonymphs

Freshly cut, clean, inverted 3 cm diameter bean leaf discs was placed on a layer of filter paper sheet placed on a distilled water-saturated cotton pad in 6 cm diameter Petri dishes, were used for each experimental arena. The filter paper was kept moist during the experimental period. Stikem Special ™ was painted around each leaf disc to form a barrier to prevent escape. One male and one female (7 days old since egg hatching) of each species (15 replicates per species) were added to leaf discs with excess food, and they were left there to mate. After 24 h, each female was transferred to a fresh arena with no food and with a 1 cm long piece of black cotton as the oviposition site. Females were left there for 24 h to standardize the level of hunger among individuals. Subsequently,

7 eggs (24 h old), or 8 newly hatched larvae, or 8 protonymphs (24 h old) of either con- or hetero-specifics were added to the arenas. Tested individuals and prey were drawn from the same colonies (kin on cannibalism). There were nine variants in each experimental series, with an arrangement per leaf arena of one adult female with seven eggs (experiment 1) and eight larvae or protonymphs (experiment 2 and 3) of each of the three species. Predation rates, survival and oviposition were recorded twice a day. Deflated eggs and shriveled corpses of the dead immatures were taken as evidence of predation. Every 24 h all the eggs and immature stages were renewed, and the eggs laid by females were removed. In experiment 1 emergence of the larvae occurred rarely in all three species. The experimental period lasted a maximum of 8 days in experiment 1 and 14 days in experiments 2 and 3.

Statistical analysis

All experiments were subjected to analysis of variance (ANOVA), using SPSS computer program. The mean predation and oviposition rates of predators provided with either con-or heterospecific prey were compared by using Duncan's multiple range tests. Data of the predation and oviposition rates were calculated as a daily mean for each female and used for interspecies comparison. Data were fitted with the assumptions of normality, not transformed, and the differences were compared for each predator species between all prey species [SMALL letters in Tables 1–3, columns 2, 3], and those among each prey species between the predators [CAPITAL letters, same table and columns]. Eggs laid during the first 24 h of the experiments were not considered in the analysis.

RESULTS
Experiment 1: Adult females feeding on con- and heterospecific eggs

Euseius scutalis and *T. athiasae* exhibited very low predation rate on eggs, while *T. swirskii* showed a higher rate on heterospecific eggs (Table 1). Female's *E. scutalis* and *T. athiasae* moved and tried to pierce eggs but had difficulties in penetrating the chorion (direct observation). Mean predation rate of *T. swirskii* was significantly higher when feeding on heterospecific eggs (ANOVA: df = 2, 44; F = 628.35; p = 0.000). Only *T. swirskii* females provided with heterospecific eggs were able to lay eggs (1.57 and 0.86 eggs/ day, respectively) (Table 1).

Table 1

Predation and oviposition for adult *Euseius scutalis, Typhlodromus athiasae* and *Typhlodromips swirskii* females when provided with con- or heterospecific eggs for 8 consecutive days

Predator	Prey	Predation* (eggs) Mean ± SE	Oviposition** Mean ± SE
Euseius scutalis	*E. scutalis*	0.38 ± 0.03 c F	0.00 ± 0.00 b D
	T. athiasae	1.16 ± 0.07 a D	0.09 ± 0.03 a D
	T. swirskii	0.68 ± 0.03 b E	0.00 ± 0.00 b D
F-value		75.032	10.161
Typhlodromus athiasae	*T. athiasae*	0.51 ± 0.05 b EF	0.02 ± 0.01 b D
	E. scutalis	1.88 ± 0.18 a C	0.48 ± 0.08 a C
	T. swirskii	0.00 ± 0.00 c G	0.00 ± 0.00 b D
F-value		78.800	36.721
Typhlodromips swirskii	*T. swirskii*	0.00 ± 0.00 c G	0.00 ± 0.00 c D
	E. scutalis	5.57 ± 0.17 a A	1.57 ± 0.08 a A
	T. athiasae	4.51 ± 0.12 b B	0.86 ± 0.07 b B
F-value		628.357	160.342
F-value		433.57	149.14

In each predator (differences within prey species) df = 2,44; P = 0.000
In a whole column (differences among each prey species within all predator species) df = 8,134; P = 0.000
* Mean number of eggs eaten / female / day
** Mean number of eggs deposited / female / day
Means in a block for each predator species followed with the same SMALL letters are not significantly different at 5 % level of probability. Means in a whole column followed with the same CAPITAL letters are not significantly different at 5 % level of probability.

Experiment 2: Adult females feeding on con- and heterospecific larvae

The adult females of *T. swirskii* generally consumed more larvae than *E. scutalis* and *T. athiasae* did (Table 2). Mean oviposition rate of *T. swirskii* was significantly higher than the corresponding rates of *E. scutalis* and *T. athiasae* (ANOVA: df = 8, 134; F = 208.52; p = 0.000). The cannibalizing of *T. swirskii* resulted in no female able to sustain oviposition. Mean predation and oviposition rates of *T. swirskii* were significantly higher, when feeding on heterospecific vs. conspecific larvae (ANOVA: F = 1999.16; and F = 213.86; p=0.000). *Typhlodromus athiasae* consumed 2 times more conspecific vs. heterospecific larvae of *E. scutalis,* and also failed to feed on *T. swirskii* larvae (Table 2). The adult females of *E. scutalis* cannibalized only 0.8 larvae per day and ate more individuals (nearly 6 times more than conspecific) of heterospecific *T. athiasae*.

Experiment 3: Adult females feeding on con- and heterospecific protonymphs

Typhlodromus athiasae consumed three times more conspecific than heterospecific protonymphs of *E. scutalis* (Table 3). *Typhlodromus athiasae* failed to lay eggs when provided with heterospe-cific protonymphs of *E. scutalis*. All the three female predators failed to predate and sustain oviposition when offered protonymphs of *T. swirskii* (Table 3). *Euseius scutalis* female consumed ten times more heterospecific *T. athiasae* than conspecific (ANOVA: F = 1189.50; p = 0.000). The cannibalizing of *E. scutalis* resulted in no female able to lay eggs. *Typhlodromips swirskii* consumed a significantly higher number of *T. athiasae* protonymphs than *E. scutalis* (ANOVA:F =397.05, P = 0.000) and also oviposited a higher number of eggs (0.94/ day) (Table 3).

DISCUSSION

Intraguild predation (IGP) is particularly common in a generalist species as they will often consume other natural enemies as well as the target pest (Polis et al. 1989; Rosenheim et al. 1995). The conspecific individual proved to be a less attractive prey for the female predators. *Euseius scutalis* and *T. swirskii* seem to feed more on hetero- than conspecific prey, probably because generalist phytoseiids, like the three species used in our study, can discriminate heterospecific prey from conspecific and feed preferentially on heterospecific prey (Schausberger 2003). Higher predation rates on heterospecifics vs. conspecifics

Table 2

Predation and oviposition for adult *Euseius scutalis, Typhlodromus athiasae* and *Typhlodromips swirskii* females when provided with con- or heterospecific larvae for 14 consecutive days

Predator	Prey	Predation* (eggs) Mean ± SE	Oviposition** Mean ± SE
Euseius scutalis	*E. scutalis* *T. athiasae* *T. swirskii*	0.80 ± 0.09 b D 5.98 ± 0.12 a A 0.45 ± 0.03 c E	0.12 ± 0.03 a D 0.10 ± 0.02 a DE 0.00 ± 0.0 b E
	F-value	1236.78	9.95
Typhlodromus athiasae	*T. athiasae* *E. scutalis* *T. swirskii*	2.97 ± 0.09 a B 1.51 ± 0.09 b C 0.00 ± 0.00 c F	0.23 ± 0.03 a C 0.17 ± 0.04 a CD 0.00 ± 0.0 b E
	F-value	427.51	19.63
Typhlodromips swirskii	*T. swirskii* *E. scutalis* *T. athiasae*	0.18 ± 0.02 c F 2.76 ± 0.07 b B 6.00 ± 0.09 a A	0.00 ± 0.0 c E 0.94 ± 0.06 b B 1.31 ± 0.05 a A
	F-value	1999.169	213.860
	F-value	938.66	208.52

In each predator (differences within prey species) df = 2,44; P = 0.000
In a whole column (differences among each prey species within all predator species) df = 8,134; P = 0.000
* Mean number of larvae eaten / female / day
** Mean number of eggs deposited / female / day
Means in a column for each predator species followed with the same SMALL letters are not significantly different at 5 % level of probability. Means in a whole column followed with the same CAPITAL letters are not significantly different at 5 % level of probability.

Table 3

Predation and oviposition for adult *Euseius scutalis, Typhlodromus athiasae* and *Typhlodromips swirskii* females when provided with con- or heterospecific protonymphs for 14 consecutive days

Predator	Prey	Predation* (eggs) Mean ± SE	Oviposition** Mean ± SE
Euseius scutalis	*E. scutalis* *T. athiasae* *T. swirskii*	0.49 ± 0.04 b F 5.17 ± 0.14 a A 0.00 ± 0.00 c G	0.00 ± 0.00 b E 0.07 ± 0.02 a D 0.00 ± 0.00 b E
	F-value	1189.500	22.892
Typhlodromus athiasae	*T. athiasae* *E. scutalis* *T. swirskii*	2.71 ± 0.09 a C 0.91 ± 0.05 b E 0.00 ± 0.0 c G	0.13 ± 0.01 a C 0.00 ± 0.0 b E 0.00 ± 0.0 b E
	F-value	494.032	748.443
Typhlodromips swirskii	*T. swirskii* *E. scutalis* *T. athiasae*	0.00 ± 0.00 c G 2.00 ± 0.10 b D 4.08 ± 0.15 a B	0.00 ± 0.00 c E 0.82 ± 0.02 b B 0.94 ± 0.05 a A
	F-value	397.054	317.100
	F-value	522.711	473.342

In each predator (differences within prey species) df = 2,44; P = 0.000
In a whole column (differences among each prey species within all predator species) df = 8,134; P = 0.000
*Mean number of protonymphs eaten / female / day
**Mean number of eggs deposited / female / day
Means in a column for each predator species followed with the same SMALL letters are not significantly different at 5 % level of probability. Means in a whole column followed with the same CAPITAL letters are not significantly different at 5 % level of probability.

have been reported for other generalist phytoseiid mite species, including *Amblyseius degenerans* (Berlese), *Typhlodromus pyri* Scheuten and *Kampimodromus aberrans* (Oudemans) (Yao and Chant 1989; Schausberger 1997, 1999). On the contrary, the generalist *T. athiasae* exhibited slightly greater predation on conspecific vs. heterospesific. The results clearly show that all three

phytoseiid species feed more on con- and hetero-specific larvae than on con- and heterospecific protonymphs. These patterns are similar to those reported on other phytoseiid species including *Neoseiulus californicus* (McGregor), *Euseius finlandicus* (Oudemans), *T. pyri*, *K. aberrans*, *A. degenerans*, *Amblyseius andersoni* Chant and *Phytoseiulus persimilis* Athias Henriot (Yao and Chant 1989; MacRae and Croft 1993; Croft et al. 1996; Schausberger 1997, 1999; Walzer and Schausberger 1999a). The fact that intra- and interspecific predation was generally lower on protonymphs than on larvae might be related to the relatively higher resistance posed by the protonymphs (Polis et al. 1989; Croft et al. 1996; Schausberger 1997, 1999; Castagnoli et al. 2002). Probably a protonymph provides more food than a larva, but this may not outweigh the energy cost of searching and handling protonymphs (prey defense) and piercing their more sclerotised tegument. We found that *T. swirskii* failed to pierce eggs of its own while *T. athiasae* failed to pierce *T. swirskii* eggs. Schausberger and Croft (1999) indicated that some species had difficulty penetrating the chorion, either indicating that their mouthparts are not adapted to hold and pierce oval-shaped eggs or the phytoseiid eggs have a protective substance on the chorion that makes penetration difficult.

Similarly to the current study, Palevsky et al. (1999) determined higher predation rates of *T. athiasae* on heterospecifics eggs than conspecific eggs. Our results of cannibalizing *T. swirskii* contradicted the report by Rasmy et al. (2004) who indicated that females of *T. swirskii* were fed on protonymphs of their own and able to sustain oviposition. The oviposition rates of *T. swirskii* fed on heterospecific were similar to the rates reported on other adequate diets at comparable environmental conditions. *Typhlodromips swirskii* female produced 1.3, 1.5, 1.0 eggs per female per day on eggs of *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae), *Aceria ficus* (Cotte) and *Rhyncaphytoptus ficifoliae* Keifer (both Acari: Eriophyidae), respectively (Abou-Awad et al. 2000; El-Sawi and Momen 2005). For *T. athiasae*, oviposition rates (eggs per female per day) from 0.18 on eggs of *Prodenia litura* F. to 2.8 on *Eriophyes dioscoridis* Soliman and Abou-Awad (Acari: Eriophyidae) have been reported (Swirski et al. 1967 b; Momen 2009). In the present study, the oviposition rates in *E. scutalis* were very low. *Euseius scutalis* female produced 0.9 and 2.03 eggs per female per day on eggs of *Agrotis ipsilon* (Hufnagel) (Lepidoptera: Noctuidae) and pollen grains of *R. communis*, respectively (El-Sawi and Momen 2005; Momen and Abdel-Khalek 2008). Cannibalizing immatures of all three phytoseiid species tested in the present study were able to reach adulthood, also all phytoseiid immatues are a suitable prey for developing stages of polyphagous phytoseiids (Momen and Abdel-Khalek, personal communication). When considering cannibalism and interspecific predation alone, *T. swirskii* will have an advantage over *E. scutalis* and *T. athiasae* by being more prone to prey upon potential competitors and by having a mechanism to avoid cannibalism. According to Overmeer (1985), heterospecific phytoseiids in the present study can be considering an alternative food source for the three adult females and immatures of generalist phytoseiid (with exception of *T. swirskii* as a prey). Kin cannibalism used in our studies may have some benefits: if nothing else is available, eating related individuals may increase the cannibal's fitness by obtaining nutrients and reducing competition. Our results emphasize the importance of knowing whether or not IGP and cannibalism occurs in a given assemblage. Since *E. scutalis* is a pollen feeder and was hardly able to sustain oviposition irrespective of con- or heterospecific prey, we suggest that *T. swirskii* and *T. athiasae* are the intraguild predator and intraguild prey, whereas they compete for the same pest. If mutual IGP does occur, then the use of intraguild predators for biological control would be a sound "no", unless the intraguild predator is the superior competitor for the pest, in which case the use of the intraguild prey would be redundant. Hence, there would be no advantage in using pairs of natural enemy species that are engaged in intraguild predation. At present it is hard to predict how *T. swirskii, T. athiasae* and *E. scutalis* will interact in the field. It is possible, that due to the abundance of phytoseiid mites in orchards, all species may be able to co-exist.

CONCLUSION

The present study has revealed (IGP) and cannibalism exist between the three species tested. How successfully *E. scutalis*, *T. athiasae* and *T. swirskii* feed, survive and reproduce on each other in the laboratory may give some indication as to what may happen (possible interaction between the three species) in the field. The ability of the species studied to utilize a phytoseiid prey suggests that they will be able to stabilize their popu-

lation levels when other food sources such as tetranychid and eriophyoid prey or pollen is unavailable. Summarizing all the experiments indicates: 1) *T. swirskii* exhibits stronger predation on heterospecific than vice versa; 2) *T. swirskii* benefits more from predation on heterospecific than conspecific; 3) when *T. swirskii* is provided as a prey, all predators suffers more mortality than *T. athiasae* and *E. scutalis* as prey; 4) *Euseius scutalis* and *T. swirskii* fed on conspecific appeared to be less favourable prey than heterospecific, while *T. athiasae* fed on conspecific immatures appeared to be favourable.

REFERENCES

Abou-Awad, B.A.; El-Sawaf, B.M. and Abdel-Khalek A.A. 2000. Impact of two eriophyoid fig mites, *Aceria ficus* and *Rhyncaphytoptus ficifoliae*, as prey on postembryonic development and oviposition rate of the predacious mite *Amblyseius swirskii*. Acarologia, 41: 367–371.

Bounfour, M. and McMurtry, J.A. 1987. Biology and ecology of *Euseius scutalis* (Athias-Henriot) (Acari: Phytoseiidae). Hilgardia, 55: 1–23.

Castagnoli, M.; Liguori, M. and Simoni, S. 2002. Interspecific predation and cannibalism in four phytoseiid species of the Mediterranean area (Acari: Phytoseiidae). In: Bernini F, Nannelli R, Nuzzaci G, de Lillo E (eds) Acarid Phylogeny and Evaluation: Adaptation in mites and ticks. Kluwer Academic Publishers, The Netherlands, 341–349.

Croft, B.A. and Croft, M.B. 1996. Intra- and interspecific predation among adult female phytoseiid mites (Acari: Phytoseiidae): effects on survival and reproduction. Environmental Entomology, 25: 853–858.

Croft, B.A.; Kim S.S. and Kim, D.I. 1996. Intra- and interspecific predation on four life stage groups by the adult females of *Metaseiulus occidentalis*, *Typhlodromus pyri*, *Neoseiulus fallacies* and *Amblyseius andersoni*. Experimental and Applied Acarology, 20: 435–444.

El-Sawi, S.A. and Momen, F.M. 2005. Biology of some phytoseiid predators (Acari: Phytoseiidae) on eggs of *Phthorimaea operculella* and *Spodoptera littoralis* (Lepidoptera: Gelechiidae and Noctuidae). Acarologia, 46: 23–30.

Janssen, A., Pallini, A., Venzon, M., and Sabelis M.W. 1998. Behaviour and indirect interaction in food webs of plant-inhabiting arthropods. Experimental and Applied Acarology, 22: 497–521.

Janssen, A., Sabelis, M.W., Magalhaes, S., Montserrat, M., and van der Hammen, T. 2007. Habitat structure affects intraguild predation. Ecology, 88: 2713–2719.

MacRae, I.V. and Croft, B.A. 1993. Influence of temperature on interspecific predation and cannibalism by *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acarina: Phytoseiidae). Environmental Entomology, 22: 770–775.

McMurtry, J.A. and Croft, B.A. 1997. Lifestyles of phytoseiid mites and their roles in biological control. Annual Review of Entomology, 42: 291–312.

Momen, F.M. 2009. Life history of the predatory mites *Typhlodromus athiasae* and *Amblyseius cabonus* (Acari: Phytoseiidae) on two pest mites as prey, with special references to *Eriophyes dioscoridis* (Acari: Eriophyidae). Archives of Phytopathology and Plant Protection 42 [In press]

Momen, F.M. and Abdel-Khalek, A. 2008. Influence of diet on biology and life table parameters of the predacious mite *Euseius scutalis* (A. H.) (Acari: Phytoseiidae). Archives of Phytopathology and Plant Protection, 41: 418–430.

Momen, F.M. and El-Sawi, S.A. 1993. Biology and feeding behaviour of the predatory mite, *Amblyseius swirskii* (Acari: Phytoseiidae). Acarologia, 34: 199–204.

Overmeer W.P.J. (1985). Alternative prey and other food resources. *In*: W. Helle and M.W. Sabelis (Eds). Spider mites: their biology, Natural Enemies and Control, Elsevier, Amsterdam, pp. 131–139.

Palevsky, E., Reuveny, H., Okonis, O., and Gerson, U. 1999. Comparative behavioural studies of larval and adult stages of the phytoseiids (Acari: Mesostigmata) *Typhlodromus athiasae* and *Neoseiulus californicus*. Experimental and Applied Acarology, 23: 467–485.

Polis, C.A. 1981. The evolution and dynamics of intraspecific predation. Annual Review of Ecology and Systematic, 12: 225–251.

Polis, G.A., Myers, C.A. and Holt R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematic, 20: 297–330.

Rasmy, A.H., Abou-El-Ella, G.M. and Hussein, H.E. 2004. Cannibalism and interspecific predation of the phytoseiid mite, *Amblyseius swirskii*. Journal of Pest Science, 77: 23–25.

Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J., and Jaffee B.A. 1995. Intraguild predation among biological control agents: theory and evidence. Bio Control, 5: 303–335.

Sabelis M. (1985): Predation on spider mites. *In*: W. Helle and M.W. Sabelis (Eds). Spider mites: their biology, Natural Enemies and Control, vol. 1B. Elsevier, Amsterdam, p. 103–129.

Schausberger, P. 1997. Inter- and intraspecific predation on immatures by adult females in *Euseius finlandicus*, *Typhlodromus pyri* and *Kampimodromus aberrans* (Acari: Phytoseiidae). Experimental and Applied Acarology, 21: 131–150.

Schausberger, P. 1999. Predation preference of *Typhlodromus pyri* and *Kampimodromus aberrans* (Ac-

ari: Phytoseiidae) when offered con- and heterospecific immature life stages. Experimental and Applied Acarology, 23: 389–398.

Schausberger, P. 2003. Cannibalism among phytoseiid mites: a review. Experimental and Applied Acarology, 29: 173–191.

Schausberger, P. and Croft, B.A. 1999. Predation on and discrimination between con- and heterospecific eggs among specialist and generalist phytoseiid mite species (Acari: Phytoseiidae). Environmental Entomology, 28: 523–528.

Swirski, E., Amitai, S. and Dorzia, N. 1967a. Laboratory studies on the feeding, development and reproduction of the predacious mites *Amblyseius rubini* Swirski and Amitai and *Amblyseius swirskii* Athias-Henriot (Acarina: Phytoseiidae) on various kinds of food substances. Israel Journal of Agricultural Research, 17: 101–112.

Swirski, E., Amitai, S. and Dorzia, N. 1967b. Laboratory studies on the feeding, development and oviposition of the predacious mite *Typhlodromus athiasae* P. and S. (Acarina: Phytoseiidae) on var-

ious kinds of food substances. Israel Journal of Agriculture Research, 17: 213–218.

Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W., and Sih, A. 2007. The influence of intraguild predation on prey suppression and prey release: A meta-Analysis. Ecology, 88: 2689–2696.

Walzer, A. and Schausberger, P. 1999a. Cannibalism and interspecific predation in the phytoseiid mites *Phytoseiulus persimilis* and *Neoseiulus californicus*: predation rates and effects on reproduction and juvenile development. Bio Control, 43: 457–468.

Walzer, A. and Schausberger, P. 1999b. Predation preference and discrimination between con- and heterospecific prey by the phytoseiid mites *Phytoseiulus persimilis* and *Neoseiulus californicus*. Bio Control, 43: 469–478.

Yao, D.S. and Chant, D.A. 1989. Population growth and predation interference between two species of predatory phytoseiid mites (Acarina: Phytoseiidae) in inter active systems. Oecologia, 80: 443–455.