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Predation preference of *Typhlodromus pyri* and *Kampimodromus aberrans* (Acari: Phytoseiidae) when offered con- and heterospecific immature life stages

Peter Schausberger*
Federal Office and Research Centre for Agriculture, Institute of Phytomedicine,
Spargelfeldstrasse 191, A-1226 Vienna, Austria
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ABSTRACT

The predation preference of singly caged adult females and nymphs of *Typhlodromus pyri* and *Kampimodromus aberrans* for con- or heterospecific immature stages as prey was tested in the laboratory. Both polyphagous predatory mite species have been previously shown to interact directly through predation on each other. The present study demonstrated that the adult females of *T. pyri* and *K. aberrans* are able to discriminate between con- and heterospecific larvae and protonymphs and that they prefer to prey upon heterospecifics when given the choice. Hunger did not reduce the propensity of the females to prefer heterospecifics over conspecifics. For proto- and deutonymphs the trends followed the results obtained with the adult females, but the preference for heterospecifics was not distinct enough to be significant. In competitive situations reciprocal predation may be a crucial mechanism in the interaction of polyphagous phytoseiid species and may contribute significantly to population persistence. The results are discussed with regard to possible associations between the ability to discriminate con- and heterospecifics and the type of feeding specialization (generalists versus specialists).
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Key words: Predation preference, reciprocal predation, mutual antagonism, predatory mites, Phytoseiidae.

INTRODUCTION

Typhlodromus pyri Scheuten and *Kampimodromus aberrans* (Oudemans) are polyphagous predatory mites that can provide biological control of spider mites (Tetranychidae) and eriophyoid mites (Eriophyidae) in orchards and vineyards (e.g. McMurtry, 1982; Helle and Sabelis, 1985; Duso, 1989; Croft and MacRae, 1992a). *Typhlodromus pyri* and *K. aberrans* partly share the same habitats and have

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* To whom correspondence should be addressed at: Department of Entomology, Oregon State University, Corvallis 2046 Cordley Hall, OR–97331, USA. Tel: 541 737 5524; Fax: 541 737 3643; e-mail: schausbp@bcc.orst.edu

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overlapping food ranges. In periods of limited food availability they can be competitors by exploiting the same prey species, but they can also interact directly through predation on each other (Schausberger, 1997, 1998a). This phenomenon has been called intraguild predation (Polis *et al*., 1989). In studies on inter- and intraspecific predation on immatures by adult females of *T. pyri, K. aberrans* and *Euseius finlandicus* (Oudemans), differences were revealed in species' tendencies to attack and feed on various stages of con- and heterospecifics (Schausberger, 1997). The females of *T. pyri* and *K. aberrans* ate more larvae and protonymphs of the other species than they did of their own. The predation rates indicated that they might have a preference for heterospecific phytoseiid prey, which presumes that they can discriminate between con- and heterospecifics. It was also found that survival and oviposition depended on the phytoseiid species used as prey. MacRae and Croft (1993) had previously shown *T. pyri* females to have higher feeding rates on heterospecific phytoseiids than on conspecifics and concluded that this species may have mechanisms for differentiating con- and heterospecific phytoseiids. Recently, several studies have been concerned with various aspects of cannibalism and interspecific predation in both adult and immature phytoseiid mites and some of the experiments were comparisons made between intra- and interspecific predation (Yao and Chant, 1989; MacRae and Croft, 1993, 1997; Croft *et al*., 1996, 1998; Monetti and Croft, 1997).

However, no specific investigations exist on the preference for con- or heterospecifics in mutual predation between competitive phytoseiids and other acarine predators, respectively. It was the objective of the present study to test the hypothesis that the polyphagous *T. pyri* and *K. aberrans* are able to discriminate between con- and heterospecific phytoseiids and that they prefer to prey upon heterospecifics when given the choice. Adult females and proto- and deutonymphs were tested on phytoseiid larvae, which are the preferred stage in intra- and interspecific predation of both adults and immatures. Phytoseiid eggs were not used here because *T. pyri* and *K. aberrans* seldom feed on them (Schausberger, 1997, 1998a). In addition, protonymphs were tested as prey for adult females. Since cannibalism and interspecific predation probably occur primarily in periods of food scarcity, it was also questioned whether starvation could alter the predation preference of the adult females.

MATERIALS AND METHODS

General methods and experimental procedure

Mass cultures of *K. aberrans* and *T. pyri*, which had originally been collected from plum and grape in Vienna and Burgenland, Austria, were maintained in the laboratory for more than 2 years. The mites used in the experiment were taken from cohorts that had been fed birch pollen (*Betula pendula* Roth) for at least two consecutive generations prior to this study. Cohorts of newly laid eggs were obtained by placing gravid females on detached apple leaves or artificial arenas with birch pollen. Eggs were collected every 24 h and transferred to separate arenas. Egg arenas were checked for larvae and proto- or deutonymphs at intervals of 24 h. Mated adult females used in the experiments were taken randomly from the rearing units. Rearing units, leaf arenas, artificial arenas and experimental cells were kept in an environmental chamber at 25 ± 1°C, 16:8 L:D photoperiod and 65 ± 5% relative humidity (RH).

Closed Plexiglass cells (1.5 cm diameter and 0.3 cm height with water available; for a detailed description see Schausberger (1997)) were used to confine the mites during the experiments. Single females and proto- or deutonymphs of one species (regarded as predators) were transferred to the cages together with four larvae or protonymphs each of both species (regarded as prey). There were five experimental series with 16–25 replicates per species each: (1) fed adult females preying upon larvae, (2) fed adult females preying upon protonymphs, (3) unfed protonymphs preying upon larvae, (4) fed deutonymphs preying upon larvae and (5) adult females starved for 24 h preying upon larvae. In experiment 3, 'predator protonymphs' were marked by a tiny water-colour point at the dorsal shield to make them distinguishable from 'prey protonymphs' moulting during the experiment. For control, four larvae or protonymphs each of both species were held in cages without predators. At the beginning of each experiment the cells were monitored for 2 h to record the first successful attack of the predator. After 24 h the number of surviving prey individuals was noticed. Since living protonymphs of *T. pyri* and *K. aberrans* can be hardly distinguished, they were mounted in lactic acid to determine their species.

Statistical analysis

Predation rates. For statistical analysis the mean net predation rates were calculated for each experiment (except for the experiment with starved females feeding on larvae) by subtracting the mean number of dead immatures found in the control groups (without an intended predator) from the mean number of dead immatures found in cages with predators. Mann–Whitney *U*-tests were used to compare the mean numbers of con- and heterospecific prey consumed by the single females and proto- or deutonymphs within a prey species between the predator species and to analyse the mean differences between the numbers of con- and heterospecific immatures predated by the single females and proto- or deutonymphs between *T. pyri* and *K. aberrans*.

Frequencies. After eliminating the cases without any prey consumption and equally partitioning the neutral cases (cells with balanced prey loss) to the biased cases (cells with prey loss biased towards a species), frequencies were analysed by four-field χ^2 tests between the species (experiments 1, 2 and 5 with Yates correction due to frequencies below five and experiments 3 and 4 without Yates correction) (Zöfel, 1992).

RESULTS

In all cases in experiments 1 and 5 (fed and starved females preying upon larvae) at which the first successful attack was recorded, the females of both species exclusively chose heterospecific larvae (Table 1). In all other experiments no feeding was observed during the first 2 h. In all experiments, in both species and in all stages tested, except for *T. pyri* protonymphs feeding on larvae (experiment 3), prey consumption was biased towards heterospecifics compared with the control groups without predators (Tables 1 and 2 and Fig. 1). χ^2 tests as well as Mann–Whitney *U*-tests revealed significance only in the experiments with adult female predators (experiments 1, 2 and 5). In cages without predators, losses of prey individuals were mainly caused by unintended inter- and intraspecific predation on larvae by newly moulted protonymphs and, to a much lesser extent, by drowned larvae. In experiments 1–3 more individuals of *T. pyri* than of *K. aberrans* survived in the control group, indicating that attacks on heterospecific larvae by protonymphs more likely occurred in *T. pyri* than in *K. aberrans*. In experiment 4 the number of survivors in the control group was similar in both species (Table 1 and Fig. 1). The frequency of cases at which prey consumption was biased towards con- or heterospecifics was significantly different between *T. pyri* and *K. aberrans* in experiments 1 (fed females feeding on larvae, $\chi^2 = 22.4$, df = 1 and $p < 0.001$) and 5 (starved females feeding on larvae, $\chi^2 = 12.25$, df = 1 and $p < 0.001$). In experiments 2 (fed females feeding on protonymphs, $\chi^2 = 2.31$, df = 1 and ns), 3 (protonymphs feeding on larvae, $\chi^2 = 1.02$, df = 1 and ns) and 4 (deutonymphs feeding on larvae, $\chi^2 = 2.11$, df = 1 and ns) the frequencies of cases with biased prey consumption were not significantly different between the species. In experiments 3 and 4 (proto- or deutonymphs feeding on larvae) no significant differences in the predation rates between the predator species within a prey species were revealed (Table 2). In addition, the mean differences between con- and heterospecific larvae predated by single proto- or deutonymphs within a predator species were not significantly different between *T. pyri* and *K. aberrans* (experiment 3 $z = -1.18$, and $n_{1,2}$ 24, 24 and experiment 4 $z = -1.52$ and $n_{1,2}$ 20, 20). In experiments 1, 2 and 5 the mean differences between con- and heterospecific larvae or protonymphs predated by adult females within a predator species were significantly different between *T. pyri* and *K. aberrans* (experiment 1 $z = -5.48$, $n_{1,2}$ 25, 25 and $p < 0.001$, experiment 2 $z = -2.39$, $n_{1,2}$ 17, 17 and $p < 0.05$ and experiment 5 $z = -3.97$, $n_{1,2}$ 16, 16 and $p < 0.001$). The predation rates of fed and starved females with larvae or protonymphs were significantly different between the predator species within each prey species in experiments 1 and 5 (see Table 2 for experiment 1; experiment 5 for prey *K. aberrans* $z = -3.16$, $n_{1,2}$ 16, 16 and

TABLE 1

Predation preference of *T. pyri* and *K. aberrans* caged singly and offered con- and heterospecific immature stages and control

Experiment	Predator		Number tested	Prey stage[a]	First prey eaten[b]		Prey loss[c]		
	Species	Stage			*K. aberrans*	*T. pyri*	*T. pyri* > *K. aberrans*	*T. pyri* = *K. aberrans*	*T. pyri* < *K. aberrans*
1	*T. pyri*	F	25	L	11	0	0	0	25
	K. aberrans	F	25	L	0	5	13	7	5
	No predator		25	L	–	–	4	7	14
2	*T. pyri*	F	17	P	0	0	1	3	13
	K. aberrans	F	17	P	0	0	6	3	8
	No predator		16	P	–	–	2	5	9
3	*T. pyri*	P	24	L	0	0	7	9	8
	K. aberrans	P	24	L	0	0	13	4	7
	No predator		25	L	–	–	7	7	11
4	*T. pyri*	D	20	L	0	0	7	1	12
	K. aberrans	D	20	L	0	0	10	4	6
	No predator		20	L	–	–	7	6	7
5	*T. pyri*	F starved	16	L	12	0	0	1	15
	K. aberrans	F starved	16	L	0	9	9	4	3

[a] Each single predator was offered four individuals each of both species.

[b] Number of cases at which the first prey eaten was recorded within 2 h after the start of the experiment.

[c] Number of cases at which prey loss was balanced or biased towards a species, respectively.

F, adult females; L, larvae; P, protonymphs; D, deutonymphs.

TABLE 2

Net predation rates of *T. pyri* and *K. aberrans* caged singly and offered con- and heterospecific larvae or protonymphs

Experiment	Predator		Prey		Net predation rate ± SD[a] (replicates)
	Species	Stage	Species	Stage	
1	*T. pyri*	F	*T. pyri*	L	0.09 ± 1.32 (25)a***
			K. aberrans	L	1.60 ± 1.20 (25)b***
	K. aberrans	F	*T. pyri*	L	1.84 ± 1.37 (25)a***
			K. aberrans	L	0.36 ± 1.31 (25)b***
2	*T. pyri*	F	*T. pyri*	P	0.04 ± 0.99 (17)a**
			K. aberrans	P	1.24 ± 1.66 (17)
	K. aberrans	F	*T. pyri*	P	1.04 ± 1.45 (17)a**
			K. aberrans	P	0.59 ± 1.68 (17)
3	*T. pyri*	P	*T. pyri*	L	0.90 ± 1.26 (24)
			K. aberrans	L	0.67 ± 1.44 (24)
	K. aberrans	P	*T. pyri*	L	0.78 ± 1.05 (24)
			K. aberrans	L	0.09 ± 1.46 (24)
4	*T. pyri*	D	*T. pyri*	L	0.15 ± 1.29 (20)
			K. aberrans	L	0.65 ± 1.37 (20)
	K. aberrans	D	*T. pyri*	L	0.45 ± 1.45 (20)
			K. aberrans	L	0.10 ± 1.57 (20)

[a] Numbers labelled by the same letters are significantly different at $p < 0.001$*** and $p < 0.01$**, using Mann–Whitney *U*-tests.

F, adult females; L, larvae; D, deutonymphs; P, protonymphs.

$p < 0.01$ and for prey *T. pyri* $z = -2.98$, $n_{1,2}$ 16, 16 and $p < 0.01$) and within prey *T. pyri* in experiment 3, respectively (Table 2).

DISCUSSION

The results of the present study demonstrate that adult females of *T. pyri* and *K. aberrans* are able to discriminate between con- and heterospecific larvae and protonymphs and that they prefer to prey upon the other species when given the choice. Hunger did not reduce the propensity of the females to prefer heterospecifics over conspecifics. It can be predicted that, in competitive situations, in particular in periods of low food availability, predation between the two species will be decidedly more severe than within each species. This kind of interaction is known as reciprocal predation, which is defined as ‘an interaction between two species (or individuals) in which each preys upon the other, so that the interaction is, in essence, competitive’ (Begon *et al*., 1996, p. 966). The classic example of mutual antagonism by reciprocal predation was provided by Park *et al*. (1965), who worked on two species of flour beetles, *Tribolium confusum* Duval and *Tribolium*

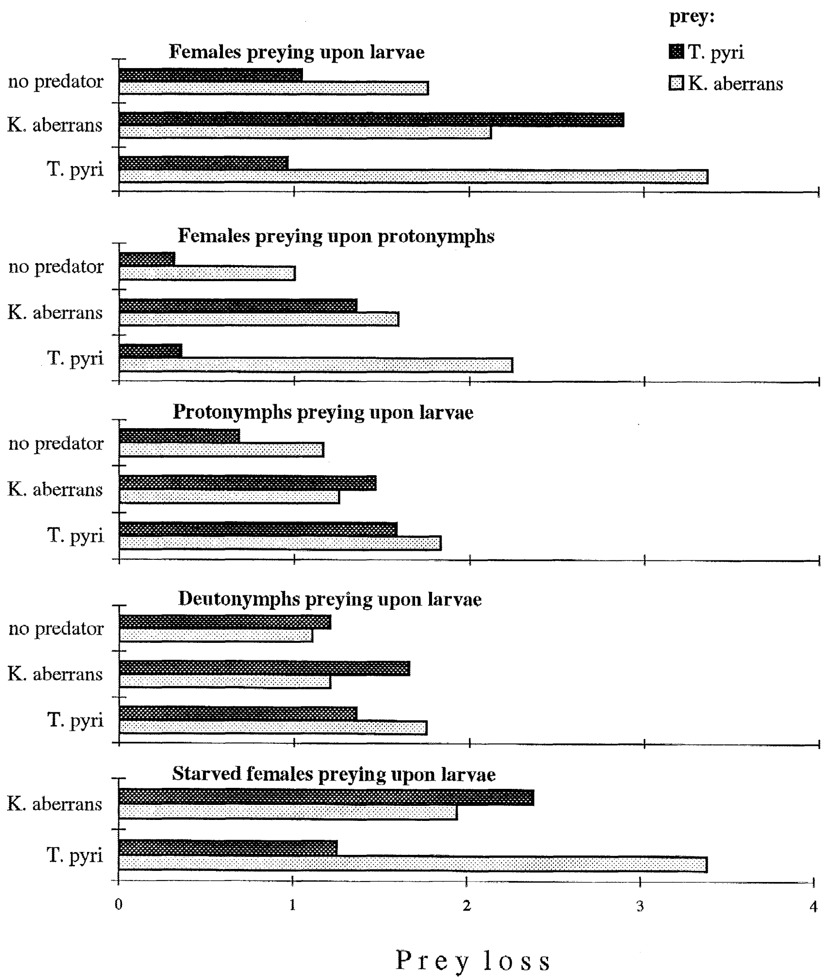

Fig. 1. Mean numbers of immature *T. pyri* and *K. aberrans* preyed upon by single females, protonymphs or deutonymphs of the two species (during 1 day) and control.

castaneum Herbst. Reciprocal predation could be a crucial mechanism in the interaction of competing polyphagous phytoseiid species.

The adult females of *T. pyri* and *K. aberrans* will not feed as much on heterospecific phytoseiids in nature as was seen in the present study, but predation on phytoseiids can greatly affect their competitive capacity, survival and reproduction at low prey levels. The preference to prey upon the immatures of heterospecific competitors over the corresponding conspecific stages might enhance the persistence of their own species. Croft and MacRae (1992b) and Schausberger (1998b) concluded from field observations and glasshouse studies, respectively, that interspecific predation was an important factor contributing to displacement of phytoseiid competitors by *T. pyri* and its persistence when other food was diminishing.

The results for proto- and deutonymphs were not clear enough to support with certainty the hypothesis that they can differentiate con- and heterospecifics. The trends followed the results obtained with the adult females, but the preference for heterospecific phytoseiid prey of proto- and deutonymphs was not distinct enough to be significant. Investigations including comparative analysis of cannibalism and interspecific predation, which could give indications on feeding preferences of immature phytoseiids, are rather scarce. Monetti and Croft (1997) found that nymphs of *Neoseiulus californicus* (McGregor) and *Neoseiulus fallacis* (Garman), two closely related species, fed significantly more on eggs of the other species and more likely reached adulthood than when feeding on eggs of their own species. In studies by Schausberger (1998a), immatures of *T. pyri* and *K. aberrans* seemed to have higher survival rates and a better chance to complete development when feeding on larvae of the other species than when cannibalizing larvae. However, more extensive choice trials and more accurate measurements of the feeding rates than presented here have to be done to elucidate the predation preferences of immature stages.

Recent comparative studies on intra- and interspecific predation of adult female phytoseiids gave rise to the hypothesis that the ability to differentiate con- and heterospecifics may be associated with the type of predation (generalist versus specialist predators). Yao and Chant (1989), who performed the first detailed studies on mutual predation between acarine predators, analysed the predation interference between *Phytoseiulus persimilis* Athias-Henriot, a highly specialized predator of tetranychid mites and *Iphiseius degenerans* (Berlese), which is more of a generalist predator. *Phytoseiulus persimilis* had similar predation rates and survival times when feeding on eggs, larvae and protonymphs of *I. degenerans* and when cannibalizing, whereas *I. degenerans* ate similar or significantly more heterospecific than conspecific immatures and had longer longevities when feeding on larvae and protonymphs of *P. persimilis* than when cannibalizing the corresponding immature stages. MacRae and Croft (1993, 1997) demonstrated adult females of *T. pyri* to have higher rates in interspecific than in intraspecific predation on eggs, larvae and protonymphs when no other prey was available, whereas *Metaseiulus occidentalis* (Nesbitt), a species with more specialized food habits than *T. pyri*, showed no significant differences in the propensity to feed on con- or heterospecifics. Croft *et al*. (1996) compared intra- and interspecific predation on various life stages of oligophagous and polyphagous phytoseiid species: the polyphagous *T. pyri* and *Amblyseius andersoni* Chant had lower or similar feeding rates on conspecific eggs, larvae or nymphs than on the corresponding heterospecific stages, whereas the oligophagous *N. fallacis* and *M. occidentalis*, depending on the stage offered, had either higher rates on immatures of their own species or on immatures of the other species. Pooling the data from the comparative studies on cannibalism and interspecific predation mentioned above, the feeding rates of the adult females indicate a distinct preference for heterospecific immatures over conspecifics in the polyphagous *T. pyri, K. aberrans, I. degenerans* and *A. andersoni*, mixed preferences in the oligophagous *M. occidentalis* and *N. fallacis* and no preference in the highly specialized *P. persimilis*. Thus, it can be hypothesized that the ability to discriminate between con- and heterospecific phytoseiids and the preference for heterospecifics over conspecifics of the adult females might be linked to the type of predation (selective versus generalist predator). The preference for preying upon heterospecifics might be the rule in generalist phytoseiids, but not in highly specialized predators like *P. persimilis*, which just may not be able to differentiate con- and heterospecific immatures.

However, detailed comparative studies between species, which are representative of different types of feeding specialization, are needed. Also, such studies could be a useful tool for the rating of phytoseiid mites in the classification system of predation types recently proposed by McMurtry and Croft (1997). The mechanisms by which phytoseiids distinguish con- or heterospecifics, whether females are able to discriminate between their own progeny and that of other conspecific females and whether polyphagous phytoseiids are able to discriminate between heterospecific phytoseiids could be major questions for exciting research areas in the future.

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