Diet of intraguild predators affects antipredator behavior in intraguild prey

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In two-predator, one-prey systems with intraguild predation and patchily distributed prey, the intraguild prey may face a choice between prey patches with and without intraguild predators. To minimize falling victim to intraguild predation, intraguild prey are expected to perceive cues specifically associated with the presence of intraguild predators. We investigate whether intraguild prey avoided intraguild predators and which cues triggered this behavior in a system composed of plant-inhabiting arthropods. We found that intraguild prey recognized intraguild predators from a distance, based on their diet: they avoided odors of intraguild predators that had consumed shared prey but did not avoid odors of intraguild predators that had fed on other diets, including a diet of conspecifics. When intraguild prey were foraging on a patch, detection of intraguild predators led to longer periods of immobility and to fewer captures of the shared prey. However, intraguild predators that were either starved or had previously consumed intraguild prey posed a higher risk to intraguild prey than did intraguild predators that had consumed the shared prey. We conclude that the cues used by intraguild prey to avoid intraguild predators are associated with the circumstances under which they encounter intraguild predators in the field and not to different degrees of danger. *Key words:* food webs, intraguild predation, predator avoidance, predator diet. *[Behav Ecol 16:364–370 (2005)]*

P redators affect prey populations not only by killing prey but also by inducing antipredator behavior (Lima, 1998; Werner and Peacor, 2003). Prey may attempt to escape from predators to avoid being killed, but this comes at the expense of other fitness-determining activities (Kotler et al., 1991; McIntosh and Peckarsky, 1999; Pallini et al., 1998; Sih and Krupa, 1996), resulting in reduced growth of prey populations. Given these costs, prey are expected to tune their antipredator behavior to the risk of being killed (Magalhães et al., 2002; Snyder and Wise, 2000; Venzon et al., 2000). Such a flexible response requires that prey are able to discriminate between predators that pose different predation risks. This may be possible when prey perceive specific cues associated with predators, which originate from the predator, the prey currently threatened by that predator (e.g., alarm pheromones), or the prey consumed previously (Brown and Dreier, 2002; Chivers et al., 1996; Cousyn et al., 2001; Kislow and Edwards, 1972; Peacor, 2003; Stabell et al., 2003; Turner et al., 1999). When predators are omnivorous, prey may avoid predators that have fed on conspecific prey, but they may lack such a response if these same predators have consumed other food sources (Persons et al., 2001; Venzon et al., 2000; Vihunen and Hirvonen, 2003).

Whereas prey responses to predators when victim and attacker represent different trophic levels are well documented, little is known of the responses of prey belonging to the same guild as their predators. When intraguild predation is not reciprocal, intraguild prey are eaten by intraguild predators, whereas both feed on a shared prey (Holt and Polis, 1997; Polis and Holt, 1992; Polis et al., 1989). To avoid predation by the intraguild predator, the intraguild prey may reduce their level

of activity, thereby becoming less conspicuous to visual hunters (Crumrine and Crowley, 2003; Okuyama, 2002; Wissinger and McGrady, 1993; Yurewicz, 2004), or move to safe sites or refuges (Finke and Denno, 2002; Moran and Hurd, 1994). Intraguild predator-prey interactions differ from bitrophic predator-prey interactions because intraguild prey and intraguild predators feed and encounter each other on patches with their shared prey. Thus, intraguild prey necessarily pay a cost of avoiding intraguild predators, because they lose opportunities to feed on the shared prey. To minimize these costs, cues triggering antipredator behavior in the intraguild prey should be specifically associated to the risk of predation posed by intraguild predators. However, investigations of these cues are still lacking. Here, we investigate the behavioral responses of intraguild prey toward their intraguild predator, and which cues elicit these responses, in a system consisting of plant-inhabiting arthropods.

Phytoseiid mites and heteropteran bugs are frequently part of the enemy complex of herbivorous arthropods in agro-ecosystems. The predatory mite *Neoseiulus cucumeris* (Oudemans) and the heteropteran bug *Orius laevigatus* (Fieber) commonly co-occur in the Mediterranean area (Castañe et al., 1999), as well as in greenhouses, where they are used as biological control agents of thrips, including the western flower thrips, *Frankliniella occidentalis* (Pergande), hereafter thrips (Chambers et al., 1993; Gillespie, 1989; Riudavets and Castañe, 1998; Scott Brown et al., 1999). *O. laevigatus* (hereafter *Orius*) feeds mainly on first and second instars of thrips larvae, but also on adults, whereas *N. cucumeris* can only feed on the first instars (Lewis, 1973). Both predators are attracted to plants with thrips (Janssen et al., 1998; Venzon et al., 1999). Hence, the two predators are likely to meet on plants with their shared prey. On those plants, *Orius* will also feed on *N. cucumeris* (Wittman and Leather, 1997). We studied the antipredator behavior of the intraguild prey, *N. cucumeris*, toward its intraguild predator, *Orius*.

A previous study showed that thrips seek refuge upon perception of odors of *Orius* that had been feeding on

conspecific thrips, but they do not respond to *Orius* that have fed on other diets (Venzon et al., 2000). This prompted the current investigation on the effect of odors associated with the diet of *Orius* on the behavior of *N. cucumeris*. First, we assessed whether *N. cucumeris* avoided odors of *Orius* that had been feeding on different diets, by means of an olfactometer. Second, we asked how diet-associated odors affected the behavior of *N. cucumeris* on a patch with thrips. Finally, we studied how the previous diet of *Orius* affected its predation rate on *N. cucumeris*, in an attempt to link antipredator behavior to predation risk.

METHODS

Stock cultures

All cultures and experiments were done at 25°C, 70% room humidity, and a 16-h light/8-h dark photoperiod. Thrips were collected from cucumber (var. Ventura RZ, Rijk Zwaan, De Lier, The Netherlands) in a commercial greenhouse near Pijnacker, The Netherlands, in May 1994 and reared in climate boxes on cucumber plants of the same variety. Twice per week, each climate box received a single cucumber plant (2–4 weeks old) grown in a herbivore-free climate room.

Neoseiulus cucumeris was reared in units consisting of a black polyvinyl chloride arena (8 × 15 cm) placed on a wet sponge in a plastic tray with water. Wet tissue was wrapped over the edges of each arena, and a glue barrier was applied on the tissue. Mites were fed a mixture of pollen of *Typha* spp and *Vicia faba* (broad bean) three times per week (Overmeer et al., 1989).

Orius were obtained from Koppert BV (The Netherlands) and reared according to a method described by Meiracker and Sabelis (1999) in plastic jars (8 × 8 × 11 cm) with two lateral holes (diameter = 4 cm) covered with fine nylon gauze. Twice per week, predators were fed eggs of the flour moth, *Ephestia kuehniella* (Zeller), and provided with bean pods as oviposition substrate and supply of moisture. Bean pods with predator eggs were collected from jars with adults and placed in a new jar with flour-moth eggs. Jars were lined with crumpled tissue to provide hiding places for the juveniles and thus reduce cannibalism (Meiracker and Sabelis, 1999).

Antipredator behavior of *N. cucumeris* toward *Orius*

A Y-tube olfactometer (Sabelis and Baan, 1983) was used to assess the response of *N. cucumeris* to odors associated with *Orius*. It consists of a Y-shaped glass tube with a similar shaped metal wire inside, running in the centre, parallel to the tube walls. The base of the tube is connected to a vacuum pump that produces an air flow from the arms (each connected to an odor source) to the base of the tube, where tested animals are introduced. The connections between the Y-tube and the odor sources were sealed with parafilm. Two anemometers were used to measure air flow in the arms of the tube, and these flows were regulated such that the wind speed in each arm was equal (approximately 0.45 m/s), ensuring that the odors formed two neatly separated fields in the basis of the Y-tube. *Neoseiulus cucumeris* were starved for 3 h before the experiment, to motivate the mites to walk upwind (Sabelis and van der Weel, 1993). To introduce a predatory mite, the vacuum pump was disconnected, a mite was placed on the metal wire, and the pump was reconnected. Observations were performed until *N. cucumeris* reached the end of one of the arms or during 5 min, after which they were removed. When five individuals made a choice, the odor sources were swapped between the arms of the Y-tube to correct for any

unforeseen asymmetry in the setup. Each replicate consisted of 20 individuals that made a choice.

To test whether *N. cucumeris* avoided plants with *Orius*, they were given a choice between plants with *Orius* and thrips and plants with thrips only. Six cucumber plants (approximately 4 weeks old) were placed in the thrip cultures during 1 week. Subsequently, the number of thrips on each plant was counted, and the plants were divided into two groups of three plants, such that each group contained approximately the same number of thrips. Each group of plants was placed in a tray (45 × 30 × 8 cm) inside a larger tray with water. A Plexiglass container (50 × 36 × 43 cm) was placed over the plants and inside the tray with water, to create an air-tight seal. The container had a gauze-covered air inlet in one wall and a similar outlet (diameter = 4 cm) in the opposite wall. Twenty-four hours before the onset of the experiment, 20 adult *Orius* were placed on one group of plants and the containers were connected to the vacuum pump to create an air flow in order to avoid condensation of water in the containers. Thus, at the beginning of the experiment, on the next day, *Orius* had been feeding on thrips during 24 h, and the two odor sources differed in the presence or absence of *Orius* as well as in the numbers of thrips on the plants. We did not replace the thrips eaten because cues emanating from newly introduced thrips could mask those emanated by thrips that had been in contact with *Orius* during 24 h.

To test whether *N. cucumeris* responded to odors emanating from *Orius*, we gave *N. cucumeris* a choice between clean air and an odor source that consisted of only *Orius* that were fed *Ephestia* eggs. A glass tube (10 cm tall × 2 cm diameter) with 20 *Orius* was connected to one of the arms of the Y-tube, and the other was connected to an identical, but empty, glass tube. Finally, the effect of the diet of *Orius* on the behavior of *N. cucumeris* was tested by giving *N. cucumeris* the choice between (1) *Orius* that had consumed either thrips or *Ephestia* eggs and (2) *Orius* that had consumed either *N. cucumeris* or *Ephestia* eggs. To obtain *Orius* that had consumed thrips and *Orius* that had consumed *N. cucumeris*, *Orius* were placed on cucumber leaves with an ample supply of each of these prey types during the 24 h preceding the experiment. To prevent escapes, cucumber leaves were floating on water-soaked cotton wool in a Petri dish (diameter = approximately 14.5 cm) covered by a lid with a hole sealed with gauze. *Orius* that had consumed *Ephestia* were collected directly from the cultures. All tubes contained a small piece of water-soaked cotton as water supply for *Orius*. Each of the odor sources consisted of 20 *Orius* that had fed on one of these diets and placed in a tube identical to the one described above. All treatments (plants with thrips versus plants with thrips and *Orius*; *Orius* that had consumed *Ephestia* versus clean air; *Orius* that had consumed thrips versus *Orius* that had been feeding on *Ephestia*; and *Orius* that had been feeding on *N. cucumeris* versus *Orius* that had consumed *Ephestia*) were replicated four times. Data were analyzed by using a replicated *G* test for the goodness of fit (Sokal and Rohlf, 1995).

N. cucumeris behavior on a patch with thrips

We tested how odors associated with the diet of *Orius* affected the behavior of *N. cucumeris* on a patch with thrips prey. One *N. cucumeris* female was placed on a cucumber leaf disc (diameter = 2.5 cm) with 10 L1-thrips larvae, which are vulnerable to predation by *N. cucumeris* (van der Hoeven and van Rijn, 1990; van Rijn et al., 2002). The leaf disc was placed inside a box receiving odors from *Orius* that had been feeding either on thrips or on *Ephestia* (obtained as described in the previous paragraph). The box (18 × 15 × 10 cm) contained two circular openings (diameter = 4 cm), covered with

mite-proof gauze, at opposite walls, one of which was connected to a glass tube with one of the odor sources, whereas the other was connected to a vacuum pump that created an air flow of approximately 0.45 m/s from the odor source to the box. The box was covered by a transparent plastic lid through which the behavioral observations on *N. cucumeris* were performed (Janssen et al., 1997). Behavior of *N. cucumeris* was recorded during 1 h by using Etholog 2.2 (Ottoni, 2000). We measured the duration of the following variables: searching (i.e., walking), resting (i.e., being immobile), cleaning (i.e., preening body or other legs with legs), and feeding on thrips (i.e., the period during which the mouthparts of *N. cucumeris* were inside the thrips). Furthermore, frequencies of encountering thrips (touching them with the front legs) and of attacking thrips (attempts to subdue them) were registered. Based on these observations, the following variables were calculated for each replicate: the time spent resting (time spent resting/observation time), encounter rate (number of encounters/observation time), success ratio (number of feeding events/number of encounters), predation rate (number of feeding events/observation time), and handling time (time spent feeding/number of feeding events). Whenever *N. cucumeris* fed on a prey item that it had attacked earlier, the time spent feeding was added to the handling time, but no encounter, attack, or feeding event was scored. The experiment was replicated 10 times for each odor source. Variables of the foraging behavior of *N. cucumeris* were compared between treatments by using a *t* test. We did not analyze differences in success ratio or in handling time because these variables were only defined in three and one replicates, respectively, in the patches in which *N. cucumeris* received odors of *Orius* that had consumed thrips (owing to low predation rates under this treatment, see Results). Encounter rates were arcsine square root transformed for the analysis, to comply with the assumptions of parametric tests (Sokal and Rohlf, 1995).

Predation by *Orius* on *N. cucumeris*

To assess how the previous diet of *Orius* affected the predation risk of *N. cucumeris*, *Orius* that either were starved or had consumed *Ephestia* eggs, *N. cucumeris*, or thrips, were offered 20 *N. cucumeris*, and their foraging behavior was observed during 1 h. Furthermore, the effect of the presence of thrips on the predation risk of *N. cucumeris* was assessed by offering 10 *N. cucumeris* and 10 thrips to *Orius* that had fed on each of these diets. The thrips used were late second instar larvae, because they are invulnerable to predation by *N. cucumeris* (van der Hoeven and van Rijn, 1990; van Rijn et al., 2002; van Maanen R, personal observation). All treatments were run with young *Orius* females. *Orius* that had consumed *Ephestia* eggs, thrips, or *N. cucumeris* were obtained in the same way as for the previous experiments. Starved *Orius* were obtained by placing *Orius* in small plastic tubes with wet cotton as water supply 24 h before the experiment. The behavior of one *Orius* female was observed during 1 h on a cucumber leaf disc (diameter = 5 cm) inside a Petri dish with water-soaked cotton wool. We recorded the same variables for *Orius* as described for *N. cucumeris* above, using Etholog (Ottoni, 2000). In addition, we scored the amount of time that *Orius* spent feeding on the leaf and the time spent feeding on *N. cucumeris* as well as the frequencies of *Orius* encountering *N. cucumeris* and attacking *N. cucumeris*. Subsequently, we calculated the same variables as for the behavior of *N. cucumeris*, for *Orius* attacking thrips and for *Orius* attacking *N. cucumeris*. Each treatment was replicated 10 times, except the treatment in which *Orius* that were fed *Ephestia* eggs were offered thrips and *N. cucumeris*, which was replicated 13 times.

We compared predation rate, encounter rate, success ratio, and handling time of *Orius* with *N. cucumeris* as prey by using a two-way ANOVA with the main effects of the previous diet of *Orius* and the presence of thrips and their interaction. When the main effect of the previous diet and/or of the presence of thrips was significant, differences were further identified by using *t* tests for the presence/absence of thrips for each diet and by using an ANOVA followed by a Bonferroni post-hoc test for replicates in presence and in absence of thrips, separately, to test for differences owing to the previous diet of *Orius*. Encounter rates and success ratios were arcsine square root transformed for the analysis, to comply with the assumptions of parametric tests.
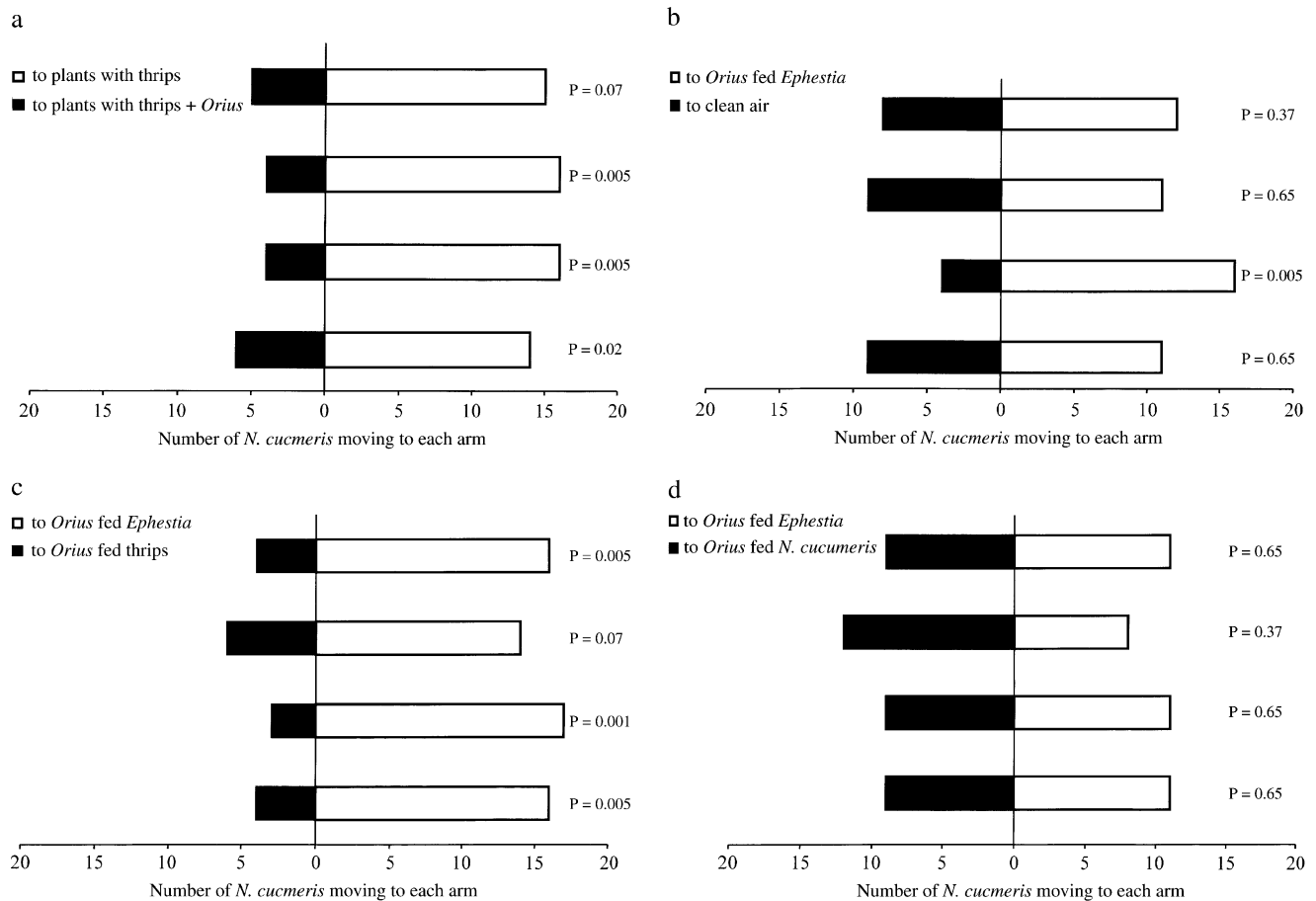
RESULTS

Antipredator behavior of *N. cucumeris* toward *Orius*

When given a choice between odors from cucumber plants with thrips with or without *Orius*, most of the *N. cucumeris* moved toward plants without *Orius* (goodness-of-fit test, $GT = 23.9$, $p < .0001$; heterogeneity among samples: $GH = 0.74$, $p = .86$; pooled effect of treatment: $GP = 23.19$, $p < .0001$) (Figure 1a). Because *Orius* had been consuming thrips during the 24 h before the experiment, plants with *Orius* contained fewer thrips than did plants without *Orius*. Hence, the preference of *N. cucumeris* could be interpreted as *N. cucumeris* being less attracted to plants with fewer thrips. However, the attraction of predatory mites to plants with prey, mediated by herbivore-induced plant volatiles (Dicke and Sabelis, 1988; Sabelis and Baan, 1983), remains after prey removal (Sabelis and Baan, 1983). Therefore, we hypothesize that *N. cucumeris* avoided odors associated with the presence of *Orius*.

To further test this hypothesis, we offered *N. cucumeris* a choice between clean air and odors of *Orius* that were collected from the culture, where they were fed eggs of the moth *Ephestia kuehniella*. *N. cucumeris* did not discriminate between these odor sources, ($GT = 8.9$, $p = .063$; $GH = 3.86$, $p = .27$; and $GP = 5.05$, $p = .08$) (Figure 1b). This shows that *N. cucumeris* do not avoid *Orius* that had been consuming *Ephestia* eggs. Next, we fed thrips to *Orius* and tested the effect of this diet on the response of *N. cucumeris*. Most of the *N. cucumeris* avoided odors of *Orius* that had consumed thrips and moved to the arm connected to *Orius* that had been feeding on *Ephestia* instead ($GT = 29.5$, $p < .0001$, with $GH = 1.38$, $p = .7$ and $GP = 28.14$, $p < .0001$) (Figure 1c). Hence, the avoidance of plants with thrips and *Orius* can, at least partly, be explained by the avoidance of *Orius* that consumed thrips. *N. cucumeris* did not discriminate between *Orius* that had been feeding on *N. cucumeris* and *Orius* that consumed *Ephestia* ($GT = 1.4$, $p = .84$, with $GH = 1.35$, $p = .72$ and $GP = 0.05$, $p = .82$) (Figure 1d). Hence, *N. cucumeris* recognized *Orius* that consumed thrips, the shared prey of *Orius* and *N. cucumeris*, but they did not recognize *Orius* that had been feeding on other diets, including *Orius* that consumed conspecifics of the predatory mites.

N. cucumeris behavior on a patch with thrips

In the next experiment, we studied whether *N. cucumeris* alters its behavior on a patch with thrips upon perception of odors associated with *Orius*. Because odors associated with *Orius* that had consumed thrips triggered avoidance in *N. cucumeris*, whereas odors associated with *Orius* that had been feeding on *Ephestia* did not, we compared the behavior of *N. cucumeris* perceiving each of these odors. *N. cucumeris* spent significantly more time resting when perceiving odors of *Orius* that had consumed thrips than when perceiving *Orius* that had fed on

Figure 1
In a Y-tube olfactometer, *N. cucumeris* were offered a choice between odors from cucumber plants with thrips and cucumber plants with thrips and *Orius* (a), *Orius* that had consumed on *Ephestia* and clean air (b), *Orius* that had consumed thrips and *Orius* that had consumed *Ephestia* (c), and *Orius* that had consumed *N. cucumeris* and *Orius* that had consumed on *Ephestia* (d). Shown are the fractions of *N. cucumeris* that chose for each of the odor sources. Each bar corresponds to one replicate (i.e., 20 individuals that made a choice). Few individuals (zero to one per replicate) did not choose one of the odor sources. *p* values of the *G* test for each replicate are given next to each bar; *p* values for each experiment are given in the text.

Ephestia (*t* test, $T_{18} = 5.008$, $p < .0001$) (Table 1). Because *Orius* is a visual hunter, this reduction of the activity level by *N. cucumeris* may reduce the risk of being detected by *Orius* (Lima, 1998; Rosenheim and Corbett, 2003). While searching, *N. cucumeris* encountered fewer thrips on patches receiving odors of *Orius* that had consumed thrips than on patches re-ceiving odors of *Orius* that had consumed *Ephestia* (*t* test, $T_{18} = 2.916$, $p = .009$) (Table 1). Moreover, the success ratio was lower on patches receiving odors of *Orius* feeding on thrips. This suggests that *N. cucumeris* became less efficient at capturing prey when perceiving odors of *Orius* that had consumed thrips. Alternatively, thrips might have become

Table 1
Foraging traits (mean ± SE) of *N. cucumeris* on a patch with thrips, receiving odors of *Orius* that had consumed either *Ephestia* eggs or thrips, and statistical analysis of differences in foraging traits of *N. cucumeris* between patches receiving different odors, using *t* tests

	Odors of *Orius* feeding on *Ephestia*	Odors of *Orius* feeding on thrips	Statistics
Time spent resting (min)	12.41 ± 3.26	39.3 ± 4.26	$t_{18} = 5.008$, $p < .0001$
Encounter rate	0.12 ± 0.12	0.04 ± 0.07	$t_{18} = 2.916$, $p = .009$
Success ratio	0.75 ± 0.18	0.33 ± 0.1	Not determined
Predation rate	1.4 ± 0.22	0.2 ± 0.2	$t_{18} = 4.02$, $p = .0008$
Handling time	823 ± 101	781	Not determined

No analysis was carried out for the success ratio and the handling time because these variables were only defined in three and one replicates, respectively, when *N. cucumeris* received odors of *Orius* that had consumed thrips. Encounter rate is the number of prey encountered per minute search time; Success ratio, the number of prey eaten per encounter; predation rate, the number of prey eaten per hour; and handling time, the total time spent handling and feeding on prey / number of prey eaten (in seconds).

Table 2

Foraging traits (mean ± SE) of *Orius* foraging on *N. cucumeris*

		Fed *Ephestia*	Fed *N. cucumeris*	Fed thrips	Starved
Predation rate	Alone	0.4 ± 0.22A	2 ± 0.33B	0.4 ± 0.27A	2.5 ± 0.17B
	In a mixture	0.33 ± 0.14A	1.8 ± 0.03B	0.3 ± 0.21A	1.8 ± 0.2B
Encounter rate	Alone	0.9 ± 0.23A	6 ± 1.57B	2.6 ± 0.69B	2.5 ± 0.16B
	In a mixture	0.73 ± 0.24A	3.6 ± 0.70B	2.2 ± 0.44B	2.6 ± 0.04B
Success ratio	Alone	0.36 ± 0.15AB	0.5 ± 0.09A	0.1 ± 0.07B	1 ± 0C
	In a mixture	0.56 ± 0.14A	0.57 ± 0.1A	0.08 ± 0.06B	0.77 ± 0.08A
Handling time	Alone	421 ± 27	711 ± 224	802 ± 142	577 ± 39
	In a mixture	423 ± 83	387 ± 79	137 ± 54	572 ± 158

Different columns correspond to *Orius* that were previously fed with different diets. Alone indicates *Orius* were offered 20 *N. cucumeris*; in a mixture, *Orius* were offered 10 *N. cucumeris* together with 10 thrips. Capital letters indicate significant differences in foraging traits of *Orius* that were fed different diets before the experiment (using a Bonferroni post-hoc test). No significant differences were found in traits measured in the presence or absence of thrips (cf. Results). Encounter rate is the number of prey encountered per minute search time; Success ratio, the number of prey eaten per encounter; predation rate, the number of prey eaten per hour; and handling time, the total time spent handling and feeding on prey / number of prey eaten (in seconds).

more alert upon perception of cues of *Orius* that had consumed conspecifics (Venzon et al., 2000). These differences resulted in a lower predation rate of *N. cucumeris* on thrips in patches receiving odors of *Orius* that had consumed thrips ($T_{18} = 4.02$, $p = .0008$) (Table 1).

Predation by *Orius* on *N. cucumeris*

The predation rate of *Orius* on *N. cucumeris* was significantly affected by the previous diet of *Orius* (two-way ANOVA, effect of diet, $F_3 = 34.33$, $p < .0001$): starved *Orius* and *Orius* that had consumed *N. cucumeris* killed more *N. cucumeris* than did *Orius* that had previously fed on *Ephestia* or on thrips (Table 2). *N. cucumeris* still ran a considerable risk of being killed by *Orius* that had consumed thrips or *Ephestia*, but this risk was lower than when *Orius* were starved or previously fed with *N. cucumeris*. The presence of thrips did not affect the predation of *Orius* on *N. cucumeris* (two-way ANOVA, effect of thrips presence, $F_1 = 2.6$, $p = .11$). The interaction term was also not significant ($F_3 = 0.78$, $p = .50$).

To further elucidate how the behavior of *Orius* was affected by the previous diet of *Orius* and by the presence of thrips, we analyzed the components of the foraging behavior of *Orius*. Encounter rates of *Orius* with *N. cucumeris* were significantly affected by the previous diet of *Orius* but not by the presence of thrips (two-way ANOVA, effect of diet, $F_3 = 19.7$, $p < .0001$; effect of thrips presence, $F_1 = 0.67$, $p = .42$). The interaction term was not significant ($F_3 = 1.12$, $p = .34$). *Orius* that had consumed *Ephestia* encountered less *N. cucumeris* than in the other treatments, which may reflect a lower searching efficiency by individuals that come directly from the cultures (Table 2). However, encounter rates with *N. cucumeris* of *Orius* that had previously consumed thrips were not lower than those of *Orius* that had fed on other diets. This suggests that the reduced activity of *N. cucumeris* perceiving odors of *Orius* that had previously consumed thrips (cf. previous section) was either not displayed here or did not result in a reduction in the encounter rate between *N. cucumeris* and *Orius*.

The previous diet of *Orius* affected the success ratio of *Orius* capturing *N. cucumeris* significantly, whereas the presence of thrips did not (two-way ANOVA, effect of diet, $F_3 = 22.83$, $p < .0001$; effect of thrips presence, $F_1 = 0.0008$, $p = .98$; interaction: $F_3 = 1.72$, $p = .17$). The success ratio was lower for *Orius* that had previously fed on thrips than in any other treatment (Table 2). This suggests that either *N. cucumeris* was more alert when *Orius* had consumed thrips than when they had fed on other diets, or *Orius* was more motivated to feed

on *N. cucumeris* when it had previously fed on the other diets or when it was starved. A combination of these two factors is also possible.

Handling times did not differ significantly depending on the previous diet of *Orius* or depending on the presence of thrips, although *Orius* tended to feed longer on *N. cucumeris* in absence of thrips than in its presence (two-way ANOVA, effect of diet, $F_3 = 0.339$, $p = .779$; effect of thrips presence, $F_1 = 0.339$, $p = .089$; interaction, $F_3 = 1.217$, $p = .315$) (Table 2).

DISCUSSION

Neoseiulus cucumeris, the intraguild prey, avoided plants with *O. laevigatus*, the intraguild predator, and with thrips, the shared prey. This avoidance was triggered by volatile cues associated with the diet of *Orius*: *N. cucumeris* avoided odors of *Orius* that had consumed thrips but not those of *Orius* that had consumed conspecific *N. cucumeris* or *Ephestia* eggs. On a patch with thrips, *N. cucumeris* reduced their activity level and captured less thrips when perceiving odors of *Orius* that had consumed thrips than when receiving odors of *Orius* that had consumed *Ephestia*. This reduced activity did not result in a lower predation risk for *N. cucumeris* on patches with *Orius*, even though *Orius* responded to the mobility of their prey. This may be because of *Orius* feeding selectively on mobile prey on the two types of patches; thus overall mortality of *N. cucumeris* remains unchanged, even though a higher proportion of *N. cucumeris* is immobile on patches receiving odors of *Orius* that had fed on thrips. Alternatively, the reduction in activity may not be an effective antipredator behavior when *Orius* occur on the same patches as *N. cucumeris*. It is also possible that the lower mobility of *N. cucumeris* reduces the perception from a distance of patches with *N. cucumeris* by *Orius*. This suggests that antipredator behavior and its consequences need to be studied at several spatial scales.

On patches with thrips, *N. cucumeris* ran a higher risk of being preyed upon by *Orius* when *Orius* was starved or had been feeding on *N. cucumeris* than when *Orius* had consumed *Ephestia* or thrips. In contrast, the predatory mite only avoided *Orius* in the olfactometer when these had been feeding on thrips, not on other diets, such as a diet of *N. cucumeris*. This seems to be at odds with the notion that prey should discriminate between dangerous and harmless predators, because the most dangerous predator would be one that has been feeding on conspecific intraguild prey. However, avoiding intraguild predators at an early stage of the interaction between

intraguild prey and predators is only possible when intraguild prey recognize intraguild predators before these feed on conspecifics, that is, while they are feeding on the shared prey. *N. cucumeris* and *Orius* are both attracted to plants with thrips (Janssen et al., 1998; Venzon et al., 1999), and hence, the two predators are expected to encounter each other on those plants. Moreover, *N. cucumeris*, *Orius*, and thrips are patchily distributed over plants (Atakan et al., 1996; Castineras et al., 1997; Higgins, 1992; Kakimoto et al., 2002). Thus, *N. cucumeris* face a choice between patches with thrips and patches with *Orius* and thrips, and they should select cues to discriminate between these two types of patches. Moreover, if *Orius* feed on *N. cucumeris* on patches with thrips, they will eat *N. cucumeris* that had been feeding on thrips. Therefore, *N. cucumeris* can also perceive those predators based on cues associated with a thrips diet. Thus, selection for the detection of specific cues associated with *Orius* that have consumed *N. cucumeris* is not expected. In this context, odors of *Orius* that feed on thrips are a reliable cue to indicate predation risk to *N. cucumeris*. Among the other cues that could betray the presence of *Orius* to *N. cucumeris* is the alarm pheromone produced by thrips. However, *N. cucumeris* use the alarm pheromone produced by second instar thrips larvae to locate patches with thrips (MacDonald et al., 2003; Teerling et al., 1993); thus, this cue can not be used to detect the presence of *Orius*. Therefore, cues associated to the diet of *Orius* seem to be the only reliable way to discriminate between profitable patches with prey and dangerous patches with prey and intraguild predators. *Ephestia* eggs are not a shared resource of *Orius* and *N. cucumeris*, which may also explain why *N. cucumeris* does not recognize *Orius* that have fed on this diet.

When all three species co-occur, *N. cucumeris* will reduce their activity level and capture few thrips as a consequence of perceiving *Orius* that have consumed thrips. On those patches, *Orius* are expected to feed mainly on thrips and less on *N. cucumeris*. Therefore, locally, the system approximates a predator-prey interaction, with *Orius* preying on thrips. Because *N. cucumeris* reduce their feeding rate on thrips (the shared prey) upon perception of *Orius*, a higher proportion of the thrips population will become unavailable to *N. cucumeris* when these co-occur with *Orius* on a patch with their shared prey. This will increase the prey density at which populations of *N. cucumeris* can persist, thereby reducing the competitive ability of *N. cucumeris* (the intraguild prey) relative to that of *Orius* (the intraguild predator; Tilman, 1989). The persistence of systems with intraguild predation hinges on intraguild prey being better competitors than intraguild predators (Holt and Polis, 1997; Polis and Holt, 1992). Therefore, the behavior of *N. cucumeris* on patches with thrips and *Orius* may decrease the local persistence of this system. However, *N. cucumeris* avoid patches with *Orius* and thrips (Figure 1, cf. a and c), and at a larger spatial scale, the distribution of these three species is expected to be affected by this behavior of *N. cucumeris*. Thus, *N. cucumeris* may escape predation by *Orius* at a metapopulation spatial scale, and this may foster the coexistence of the three species, provided that *Orius* is arrested for a sufficient amount of time on patches with thrips. Therefore, the outcome of the population dynamics in this system will depend on the relative migration rates of thrips, *N. cucumeris* and *Orius*. This suggests hitherto unexpected effects of antipredator behavior of intraguild prey toward intraguild predators on local population dynamics and on species distributions.

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