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Predators marked with chemical cues from one prey have increased attack success on another prey species

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Abstract. 1. To reduce the risk of being eaten by predators, prey alter their morphology or behaviour. This response can be tuned to the current danger if chemical or other cues associated with predators inform the prey about the risks involved.

2. It is well known that various prey species discriminate between chemical cues from predators that fed on conspecific prey and those that fed on heterospecific prey, and react stronger to the first. It is therefore expected that generalist predators are more successful in capturing a given prey species when they are contaminated with chemical cues from another prey species instead of cues from the same prey species.

3. Here, a generalist predatory mite was studied that feeds on thrips larvae as well as on whitefly eggs and crawlers. Mites were marked with cues (*i.e.* body fluids) of one of these two prey species and were subsequently offered thrips larva.

4. Predators marked with thrips cues killed significantly fewer thrips than predators marked with whitefly cues, even though the predator's tendency to attack was the same. In addition, more thrips larvae sought refuge in the presence of a predatory mite marked with thrips cues instead of whitefly cues.

5. This suggests that generalist predators may experience improved attack success when switching prey species.

Key words. *Amblyseius swirskii*, anti-predator behaviour, chemical cues, predation rate, predator–prey interactions.

Introduction

Many prey species respond to chemical cues associated with the presence of predators by exhibiting anti-predator behaviour such as fleeing, hiding, remaining motionless or aggregating (reviewed by Lima & Dill, 1990; Chivers & Smith, 1998; Kats & Dill, 1998; Dicke & Grostal, 2001; Paterson *et al.*, 2013). Because predators differ in foraging behaviour and in the risk they impose, prey are expected to tune their anti-predator behaviour by discriminating between predator species and the associated risk (Sih, 1987; Lima & Dill, 1990; Chivers & Smith, 1998; Venzon *et al.*, 2000; Persons *et al.*, 2001). One of the

ways in which prey can obtain information on predation risk is to use cues from the prey eaten by a predator (Venzon *et al.*, 2000; Persons *et al.*, 2001). In many aquatic systems, for example, prey can distinguish chemical cues from predators that fed on conspecific prey from those of predators that fed on heterospecific prey, and react stronger to the first (Wilson & Lefcort, 1993; Chivers *et al.*, 1996; Laurila *et al.*, 1997). The suggested reason for this is that prey experience more risk from predators that have recently fed on conspecifics of the prey than from predators that have fed on prey of other species. In terrestrial systems there is an increasing number of examples of prey responding differentially to cues associated with predators that fed on conspecific prey or on other prey (Venzon *et al.*, 2000; Persons *et al.*, 2001; Li & Jackson, 2005; Sullivan *et al.*, 2005; Meng *et al.*, 2006; Hoefler *et al.*, 2012).

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If cues associated with the diet of predators induce efficient anti-predator behaviour in prey, there is likely to be selection for predators that do not release such cues (Sutrisno *et al.*, 2014). So far, three papers independently proposed the idea that if diet-related chemical cues enable prey to discriminate between harmless and dangerous predators, predators may 'chemically disguise' themselves by eating other prey species (Venzon *et al.*, 2000; Lima *et al.*, 2003; Stabell *et al.*, 2003). This would result in reduced anti-predator behaviour and, consequently, increased predation success. In this study, it was investigated whether generalist predators do indeed have increased success in seizing a prey when they are marked with cues of another species of prey.

The experimental system consisted of the generalist predatory mite *Amblyseius swirskii* Athias-Henriot (Acari: Phytoseiidae) (adult diameter ~0.5 mm) and two of its prey species; first-instar larvae of the western flower thrips *Frankliniella occidentalis* (Pergande) and first-instar larvae (crawlers) and eggs of the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) (Nomikou *et al.*, 2001; Messelink *et al.*, 2008). Earlier experiments showed that juvenile survival and the developmental rate of *A. swirskii* were highest on a mixed diet of thrips and whiteflies, intermediate on a diet of thrips larvae, and lowest on a diet of whitefly eggs (Messelink *et al.*, 2008). Therefore, thrips are considered a prey of higher quality for juvenile development than whiteflies.

Whitefly eggs and crawlers (the first instar of whiteflies) are c. 0.25 mm in diameter, and are not known to exhibit anti-predator behaviour or to use protective structures to decrease predation. By contrast, first-instar thrips (up to 0.75 mm long) are able to defend themselves in various ways, for example, by counter-attacking vulnerable stages of the predator (Janssen *et al.*, 2002), and by swinging their abdomen at the attacking predator (Bakker & Sabelis, 1987, 1989), which is sometimes accompanied by the anal secretion of a droplet that may contain an alarm pheromone (Teerling *et al.*, 1993a,b; de Bruijn *et al.*, 2006). In addition, thrips larvae respond to cues associated with predation by seeking refuge in the web produced by spider mites (*Tetranychus urticae* Koch) (Pallini *et al.*, 1998; Venzon *et al.*, 2000), another herbivore species, often found on the same plants as thrips. This reduces the predation risk of the thrips larvae because the predators of the larvae have difficulties in penetrating this web (Pallini *et al.*, 1998; Venzon *et al.*, 2000). This refuge-seeking is affected by the diet of the predator (Venzon *et al.*, 2000).

We used this experimental system to test whether predatory mites marked with cues of thrips larvae had lower predation success on thrips larvae than predators marked with cues of whitefly crawlers. Such decreased predation success might be due to changes in the foraging behaviour of the predator and changes in anti-predator behaviour of the prey. A second experiment was therefore performed in which one type of anti-predator behaviour of thrips larvae was quantified, i.e. the refuge-seeking in the web of spider mites (Pallini *et al.*, 1998). It was expected that more thrips would hide in the refuge in the presence of a mite marked with cues of thrips larvae instead of cues of whitefly crawlers.

Materials and methods

Cultures

Cucumber plants (*Cucumis sativus* L. var. Aviance Z, Rijk Zwaan, De Lier, the Netherlands) were grown from seeds in herbivore-free walk-in climate rooms (25 °C, 60% RH, LD 16:8 h). Western flower thrips and spider mites were both collected from cucumber plants in a commercial greenhouse in May 1994 and since then have been maintained in our laboratory. The thrips stock was mixed with individuals that originated from chrysanthemum in experimental greenhouses of Wageningen UR Greenhouse Horticulture (Naaldwijk, the Netherlands) 3 weeks before the experiments started. Spider mites, thrips, and whiteflies were reared on cucumber plants in separate climate rooms (25 °C, 60% RH, LD 16:8 h). Whitefly crawlers were supplied by Koppert BV (Berkel en Rodenrijs, the Netherlands) on tobacco leaves. Predatory mites were reared on plastic arenas (8 × 15 cm²) that were placed on top of a wet sponge in a plastic tray filled with water (Nomikou *et al.*, 2003). The edges of the arenas were covered with tissue paper that extended to the water in the tray. In this way, the tissue served both as a barrier and as a water source. Cultures were kept in a walk-in climate room (25 °C, 60% RH, LD 16:8 h) and were supplied twice a week with ample cattail pollen (*Typha latifolia*), a food source on which the predators can develop and reproduce (Nomikou *et al.*, 2003). Small pieces of cotton wool were provided as oviposition substrates. Twice a week, cotton wool pieces with predatory mite eggs were transferred to a clean plastic arena. This ensured a steady supply of adult mites that were of the same age.

Marking of the predators

Under natural conditions, predators differing in previous diet will usually have different satiation levels, which can result in differences in their motivation to attack prey as well as different prey preference (Sabelis, 1986, 1990). All mites were therefore reared on the same diet (cattail pollen), thus avoiding differences in motivation and preference, and were subsequently marked with prey cues to mimic cues of a previous diet. To obtain marked adult predators or deutonymphs (the stage preceding adulthood), predator larvae were transferred, each to a separate leaf disc (24 mm diameter), and were allowed to develop. Subsequently, the predators were labelled with cues of whitefly crawlers, cues of thrips larvae or water. This marking was done as follows: a whitefly crawler or thrips larva was killed with the aid of a fine insect pin and the dorsum of the predatory mite was touched with this needle directly afterwards. Because the needle was sticky due to contamination with body fluids of the prey, the mite stuck to the needle and could be lifted from its leaf disc. Upon touching the experimental leaf disc, the mite grabbed the leaf and pulled itself off the needle. This resulted in a tiny, hardly visible mark (40× magnification), which was too small to quantify with a Sartorius supermicrobalance ($d = 0.0001$ mg), which is used to weigh mites (Sabelis, 1990; van Rijn *et al.*, 2005). In roughly half of the cases, thrips larvae produced an anal droplet just before being killed, and such droplets contain

alarm pheromone in *c.* 70% of the cases (P. J. A. de Bruijn, pers. comm.). The mark will therefore have contained alarm pheromones in around a third of the cases. As there are no known chemical senses on the dorsum (Chant, 1985), and predators cannot reach the dorsum with their legs to clean, predators do not try to remove the mark. We have frequently observed that the dorsum of predators became contaminated with the alarm pheromone of thrips when attempting to attack them (A. Janssen, pers. obs.). The same marking procedure was followed for the control, where the needle was not used to kill a prey, but dipped in water.

Predation of whitefly eggs

Because the mark as applied above could hinder the predators, the predation rates of predators with and without such a mark were compared on immobile prey (whitefly eggs). These prey cannot respond to the cues present on the predator's dorsum, and thus any reduction of foraging efficiency of predators with the mark relative to unmarked predators would point to effects of the presence of the mark on predator behaviour. To obtain whitefly eggs, adult female whiteflies were confined overnight in clip cages on cucumber leaves. Subsequently, leaf discs (24 mm diameter) were punched from the area that had been enclosed inside the clip cage, resulting in leaf discs containing between 20 and 70 whitefly eggs. Earlier experiments showed that adult predatory mites consume *c.* 12 whitefly eggs per 24 h (Messelink *et al.*, 2008), hence, ample numbers of prey were provided. The leaf discs were placed on wet cotton wool inside Petri dishes. Each Petri dish contained four leaf discs. In one treatment, predatory mites were marked with thrips cues as described earlier, and in the other treatment, they were marked with water as a control for the handling of the predator. Thirty-six predators were tested per treatment. All predators tested were 7 days old (post-hatching) and had a similar satiation level. After 24 h, the remaining whitefly eggs were counted. Leaf discs with whitefly eggs but without predatory mite served as a control for mortality of whitefly eggs by factors other than predation. Mean predation was compared between the two treatments and analysed using a generalised linear model (GLM) with a quasi-Poisson error distribution (R Development Core Team, 2013).

Predation of thrips larvae

Predators of the deutonymph stage, marked with thrips or whitefly cues or with water, were introduced as described earlier, each on a separate cucumber leaf disc (24 mm) with one late first-instar thrips larva (5 days post-hatching). Deutonymphs were used because they are more affected by abdominal swings of the thrips larvae than adults (R. van Maanen, pers. obs.). After 24 h, the thrips larva was scored according to whether or not it was preyed as judged by the presence of body remains. A few replicates where the thrips larva was lost, drowned, or dead but not preyed upon were excluded from the analyses, resulting in 48, 49, and 42 predatory mites that were tested with a thrips mark, a whitefly mark, and a water mark, respectively, on five different days. The proportion of thrips larvae preyed

after 24 h was compared with a generalised linear model with a binomial error distribution. Differences among treatments were assessed by stepwise model simplification through aggregation of non-significant factor levels (Crawley, 2007).

Refuge-seeking of thrips larvae

To quantify refuge-seeking as a type of anti-predator behaviour of thrips larvae in response to predators labelled with prey of different species, larvae were offered a refuge consisting of spider mite web. In the presence of predators or their cues, thrips larvae hide inside this web, which serves as a partial refuge from predators (Pallini *et al.*, 1998; Venzon *et al.*, 2000). This anti-predator behaviour is easier to interpret than other types of anti-predator behaviour of thrips larvae, such as abdominal swings with the associated production of anal droplets, which serve not only as defence, but also for communication with other thrips larvae (P. J. A. de Bruijn, pers. comm.). Discs (24 mm) were punched out of cucumber leaves in such a way that the main vein divided each disc into two halves. These leaf discs were placed on wet cotton wool in a Petri dish. A wet thread of cotton wool was placed on top of the vein to confine mites to one side of the leaf disc (Pallini *et al.*, 1998). Thirty adult spider mites were obtained from the culture and added to one half of the leaf disc, where they were allowed to feed and produce web. The spider mites did not cross the wet cotton wool; thus, half of each leaf disc became damaged and covered with web by the spider mites. After 2 days, the spider mites and the cotton wool were carefully removed using a thin insect pin, leaving the disc with spider mite eggs, faeces and a thin layer of web on the leaf surface (Pallini *et al.*, 1998). In this experiment, adult female predatory mites were used because their predation rate is three times higher than that of deutonymphs (R. van Maanen, pers. obs.). All mites were 7 days old (post-hatching) and of the same satiation level. Mites were marked with whitefly ($N = 27$) or thrips cues ($N = 31$) and introduced as described earlier, each on a separate cucumber leaf disc with one-half covered with spider mite web and one late first-instar thrips on the other half of the leaf disc. In the control ($N = 9$), no predator was added to the leaf disc to verify whether or not refuge-seeking was induced by predator cues. The experiment was carried out on six different days.

The position and predation of the thrips larvae were scored after 25 h. The proportion of thrips larvae found in the web and the proportion of dead thrips larvae were analysed with a generalised linear model with binomially distributed errors (R Development Core Team, 2013). Differences among treatments were assessed as described earlier.

Results

Predation of whitefly eggs

The average number of whitefly eggs eaten by mites marked with thrips was 7.8 (SE = 0.94) in 24 h and the average number eaten by mites marked with water was 9.6 (SE = 0.78) in 24 h; the difference was not significant (GLM with quasi-binomial

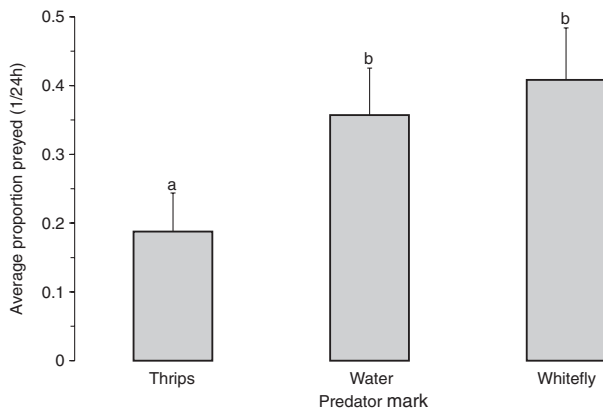


Fig. 1. The mean proportion (+SE) of thrips killed through time by deutonymph predators marked with cues from thrips, whiteflies, or water. Different letters indicate significant differences among treatments.

error distribution, $F_{1,71} = 2.0$, $P = 0.16$). This suggests that the mark did not significantly hinder the mites in their predation behaviour. No mortality of whitefly eggs was observed in the treatment without predators.

Predation of thrips larvae

Predation of thrips larvae by juvenile predatory mites in the absence of a refuge was significantly affected by the prey cues on the dorsum of the mites (Fig. 1; deviance = 6.20, d.f. = 2, $P = 0.045$). There were no significant differences among replicates carried out on different days (deviance = 7.45, d.f. = 4, $P = 0.11$). Twice as many mites marked with whitefly cues or with water consumed the thrips larva as mites marked with thrips cues (Fig. 1). Predatory mites did not spend time attempting to clean themselves when prey cues were applied on the dorsum.

Refuge-seeking of thrips larvae

Overall, there was a significant effect of treatment on the proportion of thrips in the refuge (Fig. 2; GLM with binomial distributed errors, deviance = 12.8, d.f. = 2,64, $P = 0.0017$). Significantly more thrips were found in the web when predators were marked with thrips than when predators were marked with whitefly. No thrips were found in the web in the absence of predators. These results show that thrips responded more strongly to cues associated with predators that had fed on conspecific prey than to cues from predators that had fed on other prey.

There was a significant effect of treatment on the mortality of thrips larvae (Fig. 3; GLM with binomial distributed errors, deviance = 7.21, d.f. = 2,64, $P = 0.027$). Mortality in the control (without predators) was lowest and highest in experiments with predators that had a whitefly mark. Overall, 33.3% of the thrips larvae in the web were killed and 59.5% of the larvae outside the web; the difference was almost significant (GLM

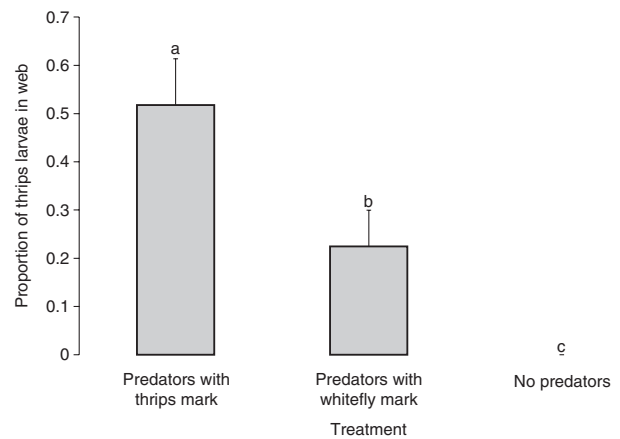


Fig. 2. The mean proportion (+SE) of thrips larvae (dead or alive) found in the spider mite web (refuge) after 24 h in the presence of predatory mites that were marked with cues from either thrips or whiteflies and in the absence of predatory mites (control). Different letters indicate significant differences among treatments.

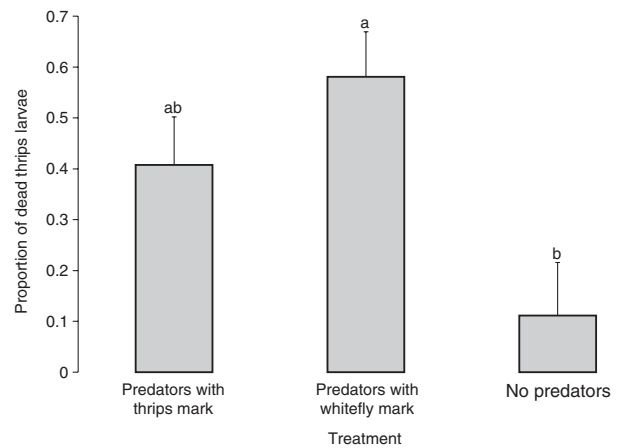


Fig. 3. The mean proportion (+SE) of dead thrips larvae after 24 h in the presence of a refuge (spider mite web) and predatory mites that were marked with cues from either thrips or whiteflies, and in the absence of predatory mites (control). Different letters indicate significant differences among treatments.

with binomial distributed errors, deviance = 3.71, d.f. = 1, $P = 0.054$).

Discussion

Predatory mites marked with thrips cues killed significantly fewer thrips larvae than unmarked predators or predators marked with whitefly cues (Fig. 1). In addition, it is shown that more thrips sought refuge in the presence of a predatory mite marked with thrips cues than one marked with whitefly cues (Fig. 2). The predatory mites under test were shown not to be hindered by the mark and were all of similar age and similar satiation level. Hence, the lower predation by predators marked with

thrips was due to a response of the thrips larvae, not to differences in the motivation to attack thrips among predators with different treatments. Thrips larvae that were exposed to predators marked with thrips cues moved into a refuge twice as often as thrips larvae exposed to a predator marked with whitefly cues. These results show that thrips larvae tried to escape from predation more often from predators with cues of conspecifics of the prey than from predators with cues of heterospecific prey.

Our data showed a marginally significant effect of refuge use on predation risk. Because the thrips larvae could choose whether to be inside or outside the web, it is possible that thrips larvae would choose to be outside the web when their predation risk was lower, and inside the web when the predation risk was higher. In other words, the refuge use of the thrips is correlated with predation risk. Experiments where thrips larvae were either confined inside or outside refuges have been reported elsewhere (Pallini *et al.*, 1998; Venzon *et al.*, 2000), showing a significant effect of refuges on predation rate.

In order to rule out the effects of predator diets on subsequent foraging behaviour, we chose to experimentally mark the predators with the body fluids of prey. Research on other systems has shown that cues emitted by damaged or crushed prey evoked less strong anti-predator behaviour than cues emanating from predators that consumed prey (Nilsson & Bengtsson, 2004; Schoeppner & Relyea, 2009). If this also holds in our system, then it implies that the differences in predation rate may be larger when the predators had been allowed to become marked in the process of feeding on different prey species.

In our experimental system, the marks of thrips and whiteflies may not have differed solely in composition but also in quantity. However, it was impossible to quantify marks as they were not visible with a 40× magnifying binocular and the mass of the mark could not be detected with a sensitive microbalance.

Thrips could also have expressed other types of anti-predator behaviour, such as swinging their abdomen (Bakker & Sabelis, 1987, 1989; Teerling *et al.*, 1993a,b) and producing droplets. When contaminated with these droplets, predators often stop attacking the thrips larva and start cleaning themselves (Bakker & Sabelis, 1989). It is not known whether these types of anti-predator behaviour contributed to reducing predation. Furthermore, when thrips larvae were killed with a needle to mark the predators, thrips might have produced an anal droplet containing an alarm pheromone. Therefore, predators marked with thrips might also have been contaminated with the thrips alarm pheromone. de Bruijn *et al.* (2006) showed that the alarm pheromone of thrips increased the vigilance of conspecific thrips. However, not all thrips larvae produced an anal droplet, and not all droplets actually contained the alarm pheromone (P. J. A. de Bruijn, pers. comm.); hence, the main result found here is predominantly due to other cues. It would be interesting to assess whether such increased vigilance promotes survival of the thrips.

Classical models of optimal diet choice (Charnov, 1976; Stephens & Krebs, 1986) consider the choice of a predator when it encounters prey of high and low quality on the same patch,

and predict that a predator should always accept the superior prey type, but should also accept inferior prey when encounter rates with the superior prey fall below a certain threshold. Lima *et al.* (2003) incorporated anti-predator vigilance into such a classical model, assuming that the vigilance of prey increases with the number of conspecific prey being attacked by the predator. They predict that anti-predator behaviour of the prey causes predators to select a more generalised diet than one might predict from classical theory on optimal prey choice. For one thing, this is caused by the predators experiencing a lower attack rate on the superior prey because of the increased vigilance, but in addition, the predators can manipulate the anti-predator behaviour of the superior prey by feeding on the inferior prey, because this may reduce the vigilance of the superior prey. Lima *et al.* (2003) suggest that predators will often benefit from 'managing' the anti-predator responses of the prey. This scenario closely resembles our idea that predators may feed on inferior prey in order to chemically disguise themselves, thus preventing strong anti-predator behaviour in the superior prey.

However, if generalist predators feed on several prey species in order to reduce anti-predator behaviour, this would result in selection on prey individuals to use other, more reliable cues associated with predators. There would also be selection for prey to use the cues originating from the consumption of other, coexisting prey species as indicators of threat. Although prey often exhibit the strongest anti-predator behaviour when the predator consumes only conspecific prey (Wilson & Lefcort, 1993; Schoeppner & Relyea, 2005), several studies have found that prey also responded to predators that had consumed heterospecific prey (Smith, 1992; Mirza & Chivers, 2001; Pollock *et al.*, 2003; Sullivan *et al.*, 2005; Turner, 2008; see Ferrari *et al.*, 2010 for review).

Our results suggest that generalist predators can reach higher predation rates on one prey species when feeding on a mixture of prey species. It is possible that generalist predators have an as yet overlooked advantage of eating different prey species: defensive prey are less easily alerted when predators switch between prey species. Predators could achieve this passively, by attacking mixtures of prey as they are encountered, or actively, by switching between prey species. Other reasons for switching are low encounter rates with high-quality prey (Charnov, 1976; Stephens & Krebs, 1986), and an increased performance on mixed diets (Waldbauer & Friedman, 1991; Messelink *et al.*, 2008). Clearly, these explanations are not mutually exclusive.

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