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Distribution and oviposition site selection by predatory mites in the presence of intraguild predators

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Abstract When intraguild prey and intraguild predators feed and reproduce in the same habitat and relatively immobile juveniles are the vulnerable stage, predation risk depends on oviposition site selection by the adult females. We studied how the availability of oviposition sites affected the distribution of two predatory mite species, *Neoseiulus cucumeris* (Oudemans) and *Iphiseius degenerans* (Berlese), over two patches that both contained food. The two plant-inhabiting species feed on pollen and thrips, prey on each other's juveniles, and prefer to oviposit on hairy parts of the leaf. When an artificial oviposition site was provided on one of two connected patches, both predator species strongly preferred this patch. Whereas the distributions of adults and eggs of *N. cucumeris* over the two patches were not affected by the presence of heterospecifics, the proportions of adults and eggs of *I. degenerans* on the patch with an oviposition site were reduced by the presence of *N. cucumeris*. A similar change in distribution was induced by cues of *N. cucumeris* on the oviposition site, without these mites being present. Hence, intraguild prey can weaken the strength of intraguild predation through patch selection, which in turn may promote coexistence of the two predator species.

Keywords Competition · Distribution · Intraguild predation · Oviposition site selection · Predator avoidance · Phytoseiid mites · *Iphiseius degenerans* · *Neoseiulus cucumeris* · Oviposition · Foraging

Maurice Sabelis—Deceased.

This paper is dedicated to Maurice Sabelis, who sadly passed away before it was submitted.

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Introduction

Animals are expected to distribute themselves over patches by balancing the availability of resources against the number of competitors and the risk of predation on these sites (Janssen et al. 1995; Grostal and Dicke 1999; Adler et al. 2001; Choh and Takabayashi 2007). When females feed and reproduce on the same patch, the distribution of animals can also be affected by the availability of oviposition sites and the predation risk of offspring at these sites (Ward 1987; Resetarits and Wilbur 1989; Nomikou et al. 2003; Rieger et al. 2004). To reduce predation risk for offspring, females can oviposit in places where their offspring are relatively protected against predation (Bentley and Day 1989; Bernays and Chapman 1994; Schoonhoven et al. 1998; Lucas and Brodeur 1999; Faraji et al. 2002a; Reich and Downes 2003). For example, females of the predatory mite *Iphiseius degenerans* (Berlese) can feed on pollen and larvae of the western flower thrips (*Frankliniella occidentalis* Pergande) in flowers on sweet pepper plants, but instead of ovipositing in the flowers, they prefer to deposit eggs in tufts of leaf hairs without food, where the eggs do not suffer from counterattacks by the thrips larvae (Faraji et al. 2002a).

In this study, we compared the distribution and oviposition site selection of the predatory mites *I. degenerans* and *Neoseiulus cucumeris* (Oudemans) in response to the presence or absence of the other species and of structures used for oviposition. The two mite species co-occur in the Mediterranean area (de Moraes et al. 2004), both feed on pollen and western flower thrips (van Rijn and Tanigoshi 1999) and they are reciprocal intraguild predators, with older, larger stages feeding on the juveniles of the other species (Montserrat et al. 2012). The few theoretical studies on reciprocal intraguild predation predict that possibilities for coexistence of such predators are limited (HilleRisLambers and Dieckmann 2003; Schellekens and van Kooten 2012), and experiments have shown that the two species studied here cannot invade each other's' populations at high densities (Montserrat et al. 2008, 2012).

Due to the life-history characteristics outlined above, the offspring of these two species would inevitably be exposed to the risk of intraguild predation in mixed populations. The *per capita* attack rate of adult *I. degenerans* on juvenile *N. cucumeris* is much higher than that of adult *N. cucumeris* on juvenile *I. degenerans* (Montserrat et al. 2006), suggesting that *I. degenerans* is a stronger intraguild predator than *N. cucumeris*. We have recently reported that adult female *I. degenerans* increase predation on juvenile *N. cucumeris* after having experienced predation on conspecific juveniles by adult females of the other species during juvenile and adult stages (Choh et al. 2012, 2014). Previous studies have shown that the two mite species avoided patches on which the other species had been present (van der Hammen et al. 2010), and that *N. cucumeris* avoided patches with cues of *I. degenerans* (Choh et al. 2010). Because both species also oviposit less on patches with heterospecific cues, this avoidance is likely to reduce the strength of intraguild predation. In addition, tufts of leaf hairs function as refuges, and reduce reciprocal intraguild predation between the two predator species on sweet pepper plants (Ferreira et al. 2011). However, the risk of predation for vulnerable juveniles will depend on where eggs are laid and hatch and female predatory mites may select sites for oviposition within their habitat that reduce intraguild predation on their offspring. To study this, we examined effects of the presence of one predator species on distribution and oviposition site selection by the other predator species when one of two patches contained potential places for oviposition. Because both patches contained ample amounts of food, the mites were expected to distribute themselves equally over the two patches if food availability were the most important determinant of their

distribution (van der Hammen et al. 2012), but based on the availability of a place to oviposit, higher densities were expected on the patch with oviposition sites. Furthermore, we tested how one species affected the distribution and the oviposition of the other species, focusing on cues left on oviposition sites by the former species. Based on these results, we discuss interactions between and coexistence of the two predator species mediated by the distribution of eggs.

Materials and methods

Mite cultures and experimental conditions

The origin of the strains of *I. degenerans* and *N. cucumeris* and the rearing methods are described in van Rijn and Tanigoshi (1999). In short, both species were reared on plastic arenas placed on top of sponges in water-containing trays. The edges of the arenas were covered with tissue paper that was in contact with the water, thus serving both as barrier and water source. The culture methods of the two predator species were different for historical reasons (i.e., different people had started the cultures). Twice per week, cultures of *I. degenerans* were provided birch pollen (*Betula pubescens* Ehrh.) as food and those of *N. cucumeris* received *Typha* sp. pollen as food (van Rijn and Tanigoshi 1999). In the cultures of both *I. degenerans* and *N. cucumeris*, small pieces of polyester thread (3 cm) were supplied as places for oviposition. All females used in the experiments were 10–14 days old since the egg stage and had no experience with heterospecifics. Because the predators came from a large, well-mixed population, the female mites were expected to have already mated. Experiments were carried out in a climate room at 25 ± 1 °C, 16:8 h L:D and 60 ± 5 % RH.

Experimental set-up

Plastic sheets were placed on top of sponges in water-containing trays, and two acrylic plates (15 × 8 cm) were put next to each other on top of these plastic sheets. The edges of the plates were covered with tissue paper that was in contact with the water in the tray, thus serving both as barrier and water source. To complete the experimental arena, the two plates were interconnected with yellow plastic tape (2 cm length, 3 cm width) that served as a bridge, allowing the mites to cross from one patch to the other (Fig. 1). Ample amounts of *Typha* sp. pollen were placed at the centre of each patch as a food source; most of the pollen was still present at the end of experiments. The two mite species can feed and reproduce on this pollen (Montserrat et al. 2008, 2012; van der Hammen et al. 2012). Although cannibalism occurs in both species, the frequency of cannibalism is low in the presence of pollen (Montserrat et al. 2008, 2012). We placed 75 adult female *I. degenerans* or 150 adult female *N. cucumeris* on the bridge one at a time, with a fine paint brush. These numbers are high, but not exceptionally so. For example, populations of *I. degenerans* on *Ricinus communis* L. plants easily reach densities of several hundred adult females per leaf (A. Janssen, pers. obs.). The size of *I. degenerans* is 0.55 ± 0.003 mm in length and 0.36 ± 0.002 mm in width (Vantornhout 2006). The size of *N. cucumeris* is reported to be similar to *Neoseiulus communis* (Hughes), which is 0.43–0.44 mm long and 0.24–0.25 mm wide (Denmark and Edland 2002). The numbers introduced were higher for *N. cucumeris* than for *I. degenerans* because individuals of the former species are smaller and less

Fig. 1 Experimental set-up, consisting of two patches (15 × 8 cm) and a bridge (2 cm long, 3 cm wide). The edges were covered with water-saturated tissue that served as barrier and water source for predatory mites. Ample amounts of pollen were placed at the centre of *each* patch. Threads served as oviposition sites and their number was manipulated as described in the methods. Mites were released on the bridge and the distribution was monitored after 10 min and 2, 4, 6, 24, 26, 28, 30, 48 h

voracious predators, and because we wished to make our results comparable to those obtained by van der Hammen et al. (2012). 10 min after their introduction, almost all mites were found on the two patches, and from 6 h after the start of the experiment onwards, we found few mites of both species on the bridge. The mites still on the bridge, especially at the beginning of experiments, were assigned to the patch that was closest.

To avoid disturbing the mites, the entire set-up was photographed after 10 min. and 2, 4, 6, 24, 26, 28, 30, and 48 h (Sony Cyber-shot DSC-W15, 5.1 Mega pixels, Japan) and the mites on each patch were counted from the photographs (Choh et al. 2010; van der Hammen et al. 2012). By examining the distributions of mites at the same intervals as in previous studies on the same experimental system (Choh et al. 2010; van der Hammen et al. 2012), we were able to compare the results. Because eggs were not clearly visible on these photos, they were counted only at the end of the experiment, 48 h after the introduction of the mites, under a microscope (magnification 10x). The eggs of *I. degenerans* are larger and have a darker colour than those of *N. cucumeris* (van der Hammen et al. 2010).

To test the effects of the presence of a place for oviposition on the distribution of adult female *N. cucumeris* and *I. degenerans*, a piece of polyester sewing thread (3 cm) was placed at a distance of 2 cm from the edge of one patch, on the side opposite the bridge. Females of both mite species lay their eggs on such threads (A. Janssen, pers. obs., van Rijn and Tanigoshi 1999). The threads for oviposition provided space for many more eggs than were laid in our experiments. Hence, competition for oviposition sites was unlikely during the experiments. To find the thread, it would be necessary for the mites to walk around on the experimental arena.

Distribution of single populations

The arenas described above were used to test how the availability of a place to oviposit affected the distribution of populations of each mite species (75 adult females of *I. degenerans* or 150 adult females of *N. cucumeris*) separately. We examined their distributions between patches with and without a thread in the absence of the other species at the time points described above. There were 10 replicates using different individual mites for each experiment to avoid pseudo-replication. The distribution of each of the two predator species over the two patches through time was compared using a linear mixed effects model (lme) with replicate as random factor to correct for temporal pseudo-replication and

$\sqrt{(N + 1)}$ numbers of mites as the dependent variable (Crawley 2007; library nlme of R, R Developmental Core Team 2010). For ease of comparison, we present the data in the figures as proportions rather than numbers. Although both predator species strongly preferred ovipositing on patches with a thread (see “Results” section), eggs were also found on patches without a thread. Hence, the distribution of the eggs over the two patches was compared with a GLM with quasi-Poisson error distributions (Crawley 2007). Owing to time and space limitations, not all replicates of all experiments could be carried out at the same time. Replicates were therefore done in blocks through time, with 2–5 replicates within each block.

Distribution of mixed populations

We furthermore tested whether the presence of one species affected the distribution of the other species under the same conditions as above. Hence, we released 75 adult female *I. degenerans* and 150 adult female *N. cucumeris* on the bridge. The order in which the two species were released was reversed in every replicate, and the interval between releasing the two species was c. 5 min. As a control for the effect of the presence of a place to oviposit, we examined the distributions of the two mite species when both patches were provided with a thread. The distributions of mites and eggs were measured as described above and each experiment was replicated ten times. The distribution of each of the two predator species over the two patches through time was compared as above. Furthermore, we compared the distribution of single populations of each species with that in the mixed populations to test whether the presence of one species affected the distributions of the other species. Because the proportion of mites on one of the patches is closely correlated to that on the other patch, we calculated the proportion of predators on the patch without a thread for each time step. Subsequently, we compared these proportions through time between the single and mixed populations by means of an lme with replicate as random factor and the arcsine($\sqrt{y}$) proportion of mites as the dependent variable. We furthermore tested for differences in egg distribution among treatments with a GLM with a quasi-binomial error distribution, followed by a posteriori contrasts through model simplification (Crawley 2007). Replicates were done in blocks as above, partially overlapping with blocks of the experiment with single populations.

Effect of heterospecific cues on the distribution of *Iphiseius degenerans*

The above experiments showed that the distributions of adult mites and their eggs were affected by the presence of heterospecifics in the case of *I. degenerans*, but not of *N. cucumeris* (see “Results” section). To further examine whether this was caused by the higher density of mites in total, we subsequently studied the distribution of adults and eggs of *I. degenerans* in response to cues of *N. cucumeris* in the absence of individuals of this species. We offered 75 adult females of *I. degenerans* two types of arenas; one arena consisted of a patch without a thread and a patch with a thread that contained cues of *N. cucumeris*, and the other arena consisted of a patch with a clean thread and a patch with a thread with cues of *N. cucumeris*. Before releasing *I. degenerans*, the threads had previously been offered to 150 adult female *N. cucumeris* as a substrate for oviposition on another arena during 24 h, together with ample amounts of *Typha* sp. pollen. Subsequently, all mites and eggs were removed from the threads with a fine paint brush so that they contained cues of *N. cucumeris* such as their faeces and chemical substances of themselves and the eggs but no individuals of this species. We introduced the threads exposed to *N.*

cucumeris to one of the patches of an arena as described above. The other patch contained no thread in one experiment and a clean thread in another experiment. All patches contained ample amounts of pollen. The distribution and oviposition by 75 adult females of *I. degenerans* were examined as above. Experiments were carried out under the same conditions as above, and each consisted of 10 replicates. Statistical analyses were performed as above. In addition, the final distributions of the mites and their eggs on patches with a clean thread or a thread with heterospecific cues were compared between single and mixed populations with a generalized linear model (GLM) with a quasi-binomial error distribution to correct for overdispersion, followed by a posteriori contrasts through model simplification (Crawley 2007; R Developmental Core Team 2010). Because it has been reported that the presence of one predator species induce egg retention in the other species (Montserrat et al. 2007), we also compared the total numbers of eggs on each of the two patches between single and mixed populations with a GLM with quasi-Poisson error distributions, followed by a posteriori contrasts as above. Because these experiments were done as a follow-up of the previous experiment, they were not done concurrently, but immediately after them. Despite this small difference in time, we think it is justified to compare the results with the experiments mentioned above because all experiments were done under the same climatic conditions (see specifications above).

Results

Distribution of single populations

When only *I. degenerans* were released on an arena, the distribution of adults over the two patches changed with time (lme, interaction of patch type with time, $F_{1,167} = 124.2$, $P < 0.0001$, Fig. 2a). Mites strongly preferred the patch with the thread (lme, $F_{1,167} = 564.0$, $P < 0.0001$, Fig. 2a). More eggs were laid on the patch with a thread than on the patch without thread (GLM, $F_{1,18} = 161.1$, $P < 0.0001$, Fig. 3a, top bar).

The distribution of *N. cucumeris* over the patches also changed with time (lme, interaction of patch with time, $F_{1,167} = 105.3$, $P < 0.0001$), and this species also strongly preferred the patch with the thread (lme, $F_{1,167} = 546.2$, $P < 0.0001$, Fig. 2b) and laid more eggs there (GLM, $F_{1,18} = 278.5$, $P < 0.0001$, Fig. 3b, top bar). Hence, the presence of a small piece of thread on a patch strongly affected the distribution and oviposition site selection by both species.

Distribution of mixed populations

When the two species were released together on an arena with a thread on one patch, the distribution of *I. degenerans* changed with time (lme, interaction of patch with time, $F_{1,167} = 54.7$, $P < 0.0002$, Fig. 2c), and most mites and eggs were found on the patch with the thread (mites: lme, $F_{1,167} = 237.5$, $P < 0.0001$, Fig. 2c; eggs: GLM, $F_{1,18} = 29.5$, $P < 0.0001$, Fig. 3a, cf. the 2nd bar). The proportion of *I. degenerans* and their eggs on the patch with the thread was reduced in the presence of *N. cucumeris* (mites: cf. Figure 2a vs. 2c, lme of fractions of mites on the patch without thread: likelihood ratio = 102.8, $df = 2$, $P < 0.0001$; eggs: Fig. 3a, cf. the 1st and 2nd bar, GLM, $F_{1,45} = 23.5$, $P < 0.0001$).

The distribution of *N. cucumeris* in mixed populations also changed with time (lme, interaction of patch with time, $F_{1,167} = 108.9$, $P < 0.0001$, Fig. 2d), and most mites and eggs were again found on the patch with the thread (mites: lme, $F_{1,167} = 518.3$,

Fig. 2 Mean fraction ($\pm$ SEM) of predatory mites on two connected patches from 10 min (1/6 h) to 48 h after their introduction. The distribution of *Iphiseius degenerans* and *Neoseiulus cucumeris* was measured on a patch without a thread connected to a patch with a piece of sewing thread, serving as oviposition site (**a–d**). **a, b** Each species released alone; **c, d** the two species together; **e, f** the two species together on two patches, each with a thread. For clarity, one of the data series in panels **e** and **f** is represented with a broken line. Asterisks indicate significant differences in the distribution over the two patches: *ns* not significant; *** $P < 0.001$. See results for changes of the distribution with time

$P < 0.0001$, Fig. 2d; eggs: GLM, $F_{1,18} = 143.8$, $P < 0.0001$, Fig. 3b). However, the distribution of this species did not change as a consequence of the presence of *I. degenerans* (mites: cf. Fig. 2b vs. 2d, lme: L-ratio = 2.16, $df = 2$, $P = 0.34$; eggs: Fig. 3b, cf. the 1st and 2nd bar, GLM, $F_{1,27} = 1.45$, $P = 0.24$).

When both patches had a thread, *I. degenerans* and their eggs in mixed populations were distributed homogeneously over the two patches (mites: lme, $F_{1,167} = 2.0$, $P = 0.15$, Fig. 2e; eggs: GLM, $F_{1,18} = 0.75$, $P = 0.40$, Fig. 3a, 3rd bar). The distribution of *I. degenerans* changed somewhat with time (lme, interaction of patch with time, $F_{1,167} = 4.61$, $P = 0.033$, Fig. 2e). The distribution of *I. degenerans* and their eggs with two threads on each patch differed significantly from that with a thread on one of the two patches (mites: cf. Fig. 2c vs. 2e, lme: L-ratio = 36.2, $df = 2$, $P < 0.0001$, Fig. 3a, cf. the 2nd and 3rd bar; eggs: GLM, $F_{1,45} = 15.5$, $P < 0.001$).

Neoseiulus cucumeris and their eggs were also distributed homogeneously over the two patches (lme, $F_{1,167} = 0.25$, $P = 0.62$, Fig. 2f, GLM, $F_{1,18} = 0.21$, $P = 0.65$, Fig. 3b, 3rd

Fig. 3 The distribution (+SEM) of eggs laid by **a** *Iphiseius degenerans* and **b** *Neoseiulus cucumeris* during 48 h on two connected patches (same experiment as Fig. 1). Patches received either a clean thread ('Thread'), a thread with cues of *N. cucumeris* ('Thread with cues') or no thread ('No thread'). The sum of the two bars equals the total average oviposition on the two connected patches. See legend to Fig. 1 for further explanation. Asterisks next to each set of bars indicate significant differences from a random distribution over the two patches within each treatment: ns not significant; *** $P < 0.001$ (GLM). Within each panel, different letters next to the pairs of bars indicate which treatments differed significantly with respect to (a–d) the distribution of eggs over the two patches (contrasts after GLM) and (x, y) the total number of eggs (summed over the two bars on the two patches, contrasts after GLM)

bar) when a thread was added to the second patch. The distribution of *N. cucumeris* did not change with time ($F_{1,167} = 0.39$, $P = 0.53$, Fig. 2f). Adding a thread to the second patch changed the distribution of *N. cucumeris* and their eggs (mites: cf. Fig. 2d vs. 2f, lme: L-ratio = 200.1, $df = 2$, $P < 0.0002$; eggs: Fig. 3b, cf. the 2nd and 3rd bar, GLM, $F_{1,27} = 102.7$, $P < 0.0001$). The total number of eggs of *N. cucumeris*, summed over the two patches did not differ among treatments (GLM, $F_{2,27} = 19.1$, $P = 0.50$, Fig. 3b).

Effect of heterospecific cues on the distribution of *Iphiseius degenerans*

We performed a series of experiments with *I. degenerans* with cues of the other species to separate the effect of heterospecific cues from the effect of total mite density, which was higher in the experiments with mixed species than with single species. When offered a

choice between a patch without a thread and one with a thread that had cues of *N. cucumeris*, *I. degenerans* preferred the latter patch (lme, $F_{1,167} = 202.2$, $P < 0.0001$, Fig. 4a) and laid more eggs there (GLM, $F_{1,18} = 47.4$, $P < 0.0001$, Fig. 3a, 4th bar), and the distribution changed with time (lme, interaction of patch with time, $F_{1,167} = 30.5$, $P < 0.0001$, Fig. 4a). The presence of cues of *N. cucumeris* on the thread had the same effect on the distribution of adult *I. degenerans* and on the oviposition pattern as the presence of *N. cucumeris* individuals (mites: cf. Fig. 2c vs. 4a, lme, L-ratio = 0.55, $df = 1$, $P = 0.76$; eggs Fig. 3a, cf. the 2nd and 4th bar, GLM, $F_{1,45} = 30.0$, $P < 0.0001$).

When offered a choice between a patch with a thread free of cues and a patch with a thread that had heterospecific cues, females of *I. degenerans* avoided the latter patch (lme, $F_{1,167} = 290.8$, $P < 0.0001$, Fig. 4b) and laid fewer eggs there (GLM, $F_{1,18} = 39.8$, $P < 0.0001$, Fig. 3a, cf. the 5th bar), and changed their distribution with time (lme, $F_{1,167} = 70.3$, $P < 0.0001$, Fig. 4b). The total numbers of eggs of *I. degenerans*, summed over both patches, was higher in the treatment with a thread with cues of *N. cucumeris* than in the other treatments (Fig. 3a, cf. the 4th bar from above with other bars).

Comparison of final distributions

The final distributions of *I. degenerans* differed among all treatments outlined above (GLM, $F_{4,45} = 31.3$, $P < 0.0001$, Fig. 5a). The preference of *I. degenerans* for the patch with a thread was significantly lower in the presence of heterospecifics than in their absence (Fig. 5a, cf. the 1st and 2nd bar). Addition of a thread to the second patch resulted in approximately equal proportions of adult mites on the two patches (Fig. 5a, 3rd bar). Cues of *N. cucumeris* on the thread resulted in a similar distribution of *I. degenerans* as the actual presence of *N. cucumeris* individuals (Fig. 5a, cf. the 2nd and 4th bar). When one patch contained a thread with heterospecific cues and the other had a thread without such

Fig. 4 Mean fraction ($\pm$ SEM) of *Iphiseius degenerans* on two patches from 10 min (1/6-th h) to 48 h after their introduction. The distribution of the mites was measured on a clean patch connected to a patch with an oviposition site with cues of *Neoseiulus cucumeris* (a), or a patch with a clean oviposition site connected to a patch with an oviposition site with cues of *N. cucumeris* (b). Asterisks indicate significant differences in the distribution between two patches: *** $P < 0.001$

Fig. 5 The final proportion (+SEM) of *Iphiseius degenerans* (a) and *Neoseiulus cucumeris* (b) on a patch with a clean oviposition site (three left-hand bars of a and all bars of b) or an oviposition site with cues of *N. cucumeris* (two right-hand bars of a). See legend to Figs. 1 and 2 for further explanation. Different letters above each bar indicate significant differences among treatments (posthoc comparisons after GLM, $P < 0.0001$)

cues, the distribution of *I. degenerans* was strongly skewed towards the latter patch (Fig. 5a, cf. the 5th bar).

The final distributions of *N. cucumeris* also differed among treatments (GLM, $F_{2,27} = 37.3$, $P < 0.0001$, Fig. 5b). The preference of *N. cucumeris* was not affected by the presence of heterospecifics (Fig. 5b, cf. the 1st and 2nd bar), and addition of a thread to the second patch resulted in approximately equal proportions of adult mites on the two patches (Fig. 5b, cf. the 3rd bar).

Discussion

When *I. degenerans* and *N. cucumeris* were separately offered a choice between a patch with a small piece of thread as oviposition site and a patch without thread, both species preferred the former patch and predominantly laid eggs on the thread. Together with earlier results (van der Hammen et al. 2012), this shows that female predatory mites distribute themselves according to the presence of food as well as oviposition sites. Physical structures that serve as potential oviposition sites (hence, having the same function as the sewing thread used in our experiments) are also present in the natural microhabitat of plant-inhabiting predatory mites and insects (Agrawal and Karban 1997; Norton et al. 2001;

Ferreira et al. 2011) and are used as refuges by juveniles (Janssen et al. 2007; Schmidt and Rypstra 2010). In the current experiments, the presence of heterospecifics weakened this preference for patches with oviposition sites in *I. degenerans*, but not in *N. cucumeris*. This change was probably a response to cues left by *N. cucumeris* on the oviposition sites. These results suggest that the two species interact by using the same oviposition site.

In classic predator–prey systems, it is known that prey select oviposition sites that function as refuges from predators (Horita et al. 2004; Bond et al. 2005; Lemos et al. 2010; Sudo and Osakabe 2013). This oviposition site selection may promote coexistence of predators and prey (Sih 1987; Krivan 1998; Lynch et al. 1998). However, one may wonder how such oviposition sites act as a refuge when they are equally accessible to either of the two species of intraguild predators (Ferreira et al. 2011), as was the case in our experiments. The answer to this question is that it takes the predatory mites time to assess the conditions on a patch and they are therefore unlikely to arrive simultaneously. Indeed, the distribution of each of the two predatory mite species over the two patches changed with time. This is consistent with the results of van der Hammen et al. (2012), who offered the same two predatory mite species two patches with different food supply, and showed that it took some time before the two species of predators reached their final distributions. Whereas we found a fast convergence (within 10 min) to the final distribution of *N. cucumeris* in an earlier study (Choh et al. 2010), where cues of *I. degenerans* were present on the entire patch and therefore easy to detect, this was not the case in the present study, where the two predators were released at the same time. Hence, the deposition of cues on patches took place only gradually in the course of our experiments. This may also explain the difference between the results of earlier experiments (Choh et al. 2010) that show that *N. cucumeris* avoided patches on which cues of *I. degenerans* were already present and the current experiments, which show no effect of the simultaneous introduction of *I. degenerans* on the distribution of *N. cucumeris*.

Our results show that patch choice is not simply determined by the presence of food (van der Hammen et al. 2010, 2012), but also by the conditions present at places where the mites can oviposit. Indeed, even when there was ample food (pollen), females of *I. degenerans* did not only change the distribution of eggs as a consequence of the presence of *N. cucumeris*, but they also did so when the oviposition site on the patch contained cues of this heterospecific predator. This shows that the changes in the distribution of *I. degenerans* in the presence of *N. cucumeris* would be caused by the presence of a population of intraguild predators or their cues rather than by the increase of competitors. Thus, if cues on potential oviposition sites are used to assess patch quality, we expect that not only assessing the amount of food, but also detecting the presence of cues indicating predation danger may require time to a predatory mite.

The asynchrony in arrival times of females of the two species also creates priority effects that may give one predator species an advantage or refuge in some patches, whereas the other species may experience the same in other patches (van der Hammen et al. 2010). Surprisingly, most studies on predator–prey interactions have focused on behavioural changes in predators or prey by fixing the other species in space (i.e., use of chemical cues or cage treatments) without testing their spatial distributions when both freely interact (Lima 2002; Hammond et al. 2007; Huang and Pike 2012). Here, we show how intraguild predators and prey that share same food source and oviposition sites change their distributions when they are allowed to move around freely.

In contrast to *I. degenerans*, females of *N. cucumeris* did not change their distribution and oviposition pattern in the presence of heterospecifics in the course of the experimental period. This may have been caused by the fact that twice the number of *N. cucumeris* than

of *I. degenerans* was released in our experiments. Hence, more cues of *N. cucumeris* than of *I. degenerans* will have accumulated on the threads. In fact, several studies reported that the density of intraguild predators or intraguild prey affects the strength of intraguild predation (De Clerq et al. 2003; Okuyama and Ruyle 2003; Holbrook and Petranksa 2004; Burley et al. 2006), suggesting density-dependent risk of predation. Further studies are needed to test whether the distribution of *N. cucumeris* would change as a result of higher concentrations of cues of *I. degenerans*.

Under conditions of well-mixed populations without refuges from intraguild predation, the two species of predators are unlikely to co-exist (Holt and Polis 1997; Sergio et al. 2007). Montserrat et al. (2008) showed that *I. degenerans* were likely to exclude *N. cucumeris*, irrespective of food levels, when similar numbers of the two species were released together. However, *I. degenerans* was excluded when populations of *N. cucumeris* had established previously, and this was due to intraguild predation by *N. cucumeris* (Montserrat et al. 2008, 2012). Thus, which of the two species was eliminated depended on initial conditions (Montserrat et al. 2008). Indeed, a recent study showed that the order of invasion affected the spatial distribution of *I. degenerans* and *N. cucumeris* (van der Hammen et al. 2010). Earlier (Choh et al. 2010), we showed that that *N. cucumeris* avoided patches with cues of *I. degenerans*, which is an intraguild predator of juvenile *N. cucumeris* (Montserrat et al. 2006). In addition, we show here that *I. degenerans* avoided patches with cues of *N. cucumeris* on potential oviposition sites. Because *N. cucumeris* could not kill eggs and adult females of *I. degenerans* under our experimental conditions (Montserrat et al. 2012), the avoidance would be a response to the potential risk of intraguild predation for offspring rather than for the individuals tested here. Taken together, these studies suggest that both predator species avoid patches that were earlier invaded by the other. It is known that intraguild prey use cues related to intraguild predators to avoid predation (Persons and Rypstra 2001; Agarwala et al. 2003; Magalhães et al. 2005; Nakashima et al. 2006). Invading patches in a different order would create patches with cues related to the risk of intraguild predation, which will subsequently affect the behaviour of intraguild prey. Such avoidance responses would reduce the strength of intraguild predation through decreases of the encounter rate in a patch. In addition, habitat structures can also reduce the strength of intraguild predation and offer opportunities for coexistence of intraguild predators and prey (Persson and Eklov 1995; Heithaus 2001; Finke and Denno 2002; Janssen et al. 2007; Schmidt and Rypstra 2010, but see Reichstein et al. 2013). For example, females of *I. degenerans* use domatia on sweet pepper leaves for oviposition and the egg batches laid in domatia suffer less predation (Faraji et al. 2002a, b). Furthermore, Finke and Denno (2002) reported that mirids and spiders, which are predators of plant hoppers, co-occur more in structurally complex habitats than in simple habitats due to reduced intraguild predation. We suggest that refuge-mediated predator avoidance may promote the coexistence of the two predator species in the same habitat.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

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