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Oviposition patterns in a predatory mite reduce the risk of egg predation caused by prey

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Abstract. 1. Predatory arthropods lay their eggs such that their offspring have sufficient prey at their disposal and run a low risk of being eaten by conspecific and heterospecific predators, but what happens if the prey attacks eggs of the predator?

2. The egg distribution and time allocation of adult female predatory mites *Iphiseius degenerans* as affected by predation of their eggs by prey, the western flower thrips *Frankliniella occidentalis*, were studied on sweet pepper plants. The predatory mites attack the first instar of thrips but all active stages of thrips are capable of killing the eggs of the predator; however the predatory mite is used for biological control of thrips.

3. The majority of predatory mite eggs was laid on the underside of leaves in hair tufts (domatia). During the experiment, females spent increasing amounts of time in flowers where they fed on pollen and thrips larvae. The risk of predation on predator eggs by thrips was lower on leaves than in flowers where the majority of thrips resides. Moreover, predation risk was higher outside leaf domatia than inside.

4. This suggests that predators avoid ovipositing in places with abundant prey to prevent their eggs from being eaten by thrips.

Key words. Domatia, oviposition, Phytoseiidae, predation, western flower thrips.

Introduction

Given that adult arthropods are more mobile than juvenile offspring, oviposition behaviour is crucial in determining development and survival of the offspring. The suitability of an oviposition site and the distribution of eggs among possible sites affect predation, hatching success, larval performance, and, thereby, indirectly, parental fitness (Resetarits & Wilbur, 1989; Rehfeldt, 1990; Heard, 1994; Resetarits, 1996). In many arthropods, oviposition is near sites with food suitable for the offspring and away from places with high offspring predation risk; however, sometimes the food itself is a prey that can counter-attack and even kill the predator or its offspring. For example, Saito (1986) observed that males of spider-mite prey *Schizotetranychus celarius* kill the larvae emerging from

the eggs left behind by their natural enemy, the predatory mite *Typhlodromus bambusae*. It is not known, however, whether these counter-attacks also affect oviposition behaviour of the predatory mite. Here, a study of oviposition behaviour of another predatory mite, *Iphiseius degenerans* (Berl.) (Acari: Phytoseiidae), is reported. Its eggs are vulnerable to counter-attack by its prey, the western flower thrips *Frankliniella occidentalis* (Pergande). The thrips is generally considered to be phytophagous because it feeds on particular plant tissues such as leaves, pollen, and nectar (Higgins, 1992; Lewis, 1997; Milne & Walter, 1997; van Rijn & Tanigoshi, 1999a). In addition to being phytophagous, thrips also feed on eggs of the phytophagous mite *Tetranychus urticae* Koch (Gonzalez & Wilson, 1982; Trichilo & Leigh, 1986; Milne & Walter, 1997) and attack the eggs of *I. degenerans* (Faraji *et al.*, in press). Thus, *I. degenerans* faces the dilemma that its prey is also its (egg) predator.

How female predatory mites deal with this dilemma was investigated in the work reported here. On sweet pepper plants, pollen, nectar, and thrips occur mainly in flowers

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(van Houten & van Stratum, 1995). Because of the counter-attacking thrips, flowers are risky oviposition sites for the predatory mite, which may cause the predators to lay eggs elsewhere (e.g. on leaves). The following questions were addressed: How does the predatory mite distribute its eggs over the plant, especially over leaves and flowers, and does this distribution lead to lower predation on their eggs by thrips?

Materials and methods

Rearing

The strain of *Iphiseius degenerans* used in the study originated from Rabat, Morocco (van Houten *et al.*, 1995) and was reared on a diet of birch pollen on arenas consisting of a grey PVC[®] sheet (30 × 21 cm) on a wet sponge in a tray of water (van Rijn & Tanigoshi, 1999b). Paper tissues were wrapped over the edges of the arena, serving as a water source and a barrier. To provide more water, each arena was divided into four using three narrow filter paper strips (1 × 30 cm). Threads of sewing cotton (0.5 mm thick, 2 cm long, black) were provided as an oviposition substrate. To obtain fresh eggs, old threads with eggs were replaced with a new thread 18 h prior to the experiments.

The population of thrips was established on chrysanthemum in 1993 at the Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, with individuals collected from chrysanthemum at the Centre for Plant Breeding and Reproduction Research in Wageningen, The Netherlands. To obtain second-instar larvae and adult thrips, five thrips females were transferred from chrysanthemum flowers to a sweet pepper leaf disc (2.5 cm). Leaf discs were put upside down on water-saturated cotton wool. In addition to the water barrier around the discs, birch pollen was added to encourage the adult thrips not to fly away from the discs and to increase their oviposition capacity (P. C. J. van Rijn, pers. comm.). Two days after introduction, females were removed from leaf discs to avoid cannibalism and competition for food with juveniles. Newly emerged larvae were transferred to new leaf discs at a density of seven to 10 larvae per disc.

Sweet pepper plants *Capsicum annuum* were grown from seeds in a greenhouse inside cages (100 × 60 × 100 cm) to prevent infestations.

Time allocation and egg distribution of *Iphiseius degenerans* on sweet pepper plants

Six potted, pest-free sweet pepper plants (35–40 cm high) with two to five open flowers were placed in a climate room at 25 °C and LD 16:8 h photoperiod. Sixteen gravid female predators (12–14 days since hatching) were released on the stem of each plant at the main branching point. The presence of individuals on/in every part of the plants was checked twice per day (09.30 and 16.30 hours) for 2 days. Because the predators are blind, it was assumed that light

would not influence their behaviour. Immediately after the last observation, the plants were dissected under a binocular microscope and predator eggs on each part of the plant were counted (i.e. flowers, stems, leaves). Experiments lasted for only 2 days because the first deposited eggs start to hatch after this period.

Under the null hypothesis that the predator's oviposition pattern is not affected by the risk of predation on predator eggs by prey, the fraction of eggs in the different plant parts was expected to be equal to the fractions of time spent on each part by the adult females. A χ^2 -test was used to compare the egg distribution with time allocation of the females.

Predation risk of predator eggs in flowers and in leaf domatia

Ten branches with one open flower and one leaf were cut from sweet pepper plants. The stems of the branches were placed individually in small jars with water. A cluster of 20 predator eggs (0–18 h old) was placed in the flowers and a similar cluster was placed inside the domatia on the underside of the leaves. Ten second-instar thrips larvae were released on the lower part of the stem.

In another experiment, branches of sweet pepper (a branch with one open flower and one leaf, $n=6$ replicates) were prepared in a similar manner to the experiment on thrips larvae. The number and distribution of predator eggs were also similar to the above-mentioned experiment. Ten adult thrips were collected in a small vial and placed in a Petri dish. The vial was opened in the Petri dish and, before the insects could escape, they were placed in a Plexiglas[®] container, which contained one sweet pepper branch. In this way, the adults were free to fly and walk either to a flower or a leaf. The number of predator eggs killed by the thrips was counted after 24 h. A *t*-test (two-tailed distribution) was used to compare the arcsin-transformed fractions of eggs killed in the flowers vs. on the leaves.

Predation risk on predator eggs inside and outside domatia

To measure predation inside and outside domatia, a cluster of 20 eggs was placed inside a leaf domatium on the lower leaf of a sweet pepper branch consisting of two leaves (12 replicates). In another treatment (15 replicates), an egg cluster was placed outside the domatia near the midrib of the lower leaf. Ten thrips larvae were released on the stem between the two leaves. After 24 h, the number of eggs eaten by thrips was counted. The *t*-test (two-tailed distribution) was used to compare the arcsin-transformed fractions of eggs killed by thrips inside vs. outside the domatia.

Results

Time allocation of females on plants

The proportion of *I. degenerans* females on each part of the sweet pepper plants (i.e. flowers, stems, and upper sides

and undersides of leaves) at four intervals from the start of the experiment (7, 24, 31, 48 h) is shown in Fig. 1. The mean proportion of *I. degenerans* in the flowers increased during the experiment (from 0.015 after 6 h to 0.564 after 48 h), whereas the proportion of females on the leaves decreased. The initial high numbers of females on the leaves was probably caused by the presence of small amounts of pollen that rained down from the flowers on the leaves. When this pollen was consumed, the females moved to the flowers to feed there.

Distribution of eggs on sweet pepper plants

The egg distribution on one of the sweet pepper plants is represented schematically in Fig. 2. Two days after releasing the female predators, a total of 407 eggs was found on the plants. Of these, two were laid in the flowers, zero on the stems, one on the upper side of a leaf, and 404 on the underside of leaves (Fig. 3). On the underside of leaves, most of the eggs (98.5%) were deposited in domatia. On the plants tested, domatia did not occur on the first seven or eight leaves and females laid on average 0.1 eggs on these leaves, whereas they laid 5.2 eggs per leaf on the next four leaves with domatia. If females do not use specific sites for oviposition, eggs would be expected to be distributed proportionally to the fraction of time spent by females on various parts of the plant. There was a significant difference ($\chi^2 = 310.5$, d.f. = 3, $P < 10^{-3}$) between observed and expected (based on the proportion of time spent) proportions of eggs on different parts of the plants (Fig. 3). This is because females oviposit significantly more eggs than expected on the underside of leaves ($\chi^2 = 137$, d.f. = 1, $P < 10^{-3}$), and significantly fewer eggs than expected in flowers ($\chi^2 = 111.4$, d.f. = 1, $P < 10^{-3}$), on stems ($\chi^2 = 41.9$, d.f. = 1, $P < 10^{-3}$), and on the upper sides of leaves ($\chi^2 = 20.3$, d.f. = 1, $P < 10^{-3}$).

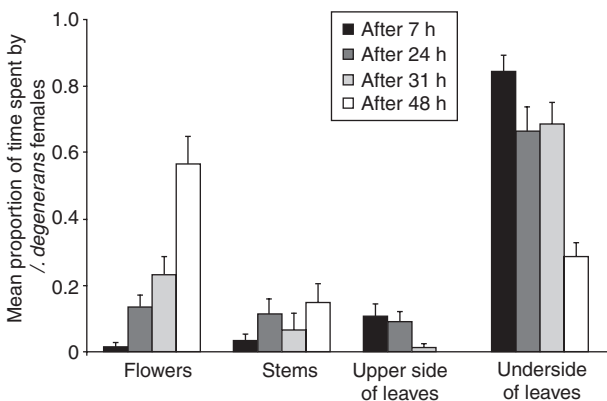


Fig. 1. Mean proportion of time allocated by adult females of *Iphiseius degenerans* on various parts of sweet pepper plants at various intervals (7, 24, 31, 48 h) after release. Shown are means +SE of six replicates, each consisting of one plant with 16 females.

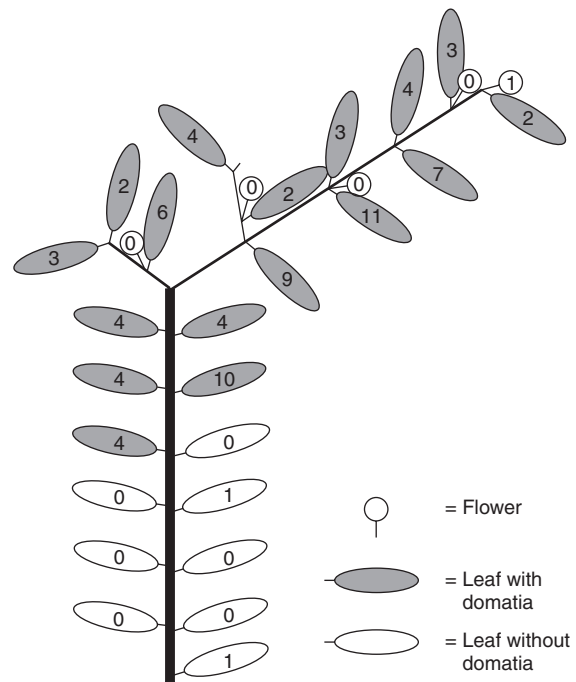


Fig. 2. An example of the egg distribution of *Iphiseius degenerans* females (16 females) on leaves and flowers of a sweet pepper plant. Numbers indicate the numbers of eggs on leaves and in flowers.

Predation risk on predator eggs in flowers and on leaves

Predation on *I. degenerans* eggs by adult and juvenile thrips was significantly higher in the flowers than on leaves (*t*-test on transformed fractions, $P < 10^{-3}$ for thrips larvae, $P < 10^{-4}$ for adult thrips). Thrips larvae killed 19.5% of all eggs on the leaves vs. 68% in the flowers while adult thrips

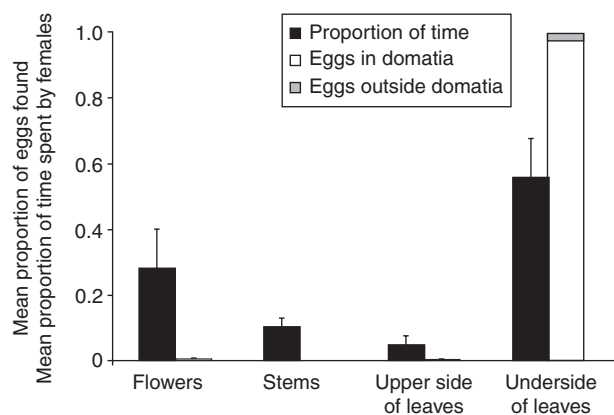


Fig. 3. Comparison of egg distribution (with SE) of *Iphiseius degenerans* on each part of sweet pepper plants (i.e. flowers, stems, upper side and underside of leaves, white bars) with mean proportion (+SE) of time spent on various plant parts (black bars, averaged over the four observation periods).

killed 8.3% of the eggs on leaves vs. 88.3% in the flowers (Fig. 4).

Predation risk on predator eggs inside and outside domatia

Thrips larvae killed significantly more eggs when clusters of eggs were located outside the domatia than when eggs were inside the domatia (*t*-test on transformed fraction, $P < 10^{-4}$; Fig. 5).

Discussion

Females of *I. degenerans* are usually found in flowers, where they feed on pollen and thrips larvae (van Houten & van Stratum, 1995). The experiments also showed that, 2 days after release, most females were found in flowers, however the females did not lay their eggs in the flowers but preferred to lay eggs on leaves, where they were laid in clusters inside tufts of leaf hairs. These so-called domatia, or acarodomatia, are common in many plant species (O'Dowd & Willson, 1997); on sweet pepper plants they occur where the mid-rib bifurcates into leaf veins. The oviposition pattern is surprising because females largely utilise ingested food for reproduction (Sabelis & Janssen, 1992), develop one egg at a time, and have to feed in between oviposition of single eggs. Because a female can produce up to three eggs per day, this means that they have to commute between flowers and leaves repeatedly. When doing so, the predators prefer to add eggs to clusters of their own (Faraji *et al.*, 2000). Being small (< 1 mm) and blind, this commuting over distances up to a few decimetres will certainly cost time and energy. This prompts the question of what benefits are associated with laying eggs away from the food source in the flowers. Other, well-studied phytoseiid species avoid such behaviour; they rather lay eggs where they feed, thus supplying their offspring with food for development (Sabelis & Janssen, 1992).

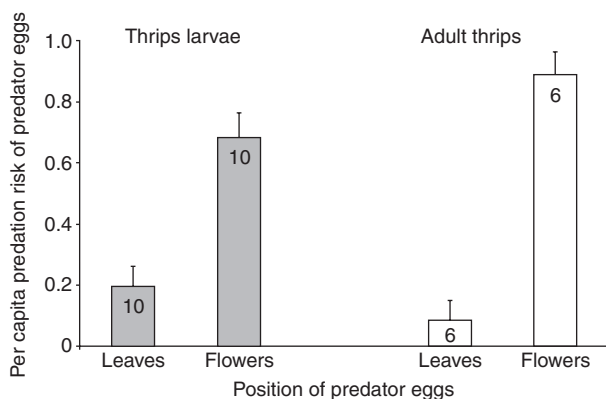


Fig. 4. Per capita predation risk (+SE) of *Iphiseius degenerans* eggs killed by thrips larvae and adult thrips in flowers and in domatia on leaves of sweet pepper branches. Numbers inside bars indicate the number of replicates.

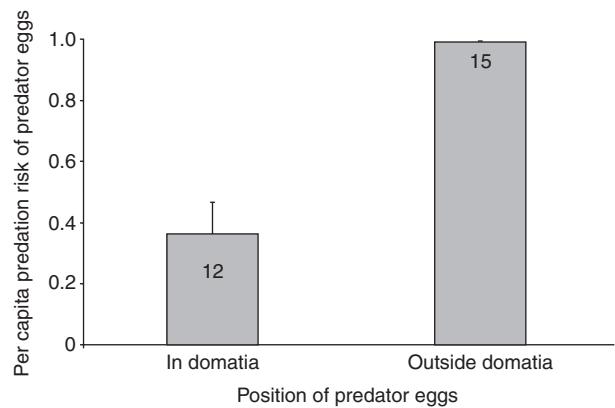


Fig. 5. Per capita predation risk (+SE) of *Iphiseius degenerans* eggs killed by thrips larvae in and outside domatia on leaves of sweet pepper branches. Numbers inside bars indicate the number of replicates.

One reason for laying eggs in domatia on leaves is that eggs are relatively safe from predation by flower-visiting predators, including counter-attacking thrips. It was indeed found that predation of eggs by thrips in flowers is higher than on leaves, and, within leaves, domatia are relatively safe sites. Admittedly, avoidance of cannibalism is an alternative explanation for avoiding oviposition in flowers, however this explanation is probably less relevant because eggs are not cannibalised (Faraji *et al.*, 2002) and juveniles disperse away from egg clusters, thereby escaping from cannibalism. Another reason for oviposition in domatia may be that domatia offer more favourable conditions (e.g. humidity).

A reason for laying eggs away from flowers may be that flowers are ephemeral. When flowers are shed before the eggs hatch, young juveniles will have to migrate from the shed flower back onto the plant. This has been suggested as an explanation for avoidance of oviposition in flowers by the predatory bug *Orius insidiosus* (van den Meiracker & Sabelis, 1993). Only some parts of the flowers are shed, however, and the predatory mites could well oviposit on the young fruit, which stays on the plant. Moreover, the ephemeral nature of the flowers cannot explain the observation that predatory mites lay eggs in domatia at the underside of leaves. Such an explanation ensues from the lower predation risk in domatia reported here.

Predators are known to affect prey distribution directly (by predation) and indirectly (through induction of anti-predator behaviour). On the other hand, prey distribution is known to affect predator distribution. Here, a new phenomenon is shown: prey affect the distribution of predator eggs because they may kill predator eggs. This results in a distribution of predator eggs that is counter-intuitive at first sight because it shows that oviposition occurs in places where eggs are safe from counter-attacking prey. Actually, these safe sites are plant-provided structures.

Plants are known to interact with the third trophic level in several ways, one of which is through the provision of shelter (domatia; Walter, 1992; Sabelis *et al.*, 1999) and food

(Sabelis *et al.*, 1999) to predators. The sweet pepper plants studied here do both. If the two facilities coincide spatially, it would be relatively easy for thrips to move into the tuft-like domatia and kill predator eggs and it would be less profitable for the plants to supply pollen and domatia. The fact that pollen and domatia are separated spatially within a plant is probably the main reason why plants benefit from these investments. The main reason why predators profit from this spatial segregation is due to the differential ecological roles associated with their life-history structure. As adults, the predators can exploit the thrips and the pollen fully and visit flowers. Eggs, and possibly larvae, are vulnerable to counter-attacks by the prey and should not be in flowers. In conclusion, plants profit from spatial segregation of domatia and pollen because of the existence of life-history structure in predator and prey populations.

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