How counter-attacking prey influence foraging and oviposition decisions of a predatory mite
Faraji, F.

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INTRODUCTION AND SUMMARY

Predation is a strong selective force on the behaviour of many organisms (Edmunds, 1974; Harvey & Greenwood, 1978; Sih, 1987, Lima & Dill, 1990). Animals can respond to predators in a variety of ways, for example by moving to an enemy-free habitat (Stain, 1979; Pierce, 1988; Stamp & Bowers, 1988; Rosenzweig, 1991; Grostal & Dicke, 1999; Pallini et al., 1999; Grostal & Dicke, 2000), moving into a refuge from predation (Sih, 1997; Pallini et al., 1998; Venzon et al., 2000), decreasing conspicuousness (Sih, 1986; Lefcourt, 1996), defending (Stamp, 1982; Bakker & Sabelis, 1989; Stamp & Bowers, 1990; Shave et al., 1994), and escaping (Yeargan & Braman, 1989; Boevè, 1991). Some of these studies show that predators do not only kill prey, but they also have non-lethal effects on reproduction (Stein, 1977; Cooper, 1984; Hafernik & Garrison, 1986; Kerfoot & Sih, 1987; Schmitz et al., 1997). Assuming that prey have limited amounts of time and energy, they must balance conflicting needs (time and energy spent on antipredator behaviour, foraging, ovipositing or mating) (Sih, 1980). To optimise time and energy expenditure, prey must adequately respond to changes in predation risk. Such flexible antipredator behaviour (as opposed to fixed; Stein, 1979; Pierce, 1988; Stamp & Bowers, 1993) requires detection of a predator (Endler, 1986, 1991). Among others, chemosensory cues are an important source of information to discover predators and to assess predation risk (Smith, 1977; Havel, 1987; Kats et al., 1988; Kats & Dill, 1998; Venzon et al., 2000). These chemicals can either originate from predators (kairomones; e.g. Weider & Pijanowska, 1993; Elliott et al., 1993) or from prey, either dead (scent of death) or alive (alarm pheromones; Chivers & Smith, 1997; Janssen et al., 1997; Pallini et al., 1999; Grostal & Dicke, 1999, 2000). Whatever the origin, these chemical cues alert other prey.

To avoid predation on their offspring, females must select a safe oviposition site. Several authors have shown that offspring survival and growth vary considerably among sites (Chesson, 1984; Resetarits & Wilbur, 1989; Petranka & Fakhoury, 1991; Kats & Sih, 1992; Knapp, 1993; Hopey & Petranka, 1994; Taylor et al., 1998). Mothers do not necessarily select sites that are best for their offspring, because they have to balance their own reproductive success against the fate of their offspring. Factors that affect this balance are the availability and suitability of food and the risk of predation, but these factors have a different weight depending on the needs of mother or that of her offspring. For one thing, arthropod females may require food to produce eggs, just as their offspring need it for development, but the amount and quality to fulfil these needs may differ between mother and offspring. If food for mother and offspring coincides in space, females should tune their own consumption and oviposition such that sufficient food is left for offspring to mature. For another, predation risk of mother and offspring may differ. If the feeding site is a risky place for offspring, females may decide to oviposit elsewhere. The decision to select an oviposition site would therefore be a compromise between costs involved in commuting by the mother between feeding and oviposition sites, the costs involved in searching for food by the offspring and benefits of lower predation risk to the offspring.

Balancing conflicting demands is not only vital for the prey, but also for predators, especially when prey counter-attack predators. For example, Saito (1986) found that bamboo spider mites attack and kill the larvae of the predator that feeds on the spider mites.
When a predator invades the web-nest of this prey, the prey parents escape from the nest. The predator feeds on the offspring, oviposits and leaves some prey for its offspring. Upon departure of the predator, the prey parents return and kill the larvae of the predator. This example shows that prey can exert strong selection on predators by counter-attacking, and it is therefore expected that such counter-attacks should be taken into consideration by ovipositing females.

In this thesis, I present the results of studies on the foraging and oviposition behaviour of a predatory mite (*Iphiseius degenerans*). In particular, I studied how counter-attacks of its prey, the western flower thrips *Frankliniella occidentalis*, modify the oviposition behaviour of the predator. The predatory mite attacks mainly the first thrips instar, whereas all active stages of thrips are capable of killing the eggs of the predator. Despite these counter-attacks, it is the predatory mite that is used for biological control of the thrips and we will therefore refer to it as ‘the predator’. Besides being involved in predatory interactions, the two species also feed on plant pollen. Thrips and adult predatory mites are found more frequently in flowers than on leaves of sweet pepper plants (van Houten & van Stratum, 1995; Kiers et al., 2000). In the flowers, they both feed on pollen and predators feed in addition on thrips larvae (see the picture on the thesis cover). Hence, flowers are a rich food source for predatory mites, but a risky site for oviposition due to the presence of counter-attacking thrips. I studied the oviposition behaviour of predatory mites in presence and absence of thrips. In Chapter 2, the egg distribution and time allocation of *I. degenerans* females on sweet pepper plants in absence of thrips is presented. The majority of predatory mites laid their eggs in clusters on the underside of leaves in domatia (tufts of hair that are present where leaf veins bifurcate, Fig. 1). Females spent increasing amounts of time in flowers where they feed on pollen and nectar. To explain the egg distribution, I tested the hypothesis that the oviposition decisions are tuned to predation risk. On leaves, fewer predator eggs were attacked by thrips as compared to flowers, since here the majority of thrips resided. Moreover, predation risk was higher outside leaf domatia than inside. This indicates that predators avoid ovipositing in flowers with abundant prey and pollen, because egg predation in the flowers is high. Since predators refrained from ovipositing in flowers in the absence of thrips, the antipredator behaviour seems to be fixed.

![Figure 1. A cluster of *Iphiseius degenerans* eggs in tufts of hair (domatia) of a sweet pepper leaf.](image-url)
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*Iphiseius degenerans* shows a strong tendency to cluster eggs inside domatia on leaves (Chapter 2, Fig. 3). This is especially remarkable because, given that the predatory mites develop one egg at a time, this implies frequent commuting between leaves, where the predatory mites oviposit, and flowers, where they feed. Moreover, ovipositing in clusters indicates that predators may spend time to find domatia with eggs, rather than ovipositing in a randomly chosen domatium. Besides these investments, there are other costs, but also potential benefits to ovipositing in clusters. For example, oviposition in clusters of conspecific eggs may lead to increased cannibalism and to increased production of daughters as a consequence of local mate competition. Costs and benefits will strongly depend on the relatedness of eggs within a cluster, since cannibalism among kin is expected to be low, while female bias increases with relatedness. Moreover, adding an egg to a cluster of own or closely related eggs may protect underlying eggs against thrips attacks. Therefore, I investigated whether *I. degenerans* discriminates between groups of heterospecific, conspecific non-kin and conspecific kin-related eggs (Chapter 3). Choice experiments showed that females preferred to oviposit close to conspecific eggs relative to heterospecific (*Neoseiulus cucumeris*, *Typhlodromus pyri* and *Phytoseiulus persimilis*) eggs. Moreover, females preferred to oviposit near eggs of kin over non-kin. Thus, females discriminate not only between conspecific and heterospecific eggs, but also between conspecific eggs of different degrees of relatedness. In this way, they avoid cannibalism by non-kin (F. Faraji, pers. obs.). Possibly, this also allows them to produce adaptive sex ratios, but this needs further experimental confirmation.

A further confirmation of the tendency to oviposit in clusters was found in Chapter 4. Females preferred to add eggs to a cluster in a domatium rather than to oviposit in an empty domatium. This shows that the observed egg clustering is not due to shortage of oviposition sites. Hence, there should be a reason for this oviposition behaviour. Two mortality factors are possibly involved: predation by thrips and cannibalism. While eggs are invulnerable to cannibalism, larvae emerging from clustered and scattered eggs were equally vulnerable to cannibalism. Hence, eggs inside clusters are not protected against predation by thrips. Only when clusters were placed in domatia, a lower proportion of eggs was killed by adult thrips compared to eggs scattered over domatia. This suggests a combined effect of oviposition in clusters and oviposition in domatia on the survival of predator eggs. Eggs at the outside of a cluster are likely to be more vulnerable to predation than eggs at the inside. If an ovipositing female adds an egg to the outside of a cluster of her own eggs, this may increase the overall fitness of the female, because it protects her eggs inside the cluster, even when the added eggs run a high risk. For this behaviour to evolve, females need to be capable of discriminating kin eggs from conspecific eggs (Chapter 3).

Although predatory mites visit flowers to acquire food (Chapter 2), flowers are not the only sites where food is present. Pollen also rains down on the leaves below the flowers and these pollen patches may offer safer oviposition sites than flowers, because of the relatively low density of thrips and other predators, which mainly reside in flowers (van den Meiracker & Sabelis, 1993; Kiers et al., 2000). If thrips would move to these pollen patches on leaves, it becomes also risky for the predatory mites to oviposit there. Hence, I studied the oviposition behaviour of predatory mites in presence of a pollen patch with thrips either present or absent (Chapter 5). In absence of thrips, predatory mites oviposited close to the pollen, whereas in presence of thrips, females oviposited further away from the food source. Because thrips stayed close to the pollen, the predatory mite eggs near the pollen were killed more frequently by thrips than eggs that were deposited further away. Oviposition behaviour of predatory mites was also studied in presence of synthetic thrips alarm pheromone (a 2:3
mixture of dodecyl acetate and decyl acetate in pentane; Teerling et al., 1993). When this pheromone was applied close to the pollen, predatory mites oviposited significantly further away from the food source. When thrips alarm pheromone was applied away from the food source, most of the eggs were found near the pollen. These results demonstrate that female predatory mites show a risk-driven flexible behaviour in response to the presence of their counter-attacking prey: they avoid oviposition at sites where their offspring is at risk of being killed by prey. Together with the finding that the mites avoid oviposition in flowers, even in absence of thrips (Chapter 2), this shows that the predatory mites use both fixed and flexible behavioural responses to reduce predation risk on eggs by thrips. It is an open question why the predatory mites show fixed behaviour with respect to flowers. Possibly, flowers are risky places to oviposit, even when no egg predators are present yet, since these will inevitably visit flowers in the future.

Since the female predatory mites are able to produce a few eggs per day and need to feed in flowers in-between ovipositions on leaves, they have to commute between flowers and leaves repeatedly. In Chapter 6, I studied how the females find these feeding and oviposition sites. Specifically, I tested their response to flower and leaf odours, and how these responses can be changed by learning and the physiological state of the predators. In a Y-tube olfactometer, both fed and starved females with no experience with pepper flowers or leaves showed a significant preference for leaf odours. However, females with experience on a pepper plant, but subsequently starved in the absence of any stimulus, strongly preferred flower odours. In contrast, satiated females collected from flowers (where they had no access to leaves), strongly preferred pepper leaf odours to flower odours. This shows that both experience and physiological state affect olfactory responses. Usually, a positive stimulus leads to an increase in response to an associated unconditioned stimulus, but here the physiological state causes the response to switch. This reversal can be explained by the fact that experienced-and-fed females tend to search for oviposition sites on leaves, whereas starved females try to locate food, which is mainly in flowers. To test whether the olfactory responses are innate, learned, or both, females were conditioned to associate oviposition and feeding sites with flower odours, by adding artificial oviposition sites to flowers. Starved females that had thus experienced food and oviposition sites together in flowers, showed a similar preference for flower odours as females that were conditioned on leaves and flowers. Fed females showed a significantly lower response to leaf odours. This is in contrast to fed females that had experienced separate food and oviposition sites. Thus, preference of *L. degenerans* is influenced by a combination of associative learning, innate response and physiological state.

The main conclusion arising from this thesis is that the foraging and oviposition behaviour of *L. degenerans* is modified by the counter-attacks of its thrips prey. On the one hand, predatory mites forage at sites where thrips occur (flowers) but on the other hand, they avoid oviposition at those sites and move to leaves to lay eggs in domatia. Predation on predator eggs by thrips is likely to be one of the main factors that has influenced the oviposition behaviour of the predatory mites. Oviposition in clusters in leaf domatia and avoidance of oviposition in flowers reduces this predation risk. Predators avoid laying eggs in flowers even in the absence of thrips, indicating that this is a fixed antipredator behaviour. In contrast, they show a flexible antipredator behaviour by avoiding oviposition near pollen patches on leaves only when thrips are present. As they produce one egg at a time and need to feed in order to develop another egg, they must commute between feeding and oviposition sites. The predators learn to use odours to locate these two sites, and switch odour preference depending on the physiological state.
Predators are known to affect the distribution of prey directly (by predation) and indirectly (through antipredator behaviour). In turn, the distribution of prey affects predator distributions, with predators searching for more profitable prey patches. Here, we show a new phenomenon: prey negatively affect the distribution of predator eggs because they would kill them, and because predators avoid oviposition at places with prey. Understanding the oviposition behaviour of predators will help us to manipulate predator-prey interactions in biological control systems such that predators have maximum impact on prey populations while suffering a minimum predation risk. This study suggests that one way to manipulate these interactions is by selecting for crops with domatia, or by addition of artificial domatia to crops (cf. Agrawal & Karban, 1997).

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REFERENCES

Chapter 1


