

## Interspecific infanticide deters predators

### Abstract

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It is well known that young, small predator stages are vulnerable to predation by conspecifics, intra-guild competitors or hyperpredators. It is less known that prey can also kill vulnerable predator stages that present no danger to the prey. Since adult predators are expected to avoid places where their offspring would run a high predation risk, this opens the way for potential prey to deter dangerous predator stages by killing vulnerable predator stages. We present an example of such a complex predator–prey interaction. We show that (1) the vulnerable stage of an omnivorous arthropod prey discriminates between eggs of a harmless predator species and eggs of a dangerous species, killing more eggs of the latter; (2) prey suffer a minor predation risk from newly hatched predators; (3) adult predators avoid ovipositing near killed predator eggs, and (4) vulnerable prey near killed predator eggs experience an almost fourfold reduction of predation. Hence, by attacking the vulnerable stage of their predator, prey deter adult predators and thus reduce their own predation risk. This provides a novel explanation for the killing of vulnerable stages of predators by prey and adds a new dimension to anti-predator behaviour.

### Keywords

Anti-predator behaviour, counterattack, interspecific killing, predator–prey interactions, stage structure.

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### INTRODUCTION

There is growing awareness that size structure or age structure is important in predator–prey interactions (de Roos & Persson 2001). For example, young, smaller stages of predator species are vulnerable to predation by conspecifics (Elgar & Crespi 1992), intra-guild competitors (Polis *et al.* 1989; Polis 1991; Palomares & Caro 1999) or hyperpredators, whereas older, large predators are invulnerable. Intriguingly, prey may also reach a size at which they can kill the younger, harmless stages of their predator (Girault 1908; Eaton 1979; Aoki *et al.* 1984; Saito 1986; Whitman *et al.* 1994; Dorn & Mittelbach 1999; Faraji *et al.* 2002a,b). Because the victim is not necessarily consumed (Eaton 1979; Palomares & Caro 1999), killing may serve other purposes than food acquisition, such as reducing the risk of predation by removing a potential source of mortality (Eaton 1979; Saito 1986; Whitman *et al.* 1994). Since most killing is of smaller individuals by larger ones (Eaton 1979; Saito 1986; Polis *et al.* 1989; Sabelis 1992; Whitman *et al.* 1994; Palomares & Caro 1999), the vulnerable stages of predators will usually not impose an immediate threat to the killer, and the killer prey will thus not experience an

instantaneous reduction of predation risk. The effect of killing vulnerable predator stages is therefore thought to affect future predation risk of the killer prey or its offspring (Eaton 1979; Saito 1986; Whitman *et al.* 1994). However, experimental evidence for such future reduction of risk is lacking. In this paper, we show that killing of harmless, vulnerable predator stages leads to an *immediate* reduction of predation risk through effects on the behaviour of dangerous adult predators.

We studied the interaction between the omnivorous western flower thrips (*Frankliniella occidentalis*) and a predator of thrips larvae, the phytoseiid mite *Iphiseius degenerans* (Faraji *et al.* 2000, 2002a,b). The thrips and predatory mite co-occur in the Mediterranean region (de Moraes *et al.* 1986; CAB International 1993). The thrips feed on many plant species and on eggs of other herbivores, such as the two-spotted spider mite *Tetranychus urticae* (Trichilo & Leigh 1986). They also kill the eggs of several species of predatory mite, including *I. degenerans* and *Phytoseiulus persimilis*, a specialist predator of spider mites that also occurs in the Mediterranean region (de Moraes *et al.* 1986), but is harmless to thrips (Faraji *et al.* 2002a,b; Janssen *et al.* submitted). Thrips larvae of all instars do not just kill the eggs, but feed on them.

Killing predator eggs for defence or killing them for food are two alternative explanations for the same phenomenon, but not mutually exclusive. Killing of predator eggs may well have started as a defence with subsequent feeding as a secondary effect, or vice versa. However, it is sometimes possible to distinguish between the two explanations; if killing of predator eggs serves to supplement plant food, it is expected that thrips larvae will kill fewer eggs on good quality host plants than on low quality plants. This is indeed what was found for western flower thrips when feeding on eggs of the two-spotted spider mite (Agrawal & Klein 2000) and when feeding on eggs of the harmless predator *P. persimilis* (Janssen *et al.* submitted). However, thrips larvae killed equally high numbers of eggs of the dangerous predator *I. degenerans* on both poor (sweet pepper,  $3.1 \pm 0.4$  eggs/larva/day) and good (cucumber,  $2.6 \pm 0.3$  eggs/larva/day) host plants. The consumption of predator eggs on the good host plant did not lead to an increase in developmental rate or survival (survival with predator eggs: 0.87, without predator eggs: 1.0; developmental time with predator eggs:  $7.3 \pm 0.76$  days; without predator eggs:  $6.6 \pm 0.29$  days, Janssen *et al.* submitted). Hence, the killing of eggs of the dangerous predator on the superior host plant does not serve to supplement food, suggesting that it has another purpose.

In this paper, we investigate the effects of killing predator eggs on the predation risk of the 'killer' prey. Specifically, we test (1) whether prey discriminate between eggs of the harmless and the dangerous predator species; (2) if killing of predator eggs affects future predation risk by the predators emerging from the eggs; (3) whether adult predators are deterred by killed eggs, and (4) if this deterrence results in a lower predation risk of thrips near the killed eggs.

## MATERIALS AND METHODS

### **Discriminating between eggs of harmless and dangerous predators**

Thrips and predatory mites were reared according to methods detailed in Faraji *et al.* (2002a,b) and Janssen *et al.* (1999). All experiments were performed in a climate room at 25 °C, 70% RH and 16/8 photoperiod. Five 1-day-old-eggs of the harmless predator (*P. persimilis*) and 5 eggs of the dangerous predator (*I. degenerans*), similar in age and size, were added manually to cucumber leaf discs (diam. 24 mm), after which one young 2nd-instar thrips larva was added to each disc. The number and identity of eggs killed and alive were counted after 24 h. We tested a total of 54 thrips larvae.

### **Predation on thrips larvae by young predators**

One young 1st-instar thrips larva was incubated with five 1-day-old eggs of the dangerous predator on a leaf disc as

described above. These eggs hatch within 24 h, and we followed the fate of the thrips larvae and immature predator for 72 h. After this period, the thrips larvae were invulnerable to predation due to increase in size (van der Hoeven & van Rijn 1990). We tested 24 young larvae, each on a separate leaf disc.

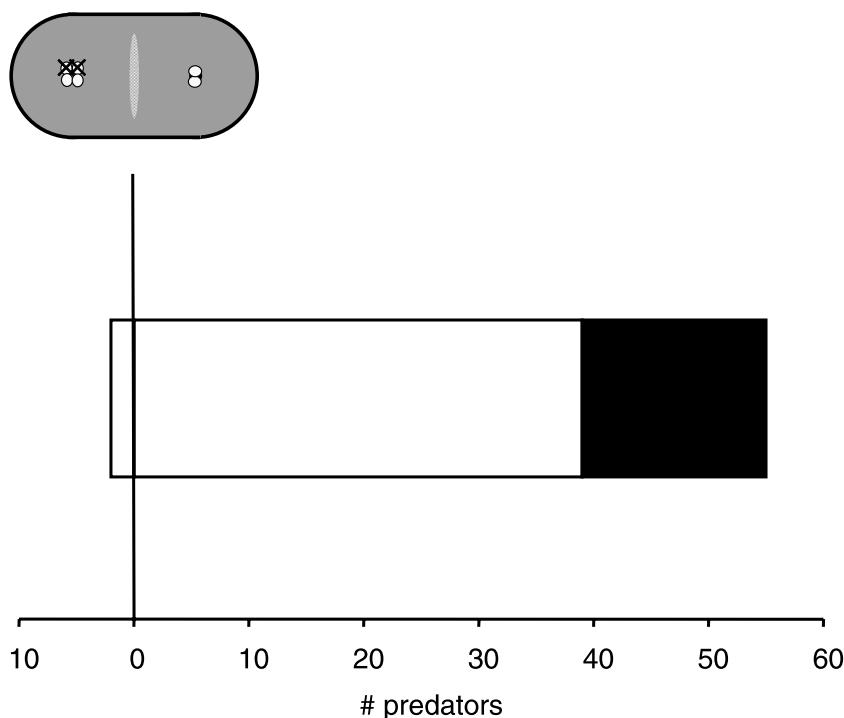
### **Oviposition of predators near damaged eggs**

We offered adult female predatory mites (*I. degenerans*) a choice between two small clusters, each consisting of two conspecific eggs. Two extra eggs were added to one randomly chosen cluster and were subsequently destroyed with a fine needle. This piercing resulted in explosion of the eggs, similar to what happens when thrips larvae kill them. Hence, both egg clusters consisted of two eggs, but one was contaminated with the contents of the destroyed eggs. To facilitate counting of new and old eggs, they were offered on an oval-shaped green plastic arena floating on water-saturated cotton wool (26 × 52 mm, see inset of Fig. 1 and Faraji *et al.* 2000). We considered eggs as being added to a cluster when they were oviposited within 2.5 mm from the cluster (Faraji *et al.* 2000). Food consisting of birch pollen was supplied at the centre of the arenas. One day after introducing the female to the experimental arena, the number of newly laid eggs was recorded and the distance from the resident eggs (inside or outside the circles) was scored. We tested a total of 100 adult female predators.

### **Predation risk of vulnerable thrips larvae near damaged predator eggs**

Arenas consisting of two leaf discs (diam. 36 mm), connected by a small strip of leaf vein (6–7 cm long, c. 3 mm wide) were cut from a cucumber leaf (inset of Fig. 2). The arenas were placed upside down on wet cotton wool in a Petri dish. Five young 1st-instar thrips larvae were placed on each leaf disc. Because the larvae could move from one disc to the other, and this would not allow a proper estimation of predation risk, we restricted movement of thrips larvae by adding a tiny amount of *Typha* pollen to each of the discs; thrips larvae will tend to aggregate near this pollen. To check further for movement of thrips larvae from one disc to the other, they were marked with red or blue fluorescent dust and each disc received larvae with one colour only.

Testing whether the deterrence of adult predators by damaged eggs results in reduced predation risk of vulnerable prey is not straightforward and therefore needs some explanation. Testing a cluster of intact eggs against a cluster of intact eggs with destroyed eggs would not be a proper set-up, because clusters of intact eggs are attractive



**Figure 1** Preference of adult female predatory mites *I. degenerans* to add eggs to a cluster of two undamaged eggs (right) or a cluster of two undamaged eggs contaminated with the contents of two destroyed eggs (left). Females were categorized as follows: those that only added eggs to one cluster (absolute preference, white bars); those that added at least one egg to one of the clusters and the rest away from both clusters (partial preference, black bars); those that added eggs to both clusters (no preference, six females, not shown); those that only oviposited away from both clusters (no preference, 37 females, not shown). Females had a significant preference to oviposit close to a cluster without destroyed eggs (Binomial test, white bars:  $P < 0.001$ , white plus black bars:  $P < 0.001$ ).

to predators (Faraji *et al.* 2000; Fig. 1) and more thrips larvae could be killed at the side with only intact eggs either because adult predatory mites avoid the cluster with damaged eggs, are attracted to the cluster with only intact eggs, or by both. Moreover, thrips larvae would also start killing eggs from the cluster of intact eggs; hence, the difference between the two sides of the set-up would disappear in the course of the experiment. Furthermore, testing damaged eggs only against no eggs would also not be a proper control because predators should also be deterred when attractive intact eggs are present close by the damaged eggs, since it cannot be expected that thrips larvae would be so efficient as to kill all predator eggs instantaneously. Therefore, the most critical test is to compare predation risk of thrips larvae that are either near damaged plus undamaged predator eggs or without any eggs.

Rather than forcing a female predator to oviposit on one of the two discs and subsequently wait for thrips larvae to damage eggs, we manually added 10 predatory mite eggs, 5 of which were destroyed on the disc with a sharp needle. Subsequently, one adult female predator, by far the most voracious stage, was released in the middle of the small strip connecting the two discs. The position of the adult predator, predator eggs, and dead and alive thrips larvae was scored after 24 h. A total of 20 replicates was carried out.

## RESULTS

### Discriminating between eggs of harmless and dangerous predators

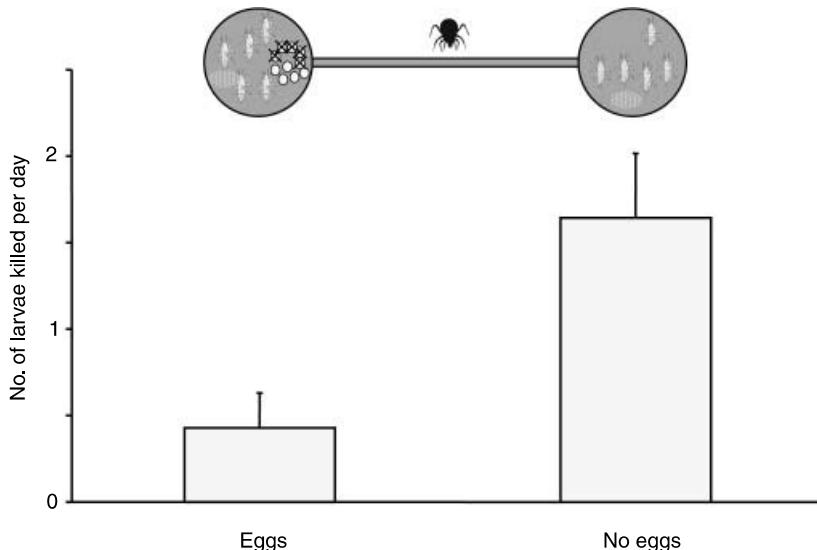
Thrips killed on average  $1.93 \pm 0.25$  eggs/day of the dangerous predator and only  $0.68 \pm 0.13$  eggs/day of the harmless predator (Wilcoxon matched pair test,  $n = 54$ ,  $Z = 4.41$ ,  $P < 0.001$ ). Hence, thrips can discriminate between eggs of the dangerous and of the harmless predator species.

### Predation on thrips larvae by young predators

Only three out of 24 thrips larvae were killed by the immature predators that hatched from the eggs, whereas the rest reached the invulnerable mid-second instar (van der Hoeven & van Rijn 1990). Thus, the juvenile predators that emerge from eggs do not pose a high risk to thrips larvae, and killing of these eggs by thrips larvae will not result in a large decrease of future predation risk.

### Oviposition of predators near damaged eggs

Predatory mites preferably added eggs to the cluster without damaged predator eggs (Fig. 1). Hence, they can recognize the remains of killed eggs and avoid adding eggs to clusters with damaged eggs.



**Figure 2** Predation on young 1st-instar thrips larvae by the predatory mite *I. degenerans* in presence (left bar + SE) or absence (right bar) of damaged and undamaged predator eggs. The difference between the numbers of larvae killed on each side was significant (Wilcoxon matched pairs:  $n = 14$ ,  $Z = 2.67$ ,  $P = 0.0077$ ).

#### Predation risk of vulnerable thrips larvae near damaged predator eggs

Most thrips larvae were found, either dead or alive, on the disc on which they were introduced. Six replicates were discarded because the predatory mite escaped from the arena, despite the presence of abundant food. In absence of thrips larvae, predators hardly ever escape from such arenas with undamaged eggs (S. Magalhães, personal observation), so these escapes are further evidence for deterrence of adult predators by the destroyed eggs. Although adult predators could easily attack thrips larvae on both leaf discs (they walked from one disc to the other within minutes), the predation risk of thrips larvae near killed eggs was 3.8 times lower than that of larvae on the leaf disc without eggs (Fig. 2). Thrips larvae killed some of the provided intact eggs (on average 1.75 of the 5 predator eggs), and they may also have killed freshly oviposited eggs, but no remains could be found. This clearly shows that the presence of damaged predator eggs indeed reduces predation risk of thrips larvae, even on a small arena as used here.

#### DISCUSSION

Thrips larvae were capable of discriminating between the eggs of a harmless and a dangerous predator, killing significantly more eggs of the dangerous predator. Except for size, this discrimination may be based on all sorts of differences in properties of the two species, but it is noteworthy that the eggs of the harmless species seem to be slightly more nutritious (Janssen *et al.* submitted). If thrips larvae kill the eggs of predators only for feeding, one would expect the thrips larvae to kill more eggs of the harmless predator, and

not of the dangerous predator. Moreover, the excessive killing of eggs of dangerous predators does not lead to an increase of juvenile survival or developmental rate on a superior host plant (Janssen *et al.* submitted), and we therefore hypothesized that it serves as a counter-attack (Saito 1986). It has been suggested that killing of juvenile predators could reduce future predation risk of the killing prey (Eaton 1979; Saito 1986; Whitman *et al.* 1994). However, the killing of predator eggs did not lead to a large reduction of future predation by the young predators that would hatch from the eggs. We found that adult predators avoid ovipositing near killed predator eggs (Fig. 1), which opens the way for thrips larvae to deter adult predators by killing predator eggs. Indeed, deterrence of adult predators by killed eggs reduced predation risk almost fourfold (Fig. 2). Hence, by attacking the vulnerable stage of their predator, prey deter adult predators and thus reduce their own predation risk.

There are several limitations to the effectiveness of the killing of eggs by thrips larvae as a means to reduce predation risk. First, predators will only be deterred by killed eggs if they can find food and reproduction sites elsewhere, and deterrence may therefore be conditional on the presence and behaviour of prey elsewhere. Second, there are several alternatives for both juvenile thrips and adult predators to avoid predation. Juvenile thrips could reduce predation risk by simply leaving areas with predator eggs. Since thrips larvae are much less mobile than predators, this escape is probably not very effective. Adult predators could kill all thrips larvae near egg clutches, thus making the area safe for their offspring. However, new larvae will emerge from thrips eggs that are inserted in the leaf tissue and cannot be killed by predatory mites, and the female predator would thus have to patrol the environment of her eggs

frequently to kill any newly hatched thrips larvae. Meanwhile, there would be no food available to the adult female, forcing her to search for food elsewhere and leave her eggs unprotected. Therefore, it is probably better for female predators to find safe oviposition sites rather than trying to kill all thrips larvae at dangerous oviposition sites. However, the decision of a female predator to either remain in an area with intact and damaged eggs may well be conditional on the kin-relatedness of the eggs and the expected reproductive success at other sites.

Our results show that prey can deter dangerous, invulnerable predators through interspecific infanticide, resulting in a reduction of their own predation risk. Numerous predators of all major taxa pass through a vulnerable stage, and we therefore expect such counter-attacks by prey to occur in many cases. Indeed, we found several reports of prey killing vulnerable predator stages (Girault 1908; Eaton 1979; Aoki *et al.* 1984; Saito 1986; Whitman *et al.* 1994; Dorn & Mittelbach 1999; Palomares & Caro 1999), including prey species that are regarded as purely herbivorous (Girault 1908; Aoki *et al.* 1984; Saito 1986; Whitman *et al.* 1994). Our findings shed new light on the function of such killing and show that size structure or stage structure of prey and predator populations may cause their interactions to be much more complex than thought so far.

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