



## Witnessing predation can affect strength of counterattack in phytoseiids with ontogenetic predator–prey role reversal



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Predators are usually larger than their prey, but because size changes during ontogeny, predator and prey roles may be reversed. Hence, an individual may be prey when juvenile, but as an adult, it may counterattack the juveniles of its childhood enemy. Earlier, we showed that juvenile predatory mites, *Iphiseius degenerans*, recognize adults of another predatory mite species that attacked and killed conspecifics of the juveniles. Upon becoming adult, these former juveniles showed an increase in attacks on juveniles of their enemy. Here, we tested whether adult females of *I. degenerans* show a similar response after witnessing attack on conspecific juveniles in the presence of suitable alternative food (i.e. pollen). We used three predatory mite species involved in reciprocal intraguild predation. We found mixed results: the rate of attack on juveniles of one species of predator, *Neoseiulus cucumeris*, did increase after witnessing the killing of conspecific juveniles, but the rate of attack on juveniles of another species, *Amblyseius swirskii*, did not increase after such an experience. Furthermore, we found no conclusive evidence for species-specific antipredator responses. It is unlikely that cues of previous predation events affected the behaviour of adult predatory mites, because the trials were conducted on new experimental arenas free of predation cues. We conclude that adult predatory mites can change their antipredator behaviour in response to having witnessed predation on vulnerable juvenile conspecifics.

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It is well established that prey change their behaviour after experiencing predators so as to reduce the subsequent risk of predation (Barbosa & Castellanos, 2005; Lima, 1998; Lima & Dill, 1990; Tollrian & Harvell, 1999). This behavioural change may occur after perceiving the predators by contact or vision (Alvarez & Nicleza, 2006; Griffin, Evans, & Blumstein, 2001) or via chemical cues such as alarm pheromones from conspecific or heterospecific individuals (de Bruijn, Egas, Janssen, & Sabelis, 2006; Ferrari, Capitanía-Kwok, & Chivers, 2006), predator-related chemicals (Alvarez & Nicleza, 2006; Chivers, Wisenden, & Smith, 1996; Dalesman, Rundle, Coleman, & Cotton, 2006; Turner, Turner, & Lappi, 2006) and via chemicals associated with predation on other conspecific prey individuals (Oku, Yano, Osakabe, & Takafuji, 2003). Furthermore, prey with such experience may show antipredator responses even to novel predator species (Ferrari, Lysak, & Chivers, 2010; Griffin et al., 2001). In addition, predation risk varies

with the species of predator. Because antipredator responses come at a cost (Abrahams & Dill, 1989; Grand & Dill, 1997; Matsumoto, Itoaka, & Nishida, 2002; Pallini, Janssen, & Sabelis, 1998), it is important for the prey to identify the enemy and to tune its antipredator behaviour to the current enemy.

Apart from the differences in predation risk imposed by different species of predator, the vulnerability of prey changes with their ontogenetic development, for example owing to increased body size. Hence, the appropriate antipredator behaviour of a prey will depend not only on predator identity, but also on prey size relative to that of its predator. In arthropods, for example, eggs and juveniles of prey are usually more vulnerable to predation than adults. Yet, adults often display behaviour to reduce predation on their vulnerable offspring. Adult females, for example, may avoid ovipositing at sites with higher predation risk (Angelon & Petranka, 2002; Blaustein, Kiflawi, Eitam, Mangel, & Cohen, 2004; Bond, Arredondo-Jiménez, Rodóriguez, Quiroz-Martínez, & Williams, 2005; Faraji, Janssen & Sabelis, 2002), and parents may protect their offspring against predators (Klug, Chin, & St Mary, 2005; Magalhães, Janssen, Montserrat, & Sabelis, 2005; Requena, Buzatto, Munguía-Steyer, & Machado, 2009; Trumbo, 1996).

Although it is generally assumed that predators attack and prey avoid predation, a species acting as a predator when adult (and

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larger) may be a prey when juvenile (and smaller). Thus, reversals of predator and prey roles may occur during ontogeny. For example, Saito (1986) showed that males and females of a spider mite prey kill larvae of their predator, and suggested that this functions as a form of biparental care. Barkai and McQuaid (1988) showed that the benthic communities of two islands off the west coast of South Africa differ considerably: on one island, the community is dominated by rock lobsters, which prevent the establishment of mussels and whelks by feeding on them, whereas the community of the other island is dominated by whelks, which attack and kill invading rock lobsters. A third example is that of predatory mites that attack first-instar larvae of the Western flower thrips, whereas all mobile stages of the thrips consume the eggs of the predatory mites (Janssen, Faraji, van der Hammen, Magalhães, & Sabelis, 2002). There are numerous other examples of such ontogenetic role reversals (Aoki, Kuroso, & Usuba, 1984; Eaton, 1979; Girault, 1908; Palomares & Caro, 1999; Polis, 1991; Polis, Myers, & Holt, 1989). However, the consequences of role reversals for the behaviour of individuals have rarely been studied (Choh, Ignacio, Sabelis, & Janssen, 2012).

We previously studied role reversals in three predatory mite species: *Iphiseius degenerans* (Berlese), *Neoseiulus cucumeris* (Oudemans) and *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae) (Choh et al., 2012). Populations of mixed stages of these species co-occur on plants in the Mediterranean area (De Moraes, McMurtry, Denmark, & Campos, 2004), where they feed on various plant-feeding and fungus-feeding mites and on plant pollen. Moreover, adults of each mite species feed on the juvenile stages of the other species. We previously showed that exposure of juvenile prey to adult predators resulted in behavioural changes after becoming adult: adult prey with such experience killed juvenile predators at a faster rate than prey that had not been exposed (Choh et al., 2012). This increased killing deterred adult predators, thus reducing predation risk for the offspring of the prey (Choh et al., 2012; Magalhães et al., 2005). Here, we investigated whether witnessing predation on juvenile conspecifics changes the behaviour of adult prey towards juvenile predators.

## METHODS

### Mite Cultures

*Iphiseius degenerans* originated from Rabat, Morocco and *N. cucumeris* was obtained from the Glasshouse Crops Research Station, Naaldwijk, The Netherlands (van Houten, van Rijn, Tanigoshi, van Stratum, & Bruin, 1995). The rearing methods are described by van Rijn and Tanigoshi (1999). *Amblyseius swirskii* was originally collected in 1997 in Israel and Jordan and was reared according to Nomikou, Janssen, Schraag, and Sabelis (2001). In short, we reared each species on separate plastic arenas placed on top of a sponge in a water-containing tray. The edges of the arenas were covered with tissue paper that extended into the water in the tray. In this way, the wet tissue served both as a barrier and as a water source. Cultures of *I. degenerans* were fed with birch, *Betula pubescens*, pollen and *N. cucumeris* and *A. swirskii* were fed with *Typha* sp. pollen twice per week. The different species were maintained on different pollen species for historical reasons. All mite species were maintained only on pollen without any animal prey as a food source. Conditions of rearing and experiments were  $25 \pm 1$  °C, 16:8 h light:dark and  $60 \pm 5\%$  relative humidity.

### Exposure to Predation on Juvenile Conspecifics

Adult females of *I. degenerans* were subjected to one of the following treatments (Fig. 1). In the first two treatments, an adult

female of *I. degenerans* (10–14 days old since egg deposition) was placed for 24 h on a plastic disc (3.2 cm diameter) on water-saturated cotton wool in a plastic container together with five conspecific juveniles (1 day old since emergence from eggs) and one adult female of another predatory mite species (*N. cucumeris* or *A. swirskii*, 10–14 days old since eggs were deposited). In this way, adult females of *I. degenerans* witnessed predation on conspecific juveniles by adult females of another predator species. The third treatment served as a control for cannibalism; as adult *I. degenerans* will kill and consume unrelated juveniles, some of the mortality observed in the first two treatments may have been caused by cannibalism. Because the frequency of cannibalism is low in the presence of pollen (Montserrat et al., 2007; Montserrat, Magalhães, Sabelis, de Roos, & Janssen, 2012), and there was ample pollen available here, cannibalism was expected to be of minor importance. Nevertheless, we incubated two adult females of *I. degenerans* as well as five juvenile conspecifics on the same disc. After 24 h, one of the two adult females of *I. degenerans* was selected randomly to be tested (see below).

Possibly, the behaviour of the adult females changes not only as a result of witnessing predation on juvenile conspecifics, but also by experiencing the presence of other predators. We therefore included two more treatments as controls (Fig. 1). In the fourth treatment, we exposed adult females of *I. degenerans* to an adult female of *N. cucumeris* and in the fifth treatment we exposed them to a conspecific adult female, but in both treatments no juvenile *I. degenerans* were present. Therefore, the adult females of *I. degenerans* did not witness predation on juveniles. It was impossible to include a control with adult *A. swirskii*, because, unlike *I. degenerans* and *N. cucumeris*, the adults of *A. swirskii* also kill eggs of *I. degenerans* and this would affect the experience of *I. degenerans* on the same disc. In all experiments, ample amounts of *Typha* sp. pollen were provided as food for all predators at the centre of the discs.

The number of juveniles of *I. degenerans* that survived this exposure to conspecific and heterospecific adult females was assessed after 24 h (Fig. 1). This survival was compared by analysing the proportion of surviving juveniles with a generalized linear model (GLM) with a quasibinomial error distribution to correct for overdispersion (Crawley, 2007), followed by analysis of contrasts between treatments, using the ‘multcomp’ package (R Development Core Team, 2010).

Immediately after this experience, the adult females of *I. degenerans* with different experience as explained above were each placed on a new plastic disc (3.2 cm diameter) together with five juvenile heterospecific predators (*N. cucumeris* or *A. swirskii*), 1 day old since egg hatching. The discs were placed on top of water-saturated cotton wool in a plastic container and had ample amounts of *Typha* sp. pollen at the centre of the disc. Because pollen is a better food source than juvenile predators (Montserrat, Magalhães, Sabelis, de Roos, & Janssen, 2008), the adult females of *I. degenerans* did not need to feed on the juvenile heterospecific predators for survival and reproduction and, thus, if they fed on heterospecific juveniles, there were likely to be other reasons to do so. The number of surviving juvenile *N. cucumeris* or juvenile *A. swirskii* was assessed 1, 3, 5 and 24 h after their introduction (Fig. 1). Because we took juveniles of *N. cucumeris* or *A. swirskii* (1 day old since hatching) from the same cohort and randomly assigned them to each treatment, there were no differences in age of the juveniles between treatments. Hence, differences in mortality will have been caused by differential predation by adult *I. degenerans* with different experience. All treatments were conducted at the same time and were replicated 18 times. Using survival analysis (Cox proportional hazards models of the survival library of R; Hosmer & Lemeshow, 1999; R Development Core Team,

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