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“Sleeping with the enemy”—predator-induced diapause in a mite

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Abstract Diapause in arthropods is a physiological state of dormancy that is generally thought to promote survival during harsh seasons and dispersal, but it may also serve to avoid predation in space and time. Here, we show that predation-related odours induce diapause in female adult spider mites. We argue that this response allows them to move into an area where they are free of enemies, yet forced to survive without food. Spider mites are specialised leaf feeders, but—in late summer—they experience severe predation on leaves. Hence, they face a dilemma: to stay on the leaf and risk being eaten or to move away from the leaf and risk death from starvation and thirst. Female two-spotted spider mites solve this dilemma by dramatically changing their physiology when exposed to predation-associated cues. This allows them to disperse away from leaves and to survive in winter refuges in the bark of trees or in the soil. We conclude that the mere presence of predation-associated cues causes some herbivorous mites to seek refuge, thereby retarding the growth rate of the population as a whole: a trait-mediated indirect effect that may have consequences for the stability of predator–prey systems and for ecosystem structure.

Keywords Diapause · Indirect effect · Predation ·
Tetranychus urticae · Trait-mediated effect ·
Typhlodromus pyri

Introduction

Diapause in arthropods is commonly considered as a means to survive harsh climatic conditions (Tauber et al. 1986; Danks 1987), but it is also hypothesised to function as a mechanism to escape from predation (Hairston 1987, 1998; Gliwicz 2003). Indeed, roach induce waterfleas (*Daphnia magna* Strauss) to enter diapause in an invulnerable stage (winter eggs; Slusarczyk 1995, 1999; Pijanowska and Stolpe 1996).

Spider mites are specialised leaf feeders (Lindquist 1998), sucking the contents of leaf parenchymal cells and excreting the excess water by defecation. They are not designed to conserve water (e.g. their body plan lacks Malpighian tubules; Lindquist 1998); if taken away from a leaf, spider mites dry out rapidly. Hence, when they choose to abandon the leaf environment, they must avoid water loss and decrease metabolic rates. A likely mechanism to achieve this is diapause development, which dramatically changes their physiology, thereby allowing dispersal away from leaves and survival in winter refuges, i.e. bark crevices and soil litter (Veerman 1985).

In temperate regions, spider mites face severe predation in late summer, because predators numerically respond to increased prey density (Rabbinge 1976; Helle and Sabelis 1985) and because predatory mites are attracted to plant SOS signals induced by phytophagy (Dicke et al. 1990). If predators become abundant or aggregate in the leaf environment, the leaf-feeding mites face a dilemma: to stay on the leaf and risk being eaten or to move away from the leaf and risk death from starvation and thirst. Seeking refuge from leaf-inhabiting natural enemies requires moving away from the leaves, which in turn requires avoiding desiccation and switching to a slow metabolic rate. Spider mites in refuges do not feed, thus precluding betrayal to

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their foes by feeding-induced plant signalling. Based on preliminary experiments (Kroon et al. 2004, 2005), we hypothesise that cues associated with predation enhance diapause induction in the two-spotted spider mite (*Tetranychus urticae* Koch). The ensuing change in metabolism would allow adult females to survive longer without food and to disperse into enemy-free space even if this harbours no food. In this article, we test whether individuals enter diapause more readily when exposed to predation-related odours, without being exposed to predators themselves.

Materials and methods

Study system

To test for the effect of predation cues on diapause incidence, we used a Greek spider mite strain referred to as ‘Thessaloniki-II’ in previous diapause studies (Koveos et al. 1993a, b; Kroon et al. 2004). At 18°C, part of the female population enters diapause when exposed to long-night photoperiods. This feature of incomplete diapause (i.e. less than 100% of individuals enter diapause) allows us to test whether predation cues have an added effect on diapause incidence. The spider mites were reared in the laboratory on detached bean leaves (*Phaseolus vulgaris* L.) under short-night photoperiod (17 h light and 7 h darkness or LD 17:7). Juvenile spider mites are most sensitive to diapause induction, and diapause becomes apparent in the adult phase. Adult females undergo a change in behaviour and a characteristic colour change from greenish to orange when entering diapause. This colour change reflects a modified carotenoid metabolism (Veerman 1985) and is used as criterion for identifying the diapause state. The predatory mite strain (*Typhlodromus pyri* Scheuten) was reared in the laboratory at LD 17:7 on plastic units and fed pollen of broad bean, *Vicia faba* L. (Kroon et al. 2004).

Experiment

To test our hypothesis, groups of juvenile spider mites (i.e. the phase most sensitive to diapause induction) on bean leaves were exposed to an air stream with volatile cues emanating from bean leaves with spider mites and predatory mites. Other groups were exposed simultaneously to cues from leaves with spider mites only (Fig. 1). The response to predation cues was quantified as the fraction of diapausing female mites in the predation treatment minus the fraction in the control.

Diapause incidence was compared between spider mites on bean leaves, either exposed to volatile chemicals emanating from an upwind source of predator-associated odour (bean leaves with spider mites and predators) or

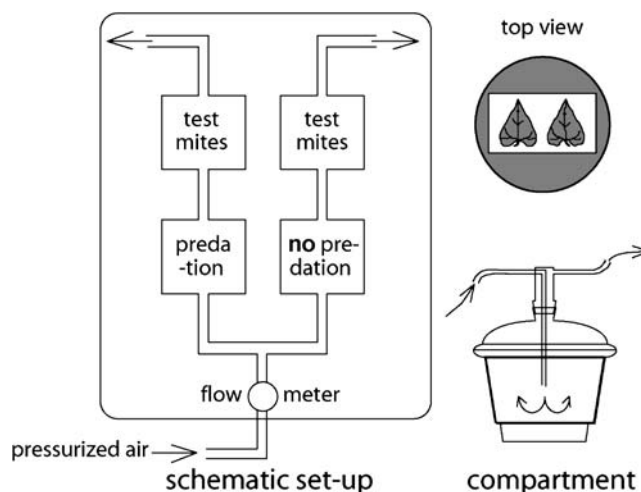


Fig. 1 Exposure of spider mites to volatile predator-associated cues in a setup with two parallel sets of serial compartments. Arrows indicate a unidirectional continuous air stream. Odour sources were placed in the upwind compartments, odour-exposed leaves in the downwind compartments (*test mites*). An odour source consisted of two bean leaves either infested with spider mites and predatory mites (*preda-tion*), or with spider mites alone (*no predation*)

exposed to cues from an upwind control odour source (bean leaves with spider mites only). The setup comprised of two parallel wind tunnels, each consisting of two interconnected compartments, i.e. glass desiccators (inner diameter at the level of the leaves—150 mm), linked with polyvinyl chloride tubelets (Fig. 1). This setup was positioned in a climate cabinet controlled at LD 10:14 and 18°C. Pressurised air entered the setup via a flow meter and the flow rate was set at 10 L/h. All four compartments contained two detached bean leaves on a layer of cotton wool on wet sponges (Fig. 1). The bean leaves in the two upwind compartments each harboured approximately 500 *T. urticae* in all developmental stages, either with ten adult female predatory mites per leaf (source of predator-associated odour) or without predators (control odour source). The downwind compartments contained the odour-exposed mites on leaves. The mites could not disperse from the leaves due to the water-soaked cotton wool surrounding the leaves.

For each replicate, groups of female spider mites were allowed to lay eggs for 24 h at LD 17:7 and 25°C on four detached bean leaves. The next day, the mites were removed and leaves with eggs were placed in the downwind compartments. The odour sources were introduced in the upwind compartments 8 days after the start of the experiment, just before hatching of the spider-mite eggs on the odour-exposed leaves. The setup was now closed and left undisturbed until the end of the experiment. Four weeks after the start of the experiment, the number of diapausing and non-diapausing female mites on each of the odour-exposed leaves were scored. This was used to

calculate two fractions of diapausing mites per treatment in each of six replicates. As a precaution, any potential asymmetries in the experimental setup were averaged out by interchanging odour sources between the two parallel compartments at the onset of each replicate experiment.

Statistical analysis

Data on diapause incidence were transformed ($\arcsin \sqrt{[\text{fraction mites in diapause}]}$) to improve normality and then subject to analysis of variance (ANOVA). Since diapause incidence can vary between replicates, due to small deviations in light, temperature or others, the replication factor was treated as a blocking factor (see Chapter 10 in Quinn and Keough 2002).

Results

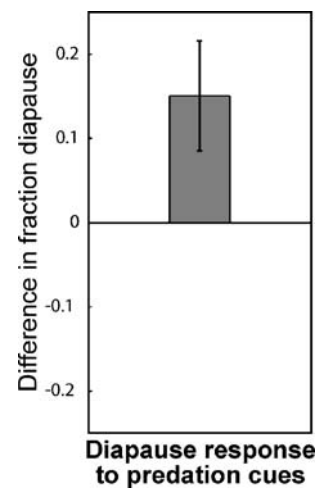
We found that diapause incidence was significantly higher when spider mites had been exposed to predation-associated cues (Fig. 2). In five out of six replicate experiments, the fraction diapause among mites exposed to these cues was higher than in the control and the average diapause response to these cues was significant (ANOVA— $F_{6,12}=3.04$, $p<0.05$; Fig. 2). On average, diapause incidence was 15% higher than in the control experiments (mean \pm standard error of the mean (SEM) over all replicates: control $24.7\% \pm 9.8$; predation cue treatment $40.0\% \pm 12.2$). Thus, when volatiles signal predation, spider mites switch to low metabolic activity and this will help them to survive outside the leaf environment. Had they not undergone this switch, they would be doomed to die within a few days due to desiccation.

Discussion

Predator-associated volatile cues can stem directly from the predators, but they can also be produced by prey in reaction to the predator, for instance when prey is alarmed, injured or dead (Dicke and Grostal 2001). For spider mites, in particular, there is evidence that they respond to odours from injured conspecifics (Janssen et al. 1997; Oku et al. 2003), but to date, the relevant chemicals have not been identified. Chemical analysis will be necessary to identify the origin of the diapause-modifying cues; odours from injured individuals seem to be a good starting point in the search for such chemical cues, but one may also think of alarm pheromones released by the spider mites upon perception of predatory mites (Janssen et al. 1997).

Evidently, part of the spider mite population responds to current predation risk by entering diapause and developing

Fig. 2 Exposure to volatile predator-associated cues increases diapause incidence among mites exposed to predation-associated cues. Error bar indicates SEM



a migratory response which brings them in a refuge without food. In doing so, they opt for a long-term physiological change, i.e. a dormant state that can only be terminated under special conditions (e.g. after a cold period; Veerman 1985), and they give up current-season reproduction, which may represent a considerable fitness cost. Hence, signals of predation—not predation per se—affect prey abundance. Since these signals are predator-induced and alter the state of prey vulnerability, these effects on the prey are indirect and trait-mediated (Schmitz et al. 2004; Ohgushi et al. 2007).

Why do not all spider mites enter diapause when signals of predation are around? Those not entering diapause may face predation risks, yet produce another generation before entering diapause under the influence of abiotic environmental factors. Thus, near the end of the summer season, spider mites face the difficult decision whether to avoid predation, enter diapause and give up current reproduction or whether to take the risk of being eaten, face competition for food, yet reproduce one more generation in the current season. Which of the two decisions is best in terms of relative fitness will vary with the biotic and abiotic conditions. Thus, one should be cautious in interpreting the diapause response to predation measured here as being low or high. The ultimate success of each of the two decisions depends on the combination of survival from predation and survival during winter, as well as on the decisions made by the other individuals in the population (as this determines the number of food competitors).

The dynamics of refuge use has received little attention. Not only may predators induce prey to seek refuge and adapt their metabolic demand to this new environment but they may also induce competition for refuge space. This lack of attention is surprising because the details of refuge use are known to matter to the stability of predator–prey models (McNair 1986, 1987; Schmitz et al. 2004; Schreiber et al. 2006). Studying the population consequences of refuge use is a promising area of research and will provide

new insight into trait-mediated indirect effects on the dynamics of predator–prey systems.

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