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The effect of predation risk on an acarine system

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Current theory on trait-mediated interactions in tri-trophic food chains shows that antipredator behaviour of the middle species can cause similar indirect effects giving rise to trophic cascades as mediated by density changes. In this article, the effect of predation risk in a tri-trophic food chain (bean plant—two-spotted spider mite prey—predatory mite, *Phytoseiulus persimilis*) is measured, both on plants (changes in leaf damage) and spider mites (changes in egg numbers, mortality rate and dispersal behaviour), under two risk scenarios. In the predator risk treatment a predatory mite was caged in an experimental cell that was placed above a leaf disc with spider mites. This prevented the predator from subduing prey while the predator was perceived by spider mites as a potential threat. In the predator cues treatment a predatory mite was introduced to the leaf disc for 24 h before placing the spider mites on the disc. Compared to control without predators, after four days we observed in both risk treatments a nonsignificant increase in plant damage per spider mite and a significant decline in spider mite fecundity. No significant effect of predation risk on spider mite mortality was observed. We also showed that the above effects are not uniformly distributed in time. For example, the spider mite fecundity and dispersal rate in the predator cues treatment were significantly different from the control only the first day. We also found that under predator cues treatment, walking activity of the spider mites increased significantly.

Keywords: food webs; indirect interaction; mites; *Phytoseiulus persimilis*; predation risk; *Tetranychus urticae*; trait-and density-mediated interaction; trophic cascades

The ability to detect and avoid predators is a crucial trait that influences survival, a key component of animal fitness. Behavioural traits related to predation risk are: habitat or diet shift, increase use of refugia, changes in time and/or activity budget (reviewed in Lima & Dill 1990; Bolker et al. 2003), delayed oviposition (Hoffmeister & Roitberg 1997) and diapause induction (Kroon et al. 2004, 2005). Abrams (1996) introduced the idea that trait responses of consumers to predators can lead to a wider range of indirect interactions (i.e. interactions between resources and predators that are mediated by consumers) in food webs than those that are mediated via direct predation effects. A classical example of indirect density-mediated interactions in food chains are trophic cascades where an increase in top predators leads to an increase in resources due to decrease in consumer densities (Paine 1980; Carpenter et al. 1985; Polis 1999; Polis et al. 2000). However, recent studies (reviewed in Schmitz et al. 2004) suggest that behavioural changes in the intervening species can also give rise to the cascading effect. In fact, whereas density effects are limited by physiological constraints of predators (the gut capacity, the rate of metabolism, etc.), trait-mediated effects caused by mere presence of predators (that need not feed on herbivores) are not limited by these constraints, and influence the entire prey population. Thus, potentially, they can lead to a strong cascading effect (Peacor & Werner 2001).

In this study we consider a tri-trophic food chain consisting of bean plants, *Phaseolus vulgaris* L., var. Katka

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(resource), the two-spotted spider mite, *Tetranychus urticae* Koch. (herbivorous consumers), and the predatory mite, *Phytoseiulus persimilis* A.-H. (predators). To study the effects of predation risk we created two types of risk treatments. In the first treatment ('predator risk'), a predatory mite was caged in a cell above the leaf disc preventing it from feeding on spider mites, while in the second treatment ('predator cues'), leaf discs were exposed to predators before placing the herbivores on them. Since direct contact of herbivores with predators was not possible in either type of risk treatment, spider mites could be warned about the potential risk by olfactory stimuli and/or by perceiving predators moving by sight (Helle & Sabelis 1985). The effects of chemical substances (called info chemicals) on the behaviour of prey mites were reviewed by others (Dicke 1986; Janssen et al. 1997; Kriesch & Dicke 1997; Pallini et al. 1997, 1999; Grostal & Dicke 1999; Oku et al. 2003a, b). The chemical compounds are either volatile and/or contact. While the former are perceived without contacting the source, the latter evoke a behavioural response only after a direct physical contact with the solid or liquid form. Our two types of risk treatments were designed to study the effect of these chemical compounds on spider mite behaviour separately. In all treatments we observed the damage caused by herbivores to the bean leaf, the total number of spider mite eggs per leaf disc, the number of dead spider mites on the disc, and the number of spider mites that escaped from the disc. In separate experiments we observed the walking pattern of spider mites on a predator-exposed leaf disc and time dynamics of *T. urticae* fecundity, mortality and dispersal rate on a leaf disc pre-exposed to predator.

Based on some recent studies, we expect that predation risk in our acarine system can cause: (1) a trophic cascading effect (Schmitz et al. 1997), (2) a decrease in fecundity (e.g. due to changes in energy budget caused by predation risk, Grostal & Dicke 1999; Oku et al. 2004, 2006), (3) increased tendency of spider mites to escape from leaf discs (Werner & Peacor 2003; Oku et al. 2003a, b, 2004), (4) an increase in herbivore mortality (Schmitz et al. 1997), (5) changes in the walking pattern of spider mites due to changes in activity level (Werner & Peacor 2003), and (6) increase in fecundity of spider mites after exposition to predation risk (postponed oviposition, Hoffmeister & Roitberg 1997).

METHODS

There were three series of laboratory experiments. The first series studied the effects of predation risk on plant damage, *T. urticae* fecundity, mortality and dispersal. The second series of experiments focused on the effect of predator cues on walking pattern of *T. urticae*. The third series of experiments evaluated the temporal effect of predation risk on *T. urticae* fecundity, mortality and dispersal.

All series of experiments used a specially designed experimental unit. The unit consisted of a disc (diameter 13 mm) cut from a bean leaf and put individually on a piece of plastic foam (35 × 35 mm and 10 mm high approximately) in a petri dish filled with water to supply the leaf disc with moisture. A predatory mite cell, assembled for the predator risk treatment, was placed on top of the leaf disc. The cell was made of two rings cut from a white plastic sheet 1-mm thick (upper one with 35 and 16 mm outer and inner diameter, respectively; bottom one with 35 and 22 mm outer and inner diameter, respectively) and glued together (Fig. 1). Fine mesh (0.2-mm opening) was glued between the rings and on top of the upper ring to form a small cell. When the cell was put above the leaf disc, there was approximately 1 mm distance between the mesh and the leaf surface allowing unrestricted movement of the herbivorous mites on the leaf disc. The predatory mite inside the cell was not able to catch the herbivorous mites, but the distance between the predator and its prey was small enough to ensure that the odour of predatory mite, i.e. volatile info chemicals released by *P. persimilis*, was perceived by spider mites as a potential threat. The cell did not physically prevent spider mites to leave the leaf disc (Fig. 1) in which case the spider mites drowned on the water saturated plastic foam.

All experiments were carried out in climate controlled cabinets at a constant temperature of 25 ± 1°C and a photoperiod of 18:6 h light:dark cycle. We used one cabinet per treatment to avoid possible interactions via volatile substances between treatments.

Predation Risk

Design of experiments

The experiment was arranged in a randomized block design with four experimental treatments per block. Leaf

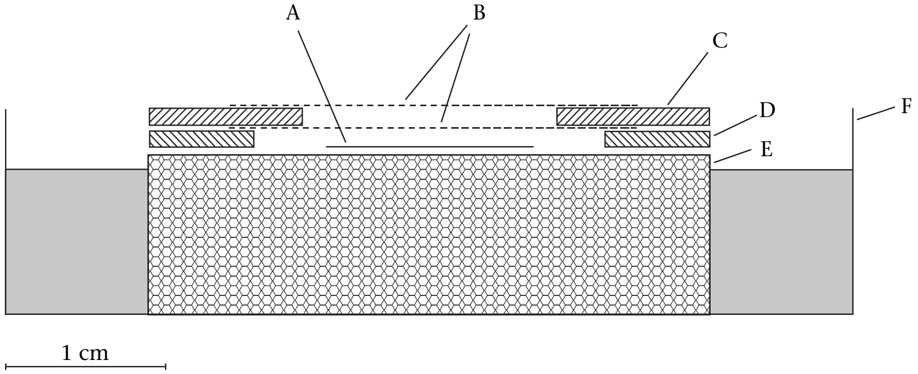

Figure 1. Side view of the experimental unit with a predatory mite cell. A = leaf disc; B = fine mesh; C = upper plastic ring; D = bottom plastic ring; E = water saturated plastic foam; F = petri dish filled with water.