How predatory mites learn to cope with variability in volatile plant signals in the environment of their herbivorous prey

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Abstract. When the chemical cues co-occurring with prey vary in time and space, foraging predators profit from an ability to repeatedly associate chemical cues with the presence of their prey. We demonstrate the ability of a predatory arthropod (the plant-inhabiting mite, Phytoseiulus persimilis) to learn the association of a positive stimulus (herbivorous prey, Tetramyces urticae) or a negative stimulus (hunger) with a chemical cue (herbivore-induced plant volatiles or green leaf volatiles). It has been suggested that the rate at which the integration of information becomes manifest as a change in behaviour, differs between categories of natural enemies (parasitoids versus insect predators; specialist versus generalist predators). We argue that these differences do not necessarily reflect differential learning ability, but rather relate to the ecologically relevant time scale at which the biotic environment changes.

Key words: associative learning, sensitisation, innate response, herbivore-induced plant volatiles, Phytoseiulus persimilis, olfactometer

Introduction

Plants are able to exploit the cognitive abilities of their inhabitants for their own interests, especially when these overlap with the interests of the inhabitants. One of many examples of this is the recruitment of arthropod predators to remove herbivorous attackers. Plants betray the presence of herbivores to predators by emitting odours induced by herbivore feeding (e.g. Turlings et al., 1995). These odours consist of blends which may vary with the species of host plant – even when attacked by the same herbivore, and with the species of herbivore – even when they attack the same species of host plant (Dicke et al., 1998; De Moraes et al., 1998). To cope with this bewildering variety
of information, predators may either specialise on one cue (innately or by imprinting) or they may adjust their behavioural response to any relevant odour associated with prey. The ability to learn associations between host and host-related cues has been extensively studied in parasitoids (Papaj and Lewis, 1993), but its role with respect to induced or constitutively released plant volatiles is little studied (but see Geervliet et al., 1998). For arthropods that are true predators, studies on associative learning and plant volatiles are in their infancy.

We studied whether and how associative learning plays a role in the orientation of the predatory mite, *Phytoseiulus persimilis* Athias-Henriot, to plant volatiles induced by feeding of their prey, the two-spotted spider mite *Tetranychus urticae* Koch. This prey mite is a phytophage with a vast array of host plants and the blends of herbivory-induced plant volatiles (HIPV) differ between hosts in qualitative and quantitative respects (e.g. Takabayashi et al., 1991, 1994). Olfactory responses of *P. persimilis* to these HIPV have been assessed for many combinations of host plant species and spider mites (Dicke et al., 1998), and using various types of experimental set-ups: Y-tube olfactometers (Sabelis and Van de Baan, 1983; Dicke et al., 1990a), vertical airflow olfactometers (Sabelis et al., 1984), wind tunnels (Sabelis and Van der Weel, 1993) and greenhouse releases (Janssen, 1999). These studies show that HIPV mediate arrestment on and attraction towards spider-mite infested plants. Among the many factors that influence these responses, the role of dietary history of the predatory mites is of particular relevance. Dicke et al. (1990b) found that *P. persimilis* reared on *T. urticae*-infested Lima bean prefer the odour from *T. urticae*-infested Lima bean over the odour from *T. urticae*-infested cucumber, and that this preference changes gradually to a preference for *T. urticae*-infested cucumber during a period of 7 days in which the predators were reared on *T. urticae*-infested cucumber (see also Krips et al., 1999 for similar results with gerbera as a host plant). The authors suggested that the predators learned to respond to cucumber odours by sensitisation, that is, by prolonged exposure the predators got used to cucumber odours and responded to them in the same way as they previously responded to bean odours (see also Takabayashi and Dicke, 1992). Papaj and Prokopy (1989) defined sensitisation as the gradual increase in response to a stimulus with repeated exposure to that stimulus. What Dicke et al. (1990b) have not yet shown is a gradual increase to cucumber odours in absence of a (positive) reinforcing stimulus (food).

We suppose that *P. persimilis* would greatly benefit from an ability to learn the association between *T. urticae*, that is its prey, and HIPV, that is the odours in the immediate vicinity of the prey. This supposition is rooted in the predator’s biology: it disperses passively on air currents, lands randomly