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Anthocorid predators learn to associate herbivore-induced plant volatiles with presence or absence of prey

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Abstract. We investigated how the plant-inhabiting, anthocorid predator, *Anthocoris nemoralis*, copes with variation in prey, host plant and associated herbivore-induced plant volatiles and in particular whether the preference for these plant odours is innate or acquired. We found a marked difference between the olfactory response of orchard-caught predators and that of their first generation reared on flour moth eggs in the laboratory, i.e. under conditions free of herbivory-induced volatiles. Whereas the orchard-caught predators preferred odour from psyllid-infested pear leaves, when offered against clean air in a Y-tube olfactometer, the laboratory-reared first generation of (naive) predators did not. The same difference was found when a single component (methyl salicylate) of the herbivore-induced plant volatiles was offered against clean air. After experiencing methyl salicylate with prey, however, the laboratory-reared predators showed a pronounced preference for this volatile. This acquired preference did not depend on whether the volatile had been experienced in the juvenile period or in the adult phase, but it did depend on whether it had been offered in presence or absence of prey. In the first case, they were attracted to the plant volatile in subsequent olfactometer experiments, but when the volatile had been offered during a period of prey deprivation, the predators were not attracted. We conclude that associative learning is the most likely mechanism underlying acquired odour preference.

Key words. *Anthocoris*, attraction, associative learning, aversion, *Cacopsylla*, infochemicals, innate response, methyl salicylate, olfactometer, pear, synomone, tritrophic interaction.

Introduction

Many plant-inhabiting insect predators are polyphagous (Sabelis, 1992). They feed on prey that are patchily distributed in space, available on specific host plants and for a limited period. Hence, they may have to switch to new prey and new host plants. To find their prey, they could use herbivore-induced plant volatiles. Each plant-herbivore combination, however, tends to produce different blends of volatiles. The predators are thus faced with a dazzling variety of information (Takabayashi *et al*., 1991; DeMoraes *et al*., 1998; Sabelis *et al*., 1999). Whether the predators rigidly specialize on certain cues or change preference by learning, is the subject of this article. We investigated whether and how anthocorid predators learn associations between (un)familiar cues and their prey.

We studied *Anthocoris nemoralis* (Fabricius), a predator that grows and reproduces best on a diet of psyllids and less so on aphids (Anderson, 1962a; Dempster, 1963). These predators feed from May to June mainly on aphids (e.g. on *Alnus* or *Salix*), but as aphid densities decline due to predation, migration or diapause, they have to switch to other prey on other host plants (Hill, 1957; Anderson, 1962b). From the end of June they often migrate into pear orchards, where they feed on pear psyllids. To locate their prey, they may use volatile plant chemicals that emanate from pear trees after induction by plant-feeding psyllids (Drukker & Sabelis, 1990; Drukker *et al*., 1992, 1995; Dwumfour, 1992; Scutareanu *et al*., 1997). Two compounds of herbivore-induced volatiles are thought to help predators find their prey: methyl salicylate and (*E,E*)-α-

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farnesene (Scutareanu *et al*., 1997). However, these two compounds also occur in herbivore-induced volatiles of other host plants. For example (*E,E*)-α-farnesene also emanates from uninfested apple buds (Kalinova, personal communication) and apples (Sutherland & Hutchins, 1973; Bradley & Suckling, 1995). By contrast, the same species of pear psyllids induce quite different blends of plant volatiles in different pear varieties. For example, the headspace of psyllid-infested trees of Beurré Hardy contains much less methyl salicylate than that of Conference (B. Drukker & M. A. Posthumus, unpublished data). Given this variability in the relation between infochemicals and prey presence, predators should possess an ability to switch selection from one odour blend to another depending on what is the currently most suitable prey (Sabelis *et al*., 1999).

Odour preference may be innate, or acquired during an individual's life time. An innate odour preference implies that it is inherited and occurs independently of an individual's experience. Such innate preferences may, however, be modified by learned inputs, but, even if the individual's response is rigid, the population's response need not be so, because flexibility may become manifest at the population level via gene frequency changes over successive generations due to selection ('genetic tracking'; Gould, 1993).

Odour preference may be acquired in three essentially different ways: imprinting, defined as learning rapidly during a sensitive period early in life – with or without reinforcement – and becoming committed to the learned stimulus (Gould, 1993; Hall & Halliday, 1998); sensitization, the gradual increase in response to a stimulus along with exposure to that stimulus, even when it has not been paired with any other stimulus (Papaj & Prokopy, 1989; Hall & Halliday, 1998); and associative learning where pairing of the conditioned (e.g. odour) and the unconditioned (e.g. food, electroshock) stimulus results in preference or aversion (Thorpe, 1963; Lewis & Tumlinson, 1988: Hall & Halliday, 1998).

In principle, acquired preferences may arise from a gradual increase in response to a stimulus – when it has not been paired with any other stimulus (sensitization), or through a close temporal and spatial pairing of stimuli (associative learning). These two forms of learning are not mutually exclusive, because close temporal pairing of two stimuli may gradually increase the response, if this pairing is repeated or exists during a prolonged period of time. However, associative learning is the case if one stimulus, offered in two different contexts, leads to opposite responses towards the stimulus: preference in one context, aversion in the other. Sensitization cannot explain such an outcome, because it requires that exposure – with or without a paired stimulus – should always lead to an increase in preference, irrespective of the context (positive, negative or neutral).

We studied the role of innate and acquired preferences, using food as the positive and food deprivation as the negative unconditioned stimulus, and one component of herbivore-induced plant volatiles (i.e. methyl salicylate) as the conditioned stimulus. First, we tested field-collected anthocorids for their response to herbivore-induced plant volatiles. Second, their offspring, reared on flour moth eggs only to deprive them of these volatiles, were tested for their innate (i.e. 'experience-free') response to methyl salicylate. Second, to elucidate a role for imprinting, we tested adult anthocorids exposed to methyl salicylate during their development and compared their response to that of adults exposed only during the adult phase. Third, to assess sensitization, we tested whether the intensity of the response increased with increasing duration of exposure to methyl salicylate in the presence of prey. Fourth, to look for associative learning, we tested whether bugs exposed to methyl salicylate in the absence of prey would develop a weaker or even opposite response, compared to that in presence of prey.

Materials and Methods

Predators

Anthocoris nemoralis adults were collected by beating branches of pear trees in orchards near Wilhelminadorp (Zeeland, The Netherlands) and in the experimental orchard 'De Schuilenburg-IPO/DLO'at Lienden (The Netherlands). They were caught during July–October in 1989, 1991, 1993 and 1994, and transferred to the laboratory. If not subjected to test the same day, they were kept in a plastic bag together with original plant material at 4°C. Sexes were not separated because previous experiments showed that males and females responded in a similar fashion to herbivore-induced plant volatiles (Drukker & Sabelis, 1990; B. Drukker, unpublished).

Y-tube olfactometer tests

A Y-tube olfactometer (Sabelis & Van de Baan, 1983; Janssen *et al*., 1997) was used to test preference for or aversion to an odour source over clean air, i.e. air uncontaminated with the odour under test (note that the uncontaminated air enters both arms of the olfactometer). The odour sources were in plastic boxes (for leaves), small Perspex chambers (for pear seedlings), or glass tubes (for methyl salicylate), connected to the two upper arms of the Y-tube. After five test runs, odour sources were swapped and the test was continued after 5 min to get rid of contamination. Unless stated otherwise, predators were starved for 4 h in clean air prior to testing. Predators were released one at a time at the downwind end of the Y-shaped wire that provided a walkway in the centre of the Y-tube, positioned horizontally. They could walk upwind along the wire and then choose either of the Y-arm (+ odour or – odour) sources. A test trial ended when the predator reached the end of one of the tube's upper arms or after 5 min. Per day, 15–30 predators were tested in total. Unless stated otherwise, three replicate experiments were carried out, each on a different day. A (two-sided) binomial test was used to evaluate the null hypothesis of an equal distribution of predators between the two arms. These tests were carried out both per replicate experiment and on pooled data.

Odour sources

Odour sources were either the complete blend of pear volatiles, or a single compound from the blend (methyl

salicylate). The complete blend emanated from detached pear leaves on wet tissue, or entire pear seedlings infested with pear psyllid nymphs (*Cacopsylla pyricola* (L.)) (headspace samples from detached leaves and pear trees/seedlings are very similar; B. Drukker, unpublished data). The total number of *Cacopsylla* nymphs (L1–5) was between 75 and 125 per plant. The number and size of the leaves and amount of honeydew were not standardized. The control stimulus came from a box with wet paper tissue, or an empty chamber.

Synthetic methyl salicylate (Aldrich, The Netherlands) was applied on discs of filter paper (2.3 mg dissolved in 0.1 mL hexane); the control consisted of hexane only. This odour source was renewed every hour. After application, the solvent was allowed to evaporate for 15 min.

This amount of methyl salicylate and the number of psyllid-infested leaves used had been proven attractive to bugs in previous experiments with anthocorids (Drukker & Sabelis, 1990; Scutareanu *et al*., 1997; B. Drukker, unpublished data). As discussed in Scutareanu *et al*. (1997), the concentration of methyl salicylate used probably reflected that found in the field.

Innate response

Three groups of orchard-collected predators were tested for their response in the Y-tube toward the odours emanating from pear psyllid-infested leaves or methyl salicylate. After testing, the predators were put in 1 litre plastic jars provided with snap beans as oviposition substrate, and fed eggs of flour moth, *Ephestia kuehniella* (25°C, 80% RH, LD 16 : 8 h). Snap beans containing the predators' eggs were collected every 2–3 days and put in a clean jar to start a new age cohort. The laboratory-reared predators were tested at an age of 2–5 weeks for their response in the Y-tube toward the odour from pear psyllid-infested leaves (two groups), or methyl salicylate (three groups). No test trials were carried out with laboratory-reared predators that were subsequently reared on psyllid-infested leaves.

Acquired response: imprinting, sensitization, operant conditioning

From the culture reared on *Ephestia* eggs, snap beans with predator eggs were transferred to new jars. Anthocorids in these jars completed their development on *Ephestia* eggs that were mixed (by stirring) with 0.1 mL methyl salicylate per 5 mL eggs. Predators were tested in the Y-tube olfactometer after 2 or 4–5 weeks of exposure (exposure starting from the egg stage). As a control, predators fed *Ephestia* eggs without methyl salicylate were tested at the same time intervals. In a separate experiment predators completed their development on *Ephestia* eggs, and were fed methyl salicylate-treated *Ephestia* eggs only for 14 h while adult (≈ 4-weeks-old). Their response was tested in the olfactometer directly after exposure to these methyl salicylate-treated eggs. In this way the effect of stage during exposure and exposure duration were studied.

Table 1. Olfactory response of orchard-caught and laboratory-reared *Anthocoris nemoralis* adults to psyllid-induced pear volatiles (PIPV) or synthetic methyl-salicylate (MeSa) (in (+) (arm), when offered against clean air (in (–)arm of a Y-tube olfactometer). $n(+, -)$ = number of predators that reached the end of the (+) or (–)arm of the Y-tube; $n(0)$ = number that did not respond within a 5-min test; %(+) = percentage of $n(+, -)$ reaching the end of the (+)arm; P = critical level (NS = non-significant).

Odour source in (+)arm	$n(+, -)$	$n(0)$	%(+)	P
Orchard-caught predators				
PIPV	23	1	78	0.011
	16	1	88	0.0042
	26	6	77	0.0093
Total	65	8	80	0.0000012
MeSa	16	0	88	0.0042
	12	3	83	0.039
	23	2	74	0.035
Total	51	5	82	0.000015
Laboratory-reared predators				
PIPV	11	18	55	1.0 NS
	21	6	48	1.0 NS
Total	32	24	50	1.0 NS
MeSa	14	2	42	0.79 NS
	18	22	44	0.81 NS
	17	6	47	1.0 NS
Total	49	30	45	0.57 NS

Imprinting during exposure early in the juvenile stage would lead to increased responsiveness to methyl salicylate in the adult phase. Sensitization would manifest itself by a gradual increase in responsiveness associated with increased exposure duration. Associative learning would lead to increased responsiveness after relatively short exposure to methyl salicylate-treated eggs and irrespective of the predator's age while exposed.

To prove a role for associative learning (operant conditioning; Hall & Halliday, 1998) it was also necessary to show a switch in response when methyl salicylate was offered together with a negative stimulus. Three groups of adult predators (4–5 weeks old) reared on *Ephestia* eggs were starved within a closed, 1 litre jar for 14 h while exposed to odour from filter paper impregnated with 7 mg methyl salicylate. The predators were tested in the Y-tube within 7 h after exposure.

Results

Innate or acquired response

In all three trials orchard-caught, adult *A. nemoralis* showed a significant preference for odour from psyllid-infested pear leaves over clean air, and also in all three trials a preference for methyl salicylate over clean air (Table 1). Descendant laboratory cultures of these adults fed *Ephestia* eggs lacked either of the two preferences (Table 1). Results obtained with

Table 2. Effect of experience with methyl-salicylate (MeSa) on olfactory response of laboratory-reared *A. nemoralis* adults to MeSa when offered against clean air in a Y-tube olfactometer. See also Table 1.

Pre-treatment with MeSa	$n(+,-)$	$n(0)$	%(+)	P
Juvenile stage, 2 weeks, well-fed	21	3	76	0.027
Egg-to-adult phase, 4–5 weeks, well-fed	18	7	83	0.0075
	20	2	75	0.041
Total	38	9	79	0.00047
Adult phase, 14 h, well-fed	16	4	88	0.0042
Adult phase, 14 h, starved	18	2	22	0.031
	22	3	23	0.017
	14	1	0	0.0001
Total	54	6	17	$< 10^{-6}$

(*E,E*)-α-farnesene (not shown in Table 1) revealed a similar course of events: parents caught in a pear orchard preferred this chemical over clean air (77% of 64 predators; $P < 5.10^{-5}$), whereas descendants reared in the laboratory lacked this preference (48% of 27 predators; NS).

Contingency table analysis showed that the difference in preference by orchard-caught and laboratory-reared *A. nemoralis* for odour from psyllid-infested pear leaves was significant ($\chi^2 = 9.2$, d.f. = 1, $P < 0.01$). The same applied for the difference in preference for methyl salicylate ($\chi^2 = 13.5$, d.f. = 1, $P < 0.001$). Orchard-caught and laboratory-reared *A. nemoralis* also showed a significant difference in their willingness to respond at all. More than 90% of 129 orchard-caught predators made a choice within 5 min, as opposed to only 60% of 135 laboratory-reared predators.

When laboratory-reared predators were fed *Ephestia* eggs treated with methyl salicylate, they switched from no preference to a clear preference for methyl salicylate over clean air (Table 2). Also, compared to the indifference of predators fed *Ephestia* eggs without methyl salicylate, this preference is significant ($\chi^2 = 16.3$, d.f. = 1, $P < 0.0001$).

It can be concluded that the preference of orchard-caught predators for odours from psyllid-infested pear leaves over clean air is not innate but acquired, because their laboratory-reared descendants – with no previous experience with psyllids and pear – did not respond, but when exposed to methyl salicylate a preference was found similar to that of the orchard-caught predators.

Imprinting

Whether exposed to methyl salicylate-treated prey early in development, from egg to adulthood, or only for 14 h as an adult (Table 2), the preference of adult predators for methyl salicylate was equally strong according to contingency table analysis. Thus, extended exposure in early development is not more effective than a short exposure during adulthood. Imprinting during the juvenile period, therefore, cannot be the main mechanism for acquiring the preference.

Sensitization

Whether exposed for 14 h, 2 weeks or 4–5 weeks, the preferences for methyl salicylate over clean air were indistinguishable by contingency table analysis (Table 2, e.g. 14 h vs. 4–5 weeks: $\chi^2 = 0.9$, d.f. = 1, $P < 0.33$). As sensitization implies that longer exposure should trigger stronger preference, we conclude that sensitization does not underly the acquired preference.

Operant conditioning

The 14-h exposure to methyl salicylate-treated prey led to a clear preference for methyl salicylate, whereas 14-h exposure to methyl salicylate in absence of prey led to avoidance of methyl salicylate (Table 2). This reversibility of the response to methyl salicylate in association with reward (prey) or punishment (hunger) represents strong evidence for associative learning.

Discussion

Learning ability

Orchard-caught anthocorids responded positively to odours from pear psyllid-infested trees, or to methyl salicylate, a constituent of this odour blend. When reared in the laboratory on a diet of *Ephestia* eggs, however, offspring of these predators did not automatically respond to these odours. Hence, an innate, unconditional response to these odours seems unlikely, since laboratory rearing does not involve selection against predators having an innate response (Lesna & Sabelis, 1999).

Laboratory-reared predators responded to herbivore-induced plant volatiles only after prior experience with them. The timing of the experience with respect to developmental phase or adult age had no impact and experience during ontogeny had the same impact on the predator's choice, as experience in the adult phase. As learning does not occur exclusively during ontogeny, imprinting *sensu* Thorpe (1963) (Hall & Halliday, 1998) cannot be the sole mechanism explaining the acquired preference. We expect that the ability to learn is distributed more or less evenly over the active lifetime of the anthocorids, but we did not test for the presence of a particular, sensitive period during adulthood, as for example just after eclosion into the adult stage, when the female must decide whether to oviposit or disperse.

Our experiments showed that experience with methyl salicylate modified the response of anthocorid predators towards this volatile, and that prolonged exposure (> 14 h) did not lead to a stronger preference. In addition, we found that the response changed depending on the context in which the cue was offered first: preference when the cue was offered together with food, aversion when offered with food deprivation. This implies that sensitization does not explain the response.

We conclude that the mechanism involved here is probably a form of associative learning, more precisely operant conditioning (Hall & Halliday, 1998). The response to the conditioned stimulus (methyl salicylate) depends on the quality of the simultaneously offered unconditioned stimulus (food or no food). Anthocorid predators are apparently capable of linking methyl salicylate to a positive (satiation) or negative (starvation) experience and subsequently adjust their response accordingly.

Changes in odour preference have been reported for anthocorid bugs. Dwumfour (1992) found that *A. nemorum*, reared on aphids, were attracted to the odour of bean leaves infested with spider mites (*Tetranychus urticae*), but not to bean leaves infested with another species of spider mite (*T. cinnabarinus*). After rearing predators for 3 days on *T. cinnabarinus* on bean leaves, the predators were attracted. Dwumfour (1992) did not show a gradual change in preference, nor did he test the same stimuli in two different contexts. Hence, based on his data a distinction between sensitization and associative learning cannot be made.

Gradual changes have been found for another predatory arthropod by Dicke *et al*. (1990). They found that the predatory mite *Phytoseiulus persimilis* reared on *T. urticae*-infested Lima bean prefer the odour from these leaves over the odour from *T. urticae*-infested cucumber leaves. This preference changed gradually within a week towards a preference for *T. urticae*-infested cucumber after the predators' transfer to *T. urticae*-infested cucumber. Dicke *et al*. (1990) suggested that sensitization explained the gradual change, but recently Drukker *et al*. (2000) presented evidence for associative learning in *P. persimilis*.

Our results again show that infochemicals do not have a single function in biology (Dicke & Sabelis, 1988). Whereas plant synomones have often been considered attractants for predators, the same components may also lead to deterrence, depending on the context, such as absence of prey (Dicke & Sabelis, 1988).

Impact of learning on response to herbivore-induced plant volatiles in the field

Our results call into question how anthocorid predators use herbivore-induced plant volatiles that betray the presence of potential prey. Along with the diminishing of a prey population on a plant, the plant receives less impulses to produce volatiles; there is evidence, however, that prey become depleted before the plant ceases odour production (e.g. Sabelis & van de Baan, 1983). During this time-lag between prey depletion and cessation of odour release, plant odours are associated by the predator with absence of prey. Associative learning will stimulate the predators to move away from that plant. Thus, food deprivation triggers the predators to switch from being arrested to being deterred by herbivore-induced plant volatiles and it reinforces aversion to these odours.

How associative learning may be implicated in finding new prey resources, is much less clear. If the aversion learnt on the original host plant fades away, the predators may either encounter new prey at random and associate ambient odours with that prey, or they may return to an innate repertoire of responses or to 'lessons' from associative learning earlier in life. We found no evidence for an innate response, but it may still emerge after aversion fades away in the absence of the paired food-odour stimuli. More research is needed to elucidate the hierarchy of responses following such fading aversion.

Understanding behavioural responses of anthocorids to herbivore-induced plant volatiles may well prove to be relevant to biological control. Possibly, the timing of immigration can be improved by applying plant volatile-based lures, by applying the elicitors of plant volatiles to plants or by using cultivars producing more attractive blends of herbivore-induced plant volatiles. Moreover, when anthocorids are released for biocontrol purposes, the efficiency of the release may be improved by allowing them to associate herbivore-induced plant volatiles and presence of prey prior to the release (Sabelis *et al*., 1999).

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