

Analysis of Prey Preference in Phytoseiid Mites by Using an Olfactometer, Predation Models and Electrophoresis

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ABSTRACT

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Prey preference of three phytoseiid species, *Typhlodromus pyri* Scheuten, *Amblyseius potentillae* (Garman) and *A. finlandicus* (Oudemans) which occur in Dutch orchards, was analysed with respect to two economically important phytophagous mites, the European red spider mite *Panonychus ulmi* (Koch), and the apple rust mite *Aculus schlechtendali* (Nalepa). Two types of laboratory experiments were carried out: (1) olfactometer tests to study the response when volatile kairomones of both prey species were offered simultaneously; and (2) predation tests in mixtures of the two prey species and comparison with calculated predation rates, using a model provided with parameters estimated from experiments with each prey species alone. In addition, the diet of field-collected predators was analysed using electrophoresis.

For each predator species the results of the different tests were consistent, in that *T. pyri* and *A. potentillae* preferred *P. ulmi* over *A. schlechtendali*, whereas *A. finlandicus* preferred *A. schlechtendali* over *P. ulmi*.

INTRODUCTION

Phytoseiid mites may feed on a variety of food sources. Some species such as *Phytoseiulus persimilis* Athias-Henriot only feed on spider mites, whereas others such as *Amblyseius potentillae* (Garman) may feed on a wide range of unrelated prey species, not restricted to the Acari. Also, plant tissue may be included in the diet of some phytoseiid species (Porres et al., 1976). Variation in prey selection behaviour, resulting in quantitative and/or qualitative differences in food intake, may result in differences in reproductive success. If this variation is genetically determined, natural selection is expected to favour those genotypes that maximize their contribution to future generations. It is there-

fore expected that phytoseiid mites do not feed indiscriminately but prefer certain food types over others.

From an applied point of view, prey specificity has been regarded as one of the criteria for pre-introductory evaluation of natural enemies (Beddington et al., 1978; Hassell, 1978; Van Lenteren, 1986) and was regarded to be an indispensable characteristic for biocontrol agents in (seasonal) inoculative release programs (Van Lenteren, 1986). In a comparison of characteristics of predatory mites that are successful in biological control, McMurtry (1982) discussed prey specificity in terms of the range of prey/food types that could be fed on and that supported survival and reproduction of the phytoseiid species. Moreover, not only the range of possible prey/food items is important in assessment of prey specificity, but also the preference of the predator (Sabelis and Dicke, 1985).

For assessment of prey preference it is essential to consider what foraging decisions are made during different stages of prey searching. (1) A phytoseiid mite that lands after aerial dispersal may decide to stay and search for prey or take off and start a new aerial voyage. If it decides to stay, it faces the decision of where to search and how long to search on specific locations. (2) After location of a prey colony, it may decide how long to stay, and which prey stages or prey species to accept and which to reject. (3) Finally, if it decides to leave the (exterminated) prey colony, it may choose whether to take off for an aerial voyage, or to disperse by walking (see Sabelis and Dicke, 1985, for review of prey-searching behaviour). Analysis of a single foraging decision may provide information on preference at that particular stage of prey selection. To obtain a more comprehensive view of prey preference it is indispensable to study foraging behaviour at different stages of prey selection.

To analyse prey preference of phytoseiid mites, we carried out two independent preference-analysis methods under laboratory conditions: (1) Investigation of the response to volatile kairomones considers decisions of the predators when prey individuals are not contacted, as is the situation after termination of an aerial voyage, or after eradication of a prey colony; a Y-tube olfactometer was used in this analysis. (2) Investigation of predation rates relates to acceptance/rejection decisions during contacts with prey items; for this analysis of prey preference we used a Markov-type predation model that accounts for feeding-state dependent behaviour (Sabelis, 1981, 1986; Dicke, 1988b).

The above two analyses are performed under artificial conditions, where only one aspect of prey selection behaviour is investigated. Moreover, field populations may undergo physiological and/or genetic changes when introduced into the laboratory (Van Lenteren, 1986). Preference analyses under field conditions constitute a significant complement to the conclusions obtained in the laboratory. For this purpose we made an electrophoretic analysis of gut contents of predators collected in orchards.

Prey selection of three phytoseiid species, *Typhlodromus pyri* Scheuten, *Amblyseius potentillae* and *A. finlandicus* (Oudemans), which occur in Dutch apple orchards, was investigated. All three phytoseiid species can feed and reproduce on the two most abundant pest-mite species that occur in Dutch orchards, *Panonychus ulmi* (Koch) the European red spider mite, and *Aculus schlechtendali* (Nalepa) the apple rust mite (Chant, 1959; Kropczynska-Linkiewicz, 1971; Overmeer, 1981; Dicke, 1988b). These two prey species can occur on different but also on the same leaves. Thus predators have to make selection decisions in all stages of the prey-selection process outlined above.

METHODS AND MATERIALS

Preference analyses

Olfactometer

To investigate prey preference on the basis of volatile kairomones, a Y-tube olfactometer was used. Predators were starved in plastic tubes at 26°C for 20 h. For a detailed description of the olfactometer, its use, and the environmental conditions, see Sabelis and van de Baan (1983), Dicke and Groeneveld (1986) and Dicke (1988a).

In the olfactometer, the predators were offered a choice between two substrates, either clean and prey-infested host plant leaves (prey vs. no prey choice), or host-plant leaves that were each infested with one of two different prey mites (simultaneous prey choice). Simultaneous prey choice was studied in a series of experiments differing in the ratio of prey numbers offered. For a comparative approach in the latter situation, prey (kairomone) quantities should be compared; this may be done on the basis of prey numbers. However, because kairomone production seems to be related to feeding on the host plant (Sabelis et al., 1984) and because prey biomass of spider mites and rust mites differs largely, we prefer a comparison on the basis of prey biomass.

Analysis of predation rates

The value of predation models that include feeding-state dependent behaviour for analysing prey preference has been established for several predator/prey interactions (Sabelis, 1986; Dicke, 1988b). For details of the methods used here, see Dicke (1988b). The basic idea is as follows. At first, the functional response of the predators to the density of each prey is determined. Two parameters of a Markov-type model are estimated for each functional response curve by trial and error. These parameters represent the feeding-state-independent behaviour (c) and the feeding-state-dependent behaviour ($z \in < -1; \infty >$). The parameter values thus obtained are used in an extended version of the model to predict predation rates in mixed cultures, under the assumption

that the parameters are not affected by the prey species being presented together. If this model prediction differs from experimentally determined predation rates in mixed cultures, and if neither a change in behaviour of the prey nor a change in walking speed of the predator can explain this difference, the conclusion is that the predator has a preference in terms of changes in success ratio or width of the searching path in response to the prey types being presented together (Sabelis, 1986). Thus, this analysis of preference uses prey numbers as a comparison index, on the basis of a model that accounts for prey biomass differences (Sabelis 1981, 1986).

In the predation model, food conversion is determined by the relative rate of gut emptying, which is the combined process of resorption, respiration, transpiration and egestion. The relative rate of respiration and transpiration (r_{rs}) and the relative rate of egestion were assumed to be similar to those of other phytoseiid species (cf. Sabelis, 1981). The parameters needed to calculate the relative rate of resorption are: maximum food content in the gut (g_{max} ; μg), somatic body weight (b ; μg), rate of oviposition (R_{ov} ; eggs day^{-1}), and weight of an egg (E ; μg). These parameters were estimated by weighing procedures using a Cahn electrobalance (g_{max} , b and E), or by experimental determination (R_{ov} ; Dicke 1988b).

The experiments were performed at $26 \pm 1^\circ\text{C}$ and $70 \pm 10\%$ r.h.

Electrophoresis

Prey preference under field conditions was analysed by tracing prey esterases in predators by means of polyacrylamide gel electrophoresis. (For procedures see Murray and Solomon (1978) and Dicke and De Jong (1988)). Recently, Fitzgerald et al. (1986) developed a technique to use this method quantitatively. Since we analysed gut contents qualitatively, conclusions on preference are based on presence/absence of each prey species' esterases. The predators were collected from leaves in an orchard where only two prey species were available. Leaves constituted the experimental unit. Prey numbers on the leaves from which predators had been collected were counted and predators were analysed individually. The data on gut contents were analysed in the context of prey densities experienced by individual predators.

Mites

Prey

The prey mites *P. ulmi* and *A. schlechtendali* were collected from commercial Dutch apple orchards. For predation experiments rust mites and spider mite eggs were collected and stored at 5°C for up to some weeks (rust mites) or two months (*P. ulmi* winter eggs). Prior to the experiments, spider mite eggs were kept at 26°C for 2–4 days and rust mites for 0.5–2 h. Rust mite adults and recently emerged spider-mite larvae were offered to the phytoseiids in the pre-

dation experiments. Leaves used in the olfactometer had been collected on the day of the experiment.

The spider mite *Tetranychus urticae* Koch was reared on Lima bean plants (for rearing conditions see Dicke (1986)). This spider mite was used to rear *A. potentillae* and *T. pyri*.

Predators

The phytoseiid mites *T. pyri* and *A. potentillae* were reared on *T. urticae* or *Vicia faba* L. pollen on plastic plates. For details on rearing methods see Dicke (1988a) and Dicke and Groeneveld (1986), respectively. *Typhlodromus pyri* had been reared on these food sources for 6–8 years, one strain of *A. potentillae* had been reared on *T. urticae* for more than 12 years, and another strain, that originated from the first one, had been reared on *V. faba* pollen for ca. 6 years. *Amblyseius finlandicus* was collected in Wageningen in 1984 from leaves of *Prunus* sp. This predator species was reared in the laboratory on *V. faba* pollen on Lima bean leaves at $26 \pm 1^\circ\text{C}$, $60 \pm 10\%$ r.h. and continuous fluorescent light. The leaves were placed upside down on wet cotton wool.

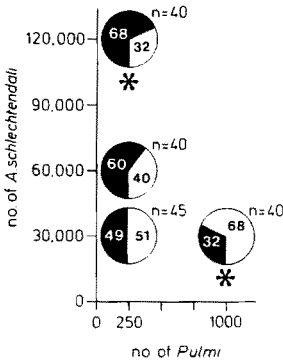
RESULTS

Typhlodromus pyri

Olfactometer

The response of 20-h-starved *T. pyri* females towards volatile kairomones is dependent on nutritional quality of the diet used for predator rearing (Dicke, 1988a). Predators reared on *T. urticae* responded to a volatile kairomone of *P. ulmi*, but not to a volatile kairomone of *A. schlechtendali* (Dicke, 1988a). These data indicate that *T. pyri* reared on *T. urticae* preferred European red spider mites to apple rust mites.

When reared on *V. faba* pollen, 20-h-starved *T. pyri* females responded to the volatile kairomones of both *P. ulmi* and *A. schlechtendali* in prey vs. no-prey choice-experiments (Dicke, 1988a). When these two prey species were offered simultaneously, the response of pollen-reared predators was dependent on the ratio of prey numbers used (Fig. 1). They walked significantly more to the end of the arm with *A. schlechtendali* when the ratio of *A. schlechtendali*:*P. ulmi* numbers was 120 000:250 but they preferred the arm with *P. ulmi* when the ratio of prey numbers was 30 000:1000. In both choice situations the rust mites outweighed the spider mites (the weight of the smallest active spider mite stage is $4 \times$ that of the largest rust mite stage). Thus, the observations of the choice between 120 000 rust mites and 250 spider mites do not permit a conclusion on prey preference on the basis of a prey biomass criterion. However, the result of the experiment where 30 000 rust mites were offered vs. 1000 spider mites demonstrates that the predators preferred *P. ulmi* to *A. schle-*



percentage response to prey species indicated on



Fig. 1. Response to volatile kairomones in a Y-tube olfactometer of *T. pyri* females reared on *V. faba* pollen and starved for 20 h. Choice between leaves infested with *P. ulmi* or *A. schlechtendali* (after Dicke, 1988a).

Numbers in sectors indicate percentage response to each prey species. Numbers above pie diagrams represent quantity of predators tested.

Asterisks indicate level of significance: * = 0.01 < P < 0.05; ** = 0.001 < P < 0.01.

chtendali. Thus, the conclusions on prey preference for *T. pyri* reared on each of the two diets are similar.

Comparison of predation rates

The predators used in these experiments had been reared on *V. faba* pollen. The relative rate of gut emptying was calculated to be 1.72 (Table 1). Estimated values for *c* and *z* that best described the predation rates in monocultures (Fig. 2) are shown in Table 2. The values for *z* indicate that the predator's success ratio sharply declines at high levels of gut fullness (Dicke, 1988b). The predicted predation rate on *A. schlechtendali* in one of the mixed cultures (2 *P. ulmi* larvae and 30 *A. schlechtendali* adults) was similar to the experimental value, but in the other mixed culture it was higher than the observed predation rate. Observed predation rates on *P. ulmi* in both mixed cultures were significantly higher than those predicted. Observations on walking speed and walking activity of the prey in mono and mixed cultures indicated that a change in these behavioural characteristics as a result of being together cannot explain the difference between predicted and measured predation rates in mixed cultures (Dicke, 1988b). Simulations showed that the differences between model calculations and observations are too high to be explained by an increase in walking speed of the predators. Varying the estimated value of r_g did not affect

TABLE 1

Values of parameters needed to calculate relative rate of gut emptying (r_g) for three phytoseiid species

	<i>T. pyri</i>	<i>A. potentillae</i> ¹	<i>A. finlandicus</i>
♀ w/full-grown egg, weight (μg)	10.5 ± 1.3 ($N=10$)	17.9	15.4 ± 0.6 ($N=13$)
Somatic body wt (μg)	2.3^2	5.1	4.4^2
Maximum gut vol (μg)	3.5^2	5.2	4.5^2
Egg wt. at deposition (μg)	1.9 ± 0.5 ($N=9$)	3.1	2.8 ± 0.3 ($N=28$)
Oviposition rate (eggs/day; 26°C)	2.0 ± 0.2^3	2.8 ± 0.5^3	2.4 ± 0.4^3
Calculated relative rate of gut emptying ⁴ (26°C)	1.72	2.50	2.33

¹Data of Sabelis (1981).

²Calculated from weight of ♀ carrying full-grown egg, under the assumption that the fraction that is made up by the somatic body weight and the maximum food content of the gut is similar for *A. potentillae* and *A. finlandicus* and for *Typhlodromus occidentalis* and *T. pyri*.

³Data of Dicke (1988b).

⁴Calculation with balance equation (Sabelis, 1986) where g_{max} was set to a slightly lower value ($=g_{\text{max}} - 0.2$) to approximate the dynamics of g_{max} during the oviposition rate determination.

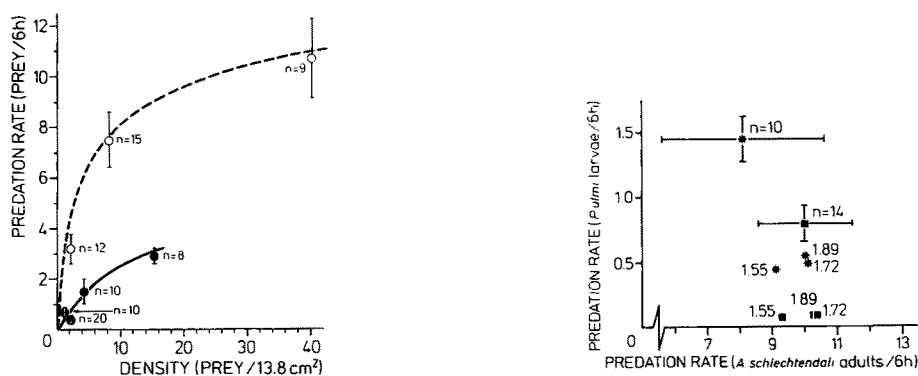


Fig. 2. Predation rates of *T. pyri* females reared on *V. faba* pollen. (Left) Functional response to prey density of *P. ulmi* larvae (—) or *A. schlehtendali* adults (---). Lines, dots and bars indicate best fit of model, mean predation rate, and standard error, respectively. (Right) Predation rates in mixed cultures of prey supply; asterisks and squares denote model predictions for the three values of r_g indicated, at prey densities of 2 *P. ulmi* larvae and 30 *A. schlehtendali* adults per 5 cm² (■) or 6 *P. ulmi* and 30 *A. schlehtendali* per 5 cm² (*); asterisk and square with bars indicate observed predation rates with 95% confidence intervals (Dicke, 1988b).

TABLE 2

Values of model parameters c and z that best describe predation rates of females of three phytoseiid species in monocultures in which *P. ulmi* larvae or *A. schlechtendali* adults were offered

	<i>Panonychus ulmi</i>		<i>Aculus schlechtendali</i>	
	c	z	c	z
Predator				
<i>Typhlodromus pyri</i>	2500	-0.94	13000	-0.95
<i>Amblyseius potentillae</i>	11000	-0.60	6000	-0.70
<i>Amblyseius finlandicus</i>	6200	-0.97	7200	-0.95

the conclusion on prey preference (Fig. 2; Dicke, 1988b). Only a drastic increase in the success ratio with respect to *P. ulmi* resulted in a predicted predation rate on *P. ulmi* that was similar to the observed value (Dicke, 1988b). It is therefore concluded that *T. pyri* reared on *V. faba* pollen preferred *P. ulmi* larvae to *A. schlechtendali* adults.

Electrophoresis

Esterases of both prey species could be detected in the gut of field-collected *T. pyri*. Esterases of *P. ulmi* were detected in 69% and esterases of *A. schlechtendali* in 6% of the predators ($N=189$). These predators were collected from leaves with known ratios of prey numbers. When the predators were classified according to these prey:prey ratios it was clear that, at all ratios, most predators contained *P. ulmi* esterases (Fig. 3), whereas at the lowest prey densities only 10% of the predators were found with rust mite esterase and no spider mite esterases; this is a low value, because 32% of the predators contained only *P. ulmi* esterases. Because the differences in detection frequencies were not the result of a lower chance of detection of rust mite esterases in *T. pyri* (see Dicke and de Jong (1988) for discussion), these data show that *T. pyri* collected in a Dutch apple orchard preferred *P. ulmi* to *A. schlechtendali*.

Amblyseius potentillae

Olfactometer

The data on the response of 20-h-starved *A. potentillae* females towards the kairomones of *P. ulmi* and *A. schlechtendali* in the prey/no-prey choice experiment (Dicke and Groeneveld, 1986) are similar to those for *T. pyri*. A nutritional difference between the diets of *T. urticae* and *V. faba* pollen also caused the difference in the response between *A. potentillae* reared on either of the two diets (Dicke and Groeneveld, 1986). Simultaneous prey choice experiments with predators reared on *V. faba* pollen led to the conclusion that *A. potentillae* preferred *P. ulmi* to *A. schlechtendali* (Fig. 4). In contrast to the

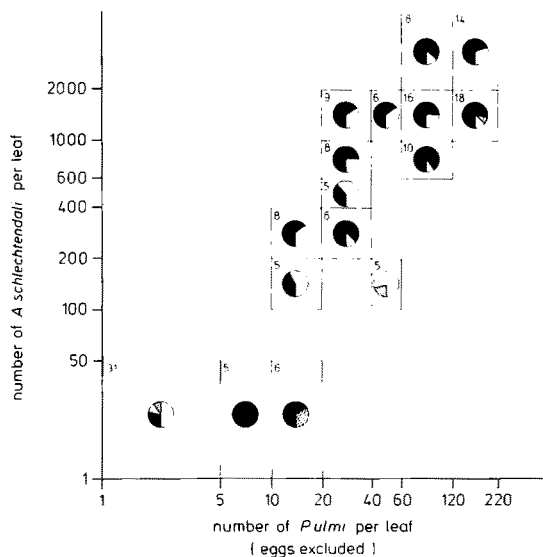


Fig. 3. Percentages of field-collected *T. pyri* with different prey esterases at several prey density combinations. Per class of prey density combinations (represented as a rectangle), pie diagram indicates the esterase percentages detected; the number in the top left corner of the rectangle indicates the number of *T. pyri* analysed. Axes on log scale. (Dicke and De Jong, 1988). Black parts of pie diagrams refer to *P. ulmi*, stippled part to *A. schlechtendali*, shaded parts to mixtures of *P. ulmi* and *A. schlechtendali*, white parts to absence of prey esterases.

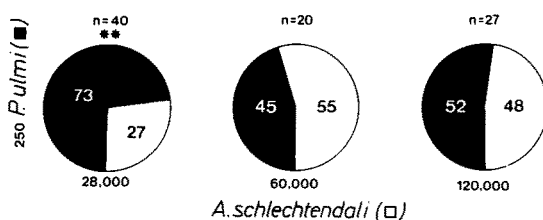


Fig. 4. Response of *A. potentillae* females reared on *V. faba* pollen and starved for 20 h to volatile kairomones in a Y-tube olfactometer. Choice between leaves infested with *P. ulmi* or *A. schlechtendali* (after Dicke and Groeneveld, 1986).

Numbers above pie diagrams represent quantity of predators tested.

For explanation of asterisks, see Fig. 1.

data for *T. pyri*, none of the prey number ratios used resulted in a preference of the arm with rust mites. Thus, *A. potentillae* reared on either of the two diets preferred *P. ulmi* to *A. schlechtendali*.

Comparison of predation rates

Amblyseius potentillae females used in predation experiments had been reared on *T. urticae*. Estimated values for r_g , c and z are given in Tables 1 and 2. The predation rates on *P. ulmi* in monocultures (Fig. 5a) are similar to those reported by Rabbinge (1976). The predicted predation rate on *A. schlechtendali* in the mixed culture (2 *P. ulmi* larvae and 50 *A. schlechtendali* adults) was similar to the observed value, but the calculated predation rate on *P. ulmi* was lower than the one observed. Differences in walking speed and activity between mono and mixed cultures are too small to explain the difference between predicted and measured predation rates (Dicke, 1988b). Moreover, simulations showed that a change in walking speed of the predators also cannot account

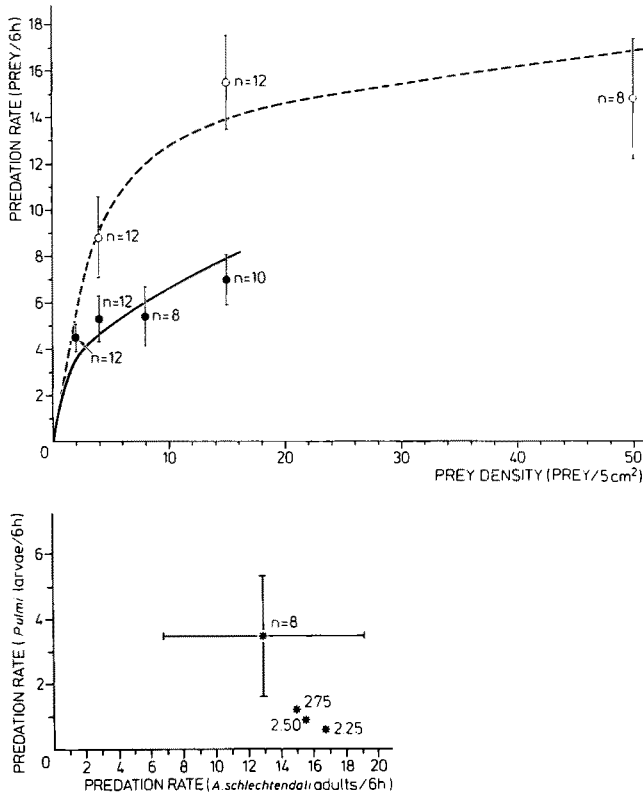


Fig. 5. Predation rates of *A. potentillae* females reared on *T. urticae*. (Top) Functional response to prey density of *P. ulmi* larvae (—) or *A. schlechtendali* adults (- -). Lines, dots and bars indicate best fit of model, mean predation rate, and standard error, respectively. (Bottom) Predation rates in mixed culture of prey supply; asterisks denote model predictions for 3 values of r_g indicated, at prey densities of 2 *P. ulmi* larvae and 50 *A. schlechtendali* adults per 5 cm²; asterisk with bars indicates observed predation rates with 95% confidence interval.

for that difference. Thus, the data show that *A. potentillae* prefers *P. ulmi* larvae to *A. schlechtendali* adults; a 10% increase or decrease in the value of r_g does not affect this conclusion (Fig. 5b).

Electrophoresis

No data on gut contents of *A. potentillae* have been obtained, because we were unable to find a Dutch orchard where European red spider mites, apple rust mites and *A. potentillae* were all present.

Amblyseius finlandicus

Olfactometer

Amblyseius finlandicus females that were starved for 20 h responded to the kairomones of *P. ulmi* and *A. schlechtendali* (Fig. 6a); response to the kairomone of *P. ulmi* was rather weak. In a simultaneous prey choice experiment in the olfactometer, the predators preferred the arm with rust mites when 35 000 rust mites were offered versus 1000 *P. ulmi* (Fig. 6b). Because the rust mites outweigh the spider mites in this choice situation, it cannot be concluded whether the predators prefer *A. schlechtendali* to *P. ulmi*. The response in the simultaneous prey choice experiment between 3500 *P. ulmi* and 17 500 *A. schlechtendali*, which represents a 1:1 biomass ratio, suggests that the predators prefer the arm with rust mites (Fig. 6b).

Comparison of predation rates

Estimated values for r_g , c and z are given in Tables 1 and 2. Predation rates of *A. finlandicus* (Fig. 7a) were much higher than those of *A. potentillae* (Fig. 5a). Partial prey consumption clearly occurred in most of the successful at-



Fig. 6. Response of *A. finlandicus* females, reared on *V. faba* pollen on Lima bean leaves and starved for 20 h, to volatile kairomones in a Y-tube olfactometer. (Left) Predators were offered prey-infested leaves (■) vs. clean leaves (□). (Right) Predators were offered a choice between leaves infested with *P. ulmi* or *A. schlechtendali*.

Numbers in sectors indicate percentage response to each prey species. Numbers above pie diagrams represent quantity of predators tested.

For explanation of asterisks, see Fig. 1.

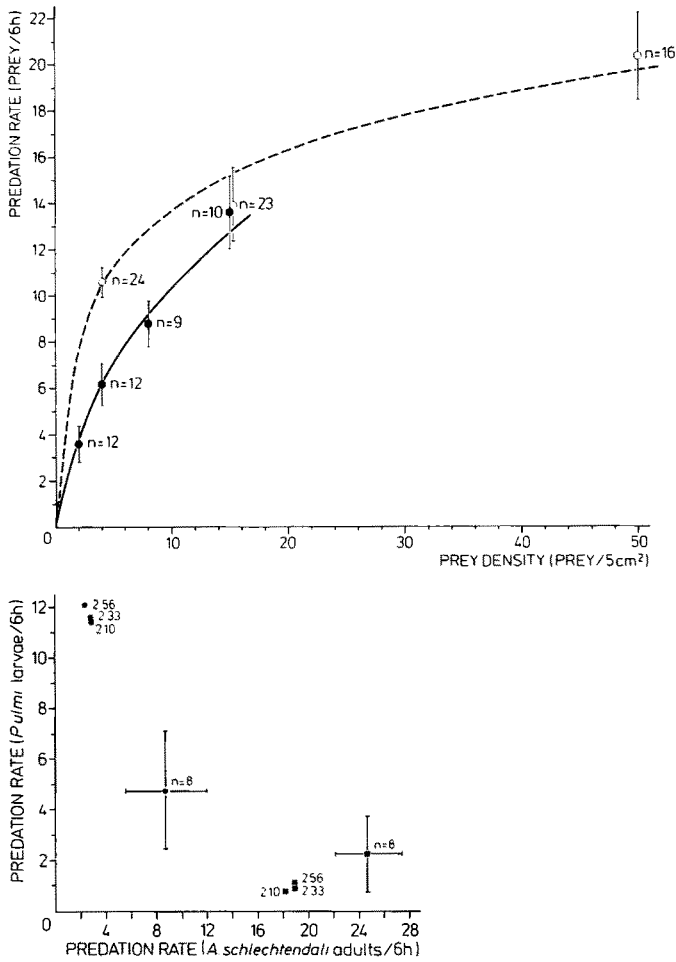


Fig. 7. Predation rates of *A. finlandicus* females reared on *V. faba* pollen on Lima bean leaves. (Top) Functional response to density of *P. ulmi* larvae (—) or *A. schlechtendali* adults (- - -). Lines, dots and bars indicate best fit of model, mean predation rate, and standard error, respectively. (Bottom) Predation rates in mixed cultures of prey supply; asterisks and squares denote model predictions for 3 values of r_k indicated, at prey densities of 2 *P. ulmi* larvae and 50 *A. schlechtendali* adults per 5 cm² (■) or 15 *P. ulmi* and 4 *A. schlechtendali* adults per 5 cm² (*); asterisk and square with bars indicate observed predation rates with 95% confidence interval.

tacks. Two mixed cultures have been offered to the predators. When 2 *P. ulmi* larvae and 50 *A. schlechtendali* adults were offered, the predicted predation rate on *P. ulmi* was similar to the observed value (Fig. 7b); however, the measured predation rate on *A. schlechtendali* was significantly higher than predicted. This indicates that *A. finlandicus* preferred apple rust mites to European

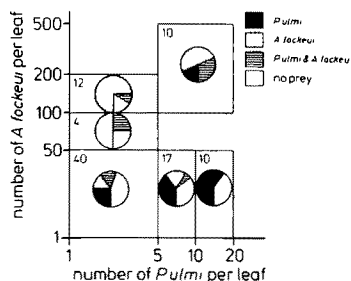


Fig. 8. Percentages of field-collected *A. finlandicus* with different prey esterases at several prey-density combinations. Per class of prey density combinations (represented as a rectangle), pie diagram indicates the esterase percentages detected; the number in the top left corner of the rectangle indicates the number of *A. finlandicus* analysed. Axes on log scale (after Dicke and De Jong, 1986).

red spider mites, which is even more obvious from the other mixed culture, where 15 *P. ulmi* larvae and 4 *A. schlechtendali* adults were offered to the predators. The predicted predation rate on *P. ulmi* is significantly higher than the observed value, whereas the predicted predation rate on *A. schlechtendali* is significantly lower than the observed rate (Fig. 7b). Simulations showed that these differences cannot be explained by a change in the walking speed of the predator; observations on walking speed and activity of prey in monocultures and mixed cultures revealed that differences were negligible (Dicke, 1988b). The data clearly show that *A. finlandicus* prefers *A. schlechtendali* adults to *P. ulmi* larvae.

Electrophoresis

Predators were collected in a Morello cherry orchard where only *P. ulmi* and the plum rust mite *Aculus fockeui* (Nalepa et Trouessart), which is closely related to *A. schlechtendali*, have been observed as prey. Spider-mite and rust-mite esterases were detected in 35% and 37%, respectively, of the predators ($N=107$; Dicke and De Jong, 1986). The range of ratios of prey numbers that were present on the leaves was small (Fig. 8). Comparison of Figs. 3 and 8 shows that *A. finlandicus* feeds much more consistently on rust mites than on *T. pyri*. In only one of the 6 classes (10–20 *P. ulmi* and 1–50 *A. fockeui*) was no predator found with rust-mite esterase. The data do not allow for a definite conclusion on prey preference of *A. finlandicus* under field conditions; data over a larger range of prey densities are needed.

DISCUSSION

Sabelis and Dicke (1985) reviewed knowledge of prey selection by phyto-seiid mites. At that time, data were available only on the response of some predator species to prey cues. This present paper is the first to give a compre-

hensive analysis of prey selection by several phytoseiid species based on several independent bioassays (Fig. 10).

The prey selection analyses carried out for *T. pyri* and *A. potentillae* invariably indicated that these predator species prefer *P. ulmi* to *A. schlechtendali*.

For *A. finlandicus*, not all analyses resulted in a firm conclusion; the predation experiments demonstrated a preference for *A. schlechtendali* over *P. ulmi*, whereas no definite conclusion could be drawn from the olfactometer experiments. However, a comparison of the decisions of all three predator species in comparative choice experiments (Fig. 10) shows that *A. finlandicus* prefers the arm with rust mite kairomone at the lowest rust-mite:spider-mite biomass ratio. No conclusion could be drawn from the analysis of field predation of *A. finlandicus*, but comparison with data on field predation by *T. pyri* indicates that *A. finlandicus* feeds much more on rust mites than on *T. pyri* (Figs. 3 and 8). Thus the conclusion on *A. finlandicus*' preference for *A. schlechtendali* over *P. ulmi*, as obtained from the comparison of observed and predicted predation rates, is not rejected.

The establishment of prey preference of these three phytoseiid species raised several questions, such as why do they exert prey preference, and why do *T.*

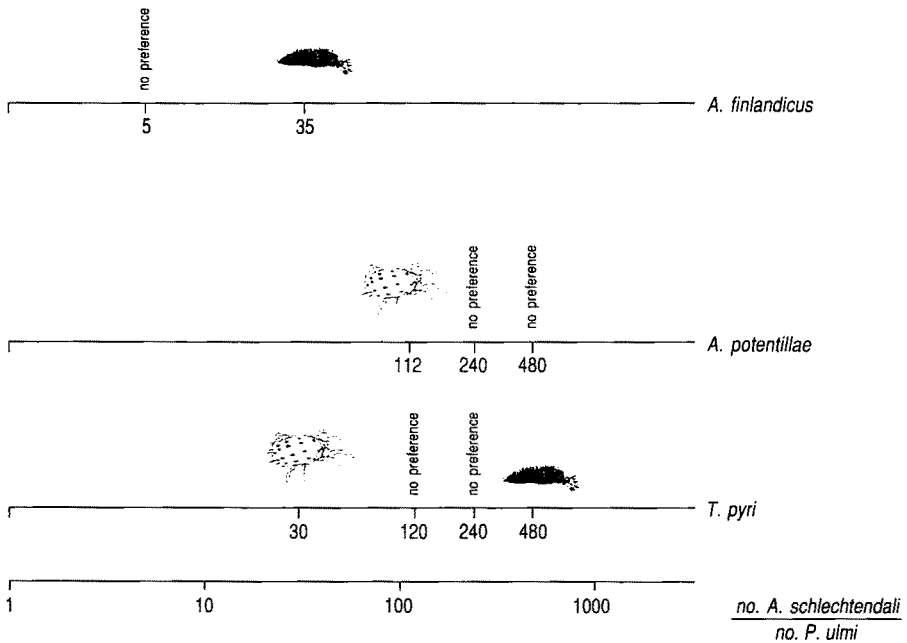


Fig. 9. Summary of data of simultaneous prey choice experiments in Y-tube olfactometer at several prey number ratios. Preferred prey species are indicated for each experiment.

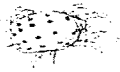








	Olfactometer	Predation	Electrophoresis
<i>Typhlodromus pyri</i>			
<i>Amblyseius potentillae</i>			
<i>Amblyseius finlandicus</i>			

Fig. 10. Summary of data on prey preference obtained from three independent analysis methods. Preferred prey species are indicated for each analysis.

pyri and *A. potentillae* prefer *P. ulmi* whereas *A. finlandicus* prefers *A. schlechtendali*?

Different prey types may differ in profitability for the predator. Dicke (1988b) determined life-history components of all three predator species, when feeding on either *P. ulmi* or *A. schlechtendali*. In addition, he investigated the effect of prey species on diapause induction in *A. potentillae*. From his data it is obvious that apple rust mites are a more profitable prey species for *A. finlandicus* than European red spider mites; to a lesser extent this was also true for *A. potentillae* and *T. pyri*. Thus, on the basis of current data, prey preference of *A. finlandicus* can be understood in terms of reproductive success, whereas this is not true for *A. potentillae* and *T. pyri*.

The functional response of predatory mites to the density of phytophagous mites has been often found to be a Type II response. Evidence for Type III responses is weak (Sabelis, 1985), but this applies the experiments with one or more developmental stages of one prey species at a time. The results presented in this paper show that other (e.g. Type III) responses may occur when more than one prey species is involved. When two prey species were presented as alternatives in olfactometer experiments, prey choice appeared to depend on the biomass ratio of the two prey species. Moreover, predation experiments in a mixture of two prey species cannot be predicted from parameters measured in monoculture predation experiments. More experiments on prey choice are needed to elucidate how the functional response to the density of one prey species is modified by the presence of alternative prey species. This may reveal Type III, or even more complex, responses that could be crucial in understanding coexistence in and stability of acarine predator/prey systems (Murdoch and Oaten, 1975; Roughgarden and Feldman, 1975; Comins and Hassell, 1976; Murdoch, 1977; Hassell and Commins, 1978; Nunney, 1980).

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