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Does prey preference change as a result of prey species being presented together? Analysis of prey selection by the predatory mite *Typhlodromus pyri* (Acarina: Phytoseiidae)

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Summary. Prey-selection behaviour of the phytoseiid mite *Typhlodromus pyri* Scheuten was analysed with a Markov-type model of feeding-state dynamics and feeding-state dependent searching behaviour (Sabelis 1981, 1986, 1989; Metz and Van Batenburg 1985a, b). All behavioural characteristics of the predator which are independent of the feeding state were represented by one parameter. The remaining feeding-state dependent characteristics were represented by a function of the feeding state, with one parameter. The best parameter values to describe a predator-prey interaction were determined by fitting the model to the predation rates in monocultures. Under the assumption that the parameter values are not dependent on the composition of prey species supply, the diet of the predators in mixed cultures was predicted from parameters estimated in monoculture experiments.

Two prey types, apple rust mite (*Aculus schlechtendali* (Nalepa)) adults and European red spider mite (*Panonychus ulmi* (Koch)) larvae were studied. A large discrepancy was observed between calculated and experimentally determined predation rates of *T. pyri* in mixed cultures: the predators actually killed 3–7 times more *P. ulmi* larvae than was predicted by the model.

The large difference between observed and predicted predation rates in mixed cultures cannot be explained by changes in the behaviour of the prey species as a result of being together. Therefore, it seems likely that the prey selection behaviour of the predator was different when prey species were presented together than when presented singly. Apparently the predatory mite *T. pyri* prefers *P. ulmi* to *A. schlechtendali*.

Key words: Prey preference – Functional response – Behaviour – Acari – Phytoseiidae

not change over a short time scale. Examples are food quality, food quantity per prey individual and defensive capacity of each prey type. Secondly, there is information that changes over a short time scale. Examples are food content of the gut, density of each prey type and prey type composition. The outcome of the acceptance/rejection decisions reflects the prey preference of the predatory mite. Sabelis (1981, 1986) showed (1) that the feeding state of predatory mites determines the probability of a successful attack after contact with prey (success ratio) and (2) that, given a particular feeding state, this probability depends a great deal on the developmental stage of the prey. He argued that in order to detect changes in prey stage preference as a result of prey stages being presented together, one must take the feeding state of the predators into account. Ideally this could be accomplished by standardizing the feeding state of the predator and investigating prey acceptance when offering a series of prey stages. This method, however, is not practical because consumption of test prey itself changes the feeding state considerably. Moreover, feeding is likely to be an integral part of the sampling process required to adapt the acceptance/rejection decision to changed conditions of prey density and prey composition. To account for a continuously changing feeding state Sabelis (1981, 1986, 1989) and Metz and Van Batenburg (1985a, b) developed a Markov-type model. The parameters of the model were estimated in monocultures of each prey stage. These estimated parameter values were used to predict the composition of the predator's diet in mixed cultures under the assumption that the feeding-state dependent success ratios would not change as a result of the prey stages being presented together. This approach of testing the null hypothesis that predator and prey behave similarly in monocultures and in mixed cultures was developed by Rabbinge (1976) and Cock (1978) and has been used in several studies (e.g., Fernando and Hassell 1980; Colton 1987; Sabelis 1981, 1986, 1989). Sabelis (1981, 1986, 1989) was the first to include feeding state of predators as the most important determinant of attack rate. He found that the difference between predicted and measured diet composition in a mixed prey-stage supply was absent or small, and concluded that prey stage composition does not affect prey stage preference. The difference between his conclusion and that of

When foraging on a leaf inhabited by a mixture of prey types, predatory mites have to decide which prey to accept and which to reject. These decisions may be based on two types of information. Firstly, there is information that does

Fernando and Hassell (1980) for the same predator-prey system is presumably due to the fact that the latter did not include feeding state of the predators (see Sabelis 1989 for discussion). In this paper we use a method similar to that of Sabelis (1986, 1989) to analyse whether prey preference changes as a result of prey species (rather than stages within one species) being presented together.

Our method, however, differs in one important respect. We were interested in prey selection behaviour of a predatory-mite species different from that studied by Sabelis (1981, 1986, 1989), i.e. *Typhlodromus pyri* Scheuten. The relationship between prey acceptance and feeding state has not yet been studied in detail in this species and such a study would be an extremely laborious task. Therefore, we simplified the model by reducing the number of parameters to three: (1) a gut-emptying constant, (2) a constant that represents the feeding-state independent part of the rate of successful attack and (3) a constant that governs the shape of the feeding-state dependent part of the rate of successful attack. Each of these parameters has been estimated by fitting model calculations to the experimentally determined functional response to each prey species. The parameters estimated in this way were then used to predict the predator's diet in a mixture of these prey species, again assuming no change in the parameters as a result of the prey species being presented together. To check whether our changes in the method affect the conclusions, our analysis method has also been applied to the data of Sabelis (1986, 1989) to compare both model calculations.

The phytoseiid mite *T. pyri* can feed and reproduce on several phytophagous prey species. The two most abundant prey species in Dutch apple orchards are the European red spider mite, *Panonychus ulmi* (Koch) and the apple rust mite, *Aculus schlechtendali* (Nalepa), two economically important acarine pests. The predators frequently encounter both prey species in a given foraging bout because both often occur on the same leaves. Therefore it is especially appropriate to ask whether composition of prey-species supply affects prey preference in this system.

Methods and materials

The methodology is essentially the same as that used by Sabelis (1986, 1989). He used a predator species for which the necessary behavioural data were already available. Such data were not available on the foraging behaviour of *T. pyri*. Instead of performing these experiments to determine the necessary parameters, we simplified the procedure to obtain estimates of the attack rate, σ , as follows. Sabelis (1981, 1986) calculated the attack rate from walking speed and activity of prey and predator, width of searching path, success ratio of the predator and density of the prey. All these components of σ were determined in relation to the level of gut fullness or satiation (s) for four phytoseiid species and several stages of the two-spotted spider mite. These parameters can be divided into components dependent on s and components independent of s , so that the attack rate (σ) may be represented as follows:

$$\sigma = C * f(s) * D, \quad (1)$$

where C (mm²/day) represents components of the above-mentioned parameters that are not affected by s , $f(s)$ repre-

sents components that are dependent on s and D is prey density (mm⁻²). Sabelis (1981, 1989) demonstrated that the success ratio is the parameter that depends most on s . The shape of the function $f(s)$ may therefore be assumed to resemble the success ratio curves as measured for several species of predatory mites by Sabelis (1981). Success ratio usually varies over s in a convex or concave negative exponential fashion. We chose a one-parameter function for $f(s)$ that describes a set of convex and concave curves:

$$f(s) = \frac{1-s}{1+z*s} \quad z \in \langle -1, \infty \rangle \quad (2)$$

where z is a constant.

Thus, the relationship between σ and D , the functional response, is dependent on two unknown constants: C and z , that reflect the predator's behaviour. If the functional response is determined experimentally, values for C and z can be found by fitting the model to the experimental data. These estimates of C and z (C^* and z^*) with respect to each of the two prey species are used in the model to predict predation rates in the mixed culture.

To investigate to what extent the conclusions depend on the shape of $f(s)$, we also made an analysis with a sigmoid function of $f(s)$ instead of only convex and concave curves. We used the Weibull function for that purpose:

$$f(s) = 1 - \exp(-a*s^b), \quad (3)$$

where a and b are unknown parameters, determining the scale and shape of $f(s)$ respectively. The use of this function results in a three-parameter function for σ , with three unknown constants a , b and C .

Mites

The prey mites, *P. ulmi* and *A. schlechtendali*, were collected in commercial Dutch apple orchards. Winter eggs of *P. ulmi* on apple twigs were collected in March and stored at 5° C. The emerging larvae (after 2–4 days at 26° C) were used immediately in predation experiments. *Panonychus ulmi* larvae that had been collected in an orchard during summer were used for some of the experiments. Apple rust mites were collected on apple leaves in an orchard during July/August and stored in the laboratory at 5° C in plastic bags. Within 30 min to 2 h after transfer of the leaves to 26° C, we selected the largest active mites for immediate use in the predation experiment. Although apple rust mites can be stored at 5° C for up to 2–3 months, the mites that were used in the experiments had been stored for a maximum of 3–4 weeks.

Predatory mites were obtained from W.P.J. Overmeer and A.Q. van Zon (Amsterdam) (for details see Overmeer 1981) and reared on *Vicia faba* L. pollen on plastic plates for ca. 5 years. During the last 2 years pollen of *V. faba* variety Suprifin (Janssen Zaad B.V., Dinxperlo, The Netherlands) was used. Young females in the oviposition phase (3 days since the final moult) were used in the experiments.

Predation experiments

Predation was measured on plastic discs on wet cotton wool. These discs (1385 sq mm) were transparent and pro-

vided with a millimetre grid on the underside. The grid facilitated counting of large numbers of these small rust mites. Prey densities were set at 1, 2, 4, 8 or 15 *P. ulmi* larvae or 4, 8, or 40 *A. schlechtendali* adults per disc for the monocultures and 2 or 6 *P. ulmi* larvae in combination with 30 adult *A. schlechtendali* for the mixed cultures. One female predator was introduced on each disc immediately after placing the prey on the disc. At regular intervals, varying from 30 min (density 1 *P. ulmi* or 2 *A. schlechtendali* per disc) to 2 h (15 *P. ulmi* or 40 *A. schlechtendali* per disc) the prey consumption was recorded and prey were replenished. In addition, drowned prey were replaced and predator eggs removed. This procedure was executed during 8 h before the experiment started and served as an adaptation period, to reach a steady state of the food content of the gut (Rabbinge 1976; Sabelis 1981, 1986). After the adaptation period, predation was measured over the next 6 h by treating the discs as had been done during the adaptation period. The experiments were performed in a climate room at $26 \pm 1^\circ \text{C}$ and $60 \pm 10\%$ r.h.

Weighing procedure

In order to quantify feeding and food conversion the weights of the prey types, predator females and eggs were determined. Both prey species were weighed using a quartz fiber fish pole balance (Lowry and Passonneau 1971), whereas predator females and their eggs were weighed using a Cahn electrobalance.

Behaviour of prey

A difference between measured predation rates in mixed culture experiments and predicted rates based on monoculture experiments does not necessarily mean that the predator's prey preference differs in monocultures and mixed cultures. It is necessary to exclude that the behaviour of one prey species is affected by the other species so as to change its rate of encounter with the predator as a result of the two species being presented together. Therefore, two aspects

of prey behaviour were studied in monocultures and mixed cultures: percentage time spent moving and walking speed. Prey densities were set at 2, 4 or 8 *P. ulmi* larvae or 4, 15 or 50 *A. schlechtendali* adults per disc (500 sq mm) for monocultures and 2 *P. ulmi* larvae and 50 *A. schlechtendali* adults per disc in mixed cultures. To measure the percentage time spent moving, instantaneous observations of the mites were made at 30 min intervals: each prey individual was classified as walking or motionless. Occasionally some mites drowned during the experiment. These were then replaced by new individuals. Using a 'drawing tube' connected to a stereo microscope walking paths were drawn on graph paper with a millimeter grid. With a drawing tube one eye sees the experimental arena and the other sees the drawing paper, which facilitates drawing the trail directly. A trail was followed during 3 min, except when the mite stopped before this time limit was reached. Only trails of more than 1 min were analysed. Walking speed was established by counting the number of mm squares traversed, transforming this to the path length (Reddingius et al. 1983) and dividing path length by the time elapsed.

Results

Food conversion parameters

Relative rate of gut emptying. Ingested food leaves the gut through resorption and egestion:

$$r_G = r_A + r_E,$$

where r_G is the relative rate of gut emptying, r_A is the relative rate of food absorption from the gut and r_E is the relative rate of egestion. r_A can be estimated with a 'mass balance equation' (Sabelis 1986):

$$r_A * s_{\max} = r_B * B + r_O * E,$$

where s_{\max} is the maximum food content of the gut, r_B the relative rate of weight loss by respiration and transpiration, B the somatic body weight (total weight minus gut content, weight of integument and terminal oocyte), r_O the

Table 1. Parameters needed to calculate the relative rate of gut emptying (r_G)

Parameter	Symbol	Value	<i>n</i>	Remark
Weight of young oviposition female just before egg deposition	<i>W</i>	$10.5 \pm 1.3 \mu\text{g}$	10	
Somatic body weight	<i>B</i>	2.3	–	Calculated from <i>W</i> on the assumption that <i>B</i> takes up the same proportion of <i>W</i> (0.22) as in other phytoseiid species (Sabelis 1981)
Maximum food content of the gut	s_{\max}	3.5 ^a	–	Calculated from <i>W</i> on the assumption that s_{\max} takes up the same proportion of <i>W</i> (0.33) as in other phytoseiid species (Sabelis 1981)
Weight of freshly laid egg	<i>E</i>	$1.9 \pm 0.5 \mu\text{g}$	9	
Rate of oviposition	r_O	$2.0 \pm 0.3/\text{day}$	44	Temperature $26 \pm 1^\circ \text{C}$
Relative rate of resorption and transpiration	r_B	0.60	–	Assumed to have the same value as for other phytoseiid species (Sabelis 1981), temperature 26°C
Relative rate of egestion	r_E	0.15	–	Assumed to have the same value as for other phytoseiid species (Sabelis 1981), temperature 26°C

^a Value of s_{\max} used in balance equation to calculate r_G (according to Sabelis 1986, 1989) was set to a slightly lower value ($=s_{\max} - 0.2$) to approximate the dynamics of s_{\max} during the oviposition rate determination

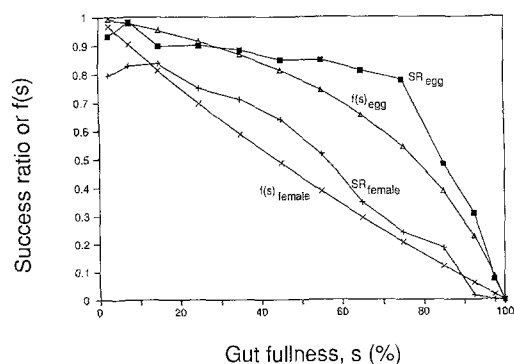


Fig. 1. Comparison of experimentally derived success ratio curves with $f(s)$ curves resulting from estimated z values (see text for more details)

rate of oviposition and E the weight of an egg at deposition. Each of the relative rates is dependent on temperature. The values for all these parameters are given in Table 1. In addition to the assumptions made by Sabelis (1986, 1989) we assumed that (1) somatic body weight and s_{max} of *T. pyri* represent similar proportions of the weight of a female in the oviposition phase as has been established for four other phytoseiid species (Sabelis 1981). (2) r_B and r_E , whose contribution to r_G is small compared to that of r_O were assumed to have the same value as those of other phytoseiid species: $0.04 * (\text{temperature} - 11)$ and $0.01 * (\text{temperature} - 11)$ respectively (Sabelis 1981). Using the parameter values in Table 1 r_G was calculated to be 1.72 day^{-1} at 26°C .

Ingestible weights of the two prey types. *Panonychus ulmi* larvae weighed $0.77 \pm 0.07 \mu\text{g}$ ($n=28$). *Aculus schlechtendali* adults weighed $0.20 \pm 0.06 \mu\text{g}$ ($n=27$). We used values of 0.8 and $0.2 \mu\text{g}$ respectively for the ingestible weights of these prey types. For *P. ulmi* larvae especially, this is an overestimation since a significant portion of their biomass, consisting of integument and legs, is not ingestible. However, the model is not very sensitive to the weight of *P. ulmi* because, at high values of s , prey are only partially ingested. In the model we divided the gut volume ($3.5 \mu\text{g}$) into 35 volume classes of $0.1 \mu\text{g}$ each. Thus a *P. ulmi* larva is equivalent to 8 classes and an adult *A. schlechtendali* to 2 classes. This grid of gut content classes is fine enough to account for partial ingestion of both prey types at high levels of gut fullness.

Predicted and measured diet in mixed cultures

(a) *Phytoseiulus persimilis*. Sabelis (1986) used empirically determined behavioural data in the model. To investigate whether our indirect and simplified method of estimating the attack rate affected the conclusions, we first used it to reanalyse predation of *P. persimilis* in a mixture of eggs and preoviposition females of *T. urticae*. Estimations of C and z are given in Table 2a. The estimations of C are well within an order of magnitude of the experimental values derived by Sabelis (1989): 640 and $1180 \text{ mm}^2/\text{day}$ for prey eggs and prey females respectively. The curves of $f(s)$ resulting from the estimated z values also compare rather well with experimentally derived success ratio curves (Fig. 1). Our predictions (Fig. 2) do not differ appreciably from those made by Sabelis (1986, 1989). Model calcula-

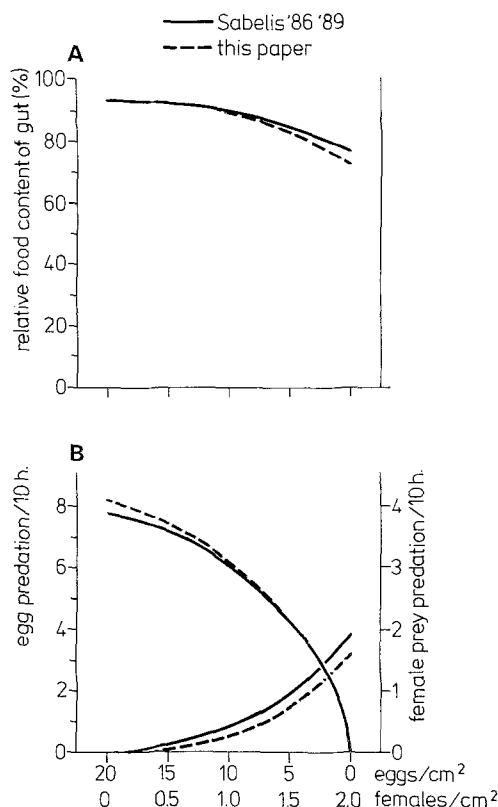


Fig. 2A, B. Comparison of model steady state calculations for *Phytoseiulus persimilis* in mixed cultures of *T. urticae* eggs and females. Continuous lines represent calculations by Sabelis (1986) who included experimentally determined behavioural characteristics into the model. Dashed lines represent calculations made with indirectly estimated behavioural parameters. **A** Relative food content of the gut. **B** Predation rates

Table 2A, B. Values of attack rate parameters that result in best fit of model to measurements of predation rates in monocultures

A Predator: *Phytoseiulus persimilis*

Prey	C (mm^2/day)	z
<i>T. urticae</i> eggs	550	-0.72
<i>T. urticae</i> preoviposition females	800	0.30

B Predator: *Typhlodromus pyri*

Prey	a	b	C (mm^2/day)	z
One-parameter function for $f(s)$				
<i>P. ulmi</i> larvae	-	-	2500	-0.94
<i>A. schlechtendali</i> adults	-	-	13000	-0.95
Weibull function for $f(s)$				
<i>P. ulmi</i> larvae	1.08	10	3000	-
<i>A. schlechtendali</i> adults	1.06	10	10000	-

tions of relative gut fullness are also similar (Fig. 2). In short, our simplifications have not affected the conclusions on prey preference of *P. persimilis* and may be applied to an analysis of prey species preference in *T. pyri*.

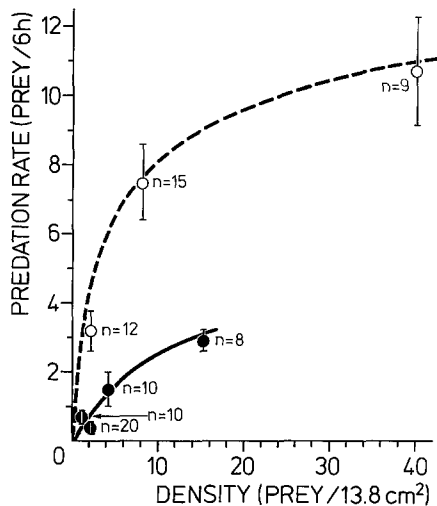


Fig. 3. Functional response of *Typhlodromus pyri* to the density of *Panonychus ulmi* larvae (—) or *Aculus schlechtendali* adults (---). The lines represent steady state calculations made with the model, where $f(s)$ is represented by the one-parameter equation (Eq. 2). The mean measured predation rate is indicated by a dot, the bar represents the standard error

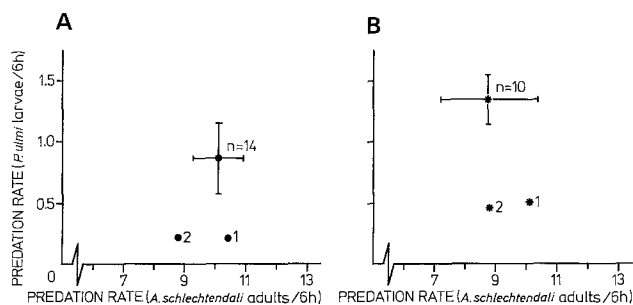


Fig. 4A, B. Comparison of measured and predicted predation rates of *Typhlodromus pyri* in mixed cultures of *Panonychus ulmi* larvae and *Aculus schlechtendali* adults. Dot with bars (representing standard errors) indicates measured predation rates. Numbered dots represent predicted predation rates when using (1) the one parameter or (2) the two parameter function for $f(s)$. **A** 2 *P. ulmi* larvae and 30 *A. schlechtendali* adults per disc; **B** 6 *P. ulmi* larvae and 30 *A. schlechtendali* adults per disc

(b) *Typhlodromus pyri*. Predation rates in monocultures of each prey species are presented in Fig. 3. The best fit of the model to each functional response is shown for the simulation where $f(s)$ was represented by the one parameter (z) function (Eq. 2). Estimations of C and z are presented in Table 2b. For both prey species the value of z^* indicates that $f(s)$ is a convex curve, that steeply declines at high values of s . The observed and predicted predation rates in the mixed cultures are given in Fig. 4. The 95% confidence intervals of the observations indicate that the predicted values for the predation rates on apple rust mites do not differ from the observations. However, the experimental values for the rate of predation on European red spider-mite larvae differ greatly from the prediction: for *P. ulmi*, observed rates are 3–7 times higher than predicted ones.

When the Weibull function is used to represent $f(s)$, predicted rates of the predation in mixed cultures also differ greatly from experimental values (Fig. 4, Table 2 for esti-

Table 3A, B. Walking speed and activity of prey in monocultures and mixed culture (2 *Panonychus ulmi* and 50 *Aculus schlechtendali* per 500 sq mm)

A. P. ulmi

Density	Activity (%)	<i>n</i>	Walking speed ^a (mm/s)	<i>n</i>
Mono culture				
2	60–70	30	0.19 ± 0.06 a*	6
4	60–70	40	0.20 ± 0.06 a	10
8	60–70	64	0.22 ± 0.03 b	13
Mixed culture				
2	70–80	12	0.15 ± 0.05 b	24

* Walking speed data were analysed by ANOVA: $F = 5.09$, $df = 3, 49$, $P = 0.004$. Subsequently, significant differences were detected with the Tukey test. Walking speed values followed by the same letter are not significantly different (5% level)

^a Mean ± standard deviation

B. A. schlechtendali

Density	Activity (%)	<i>n</i>	Walking speed ^a (mm/s)	<i>n</i>
Mono culture				
4	50–60	28	0.07 ± 0.02 b*	9
15	60–70	75	0.07 ± 0.01 b	9
50	50–60	150	0.06 ± 0.02 a	9
Mixed culture				
50	50–60	300	0.05 ± 0.02 a	30

* See Table A. ANOVA: $F = 5.94$, $df = 3, 53$, $P = 0.002$

^a See Table A

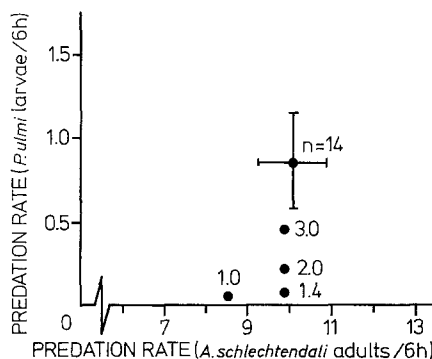


Fig. 5. Comparison of measured and predicted predation rates of *Typhlodromus pyri* in a mixed culture of 2 *Panonychus ulmi* larvae and 30 *Aculus schlechtendali* adults. Dot with bars (representing standard errors) indicates measured predation rates. Predictions were made with different values of r_G (indicated in the Fig.). C (mm^2/day) and z values at different r_G values (day^{-1}):

$r_G = 1.0$: *P. ulmi*: $C = 3000$, $z = -0.97$;
A. schlechtendali: $C = 30000$, $z = -1.00$
 $r_G = 1.4$: *P. ulmi*: $C = 2900$, $z = -0.93$;
A. schlechtendali: $C = 15000$, $z = -0.97$
 $r_G = 2.0$: *P. ulmi*: $C = 2900$, $z = -0.90$;
A. schlechtendali: $C = 15000$, $z = -0.85$
 $r_G = 3.0$: *P. ulmi*: $C = 2700$, $z = -0.85$;
A. schlechtendali: $C = 10000$; $z = -0.30$

mated values of a , b and C). The conclusions thus do not depend on the function used for $f(s)$.

Are deviations in predation rates from prediction due to changes in predator or prey behaviour?

The difference between observed and predicted predation rates of *T. pyri* in mixed cultures is too large to be explained by differences in the walking activity or speed of prey or predator. In fact prey behaviour in a mixed culture is little different from that in monoculture. Some significant differences in prey activity or walking speed occur between monocultures (Table 3), but not between the mixed culture and corresponding monocultures.

Clearly, foraging decisions of *T. pyri* are not affected by the food content of the gut alone but also by the composition of prey species supply. *Typhlodromus pyri* appears to change its behaviour in the mixed culture, feeding more on *P. ulmi* than expected from its behaviour in monocultures.

We next asked whether variation in either food conversion parameters or attack rate parameters affected this conclusion:

(1) Food conversion parameters. We varied r_G from 1.0 to 3.0 (26°C) and determined C^* and z^* values for each value of r_G . When the value of r_G was as low as 1.0 no fully satisfactory fit for the functional response could be obtained. In that case, C and z values that resulted in the best possible fit were used to predict predation rates in mixed cultures. Figure 5 shows that our conclusion is not affected by drastic changes in r_G .

(2) Attack rate parameters. Figure 6a shows the product of $C^*f(s)$ (which describes the relationship between attack rate (σ) and prey density (D)), over s for several values of a , b and C (sigmoid function of $f(s)$) with respect to *P. ulmi* as prey. Note that by convention always $f(1.0)=0.0$. The corresponding predicted predation rates in mixed culture are shown in Figure 6b. In these calculations, values of a^* , b^* and C^* with respect to *A. schlechtendali* were determined from the best fit of the functional response. Figure 6 shows that only when $f(s)=1$ (independent of gut fullness for all gut-content classes except the highest class, line 1 in Figure 6a), predicted predation rates in the mixed culture are similar to the measured rates. Similar manipulations of $f(s)$ describing the interaction between *T. pyri* and *A. schlechtendali* were carried out. Here, values of a^* , b^* and C^* for $f(s)$ describing the interaction between the predator and *P. ulmi* were determined from monocultures with this prey species. Calculations revealed that changes that resulted in increased predicted *P. ulmi* predation cause a strong decrease in *A. schlechtendali* predation. No change in $f(s)$ for the *T. pyri*-*A. schlechtendali* interaction resulted in predicted predation rates for the mixed culture that resembled the observed rates. Thus, a severe change in the success ratio with respect to *P. ulmi* is the only factor capable of making the model calculations correspond with the experimental predation rates.

Discussion

Causal analysis

Sabelis (1986, 1989) developed a method for causal analysis of prey preference in phytoseiid species, for which data on

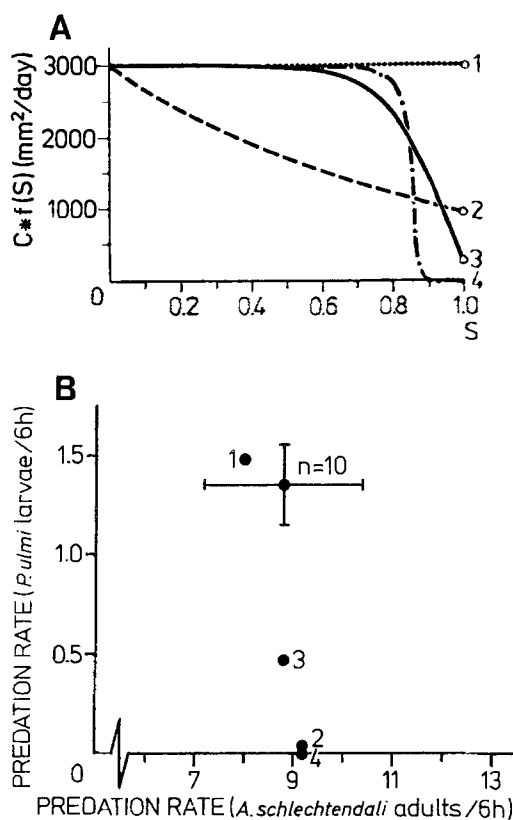


Fig. 6A, B. Effect of varying model parameters a and b in $f(s)$ (equation 3) for the interaction of *Typhlodromus pyri* and *Panonychus ulmi*. *T. pyri* - *A. schlechtendali* interaction: $a^*=1.06$; $b^*=10$; C^*10000 mm²/day. *T. pyri* - *P. ulmi* interaction:

- 1: $a^*=0.10$; $b^*=10$; $C^*=3000$ mm²/day
 2: $a^*=1.18$; $b^*=15$; $C^*=3000$ mm²/day
 3: $a^*=1.08$; $b^*=10$; $C^*=3000$ mm²/day
 4: $a^*=1.18$; $b^*=50$; $C^*=3000$ mm²/day

A Effect on the value of $C^*f(s)$ at several levels of gut fullness (s). **B** Comparison of the predicted predation rates in a mixed culture of 6 *Panonychus ulmi* larvae and 30 *Aculus schlechtendali* adults with the measured predation rates

behaviour and food conversion were available. Based on these data we made some assumptions on the general shape of the attack rate, σ , as a two-parameter function of the satiation level, s . Together with data on food conversion, the predation model is fully defined except for two parameters to be estimated by setting their value such that measured and calculated predation rates in prey monocultures are made to correspond. After comparison of predicted and measured predation rates in mixed cultures one may decide whether additional observations are needed.

Current results with mixed prey cultures indicate that *T. pyri* prefers *P. ulmi*. Independent tests suggest this pattern is robust. Dicke (1988) investigated prey preference of *T. pyri* by studying the response of a laboratory population towards prey kairomones. Dicke and De Jong (1988) analysed the diet of a field population of *T. pyri* by electrophoresis of gut contents. The conclusions of both studies are consistent with the conclusion drawn here.

Functional analysis

Given these results of the causal analysis, one may question why *T. pyri* prefers European red spider mites. Two func-

tional arguments would predict the opposite, a preference for apple rust mite: (1) the predator's intrinsic rate of increase is higher when fed apple rust mites exclusively than when fed European red spider mites exclusively (Dicke et al. 1989a). (2) Under selective feeding the time needed to find and catch a prey is longer than when both prey species are accepted. Thus, selective feeding results in a lower level of gut fullness and thereby in a lower rate of absorption of food from the gut (Sabelis 1986) and thereby a lower rate of oviposition.

It seems then, that *T. pyri* sacrifices a high intrinsic rate of increase in order to increase the proportion of *P. ulmi* in its diet. Why would they do so? A prey type may be more preferred e.g. because it (1) is attacked and caught more easily, (2) has a more profitable composition of nutritious compounds, (3) contains less toxic components that need to be detoxified or (4) is a more prolific organism, that provides more prey and for a longer period. Do one or more of these arguments provide an indication why *T. pyri* prefers *P. ulmi*?

Regarding (1), rust mites are smaller and probably have a thinner integument than spider mites. Therefore, it is inconceivable that rust mites are more difficult to get hold of than European red spider mites. Behavioural observations support this view (Dicke, unpublished work). Regarding (2), by inducing 'specific hunger' food quality affects subsequent food selection behaviour in many organisms (Dethier 1976), including phytoseiid mites (Dicke et al. 1989b). The behavioural response of females of *T. pyri* and *Amblyseius potentillae* (Garman) to volatile kairomones is affected by the diet on which predators are reared: when reared on broad bean pollen, these predators have a 'specific hunger' for carotenoids (Dicke et al. 1986; Dicke and Groeneveld 1986; Dicke 1988). *Amblyseius potentillae* needs carotenoids for diapause induction (Overmeer 1985; Van Houten et al. 1987). The amount needed is small: females that feed on a carotenoid source can supply their offspring with enough carotenoids for diapause induction (Van Zon et al. 1981). Both *P. ulmi* and *A. schlechtendali* may provide the predators with carotenoids (Van der Geest 1985; Dicke et al. 1989a). However, Dicke et al. (1989a) observed that these two prey species are not identical in this respect. After transfer of *A. potentillae* females to a carotenoid-deficient diet, previous feeding on *P. ulmi* exerted a longer-lasting effect on diapause induction in the offspring than previous feeding on *A. schlechtendali*. Whether this is caused by a quantitative or qualitative difference in carotenoid content is not clear. Behavioural data indicate that these nutrients are also important for *T. pyri*, but their function for this predator species remains unknown (Dicke 1988). In short, the effect of a difference in carotenoid-content of the two prey species on prey preference of *T. pyri* remains an open question.

Regarding (3), nothing is known about toxic compounds in apple rust mites and European red spider mites.

Regarding (4), it is important to note that European red spider mites and apple rust mites do not occur in spatially separated patches. They are frequently found together on the same leaf. Hence, when nutritional quality and toxic load would not differ between the two species, the predators would do better by feeding non-selectively (the more so because time spent feeding is small compared to intercatch time intervals, even at high prey density).

Our experiments to date, however, show that *T. pyri*

feed selectively and prefer the less profitable prey species. This incongruous result may be the consequence of an oversimplified definition of fitness. Profitability of each prey has been measured only at high prey density, thus representing a measure of potential fitness at such densities (Dicke et al. 1989a). The actual availability of prey in the environment is also an important determinant of prey profitability. This factor is obviously rather difficult to estimate, especially since prey availability is a function of predator-prey dynamics and may be negatively influenced by preferential predation. The evolution of prey preference may well be constrained by its own effect on prey availability or the effect of other predator species on it. In other words, competition for food may have played an important role in structuring prey preferences in predator-prey communities of plant-inhabiting mites. We plan to test this hypothesis in future studies (M. van Baalen and M.W. Sabelis).

In conclusion, we cannot presently explain why *T. pyri* prefers *P. ulmi* to *A. schlechtendali*. Future investigations should focus on nutritional differences between prey species, nutritional demands of the predator and the possible effect of competition among predator species on prey preference of *T. pyri*.

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