

Do Phytoseiid Mites Select the Best Prey Species in Terms of Reproductive Success?

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(Accepted 16 September 1988)

ABSTRACT

Dicke, M., Sabelis, M.W., de Jong, M. and Alers, M.P.T., 1990. Do phytoseiid mites select the best prey species in terms of reproductive success? *Exp. Appl. Acarol.*, 8: 161–173.

Optimal foraging theory predicts that predators prefer those prey species that are most rewarding in terms of reproductive success, which is dependent on prey quality and prey availability. To investigate which selection pressures may have moulded prey preference in an acarine system consisting of two prey species and three predator species, we tested whether prey preference of the predators is matched by the associated reproductive success.

The predators involved are *Amblyseius finlandicus* (Oudemans), *Am. potentillae* (Garman) and *Typhlodromus pyri* Scheuten. The prey species are the apple rust mite (*Aculus schlechtendali* (Nalepa)) and the fruit-tree red spider mite (*Panonychus ulmi* (Koch)).

Reproductive success was assessed in terms of intrinsic rate of increase and for one predator also in terms of diapause induction. All three predator species reached highest reproductive success on the same prey species: apple rust mite. This was most pronounced for the predator *Am. finlandicus*, because its larval stage suffered severe mortality when feeding on *P. ulmi*.

An independent study on prey preference of the three predator species (Dicke et al., 1988) revealed that *Am. finlandicus* prefers *Ac. schlechtendali* to *P. ulmi*, whereas the other two predator species have the reverse preference.

Thus, on the basis of current data, prey preference of *Am. finlandicus* can be understood in terms of reproductive success. However, this is not so for prey preference of *T. pyri* and *Am. potentillae*. Investigations needed for a better understanding of prey preference of the last-named two predator species are discussed.

INTRODUCTION

Reproductive success of a predator is likely to depend on the prey species consumed. Intraspecific variation in prey preference may therefore lead to significant differences in the contribution of each individual predator to the next

generation. If prey preference has a genetic basis, natural selection will favour genotypes coding for preferences that maximize the genetic input into future generations. Predictions of how natural selection will operate are not at all straightforward. These depend on prey-species availability which in turn may depend on prey-species availability which in turn may depend on mutual interactions between prey species. Moreover, when more than one predator species forages on the same set of prey species, prey-species availability also depends on the preference of each predator species and on the possible existence of mutual interactions between predator species.

To investigate which selection pressures may have moulded prey preference, it is a reasonable first step to test whether prey preferences of the predators are matched by the associated reproductive success. This hypothesis assumes equal availability of all prey species included in the diet. Under this assumption, reproductive success can be measured as the number of offspring produced by a predator in a given period of time when the prey species under consideration is abundantly available.

In this paper we test this hypothesis for the case of three phytoseiid species that are commonly found in Dutch apple orchards: *Typhlodromus pyri* (Scheuten), *Amblyseius finlandicus* (Oudemans) and *A. potentillae* (Garman) (Overmeer, 1981; Gruys, 1982; McMurtry and van de Vrie, 1973). The major part of the diet of these predators consists of two phytophagous mite species that are considered to be pests (Easterbrook, 1979; Van de Vrie, 1973; Van Epenhuijsen, 1981; Gruys, 1982) and therefore far more abundant than any other potential prey species: the European red spider mite, *Panonychus ulmi* (Koch), and the apple rust mite, *Aculus schlechtendali* (Nalepa).

Typhlodromus pyri and *Am. potentillae* prefer *P. ulmi* to *Ac. schlechtendali*, whereas *Am. finlandicus* has a reverse preference (Dicke et al., 1988). These preferences are firmly established because they were assessed by three independent methods: (1) olfactometer experiments; (2) predation experiments; and (3) electrophoretic diet analysis of predators collected in the field. The preferences assessed by each of these methods were fairly consistent for each predator species (Dicke et al., 1988). To determine the pay-off of these preferences, we investigated two components considered to be major determinants of reproductive success on each of the two prey species: (1) The intrinsic rate of population increase, r_m ; this characteristic was estimated for predators that were provided with an ample prey supply. (2) Diapause induction when feeding on either prey species. Under the null hypothesis we expected reproductive success to match the prey preferences assessed earlier (Dicke et al., 1988). If this hypothesis does not hold, there are good reasons to believe that either prey availability as a prey species characteristic (e.g. in terms of intrinsic rate of increase) or some form of competition affecting prey availability has played a role in moulding prey preferences of phytoseiid mites.

MATERIALS AND METHODS

Mites

The predatory mites were reared in the laboratory on pollen of broad bean (*Vicia faba* L.), variety Suprifin (Janssen Zaad, Dinxperlo, The Netherlands) at $26 \pm 1^\circ\text{C}$ and $60 \pm 10\%$ relative humidity (r.h.) under continuous fluorescent light. Pollen was collected from the flowers by hand, dried at 40°C during 1–2 days and stored at -20°C . The pollen was supplied on plastic plates, surrounded by wet tissue (provision of water) and sticky glue (prevention of escape) (Overmeer, 1985b).

Amblyseius potentillae and *T. pyri*, obtained from A.Q. van Zon and W.P.J. Overmeer (University of Amsterdam), had been reared on broad-bean pollen for approximately 7 years since collection. The origin of these predators' culture is given by Overmeer (1981). *Amblyseius finlandicus* had been collected from ornamental *Prunus* sp. in Wageningen in 1985.

Prey mites were collected in apple orchards. Leaves with *Ac. schlechtendali*, and twigs with winter eggs and leaves with summer eggs of *P. ulmi* were stored at 5°C until needed for experimental work.

Estimating intrinsic rate of increase

For each predator species we were interested in relative values of r_m on a diet of either of the two prey species. The following life-history components were determined experimentally: (1) development time; (2) mortality; and (3) initial oviposition rate, measured during the first 3 days of the oviposition period. This 3-day restriction was made because provision of prey, especially the tiny rust mites, was laborious. Sex-ratios were obtained from the literature (Rabbinge (1976) for *Am. potentillae*, Overmeer (1981) for *T. pyri*, and Sabelis (1985b) for *Am. finlandicus*), assuming sex allocation by phytoseiid mites does not depend on the prey species.

The intrinsic rate of increase (r_m) was estimated (according to Lotka, 1925) over a 10-day oviposition period, assuming that oviposition rate and mortality of ovipositing females were constant over this period (Sabelis, 1981, 1985c). Oviposition periods of phytoseiid mites usually last longer than 15 days at 25°C (Sabelis, 1985c) and therefore this 10-day period is certainly not too long. A sensitivity analysis for the effect of longer oviposition periods was carried out. Because the estimate of r_m is calculated on the basis of an incomplete life-table, it will be referred to as r'_m .

Determination of life-history components.

Predator eggs, collected at 4-h intervals, were transferred to leaf discs (2-cm diameter) that were placed with the adaxial side on water-soaked cotton wool. Apple leaf discs were used for *Am. potentillae* and *T. pyri*, and *Prunus* sp. leaf

discs for *Am. finlandicus*. A rooflike structure (sides 0.5×0.5 cm) was placed on each disc to provide the predators with a shelter (Overmeer, 1985b). Provision of food was initiated just before egg-hatching was expected to occur. In this way, emerging larvae encountered food immediately. New prey items were supplied at 8-h intervals to guarantee a continuous ample prey supply. The number of prey mites that was supplied at each 8-h interval was tuned to the prey requirements of each predator stage: 5, 10, 15 or 25 *P. ulmi* larvae, or 25, 25, 40 or 60 *Ac. schlechtendali* adults for larvae, protonymphs, deutonymphs and adults of the predators, respectively.

To obtain prey of the right stage, leaves with *P. ulmi* eggs were taken from cold storage and kept at 26°C ; newly emerged larvae were collected and transferred to the leaf discs. Active *Ac. schlechtendali* adults were collected from the cold-stored leaves and placed on the leaf discs immediately. The leaf discs were observed at 8-h intervals to see whether the predators had developed into the next stage. A moult was recorded only if the exuvium was found, which was then discarded. When a female deutonymph was 24 h old, one or two adult males were placed on the disc to allow for mating as soon as possible after the final moult. Oviposition was recorded at 8-h intervals during 72 h after the first egg had been recorded. All observed eggs were removed from the disc.

Drowned predators were not included in the calculation of mortality.

The experiments were carried out in climatic rooms at $26 \pm 1^\circ\text{C}$ and 50–70% r.h. For each predator species the experiments were carried out within a period of 3 months.

Effect of prey species on diapause induction.

Diapause induction in *Am. potentillae* depends on food quality; availability of carotenoids is indispensable (Van Zon et al., 1981; Veerman et al., 1983). When mothers feed on a carotenoid source, their offspring earn a carotenoid legacy and do not require dietary carotenoids to enter diapause (Van Zon et al., 1981). When feeding on spider mites or rust mites, *Am. potentillae* females enter reproductive diapause under short-day conditions (Overmeer and Van Zon, 1983a; Dicke, unpublished data, 1985). To compare the effect of either *P. ulmi* or *Ac. schlechtendali* on diapause induction, *Am. potentillae* was reared on either prey species for at least 3 weeks. Subsequently, adult females were transferred (2–3 h since the last prey supply) to a rearing unit on which *V. faba* pollen was the only food source (26°C , L:D 24:0). Broad-bean pollen is a carotenoid-poor food source for *Am. potentillae* (Overmeer and van Zon, 1983a). Eggs were collected at 24-h intervals and reared to adulthood on *V. faba* pollen at low temperature and short day conditions ($18 \pm 1^\circ\text{C}$, L:D 8:16). When matings were observed, the rearing plates were inspected for presence of eggs at 2-day intervals. When eggs were found, females were individually isolated on plastic discs (diameter 2 cm) 4 days later in presence of *V. faba* pollen, to determine the percentage of predators that oviposited (non-diapause females). This isolation phase lasted for 7 days. When eggs had not been ob-

served on a plate during 18 days after the first mating, the experiment was terminated and all females were classified as having entered diapause.

To investigate whether differential effects on diapause induction by rust mites and spider mites are a result of feeding from different plant tissues (Jeppson et al., 1975), another spider mite, *Tetranychus urticae* Koch, also was used as prey during the initial phase. A dietary effect on diapause induction has not been recorded for *T. pyri* (Dicke, 1988) and it has not been studied for *Am. finlandicus* (Overmeer, 1985a). The current analysis was restricted to *Am. potentillae*.

RESULTS

Intrinsic rate of increase.

The data of life-history components are presented in Table 1 (development time and oviposition rate) and Table 2 (mortality), and the estimated values of r'_m in Table 3. Values of r'_m hardly increased when they were estimated for a 20-day period instead of a 10-day period (Table 3). Mortality of *Am. potentillae* and *T. pyri* did not occur during the experiment (Table 2) and therefore a value of $l_x=1.0$ was used to estimate r'_m . When using a more realistic value of $l_x=0.9$, the r'_m values decreased only slightly (Table 3).

Amblyseius potentillae has a longer development time when feeding on *P. ulmi* larvae than on *Ac. schlechtendali*. Mortality has not been observed, and

TABLE 1

Development time and oviposition rate of *Am. potentillae*, *Am. finlandicus* and *T. pyri*, when feeding on an ample supply of *P. ulmi* larvae or *Ac. schlechtendali* adults at 26 °C

Predator species	Food species	Development time ¹ (larva → egg; h)	Oviposition rate ¹
<i>Am. potentillae</i>	<i>Ac. schlechtendali</i>	133 ± 21 a (n=21)	2.9 ± 0.4 a (n=20)
	<i>P. ulmi</i>	153 ± 26 b (n=22)	2.7 ± 0.4 a (n=17)
<i>T. pyri</i>	<i>Ac. schlechtendali</i>	173 ± 8 a (n=22)	2.0 ± 0.7 a (n=22)
	<i>P. ulmi</i>	163 ± 11 b (n=22)	1.9 ± 0.1 a (n=22)
<i>Am. finlandicus</i>	<i>Ac. schlechtendali</i>	172 ± 47 a (n=12)	2.3 ± 0.5 a (n=12)
	<i>P. ulmi</i>	172 ± 24 a (n=23)	2.4 ± 0.3 a (n=23)

¹Mean ± standard deviation. Values for the same predator species in the same column followed by the same letter are not significantly different ($\alpha=0.05$, Student *t*-test).

TABLE 2

Influence of diet on mortality of *Am. potentillae*, *Am. finlandicus* and *T. pyri*

Predator species	Food species	% larvae becoming protonymph	% protonymphs becoming adult	% adult females surviving first 72 h of oviposition period
<i>Am. potentillae</i>	<i>Ac. schlechtendali</i> ¹	100 (37) ²	100 (35)	100 (20)
	<i>P. ulmi</i>	100 (37)	100 (37)	100 (17)
<i>T. pyri</i>	<i>Ac. schlechtendali</i>	100 (39)	100 (36)	100 (22)
	<i>P. ulmi</i>	100 (41)	100 (39)	100 (22)
<i>Am. finlandicus</i>	<i>Ac. schlechtendali</i>	86 (42)	100 (28)	92 (13)
	<i>P. ulmi</i>	46 (131)	86 (47)	96 (24)
	no food	6 (36)	0 (2)	-

¹*Ac. schlechtendali* adults; *P. ulmi* larvae.²Numbers in parentheses indicate number of predators.

TABLE 3

Estimated rates of population increase (r'_m) for *Am. potentillae*, *Am. finlandicus* and *T. pyri* when feeding on *P. ulmi* larvae or on *Ac. schlechtendali* adults

Predator	Prey	l_x survival	m_x reproduction rate (eggs/day)	s^1 sex-ratio	egg-egg development (days)	r'_m (day ⁻¹)	
						10-day period	20-day period
<i>Am. potentillae</i>	<i>Ac. schlechtendali</i>	1.0	2.9	0.69	7.92	0.240	0.247
		0.9	2.9	0.69	7.92	0.231	0.239
	<i>P. ulmi</i>	1.0	2.7	0.69	8.63	0.221	0.228
		0.9	2.7	0.69	8.63	0.212	0.220
<i>T. pyri</i>	<i>Ac. schlechtendali</i>	1.0	2.0	0.39	9.54	0.142	0.156
		0.9	2.0	0.39	9.54	0.134	0.149
	<i>P. ulmi</i>	1.0	1.9	0.39	9.92	0.135	0.149
		0.9	1.9	0.39	9.92	0.127	0.142
<i>Am. finlandicus</i>	<i>Ac. schlechtendali</i>	0.84	2.4	0.62	9.13	0.175	0.186
	<i>P. ulmi</i>	0.39	2.3	0.62	9.33	0.125	0.140

¹females/ (females + males).

rates of reproduction were similar for *Am. potentillae* feeding on either prey species. These differences result in a higher r'_m for *Am. potentillae* when feeding on apple rust mites than when feeding on European red spider-mite larvae. It is therefore concluded that *Ac. schlechtendali* is a better prey species for *Am. potentillae* than *P. ulmi*, in terms of r'_m .

Typhlodromus pyri developed faster on *Ac. schlechtendali* than on *P. ulmi*. No difference was observed for the rate of reproduction, which was rather high compared to data by Overmeer (1981), who reported a reproduction rate of 0.6

eggs female⁻¹ day⁻¹ on *P. ulmi* as prey (25°C). No mortality has been recorded. Thus, *Ac. schlechtendali* is a better prey species for *T. pyri*: r'_m is higher on apple rust mites than on European red spider-mite larvae as prey.

Amblyseius finlandicus developed equally fast on *Ac. schlechtendali* and on *P. ulmi* larvae. Also, oviposition rates were similar. However, these two prey species are not of equal value to this predator species: larvae had a much higher mortality when feeding on *P. ulmi* larvae than when feeding on *Ac. schlechtendali* ($P < 0.001$; *G*-test, Sokal and Rohlf, 1981). Gut colour indicated that all larvae which developed into protonymphs had fed, whereas larvae that died consisted of both fed and unfed individuals. In *T. pyri*, none of the larvae had fed, whereas in *Am. potentillae* 20% of the larvae had fed. This led to the hypothesis that *Am. finlandicus* larvae need food to complete larval development, but have difficulties in using *P. ulmi* larvae for that purpose. We therefore studied mortality when no food was offered: almost all larvae died (Table 2), which indicates that *Am. finlandicus* needs food to reach the protonymphal stage.

Because of differences in larval mortality, *Ac. schlechtendali* is considered a better prey species for *Am. finlandicus*: r'_m is much higher on *Ac. schlechtendali* than on *P. ulmi* larvae as prey.

Effect of prey species on diapause induction in Am. potentillae

When female *Am. potentillae* were transferred from *P. ulmi* or *Ac. schlechtendali* to a diet of *V. faba* pollen, the percentage offspring entering reproductive diapause decreased when the time interval between transfer of the mother and oviposition increased. However, this effect was stronger when the former diet of the mothers had consisted of rust mites than when they had fed on spider mites (Fig. 1). When females fed on spider mites before transfer to broad-bean pollen, a reduction in percentage diapause in their offspring was manifest by the 3rd day after the transfer to the carotenoid-deficient diet. When fed on rust mites before transfer, this effect occurred on the 1st day after transfer. No difference in effect was observed between experiments in which the mothers had fed on either of the two spider-mite species, *T. urticae* or *P. ulmi*, before transfer.

DISCUSSION

Life-history components.

Despite much literature data on development time and/or oviposition rate of the three phytoseiid species studied (Herbert, 1961; Kropczynska, 1970; Kropczynska-Linkiewicz, 1971; Zaher and Shehata, 1971; Van de Vrie, 1973; Rabbinge, 1976; Amano and Chant, 1977, 1986; McMurtry, 1977; Overmeer, 1981; Sabelis, 1981; Hayes and McArdle, 1987), we made a new investigation

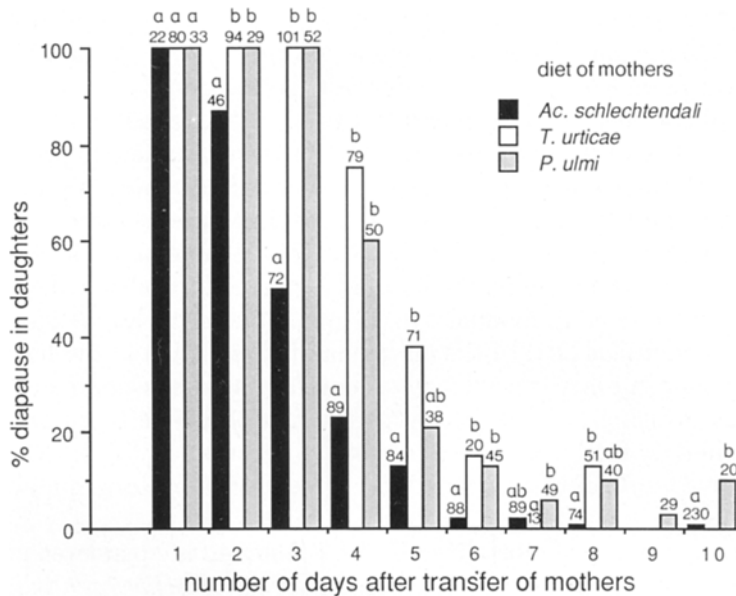


Fig. 1. Effect of diet of *Am. potentillae* mothers on diapause induction in offspring, produced after transfer of mothers from a carotenoid-containing diet of phytophagous mites to the carotenoid-deficient diet of *V. faba* pollen. Numbers above bars indicate number of predators observed. Different letters above bars for the same day indicate significant differences ($\alpha=0.05$, *G*-test, Sokal and Rohlf, 1981).

for the following reasons: (1) Changes in life-history parameters may occur with increasing time-periods of laboratory rearing of a phytoseiid strain: e.g. in the course of one year the oviposition rate of *T. pyri*, when feeding on *V. faba* pollen, more than doubled for predators that had been reared on this food source (Overmeer, 1981; Overmeer and van Zon, 1983b). Thus, for a comparative analysis of life-history components, experiments using one predator strain should be carried out within a short period of time. (2) Only Kropczynska (1970) and Kropczynska-Linkiewicz (1971) made a comparative analysis of development time and reproduction rate for these predator species when feeding on either *P. ulmi* or *Ac. schlehtendali*. However, no record was made of prey stages or time-interval of observations to determine development time. Drawing conclusions on the significance of the reported differences is therefore difficult (Sabelis, 1985a). Despite these reservations, however, the data of Kropczynska (1970) and Kropczynska-Linkiewicz (1971) concerning the development rates of *Am. potentillae*, *Am. finlandicus* and *T. pyri* have been compared with our data (Table 4). Although quantitative differences exist, qualitative conclusions on relative development times of *Am. potentillae* and *T. pyri* are similar in both studies. However, a large discrepancy exists with respect to *Am. finlandicus*.

TABLE 4

Development times of three phytoseiid species, when feeding on *Ac. schlechtendali* or *P. ulmi* at 25—26°C

Predator species	Prey species	Development time		Source
		Egg→ adult (h)	Ratio ¹	
<i>Am. finlandicus</i>	<i>Ac. schlechtendali</i>	259		Kropczynska (1970)
	<i>P. ulmi</i>	182	1.42	
<i>Am. finlandicus</i>	<i>Ac. schlechtendali</i> (adults)	164	0.94	Present paper
	<i>P. ulmi</i> (larvae)	175		
<i>Am. potentillae</i>	<i>Ac. schlechtendali</i>	211	0.93	Kropczynska-Linkiewicz (1971)
	<i>P. ulmi</i>	228		
<i>Am. potentillae</i>	<i>Ac. schlechtendali</i> (adults)	132	0.94	Present paper
	<i>P. ulmi</i> (larvae)	140		
<i>T. pyri</i>	<i>Ac. schlechtendali</i>	250	0.95	Kropczynska-Linkiewicz (1971)
	<i>P. ulmi</i>	262		
<i>T. pyri</i>	<i>Ac. schlechtendali</i> (adults)	163	0.96	Present paper
	<i>P. ulmi</i> (larvae)	170		

¹Time on *Ac. schlechtendali*/time on *P. ulmi*.

Larvae of many phytoseiid species do not need food to develop into the protonymph stage (e.g., Chant, 1959; Amano and Chant, 1986), although feeding may occur, as has been noticed for *Am. potentillae* in the present study. Apparently, only *Am. finlandicus* larvae need food to complete the larval stage (Chant, 1959; Amano and Chant, 1986). This raises the question of why *Am. finlandicus* larvae are obligate feeders. This question is also relevant in the light of observations of large numbers of all stages of *Am. finlandicus* on trees on the leaves of which hardly any prey could be found (Sabelis and van de Baan, 1983; and present observations on collection site of *Am. finlandicus*). Do *Am. finlandicus* larvae rely on other food sources that are generally available? Present knowledge indicates that, if leaf sap or phyllosphere microorganisms are such a food source, they were insufficiently available in the experimental setups (Chant, 1959; Amano and Chant, 1986; and the present paper).

Effect of prey species on diapause induction in Am. potentillae

Amblyseius potentillae females that feed on *T. urticae* supply their offspring with sufficient carotenoids to enter reproductive diapause (Van Zon et al., 1981). In addition, daughters produced during the first 3 days after transfer from a *T. urticae* diet to *V. faba* pollen enter diapause under short-day conditions. In the offspring produced thereafter the percentage entering diapause declines with time. When the mothers had been feeding on the spider mite *P. ulmi*, the effects are similar. However, when the mothers had been feeding on the rust mite *Ac. schlechtendali*, the decline occurs already after the first day. When predators are transferred from one food source to another, the percentage of the former food in the gut declines exponentially after transfer to a new diet (Sabelis, 1981). This percentage amounts to 8.2 ($= \exp(-2.50 \cdot 1)$) after 1 day and 0.06 ($= \exp(-2.50 \cdot 3)$) after 3 days (relative rate of gut emptying obtained from Dicke et al., 1988). The data show that spider mites and rust mites affect diapause induction in *Am. potentillae* differently. It cannot be concluded from this experiment which prey component is involved. Because carotenoids are known to affect diapause induction, chemical analysis of quantitative and qualitative carotenoid content of spider mites and rust mites would be worthwhile. Current knowledge indicates that only carotenoids with provitamin A function relieve the deficiency of the diet with respect to photoperiodic diapause induction (Veerman et al., 1983). However, no investigation has been made on the qualitative differences between such carotenoids regarding the effect on diapause induction. To date, other nutrients that affect diapause induction in mites are not known.

It will be interesting to investigate whether the differences in nutritive value of *P. ulmi* and *T. urticae* on the one hand, and *Ac. schlechtendali* on the other, are caused by differences in their feeding habits. Spider mites have much longer stylets and can penetrate the parenchyma, whereas rust mite stylets can only penetrate the epidermal cells (Jeppson et al., 1975). Plants infested by rust mites not only show damaged cells in the epidermis but also in deeper cell layers (Schliesske, 1977). However, it is not known whether this damage results in uptake of nutrients from the parenchyma by rust mites.

In conclusion, spider mites constitute a superior prey for *Am. potentillae* in terms of diapause induction.

Prey preference and reproductive success

Table 5 summarizes the data on prey preference (Dicke et al., 1988b) and reproductive success. For *Am. finlandicus*, r'_m is much higher on *Ac. schlechtendali* than on *P. ulmi* larvae, because of high larval mortality of predators feeding on *P. ulmi*. This difference in reproductive success matches prey preference.

As a result of low development rates when feeding on *P. ulmi* larvae, *Am. potentillae* and *T. pyri* also have lower r'_m values when feeding on this prey

TABLE 5

Prey preference and best prey species in terms of reproductive success parameters of three species of phytoseiid mites

Predator species	Preferred prey species	Best prey species in terms of	
		r'_m	Effect on diapause induction
<i>Am. finlandicus</i>	<i>Ac. schlechtendali</i>	<i>Ac. schlechtendali</i>	
<i>Am. potentillae</i>	<i>P. ulmi</i>	<i>Ac. schlechtendali</i>	<i>P. ulmi</i>
<i>T. pyri</i>	<i>P. ulmi</i>	<i>Ac. schlechtendali</i>	

species. This is most obvious for *Am. potentillae*. However, because the least vigorous *P. ulmi* stage was used, the difference in r'_m values would be expected to be larger when other *P. ulmi* stages are used (Sabelis, 1985a). In terms of diapause induction, *P. ulmi* is a better prey species for *Am. potentillae* than is *Ac. schlechtendali*. This is of importance at the end of the season. Current data, therefore, suggest that *Ac. schlechtendali* is a better prey species for *T. pyri* and, at least during the beginning of the season, also for *Am. potentillae*. This conclusion implies that prey preference of these predator species does not match reproductive success. As argued in the introduction, this may be due either to prey availability as a prey-species characteristic, or by prey availability as a result or competition between prey species or competition between predator species. Prey characteristic availability is dependent on the intrinsic rate of prey population increase (r_m). Estimated values of r_m early in the season are higher for *Ac. schlechtendali* (based on the data of Easterbrook, 1979) than for *P. ulmi* (based on the data of Rabbinge, 1976); (P. van Rijn and M.W. Sabelis, unpublished data, 1987). From July onwards, this difference is reversed because of production of overwintering deutogyne female *Ac. schlechtendali*. This makes *Ac. schlechtendali* a better prey species during the first half of the season and *P. ulmi* a better prey species during the last half. In addition, at the end of the season, prey effects on diapause induction also render *P. ulmi* a better prey species for *Am. potentillae*. Does this suggest that predatory mites should change prey preference during the season? Investigation of field-collected predators are needed. Electrophoretic diet analysis of *T. pyri* collected in August and September showed preference for *P. ulmi* (Dicke and de Jong, 1988), but no field data for the first half of the season are available.

Prey characteristic availability of *P. ulmi* and *Ac. schlechtendali* also are important to *Am. finlandicus*. However, because of the large difference in r'_m values of *Am. finlandicus* when feeding on *P. ulmi* or *Ac. schlechtendali*, the effect of a change in characteristic prey availability is less pronounced for *Am. finlandicus* than for *T. pyri* or *Am. potentillae*.

In conclusion, prey preference of *Am. finlandicus* shows reasonable corre-

spondence with reproductive success. For *Am. potentillae* and *T. pyri* the situation is more complex. Reproductive success in terms of r'_m does not match prey preference of these predator species. Differences in characteristic prey availability may account in part for this discrepancy. To increase understanding of the conditions that have moulded prey preference of phytoseiid mites, future investigations should concentrate on, e.g., (1) possible role of competition between predator species or between prey species, (2) prey preference early in the season, and (3) the effect of interspecific differences in carotenoid content of prey species on overwintering ability of predatory mites.

ACKNOWLEDGEMENTS

We thank P.J.C. van Lenteren and O.P.J.M. Minkenberg for comments on the manuscript, and P.J. Kostense for preparing the Figure.

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