



## Intraspecific variation in induction of feeding preference and performance in a herbivorous mite

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**Abstract.** Induction of food preference has often been observed in herbivorous insects. The term is used to indicate preference of individuals for the host plant they have already experienced over one they have not experienced. A typical set-up is one where individuals first feed on host X or Y, and are then offered a choice between host X and Y. This set-up – and hence the body of empirical data – has been criticised for lack of a control treatment to untangle the effects of the separate hosts. In this study, we use a design with a third, unrelated host as control to investigate induction of preference in the herbivorous arthropod, *Tetranychus urticae*. We provide evidence of induced preference, as well as induced performance, and show that there is considerable variation in these two traits among strains. We suggest induced resistance to toxic secondary plant chemicals as one potential explanation for induced performance. This in itself suggests associative learning as the most likely candidate learning mechanism for induction of preference in this species. Phenotypically plastic effects underlying induced performance may be a general aspect of induction of preference in herbivorous arthropods, which warrants closer attention to these phenomena.

### Introduction

In phytophagous insects, learning may play an important role in selection of host plants for feeding and/or oviposition (reviews in Papaj and Prokopy (1986, 1989); Szentesi and Jermy (1990), Bernays (1993, 1995a, 1995b)). Two distinct kinds of learning can be identified: associative and non-associative learning. Non-associative learning involves a gradual change in response to a (conditioning) stimulus. The response can either wane (habituation) or increase (sensitization). Both types of learning have been observed in phytophagous insects, e.g. habituation of *Schistocerca gregaria* to a feeding deterrent (Szentesi and Bernays 1984) and rejection by *Locusta* nymphs of unpalatable leaf material at a progressively earlier stage in food selection with experience (Blaney and Simmonds 1985). In associative learning, behaviour is changed due to an unconditioned stimulus which has become associated with a conditioned stimulus. A special kind of associative learning is food

aversion learning, where “learned associations develop between the taste of a food and a subsequent nausea or other negative internal effect” (Bernays 1993), rendering such a food unacceptable.

A separate category in the literature on insect learning has been termed induction of feeding preference by Jermy et al. (1968; review in Szentesi and Jermy 1990). The term is used when individuals prefer the host plant they have already experienced over one they have not experienced. A typical experimental set-up is one where individuals first feed on host X or Y, and are then made to choose between host X and Y. The result can be a change in the rank order of preference of host plants or, more commonly, only a change in the distinctness of preference (Papaj and Rausher 1983; Szentesi and Jermy 1990). Induction of preference has been reported for many larvae of Lepidoptera, but also for species in Orthoptera (1 species), Phasmatodea (2), Heteroptera (1), Homoptera (2), and Coleoptera (6). The test set-up of induction experiments (and hence the body of empirical data) has been criticised by Bernays and Weiss (1996), on the grounds that such experiments can only show the relative changes in preference, but cannot reveal possible learning mechanisms controlling it. Are the effects of conditioning the result of aversion to one food type, attraction to the other, or both? Some kind of control treatment is necessary to untangle these effects and pave the way for understanding the mechanisms behind food preference induction (associative learning, habituation (e.g., De Boer 1992), sensitization).

Recently, induction of feeding preference has also been found in the two-spotted spider mite, *Tetranychus urticae* Koch (Agrawal et al. 2002). We present further evidence for induction of feeding preference in *T. urticae*, and report on variation among strains of the species. We describe two experiments. First, in the food induction experiment, the effect of previous food experience (bean, tomato or cucumber) on subsequent preference for tomato or cucumber was investigated, using eight strains of *T. urticae*. We use bean as an unrelated host plant (i.e., from a different plant family) to control for changes in preference for tomato or cucumber. Second, we examined the preference-performance relationship and possible induction of performance for mites of two of the strains – one adapted to cucumber, and one adapted to tomato.

## Materials and methods

*Tetranychus urticae* is a polyphagous herbivore recorded from over 900 plant species (Bolland et al. 1998) and it is a well-known pest of many crops (Helle and Sabelis 1985). Eight strains of mites were collected from commercial greenhouses and two research stations in The Netherlands and in Poland, whereby inquiries were made as to the crop frequency and history in the greenhouse compartments the mites were collected from (Table 1). There are two important distinctions between the commercial greenhouses and the research stations: greenhouse compartments are much larger in commercial greenhouses, and crops alternate much less fre-

Table 1. Characteristics of the eight strains used in this study. NL refers to The Netherlands, PL to Poland. See text for further details.

Strains	Origin	Type	Collected on	Frequency	Since
Nootdorp, NL	Greenhouse	green	Cucumber	Continuously	12 yr
Pijnacker, NL	Greenhouse	green	Cucumber	Continuously	14 yr
Asten, NL	Greenhouse	green	Cucumber	Alternating	>5 yr
Schijndel, NL	Greenhouse	red	Cucumber	Alternating	>8 yr
De Meern, NL	Greenhouse	red	Tomato	Continuously	13 yr
Houten, NL	Greenhouse	red	Tomato	Continuously	>8 yr
Warsaw, PL	Res. station	red	Tomato	Alternating	unknown
Naaldwijk, NL	Res. station	red	Tomato	Alternating	unknown

Table 2. Two-way ANOVA of the effects of conditioning plant and strain type on preference for cucumber. Data were angularly ( $\arcsin[\sqrt{I}]$ ) transformed before analysis.

Source	df	MS	F	<i>p</i>
Strain (S)	7	0.027	1.01	0.39
Conditioning (C)	2	0.245	9.19	<0.001
S × C	14	0.0505	1.90	0.048
error	54	0.0266		

quently. Distinguishing the eight strains by origin, crop frequency and history, we obtained two strains of *T. urticae* from tomato (*Lycopersicon esculentum*) cultivars which had been grown continuously for many years, two strains from cucumber (*Cucumis sativa*) which had been grown continuously for many years, two strains from greenhouses with alternating crops of tomato and cucumber and two strains from the research stations with frequently alternating crops. Several strains were of the red form of *T. urticae* (sometimes referred to with the synonym *T. cinnabarinus*, see Bolland et al. (1998)), while others were of the green form. The difference in colour (carmine red vs greenish) becomes manifest in the adult females. Strains collected from cucumber were grown in the lab on detached leaves of cucumber (cv. ‘‘Corona’’) and those from tomato on detached leaves of tomato (cv. ‘‘Money-maker’’). The same plant varieties were used throughout the experiments. Cucumber is susceptible to mite attack, but tomato is known as a hostile host due to secondary compounds in leaves and sticky exudates of glandular hairs (Fry 1990, 1999; Chatzivasilieiadis and Sabelis 1997, 1998; Chatzivasilieiadis et al. 1999, 2001).

To avoid age-dependent effects, egg waves were produced for the experiments, i.e. eggs laid in three days by many adult females on detached leaves, placed on wet cotton-wool. All experiments were carried out in a climate room at 23 °C, 70% relative humidity and 17:7 h light:dark period.

Table 3. Two-way ANOVA of the effects of food-plant choice (tomato or cucumber) and food history (Test period I tomato or cucumber + Test period II tomato or cucumber) on oviposition rate in Test period II of the Tomato strain Naaldwijk. Data were square-root transformed.

Source	Df	MS	F	<i>p</i>
Choice (C)	1	0.021	0.0178	0.893
History (H)	3	11.6	9.82	<0.001
C × H	3	2.03	1.72	0.165
error	171	1.18		

Table 4. Two-way ANOVA of the effects of food-plant choice (tomato or cucumber) and food history (Test period I tomato or cucumber + Test period II tomato or cucumber) on oviposition rate in Test period II of the Cucumber strain Nootdorp. Data were square-root transformed.

Source	Df	MS	F	<i>p</i>
Choice (C)	1	1.12	0.955	0.331
History (H)	3	23.5	20.0	<0.001
C × H	3	2.66	2.26	0.086
error	104	1.17		

#### *Effect of previous food experience on host preference*

To obtain groups of mites with different food experience, egg waves were produced for all 8 strains on three hosts: tomato, cucumber and bean (*Phaseolus vulgaris*) as a control host. Three-day-old adult females of these groups were used to measure host preference. Individual choice arenas were made by connecting two leaf disks (Ø 10 mm, one of tomato and one of cucumber) with a bridge of transparent plastic, with an insect pin in the middle of the bridge (see Figure 1). To prevent leaf desiccation, the arenas were placed on wet cotton-wool. Adult females were taken with a fine brush directly from the host leaf and put individually on top of each pin. Pilot experiments with this set-up showed that the mites readily descend from the pin, generally inspect both leaf disks (by walking and occasionally probing) and settle at one site after approximately 4–5 h. Therefore, the choice of the mites was scored as the position after 6 h. Mites found on the pin, the plastic bridge or the cotton-wool were scored as “no choice” and excluded from further analysis.

#### *Preference-performance relation and induced performance*

This experiment was carried out with mites of the Tomato strain “Naaldwijk” and the Cucumber strain “Nootdorp”. The experimental design to measure the preference-performance relation is illustrated in Figure 1. Egg waves were produced on bean leaves. The preference of adult females from these egg waves was measured as described above, except that the choice of mites was now scored after 24 h. In this way, two groups of mites were obtained: those preferring cucumber and those

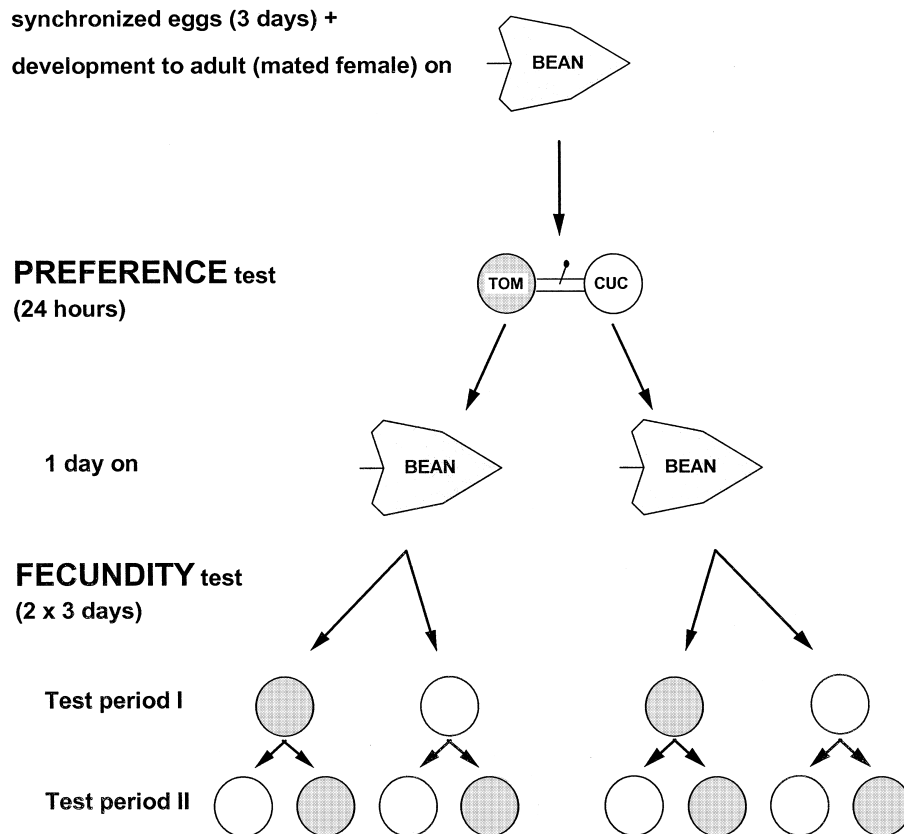


Figure 1. Experimental design of the preference-performance test. See text for further details

preferring tomato. The mites were then placed on bean leaves for one day, to cancel any effect (e.g., conditioning) of the choice test on subsequent performance (i.e., oviposition rate; Egas and Sabelis 2001). For both groups, individuals were randomly assigned to a leaf disk of either tomato or cucumber to measure oviposition rate as the number of eggs laid in three days (Test period I). This procedure was repeated (Test period II; see Figure 1) to measure induced effects of performance on any of the two host plants.

## Results

### *Effect of previous food experience on host preference*

In all cases, more than 50% of the individuals tested preferred cucumber, except for bean-reared females of the Naaldwijk (tomato) strain and tomato-reared females of the De Meern (tomato) strain, which had no distinct preference (Figure 2). Al-

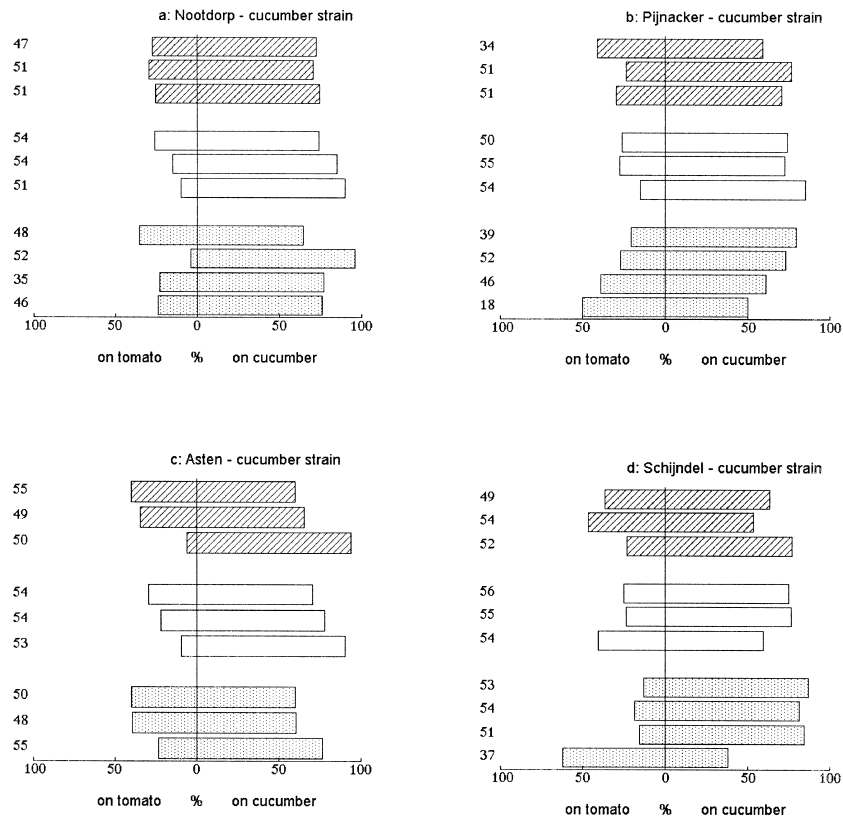


Figure 2. Fraction of spider mites choosing tomato or cucumber, for the eight strains used in this study. Hatched bars: individuals reared on tomato; open bars: individuals reared on cucumber; shaded bars: individuals reared on bean. Numbers refer to the number of individuals used in each replicate. Asterisks denote significantly different preferences within strains (\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ )

though differences in preference are small, there are significant effects of conditioning and these differ among strains (2-way ANOVA, Table 2). The preference for cucumber of mites reared on cucumber was significantly higher than that of mites reared on bean or on tomato (Tukey post-hoc test; bean vs cucumber:  $p = 0.002$ ; tomato vs cucumber:  $p = 0.001$ ).

Analysing all strains separately showed that three (tomato) strains had significant intra-strain differences in preference: the De Meern strain (fig. 2e; Kruskal-Wallis:  $H_{3,3,3} = 5.956$ ,  $p < 0.05$ ), the Warsaw strain (fig. 2f; Kruskal-Wallis:  $H_{4,3,3} = 5.791$ ,  $p = 0.05$ ) and the Naaldwijk strain (fig. 2h; Kruskal-Wallis:  $H_{5,3,3} = 8.508$ ,  $p < 0.01$ ). In the De Meern strain, preferences were only significantly different from each other when mites were reared on cucumber and tomato (Kruskal-Wallis post-hoc (equal sample sizes):  $q_{\infty,3} = 3.37$ ,  $p < 0.05$ ), indicating induced preference for both cucumber and tomato. In the Warsaw strain, none of the pairwise comparisons was significant, because the effects of conditioning were

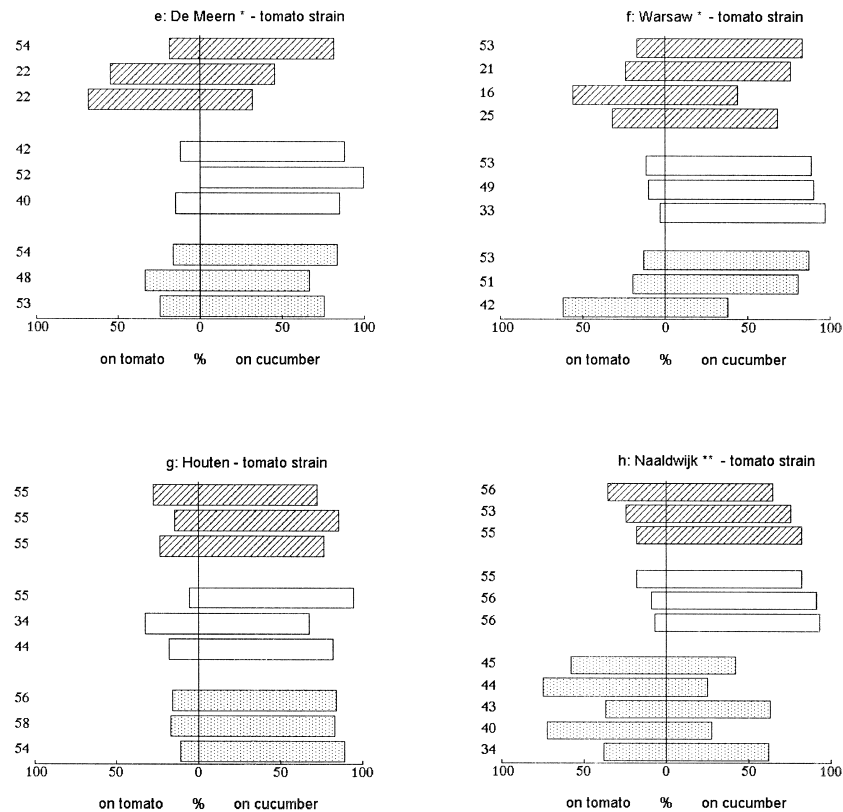


Figure 2. Continued

small. In the Naaldwijk strain, preferences were significantly different only when mites were reared on cucumber and bean (Dunn's post-hoc (unequal sample sizes):  $Q_3=2.83$ ,  $p<0.05$ ), indicating induced preference for cucumber but failing to indicate induced avoidance of tomato.

#### *Preference-performance relation and induced performance*

Mites of both the Tomato strain "Naaldwijk" and the Cucumber strain "Nootdorp" preferred cucumber over tomato (Figure 3; Goodness of fit, Tomato strain:  $G=5.05$ ,  $p<0.05$ ; Cucumber strain:  $G=26.1$ ,  $p<0.001$ ). However, in the Tomato strain this preference was slight. Both preferences were in line with those found in the previous experiments (see fig. 2a and 2h, bean-conditioned replicates).

Host plant choice did not affect subsequent oviposition rate, but the host plant for ovipositioning did (2-way ANOVA on Test period I; Cucumber strain: Choice  $F_{1,108}=2.08$ ,  $p=0.152$ , Host  $F_{1,108}=90.2$ ,  $p<0.001$ , interaction  $F_{1,108}=2.38$ ,  $p=0.126$ ; Tomato strain: Choice  $F_{1,175}=2.22$ ,  $p=0.128$ , Host  $F_{1,175}=68.3$ ,  $p<0.001$ , interaction  $F_{1,175}=3.79$ ,  $p=0.053$ ). Mites choosing tomato performed equally well as mites

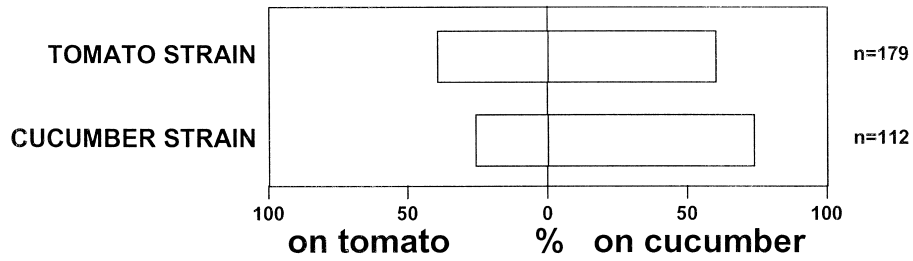


Figure 3. Fraction of spider mites choosing tomato or cucumber, for the Tomato strain “Naaldwijk” and the Cucumber strain “Nootdorp”. Numbers refer to the number of individuals used in each test

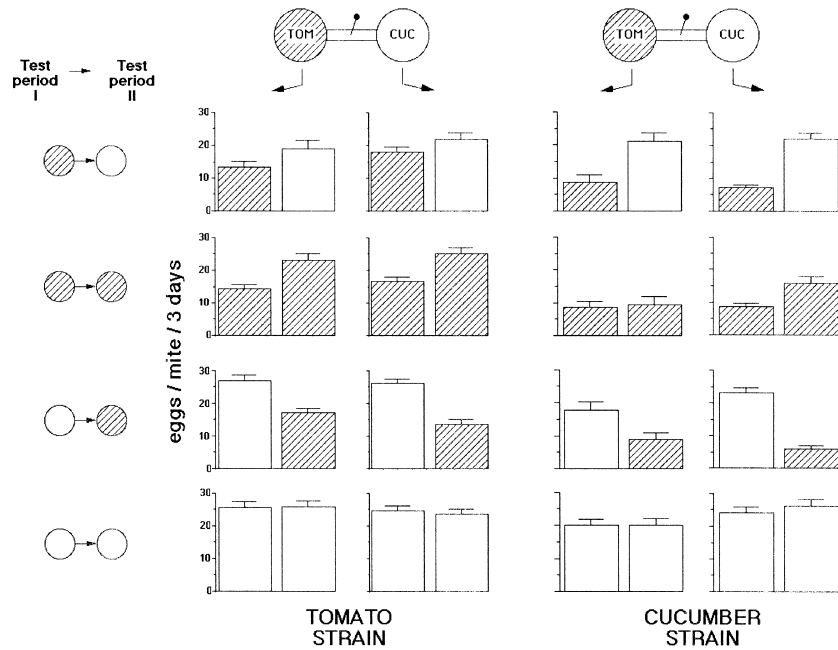


Figure 4. Average oviposition rates (number of eggs per individual per three days) of the Tomato strain “Naaldwijk” and the Cucumber strain “Nootdorp”, choosing tomato or cucumber, in Test period I and II. Open bars: oviposition rate on cucumber; hatched bars: oviposition rate on tomato. The error bars indicate 1 s.e.

choosing cucumber (although in the Cucumber strain the interaction term was bordering significance, indicating a slightly higher oviposition rate on cucumber of mites that had chosen cucumber). For both strains, performance on tomato was lower than on cucumber (Figure 4; Test period I).

Analysis of the effects of food choice and food history on oviposition rate in Test period II did not show significant differences with food choice (as in Test period I), but did show significant differences with food history for both strains (Figure 4, Tables 3 and 4). In the Tomato strain, this effect was due to mites, having a lower oviposition rate when first on cucumber and then on tomato (C → T), com-

pared to the other three combinations (Tukey post-hoc test:  $C \rightarrow T$  vs.  $C \rightarrow C$ ,  $p < 0.001$ ;  $C \rightarrow T$  vs.  $T \rightarrow T$ ,  $p < 0.001$ ;  $C \rightarrow T$  vs.  $T \rightarrow C$ ,  $p = 0.061$ ) and not due to mites having a lower oviposition rate when both periods were on tomato ( $T \rightarrow T$ ; Tukey post-hoc test:  $T \rightarrow T$  vs.  $C \rightarrow C$ ,  $p = 0.976$ ;  $T \rightarrow T$  vs.  $T \rightarrow C$ ,  $p = 0.339$ ), or when both periods were on cucumber ( $C \rightarrow C$ ; Tukey post-hoc test:  $C \rightarrow C$  vs.  $T \rightarrow C$ ,  $p = 0.152$ ). Hence, during Test period II the tomato strain showed increased oviposition rate on tomato (but not on cucumber) after spending Test period I on tomato (Figure 4). This induction of performance even compensated for the initial difference in oviposition rate on tomato and on cucumber. In the Cucumber strain the same effect occurred, albeit less pronounced because oviposition on tomato always remained lower than on cucumber (Tukey post-hoc test:  $C \rightarrow T$  vs.  $C \rightarrow C$ ,  $p < 0.001$ ;  $C \rightarrow T$  vs.  $T \rightarrow C$ ,  $p < 0.001$ ;  $C \rightarrow T$  vs.  $T \rightarrow T$ ,  $p = 0.041$ ;  $T \rightarrow T$  vs.  $C \rightarrow C$ ,  $p < 0.001$ ;  $T \rightarrow T$  vs.  $T \rightarrow C$ ,  $p = 0.004$ ;  $C \rightarrow C$  vs.  $T \rightarrow C$ ,  $p = 0.984$ ).

## Discussion

Induction of feeding preference for cucumber was found when the data from all strains were taken together (ANOVA in Table 2). The effects were small and mostly modifications of the degree of preference, not of rank order (in line with previous studies; Papaj and Rausher 1983). These results add to recently reported evidence of preference induction in *T. urticae* (Agrawal et al. 2002). The strains varied in their response to conditioning: none of the strains with a (continuous or alternating) history on cucumber (the benign host) showed significant effects of induction, but three of the strains with a history on tomato (the hostile host) did. In the Warsaw strain, preferences differed among treatments, but differences were too small to conclude on induced preference for cucumber or tomato (fig. 2f). In the De Meern strain, neither preferences of cucumber-reared mites nor of tomato-reared mites were significantly different from preference when reared on bean, the control plant (fig. 2e). Hence, we cannot formally conclude that conditioning with either plant induces a different preference. The preferences of bean-reared mites, however, were in between those of tomato-reared and cucumber-reared mites, and the differences between bean-reared and cucumber-reared mites were small. Therefore, we conclude that this strain showed indications of induced preference for tomato but not for cucumber. In the Naaldwijk strain the data point to induced preference for cucumber and induced avoidance of tomato, although only the former effect was significant. However, in this strain the preference of mites reared on bean appears to be more variable and appears quite different from both tomato and cucumber (fig. 2h). Hence, the nonparametric test we use may not be powerful enough to detect the differences. Indeed, the same data (but arcsin square root transformed) in an ANOVA test indicated that preferences were significantly different both when mites were reared on cucumber and on tomato (ANOVA:  $F_2 = 12.00$ ,  $p = 0.0039$ ; Tukey post-hoc test: bean vs. cucumber  $p = 0.0039$ , bean vs. tomato  $p = 0.045$ , cu-

cucumber vs. tomato  $p=0.30$ ). Hence, induced avoidance of tomato seems marginally significant.

Interestingly, if we would not have included bean as a control, we would have concluded that conditioning on cucumber increases preference for cucumber, compared to conditioning on tomato (2-way ANOVA excluding bean data; strain (S):  $F_{7,7} = 0.525$ , *n.s.*; conditioning (C):  $F_{1,33} = 17.1$ ,  $p < 0.001$ ; S  $\times$  C:  $F_{7,33} = 1.68$ , *n.s.*). This clearly shows the need for an unrelated control for comparison of changes in preference (Bernays and Weiss 1996). Having included the control, we conclude for the De Meern strain that experience with tomato has a positive effect on preference for tomato (through habituation or associative learning). On the other hand, in the Naaldwijk strain experience with tomato has a negative effect on preference for tomato (through sensitization or associative learning), whereas experience with cucumber leads to higher preference for cucumber (through habituation or associative learning).

There was no correlation between individual host plant choice and oviposition rate in the Tomato strain (Naaldwijk) and the Cucumber strain (Nootdorp). However, at the population level both strains preferred cucumber over tomato, and had a higher oviposition rate on cucumber than on tomato. Induction of performance on tomato was found in the Tomato strain and, to a lesser extent, in the Cucumber strain (Figure 4). Feeding on cucumber did not lead to induced performance in either strain.

A possible alternative explanation for the results on induction of preference could be that in rearing the mites on different host plants, we selected against mites that performed badly on the host plant (i.e., low oviposition rate, pre-adult mortality and slow development time). If performance correlates well with preference, it is reasonable to expect higher preference for the host plant the mites were raised on – just like we expect under induced preference. However, on bean and cucumber all mites perform very well: pre-adult mortality is virtually zero and the range of differences in development time among individuals is very small ( $\ll$  one day). Selection can therefore play no role on these two hosts. However, on tomato (a more hostile host) selection may have acted on the individuals hatching and developing from the egg wave. This alternative explanation presupposes a strong preference-performance relation, but this assumption does not hold. In our test of the preference-performance relation in the Tomato strain Naaldwijk and the Cucumber strain Nootdorp, we found no correlation between individual host plant choice and oviposition rate. This finding is corroborated by another recent study on induced preference and the preference-performance relationship in *T. urticae* (Egas and Sabelis 2001). Individuals of the Naaldwijk strain and a different Cucumber strain were subjected sequentially to three choice tests between tomato and cucumber, and then to a performance test on each host plant. During the three consecutive choice tests, mites of both strains learned to avoid tomato and to prefer cucumber. The performance test showed that cucumber allowed for higher oviposition, survival, and development than tomato, and that there was no effect of individual choice history on these three performance measures. Taken together with the results presented here, individual choice behaviour in *T. urticae* appears to be a probabilistic pro-

cess, with the probability of choosing cucumber increasing with experience. Hence, on the individual level, *T. urticae* females only show a strongly positive preference-performance relationship if they are allowed to learn the difference between host plants. In absence of a strong preference-performance relationship, we think it very unlikely that the effects of induced preference on tomato are caused by selection on performance in the egg wave. It is important to note that, in principle, a preference-performance relationship in adult females does not necessarily imply a performance-preference relationship among offspring (emerging from the egg wave). Therefore, in future experiments the only way to bypass this problem is to decrease the time the individuals are exposed to the conditioning host plant such that mortality becomes negligible.

A potential mechanism for induced performance on tomato comes from two bodies of evidence. Firstly, Chatzivasileiadis et al. (2001) have shown that in the Nootdorp strain increased resistance to the tomato toxin 2-tridecanone can be induced. This mechanism could also act in the Naaldwijk strain to enhance oviposition rate on tomato. Since 2-tridecanone has a turnover rate in *T. urticae* of less than two days (Chatzivasileiadis et al. 1999), our experimental set-up provided ample time for this effect to become apparent. Secondly, Agrawal et al. (2002) have shown that increased performance on tomato can be cancelled by inhibition of detoxifying enzymes. Mites conditioned on tomato had increased oviposition rate on tomato, compared to mites conditioned on bean. When treated with an inhibitor of P-450 enzymes, both treatments showed equal oviposition rates, which was reduced by  $\pm 70$ –85% compared to mites conditioned on tomato. Hence, induced resistance to tomato toxins may be an important mechanism for induced performance.

Combining these two bodies of evidence, we propose that induced performance may lead to a change in preference for tomato. Although sensitization and/or habituation are more parsimonious hypotheses for induction of preference (because they do not assume a causal relationship between the increase in performance and subsequent preference), to us this would suggest associative learning (specifically: food aversion learning) as the mechanism underlying induction of preference in *T. urticae*. Indeed, the effect of induced performance is small in the Nootdorp strain, and it did not show significant changes in preference. In the Naaldwijk strain, the effect of induced performance was large, and there was a clear (although marginally significant) effect of induced avoidance of tomato.

In conclusion, this study provides evidence of induced preference and performance in the two-spotted spider mite *T. urticae* and shows that there is considerable variation in these two traits among strains. We suggest induced resistance to toxic secondary plant chemicals as one potential explanation for induced performance, which in itself suggests associative learning as the most likely candidate learning mechanism underlying induction of preference in this species. Phenotypically plastic effects underlying induced performance may be a general aspect of induction of preference in herbivorous arthropods, which warrants closer attention to these phenomena.

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