Host Selection by the Herbivorous Mite
Polyphagotarsonemus latus (Acari: Tarsonemidae)

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Abstract This study examined the host-selection ability of the broad mite *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae). To make long-distance-shifts from one host plant patch to another, broad mites largely depend on phoretic association with whiteflies. However, the host plants of whiteflies and broad mites are not necessarily the same. We determined the host-preference and acceptance of free-moving and phoretic broad mites using two behavioral bioassays. We used a choice test to monitor host selection by free-moving mites. In the case of phoretic mites, we compared their rate of detachment from the phoretic vector *Bemisia tabaci* placed on leaves taken from various host plants. The suitability of the plant was further determined by monitoring mite's fecundity and its offspring development. We compared the mites' responses to young and old cucumber (*Cucumis sativus* cv. 'Kfir') leaves (3rd and 8–9th leaf from the apex, respectively), and two tomato (*Solanum lycopersicum* cvs. 'M82' and 'Moneymaker'). Free-moving mites of all stages and both sexes preferred young cucumber leaves to old cucumber leaves and preferred young cucumber rather than young tomato leaves, demonstrating for the first time that broad mites are able to choose their host actively. As for phoretic mated females, although eventually most of the mites abandoned the phoretic vector, the rate of detachment from the whitefly vector was host dependent and correlated with the mites' fitness on the particular host. In general, host preference of phoretic female mites resembled that of the free-moving female. Cues used by mites for host selection remain to be explored.

Keywords Broad mite · phoresis · behavior · *Cucumis sativus* ·
Solanum lycopersicum

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Introduction

Host selection is one of the most crucial stages in the life cycle of an organism. For minute herbivorous organisms such as mites, with limited locomotory abilities, the host plant is not merely a source of food, but a habitat to live on for several generations. Although herbivorous mites are an economically significant group of pests, not much is known about their host selection behaviour. This is especially true for the broad mite, *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae). This minute, 0.2 mm mite is found on plants of nearly 60 different families and is presumably polyphagous (Gerson 1992). Most of the information on the relationship between the broad mite and its host has been inferred from observations on the prevalence or extent of damage on certain hosts, but its host-choosing ability is not clear. Cross and Bassett (1982) suggested that different feeding strains (host races) specialize on different host plants, but they presented no experimental evidence for this. Broad mites are commonly found on the lower surfaces of young apical leaves and in flowers, where they deposit their eggs (Gerson 1992). This indicates broad mite's ability to adjust their local position on the constantly growing plant by detecting declining host suitability and migrating towards more attractive sites for feeding and oviposition.

Mite dispersal occurs through various means. Within the infested plant, the broad mite population appears continuously to move upwards, presumably via the males carrying pharate females to apical plant parts and thus 'choosing' their oviposition sites (Gadd 1946). To colonize distant habitats, mites may use several modes: walking, passive aerial dispersal (anemochory), and phoresy, i.e., being carried by other organisms. The broad mite is known to have a specific phoretic association with whiteflies (Homoptera: Aleyrodidae) (Palevsky et al. 2001; Soroker et al. 2003). Although the broad-mite-whitefly phoretic association appears to be facultative, monitoring of broad mites with sticky traps near greenhouses clearly indicated the importance of phoresy in broad mite dispersal and epidemiology, and also suggested that passive dispersal by wind is limited to less than 10% (Soroker et al. 2003). The phoresy of the broad mite is sex specific and mainly characterizes mature females (Palevsky et al. 2001). Since it is phoretic on whiteflies, commonly on polyphagous *B. tabaci*, active host choice behavior of the broad mite may seem superfluous, but the host preferences of both species are not necessarily the same. Moreover, as both herbivores were reported to induce plant defense mechanisms (Grinberg et al. 2005; Zarate et al. 2007) and cause severe damage to the plant, they are potential competitors for the plant resources.

The aim of the present study was to explore the host selection ability and host acceptance of phoretic and free-moving broad mites, using behavioral assays that we developed for this poorly characterized pest.

Material and Methods

Broad Mite and Whitefly Culture

Broad mite cultures were established on young cucumbers at the Plant Protection Institute of the Agricultural Research Organization (ARO), Bet Dagan, Israel, as

described in Palevsky et al. (2001), and were maintained at 19–27°C and 30–60% RH. Female whiteflies, *B. tabaci* B-biotype, were collected from a laboratory colony reared at ARO and kept frozen for 24 h at −20°C for the phoretic bioassays.

Plant Cultivation and Preparation

Experimental plants were grown in pots (1 L) with standard fertilization in a growth room at about 24ºC, as described by Grinberg et al. (2005). Young leaves (3rd leaf from the apex) or old leaves (8th or 9th leaf from the apex) of cucumber (*Cucumis sativus* cv. 'Kfir') and young leaves of two tomato varities (*Solanum lycopersicum* cvs. 'M82' and 'Moneymaker' (Mm)) were used.

Host Preference of Free-Moving Broad Mite

Host preference of free-moving mites was examined using a choice test. A mite-infested cucumber leaf, with 101 ± 13 individuals (mean±SE), served as a source of the mite population. The bioassay was conducted in a Petri dish (9 cm diameter), and two types of leaves were compared at each test:

(1) Cucumber young vs. cucumber old leaves, $n=12$; (2) Cucumber young vs. tomato Moneymaker young leaves, $n=8$; (3) Young leaves of tomato Moneymaker vs. those of tomato M82, $n=8$. Each Petri dish was considered as a replicate. The leaf, infested by all stages of broad mite, was placed in the center of the plate and 1.8 cm discs of uninfested leaves were placed at equal distances of 1.2 cm on its four sides. To compensate for a possible side bias, leaves from the same host type were placed on the opposite sides of the infested leaf. The arrangement of the leaves in the plates was randomized. Host choice was evaluated by counting the numbers of female, male and larvae that reached the various host leaves after 1, 2, 4, 6 and 8 h, using a stereomicroscope (Olympus SZX12, AT 40×magnification). For exact evaluation of the mite populations at the end of the assay (after 24 h), the leaf discs were washed with 70% ethanol and all the mites (male, female and larvae) were counted under the stereomicroscope.

Host Selection of Phoretic Broad Mite

Host selection by phoretic broad mites was studied using a detachment bioassay. Host plants varieties used for this study were the same as in the former Section. This bioassay compares the rate of broad mite detachment from their phoretic host (whitefly), onto leaf discs from several different host plants. In order to obtain phoretic broad mites, frozen *B. tabaci* adults were placed on cucumber leaves infested with broad mites, and mites (on average seven individuals) were allowed to attach to whiteflies during about an hour (e.g. Soroker et al. 2003). It was proven that frozen whiteflies remained attractive to broad mites for at least 8 h (Palevsky et al. 2001). The numbers of mites attached onto the whiteflies were noted. Subsequently, one whitefly loaded with broad mites was placed on each leaf disc (2.8 cm diameter) in Petri dishes (3.5 cm diameter) containing a piece of water saturated filter paper. The rate of mite detachment from the whiteflies at 24–26°C was measured by counting the numbers of mites remaining on the whiteflies at

several time intervals: 10 and 30 min, and 2, 4, 6, 8 and 24 h. This experimental setup was replicated for 19–37 times for each host plant. The results are presented as percentage of detached broad mites at various time intervals.

Following the detachment bioassay, the leaf discs were incubated in a controlled environment (25°C, 14L:10D), and the host plant suitability for broad mites was determined. Egg laying usually begins within 24 h after colonization of a suitable host (Grinberg, unpublished data), and *P. latus* generation time at 25°C is 6 days (Gerson 1992). To monitor population build-up, the numbers of eggs laid by adult females, and numbers of developing larvae, were counted after 24, 48, 72 and 96 h. After 7 days the leaf discs were washed with 70% ethanol and total progeny (males, females and larvae) were counted under the stereomicroscope. The numbers of eggs, larvae and total progeny per female were calculated for each replicate.

Data Analysis

All statistical analyses were done using SAS 8.03 software. Host selection by free-moving mites was calculated as the percentage of mites from each group (females, males or larvae) out of the total number of mites that selected new leaf discs (total dispersing mites). Wilcoxon Signed Rank test was used to evaluate mite discrimination between the leaves of two host plants. Probit analysis (PROC PROBIT) was used to compare host preferences of males, females and larvae by comparing proportion of individuals of each group (males, females and larvae) that preferred one of the hosts out of total individuals that were found on both kinds of leaves at the end of experiment. Host selection of free moving female mites between cucumber and tomato leaves was analyzed over time using the repeated measures ANOVA (PROC GLM) procedure using the Greenhouse-Geisser adjustment in lieu of a sphericity test to the arcsin-transformed data on proportions of total female mites. The same procedure was used to analyze the behavior of phoretic mites, using proportions of detached mites, and the rates of mite detachment onto the various hosts over time. The effects of leaf type, time and the time x leaf type interaction were tested over the variation within leaf type. In the case of significant time x leaf type interaction, leaf type groups were subjected to *t* -tests (LSD) at each time point, followed by the Bonferroni correction, to investigate the host differences by time. The numbers of individuals counted in assessment of host suitability were subjected to the square root transformation ($\alpha=0.001$). Differences in host suitability were evaluated by one-way ANOVA, followed by Scheffe's test on the transformed data ($\alpha=0.05$). Goodness-of-fit test was used to examine the sex ratio of progeny.

To assess correspondence between the broad mite detachment rate and host suitability (total progeny), detachment rate and progeny per female for each leaf disc (replicate) were compared by pooling all the host plants. The Pearson correlation among the transformed data was tested ($\alpha=0.05$).
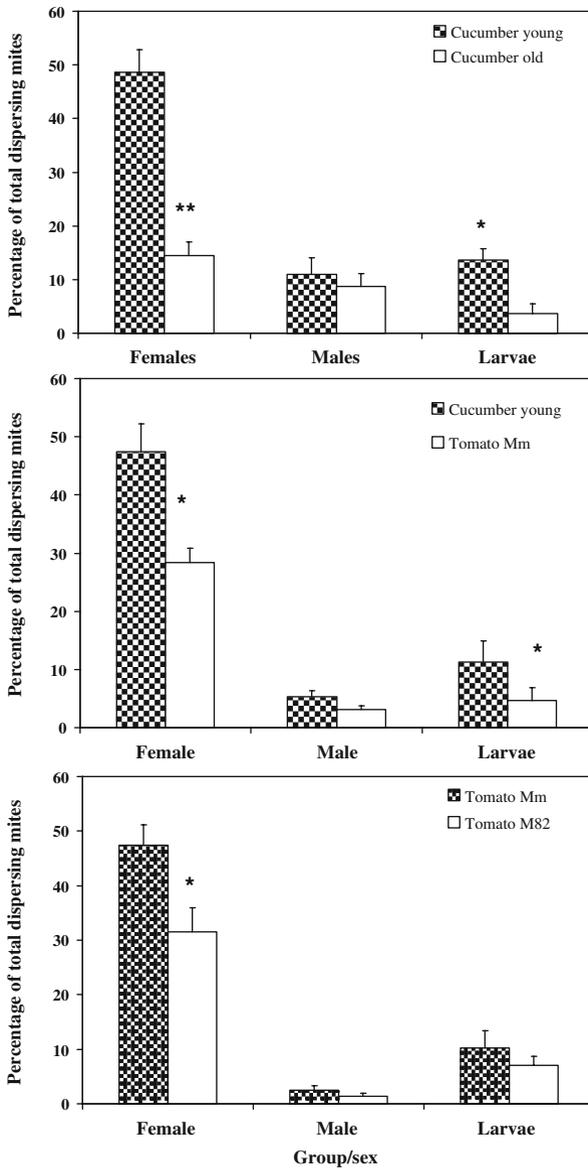
Fig. 1 Host selection of free-moving broad mites between: **a** cucumber (Kfir) leaves of two ages: young (3rd leaf from the apex) and old (8–9th leaf from the apex) **b** Young leaves of *Cucumis sativus* (Kfir) and *S. lycopersicum* cv Moneymaker **c** Young tomato leaves from two different varieties, Moneymaker (Mm) and M82. The figures represent the percentage of mites (males, females or larvae) that selected a particular host, out of the total number of dispersing mites (average±SE of 8–12 replicates). Asterisk indicates a significant choice within a group (females, males or larvae, Wilcoxon signed Rank test, *P<0.05; **P<0.01).

Results

Host Selection of Free-Moving Broad Mite

The ability of broad mites on a fast-deteriorating host, i.e., mite-infested detached leaf, to select a new host was examined. Evaluation of the mite population after 24 h showed that the relative proportions of males, females and larvae varied among the different leaves, but the population of dispersing mites was generally female biased: 46–56% of the females left the infested leaf for a new one, compared to 16–45% of the males and 8–24% of the larvae, respectively. Larvae and adult females of *P. latus* showed a significant preference for young cucumber leaves when offered a choice between young and old cucumber leaves, or between young cucumber and young tomato 'Moneymaker' leaves (Fig. 1). Female mites also showed a significant preference for 'Moneymaker' variety of tomato, compared to that of 'M82' variety. Preference of males was not significantly different from that of females and larvae (Probit procedure (SAS); $P>0.05$), but due to low number of males, direct statistical analysis of male behavior did not reveal a significant host preference.

The time course of leaf choice by female broad mites that were offered cucumber 'Kfir' and tomato 'Moneymaker' young leaves is shown in Fig. 2. Preference for cucumber was detected for the whole time span ($F=6.06$, df=1, $P=0.027$) and increased significantly with time ($F=57.4$, df=4, $P<0.0001$).

Host Selection of Phoretic Broad Mite

Figure 3 presents the time course of the detachment of phoretic broad mites from their vector on various host plants: young and old cucumber leaves, and two tomato varieties. Detachment of mites started shortly after the broad mite-loaded whiteflies were placed on the leaf discs. By 24 h most broad mites had detached, and dispersed on the leaves. However, the rate of detachment was host-dependent (ANOVA,
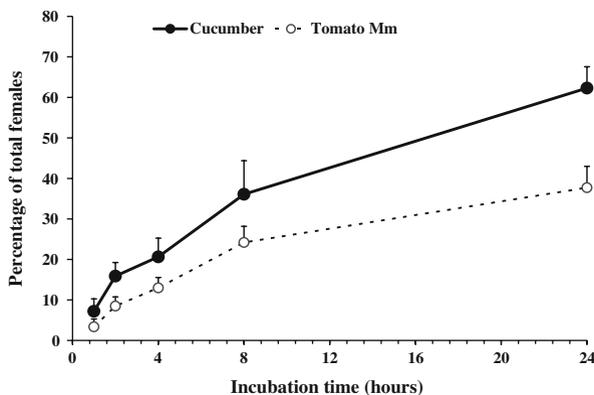

Fig. 2 Time course of host selection of free–moving female broad mites between young cucumber leaves (Kfir) and tomato (Moneymaker) leaves. Results are the percentage of total females that arrived to each leaflet type (average±SE; $n=8$). Repeated Measures ANOVA revealed a host effect, $F=6.05$, df=1, $P=0.027$; time effect, $F=57$, df=4, $P<0.001$; Plant×Time interaction, $F=1.1$; df=4, $P=0.35$.
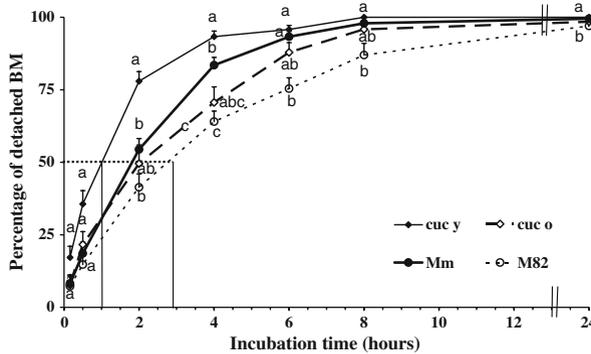
Fig. 3 The effect of different host plants on broad mite detachment ratio. Results are average±SE of at least 19 replicates. Repeated Measures ANOVA indicates: Host effect, $F=14.62$, $P<0.0001$; Time effect, $F=311.75$, $P<0.0001$; Interaction Host×Time, $F=3.38$, $P<0.0001$. Different letters at each time interval indicate groups that statistically different, t-tests (LSD) followed by Bonferroni correction, $P<0.0012$. Dotted line at 50% points at time interval required to attain detachment of 50% of mites onto leaves from different plant.

Repeated Measures, Time x Plant, $F=3.38$; $P<0.0001$, df=18, Table 1). The fastest detachment was observed on young cucumber leaves, 50% in about 1 h and 100% within 8 h, followed by tomato 'Moneymaker'. The slowest detachment occurred on tomato 'M82', where 50% of the mites detached after more than 2 h but some individuals did not detach even after 24 h. Detachment rates on young cucumber and tomato 'Moneymaker' did not differ significantly at most time points, except at 2 and 4 h (ANOVA, followed by t-tests (LSD) with Bonferroni correction, $P<0.05$), but detachment on both differed significantly from that on 'M82' at 4, 6 and 8 h ($P<0.05$). Finally, the detachment rate of mites to old cucumber leaves was highly variable and did not differ significantly from the others, probably due to high variation in leaf quality.

The fitness of the broad mites on the various hosts was determined during seven days following the detachment bioassay. Table 2 shows that reproductive performance was significantly host-dependent (ANOVA, the F values ranging between 21.3–37.4, depending on the parameter tested, $P<0.001$). The highest numbers of progeny developed on young cucumber leaves, followed by the progeny on tomato 'Moneymaker' leaves. Very few eggs were laid on 'M82' and old cucumber leaves, and thus significantly fewer progeny developed on these two

Table 1 Repeated Measures Analysis of Variance (7 Counts on 4 Hosts) of Phoretic Broad Mite Detachment

Source of variation	Sum of squares	Mean Square	F	df	P
Plant	7.58	2.52	14.62	3	<.0001
Error	11.07	0.17		64	
Time	74.72	12.45	311.75	6	<.0001
Time * Plant	2.42	0.13	3.38	18	<.0001
Error (time)	15.33	0.03		384	

Table 2 The Effect of Host Plant on Broad Mite Development

Host Plant	Progeny after 7 days				
	Larvae	Female	Male	Total	n
C. sativus young (3rd leaf)	2.6±0.36 b	1.6±0.14 a	0.7±0.07 a	4.8±0.48 a	37
C. sativus old (8–9th leaf)	0.1±0.04 c	0.4±0.06 b	0.2±0.05 b	0.6±0.10 b	19
L. esculentum Mm	2.0±0.30 a	1.1±0.07 a	0.4±0.06 a	3.6±0.40 a	26
L. esculentum M82	0.4±0.11 bc	0.5±0.05 b	0.1±0.03 b	1.1±0.15 b	19

Two leaf ages of *Cucumis sativus* 'Kfir' and two tomato varieties, Moneymaker (Mm) and M82, were compared. Results are presented as progeny numbers that developed on the leaf disc during 7 days following the phoretic bioassay. The results are average numbers per female±SE, *n*=number of replicates. Different letters within a column indicate statistically significant difference (ANOVA, followed by Scheffe's test on transformed data, *P*<0.05)

hosts. The sex ratio of adult progeny varied but was significantly female biased (χ^2, *P*=0.0027).

To study the dynamics of host recognition and acceptance by the phoretic mites, we evaluated the correlation between these two phenomena over time. The time course of female detachment was expressed as the percentage of detached mites at each time point, whereas the subsequent reproductive success was expressed by the numbers of eggs and newly emerged larvae counted after 72 h, as well as the total progeny after 7 days (Fig. 4). We hypothesized that detachment would occur fastest on the most suitable host. Significant positive correlation was indeed detected between female detachment levels at intervals from 30 min onwards, and subsequent broad mite performance on the different hosts. However, this relationship was complex: initially detachment levels showed low correlation (Pearson correlation,
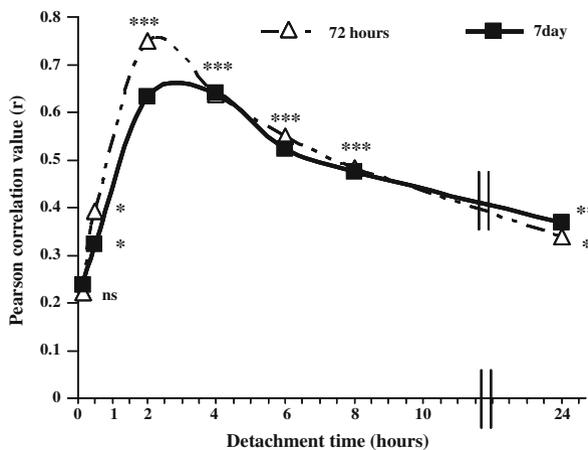

Fig. 4 Correspondence between broad mite detachment and host suitability. Data are Pearson correlation values of comparison between progeny that developed after 72 h (black line) and 7 days (dotted line) and the detachment ratio at a number of time intervals. Results of a two-tailed test are indicated for all comparisons; *P<0.05, ** P<0.01; ***P<0.001, df=54.

R=0.2 to 0.4) with total progeny numbers, but later the correlation strengthened and attained values of R=0.6 to 0.75 after 2 h. In general, mites' detachment after 2 h predicts reproductive success of females. By 4 h the majority of the mites had detached, and subsequently the correlation weakened. The highest correlation was observed with the 72 h progeny. We attributed the somewhat lower correlation with broad mite performance after 7 days to deterioration and senescence of the detached leaf; this was especially significant in the case of cucumber leaves.

Discussion

Our findings show, for the first time, that both free-moving and phoretic broad mites are capable of active-host-choice. In the case of a free-moving population, both larvae and adults are capable of host discrimination in choice tests. The adult females are the majority among selecting individuals. This female selecting ability casts doubts on the significance of male choice of future oviposition site for females, based on Gadd's observation of males carrying around pharate females (Gadd 1946).

In the present study, broad mites exhibited clear preferences. Mites bred on cucumbers readily discriminated between two ages of cucumber leaflets, preferring the young ones. They also discriminated between young cucumber leaves and tomato leaflets, and between leaflets of similar age from two tomato varieties. As can be deduced from the relative detachment rates of phoretic broad mites onto various hosts, the preference of phoretic females is similar to that of free-moving ones. Preference for young leaflets could be anticipated, since apical plant parts were previously reported as the most common oviposition site (Gerson 1992). Broad mites could be repelled to some extent from tomato, especially the M82 variety. Tomato is known as a rather "hostile" host for *Polyphagotarsonemus latus* and there is only a single report of broad mite damage to tomatoes (Cross and Bassett 1982). The basis for broad mite discrimination between the two tomato varieties needs further elucidation, and may provide us with a clue regarding the chemical attractants/repellents that differentiate tomato genotypes.

Preference for cucumber over tomato in cucumber-reared mites could be also explained by induced preference to food of origin, which is a well documented phenomenon in phytophagous insects and may involve some kind of non associative learning mechanism (Schoonhoven et al. 1998). Another possibility could be that over generations reared in the laboratory, a cucumber race was formed, which shows innate preference for cucumber. Formation of host races is a prevalent phenomenon in Acari (Magalhães et al. 2007 and references therein). The existence of specialized host races — "biotypes" — was reported in a number of presumably generalist species of phytophagous mites, e.g., the spider mite *Tetranychus urticae* (Agrawal 2000; Gotoh et al. 1993) and the rust mite, *Abacarus hystrix* (Skoracka and Kuczynski 2006), and was suggested also for broad mite (Cross and Bassett 1982). Demonstrating a relation between broad mite preference and performance provides some support for such possibility.

In general, the preferences of adult females and the performance of their offspring do not always correlate (Thompson 1988; Mayhew 1997). However, the finding that

the highest reproductive performance occurred on the most preferred host indicates that in the case of the broad mite, female host choice is probably adaptive. A significant positive correlation ($r=\sim0.75$) was found between female host preference and the suitability of the given host for progeny development. A similar level of correlation was observed by Yano et al. (1998) and Agrawal et al. (2002), regarding host selection by the spider mite, *T. urticae*. Yano et al. (1998) suggested that under natural conditions, the mite's host range was partly determined by selection against females that settled on unfavorable host plants: there was low fecundity on these hosts and females repeatedly escaped from them. It has been also noted that when there is trade-off in performance on different hosts, the positive correlation between host plant suitability and its acceptability might enhance host race formation.

Although the role of such correlation in restricting gene flow has been described in several models of sympatric speciation (*e.g.* Fry 2003 and references therein), the fact that in our study cucumber-reared broad mites exhibited similar reproductive success on plants from two different botanical families, *Cucurbitaceae* and *Solanaceae*, does not support a host-race scenario. On the other hand, performance (survival and fecundity) varied between two tomato varieties and two different ages of cucumber leaves. Such situation probably resulted from differences in plant nutritional quality and/or defensive capabilities rather than host race specialization.

Many factors have been hypothesized to be important for host discrimination by phytophagous arthropods, e.g., secondary and primary metabolites, plant morphology and phenology (Schoonhoven et al. 1998). Often, it is the balance between opposing positive and negative cues presented by phytochemicals that determines whether a plant is accepted or rejected by the herbivore (Huang and Renwick 1993; Renwick and Chew 1994; Krokos et al. 2002). The cues that guide broad mite behavior and the distances at which the broad mite perceives them are still unknown, but Smith (1935) reported that active mite individuals 'crossed' (presumably by walking) an 18-inch (45-cm) space between plants.

The evolution of broad mite host selection should be also viewed in the ecological context, in particular in the frame of the mite's phoretic association with whiteflies. This association plays a major role in providing host choice opportunities for the broad mite. Whiteflies and broad mites usually complete their development on the same plant and even on the same leaf on which they hatched (Byrne and Bellows 1991). It is therefore clear that female host choice is critical for both species. The degree of overlap between the host ranges of the two species is still not clear, but obviously the broad mite can choose only between those hosts on which its phoretic vector lands. We hypothesize that detachment is induced by stimuli from the vector and/or the host. Stimuli provided by the vector are expected to be associated with landing on the host (*e.g.*, reduced tactual inputs from air currents), or host acceptance, as expressed by feeding and/or oviposition behavior of the vector (tactual and/or chemical cues). In the case of the common vector, *B. tabaci*, it is unknown how long they carry broad mites. It has been reported that the adult lives for about a week or more (Byrne and Bellows 1991) and exhibits two different flight patterns: short-distance and long-distance flights (Berlinger 1986). Short-distance flights are restricted to the plant canopy and to travels from plant to plant within a field. These flights cover less than 15 ft (about 5 m; Berlinger 1986). Long-distance

flights occur when the insect is caught in air currents and drifts passively, and may be carried to several hundred meters of height and over distances of kilometers. From several studies on whiteflies such as *B. tabaci*, it is clear that an initial landing on a plant does not implicate acceptance. A whitefly may choose to stay on suitable hosts or move away from unsuitable ones. For example, adult females of *B. tabaci* avoid plants occupied by its predators (Nomikou et al. 2003), but how they react to the presence of conspecifics, to broad mites or their natural enemies, is still unknown. The nature of broad mite-white fly association is still an unsolved issue: is there a "conflict of interests" between the mite and its vector? Alternatively, do they benefit from cooperative host exploitation? Such parameters may influence whitefly landing decisions, subsequently affecting broad mite host possibilities and ultimately having fitness costs, thus shaping the evolution of the broad mite detachment and host selection strategy.

To disclose phoretic broad mite-host interactions, in our experimental set up, we eliminated the vector dimension, behavior and stimuli, except for the effect of landing, which was simulated by placing the dead, broad mite-loaded vector on the experimental leaf. We repeatedly observed that BM remain attached unless the vector is moved to another leaf (Alagarmalai, unpublished observation). As time passed, the broad mite detached from the vector, indicating that landing itself might provide stimuli for detachment. However, the rate of detachment differed on different hosts, indicating a definite role for host-plant derived cues. The fact that, once detached, mites were never observed to climb back up and re-attach to the vector, indicates that a "final decision" on host acceptance is taken before the actual tasting of the plant, and thus adaptive learning of the host cannot play a role in this behavior. Since in our bioassay we used dead whitefly as vectors, our results also indicate that this choice is made by the mite, leading to the suggestion that the mite does not rely fully on the choice made by the whitefly.

The increased detachment with time and the high correlation between mite detachment after 2–4 h and subsequent performance, suggest that the majority of mites do not detach upon each whitefly landing event. It appears that the mite's behavior is adapted to the explorative behavior of its phoretic vector. In fact, whiteflies were observed in the laboratory to make either short stops of less than 10 min, or longer ones of more than 1 h, during which probing presumably takes place (Bernays 1999). We can assume that when these short stops are associated with an unacceptable host, most of the attached broad mites do not "accept the whitefly decision", and stay attached. On the other hand, if the whitefly stays on the host for longer than 8 h, the broad mites will usually descend, since the likelihood of an opportunity to switch host is diminishing. Our present data could suggest three strategies of broad mite detachment behavior adopted by different individuals after whitefly landing: the non-selective drop-off strategy of fast detachment; the selective targeted landing strategy, which includes preliminary evaluation of the potential host; and the less selective, delayed "emergency landing" strategy. Whitefly landing itself could be triggering the detachment. However, the fact that the majority of mites do not detach shortly after whitefly landing supports the idea that the majority of detachments events are selective. The targeted landing strategy appears to be optimal; however, under natural conditions, characterized by complex adaptations and trade-offs, the other two strategies also have their benefits, and these benefits

apparently contribute to maintenance of these traits in broad mite populations. The mites employing the targeted landing strategy detach upon detection of suitable cues, which are most likely chemical. Plant chemistry is probably the most important source of information contributing to the final decision of the female mite to detach or not. In case of phoretic mites, these stimuli are presumably volatile, since the mite detaches (or commits to detachment) from the vector prior to tasting the host.

In conclusion, the broad mite exhibits host selection and host preference which are correlated with its potential performance on the host. The detachment of phoretic mites is presumably guided both by host chemical cues and by the behavior of its vector. Specific cues involved in mites' detachment from the vector and/or plant-host discrimination remain to be discovered. It will be also interesting to determine whether host preference behavior of broad mites is affected by the presence of competitors, natural enemies, or induced plant-defense mechanisms.

The assays that we developed offer a simplified experimental set-up to facilitate the study of broad mite behavior and can be implemented in screening genotypes for resistance.

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