



Predatory behavior of *Delphastus pusillus* in relation to the phenotypic plasticity of *Bemisia tabaci* nymphs

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Abstract

Phenotypic plasticity in *Bemisia tabaci* is expressed, among others, through the degree of nymphal setosity. We tested the hypothesis that the setose phenotype of nymphs can act as a defense mechanism against the predatory coccinellid *Delphastus pusillus*. Since it has been shown that the relative number of each phenotype is directly correlated with the tomentosity level of the host leaf, our study included characterization of *D. pusillus* predatory activity when exposed to the different nymphs upon two different leaf types: glabrous and tomentose. Leaf trichomes were found responsible for differences in durations of observed events, their frequency and transitions between events, leading to a break in the predatory sequence regularly found on glabrous leaves. However, despite this break, observational data and functional response tests showed no differences in prey consumption when the predator was exposed to each prey type separately. This is explained by a particular foraging behavior displayed by *D. pusillus* on tomentose leaves that included walking upon leaf trichomes while performing a vertical introduction of the head between the trichomes, thus reaching the leaf surface. Differences in handling times between the nymph phenotypes were recorded during direct observations of patch time allocation, but these did not result in significant differences in the number of prey eaten. Moreover, our estimates of handling time, calculated with a type II functional response equation, also failed to show these differences. However, foraging predators were more prone to discover smooth nymphs than setose nymphs when the former were offered on tomentose leaves. The significance of these findings in the context of predator-prey-plant interactions is discussed.

Introduction

In numerous whitefly species (Homoptera: Aleyrodidae), fourth instar nymphs, usually referred to as pupae, are characterized by waxy secretions, setae and cuticular or wax extrusions. As a result, almost all the historical taxonomic identifications of this group are based on the morphology of this instar (Gill, 1990; Gerling, 1990a; Byrne & Bellows, 1991; Rosell et al., 1997).

One of the most investigated whitefly species is the tobacco or sweet potato whitefly *Bemisia tabaci* (Gennadius). The fourth nymphal stage of this species, like some others in its family, develops different phenotypes on different host plants. One expression

of these variations is the existence of visible setae on the nymph's dorsum, which has been recorded from nymphs developing on tomentose host-plant leaves (Mound, 1963; Bink-Moenen & Mound, 1990; Rapisarda, 1990; Gerling & Mayer, 1996; Rosell et al., 1997). Recently, Guershon & Gerling (unpubl.) demonstrated that the appearance of these setose nymphs is a direct response of the wandering crawler to a stimulus received through contact with leaf trichomes. Moreover, the percentage of such responding nymphs within a leaf population is directly correlated to the density of trichomes on the tomentose leaf.

Although little is known about the possible ecological significance of the aforementioned whitefly

secretions, wax and/or setae, assumptions about their possible defensive role against natural enemies have been raised (Gerling, 1990b). Such role has been shown for morphological features in other insects and arthropods (Olmstead & Denno, 1992; Evans & Schmidt, 1990; Gerling, 1990b; Gross, 1993, Honda & Luck, 1995). Our aim in the present study was to investigate whether whitefly pupal setosity has a defensive role against one of its predators, *Delphastus pusillus* LeConte (Coleoptera: Coccinellidae), which is considered a potential biological control agent of whiteflies (Heinz et al., 1994; Heinz & Zalom, 1996; Obrycki & Kring, 1998).

Materials and methods

Plants. Two cotton varieties (provided by The Israel Cotton Production & Marketing Board) were categorized by the different degrees of trichome density on their leaves. Average number of trichomes per 25 mm² was 206.8 (SD = 31.3, N = 75; 15 leaves with 5 measures per leaf) for a hybrid (Michlo 195/86) variety which was categorized as tomentose, while a second variety, Acala SJ2, had leaves with 2.7 trichomes in average (SD = 0.23, N = 75; 15 leaves 5 measures per leaf) and was categorized as glabrous. Plants were grown from seed in 150 ml plastic pots. The same plant varieties were used for whitefly rearing as for the experiments. Only third mainstem node leaves were used for observations and experiments.

Insects. Predators and prey came from laboratory cultures. *B. tabaci* was reared in greenhouses on cotton plants. In the experiments, only fourth instar whiteflies were used as prey. Since leaf tomentosity provides the trigger for whitefly setosity, we used the two different plant categories to obtain different nymph phenotypes. Thus, two groups of *B. tabaci* were identified: smooth nymphs with less than two setae ($\approx 95\%$ with none) reared on the glabrous plants, and setose nymphs with four or more setae ($\approx 80\%$ with six) developing on the tomentose leaves.

A laboratory colony of the coccinellid *D. pusillus* was established and reared in climatic chambers, feeding on *B. tabaci* in either tomentose or smooth cotton plants. The colony source was a culture kept in the Biological Control Industries at Kibbutz Sede Eliyahu (the stock originated with Dr. Lance Osborne, University of Florida at Apopka). Environmental conditions

were standardized for all cultures and experiments: 25–27 °C, r. h. 50–60% and an L14:D10 ratio.

Behavioral analysis. We used several methods to quantify different aspects of the predatory behavior of *D. pusillus* and to characterize its predator-prey interactions with each of the two different *B. tabaci* types. Due to the aforementioned relationship between nymph phenotype to leaf surface, the substrate was included within the studied parameters. Direct observations were made on different leaves bearing different whitefly phenotypes. Duration of displayed events, their frequency and the frequency of transition from one event to another were quantified during the observations. Besides the direct observations we used two additional methods for the behavioral analysis: patch time allocation (Morrison & Lewis, 1981; Galis & van Alphen, 1981), in which the time devoted to each behavior displayed by the predator while on a prey patch was recorded; and the predator's functional response (Holling, 1959), which allows the calculation of variables with biological significance (predatory or attack rate and handling time). All experiments involved only adult females of *D. pusillus*, selected randomly from the beetle colony. To standardize hunger and avoid satiation during observations, the female predators were starved for 24 h prior to each test.

I. Description and quantification of behavior. Twenty observations of the behavior of a single predator were performed on each leaf type. The leaves bore a naturally growing population of fourth instar *B. tabaci*. These observations, lasting 30 min each, were recorded and analyzed using an event recorder ('The Observer[®]', Noldus, 1991). Based on preliminary observations, the behavior of the observed beetles was categorized according to six events: walking (usually foraging on the substrate); handling (from contact with prey until starting feeding); feeding on nymph (sucking prey fluids observable through the almost transparent cuticle of the nymph); feeding on whitefly adults; feeding on honeydew drops; and 'others' (including any non-listed observed behavior such as preening or standing still). The duration of the recorded events was compared using a *t*-test (after a square root transformation) and the frequencies of display and the frequencies of transition between pairs of event were compared using an *X*² analysis. The total activity rate of the predator (defined by the total number of events displayed by the predator during the observation time) was compared between leaf types

using a *t*-test after a square root transformation of counts (Sokal & Rohlf, 1981).

II. Time allocation study. In order to assess the patch time allocation of the predator, the beetles were exposed separately to each of the two nymphal phenotypes in Petri dishes (5 cm in diameter) lined with one of the following substrates: a tomentose leaf, a glabrous leaf, or moistened filter-paper which served as a 'neutral' substrate. In all cases, 15 whitefly pupae were distributed randomly on each substrate. Each treatment was replicated 15 times. Beetles were cooled in the refrigerator for 2–4 min to slow them down, introduced into the test arenas and observed for 30 min. The proportions of total time devoted to each event during the observation period were compared among the three substrates using a one way analysis of variance (ANOVA). Data were transformed (arcsin of the proportions' square root) before analysis (Sokal & Rohlf, 1981).

III. Functional response study. These experiments offered several conditions in order to conform with the mathematical and statistical assumptions of Holling's (1959) functional response model. To standardize hunger, predator females were starved for 24 h. Single predators were exposed to prey for 24 h. The test arena comprised a Petri dish (9 cm in diameter), lined with one of three different substrates: moistened filter paper, tomentose, or glabrous leaves. Prey consumed or killed were replaced every 3 h during the photophase (Houck & Strauss, 1985). The following prey densities were introduced: 1, 2, 4, 10, 20 and 30 whiteflies per dish. Each density was replicated seven times for each whitefly type (smooth and setose).

According to Holling's type II functional response model, which often typifies arthropod predators (Foglar et al., 1990), the behavior of a single predator is described by the equation:

$$Na = \frac{aNT}{1 + aNTh},$$

where Na is the number of prey consumed, N is the prey density and T is the total time of exposure. Th and a are two biologically significant constants in the model: Th represent the handling time (including piercing, feeding and digestion times) and a stands for the attack rate.

Several methods have been proposed to estimate the parameters a and Th (Houck & Strauss, 1985). We used an iterative nonlinear least squares technique that is considered to produce a less biased estimate

than other commonly used methods such as reciprocal transformation (Livdahl & Stiven, 1983; Juliano & Williams, 1987; Foglar et al., 1990; Fan & Petil, 1994; Williams & Juliano, 1996). The calculations and statistical comparisons were performed using the SAS derivative free procedure NLIN (SAS Institute Inc., 1988).

Results

Quantification of behavior and time allocation. Figure 1 shows the ethogram of *D. pusillus* predatory behavior as displayed while preying on fourth instar *B. tabaci* on different leaf types. On glabrous leaves, the beetle's behavior was characterized mainly by the following sequence: walking- handling- feeding and others, which was generally repeated. When a whitefly adult was encountered, a rapid attack took place; whereas when a nymph was encountered, the predator first handled the prey, apparently seeking a place to pierce the integument, and then started to suck its fluids. Encounters with prey items occurred during apparent random foraging on the leaf surface, with the mouthparts performing short scanning-like movements (especially the palpi).

On tomentose leaves, the main sequence still existed, but it was repeatedly interrupted. The beetles walked on top of the trichomes rather than on the leaf surface itself. This greatly decreased the potential probability of encountering prey. However, the beetle frequently displayed a diving motion, dipping its head between the leaf hairs to reach the leaf surface. Our observations indicated that this was in fact the only way the beetle could locate its prey. Feeding on adult whitefly did not occur on tomentose leaves, whereas honeydew feeding was recorded only on these leaves. As noted, the beetles' behavior was compared between the different leaf types using three quantification parameters: duration of events, their frequency and the frequency of transitions between events. Significant differences between the leaf types were found for the duration of the events 'walking' and 'others', with higher values on the tomentose leaves for both (*t*-test, $P < 0.05$). Differences in the frequency at which each event was displayed were significant for 'walking' and 'handling' (Figure 2; X^2 analysis, $P < 0.05$). Likewise, a comparison of predator activity rate distribution on each leaf type, shows a significant difference between the leaves, being lower for those beetles performing on tomentose leaves (Figure 3; *t*-test, $P < 0.05$).

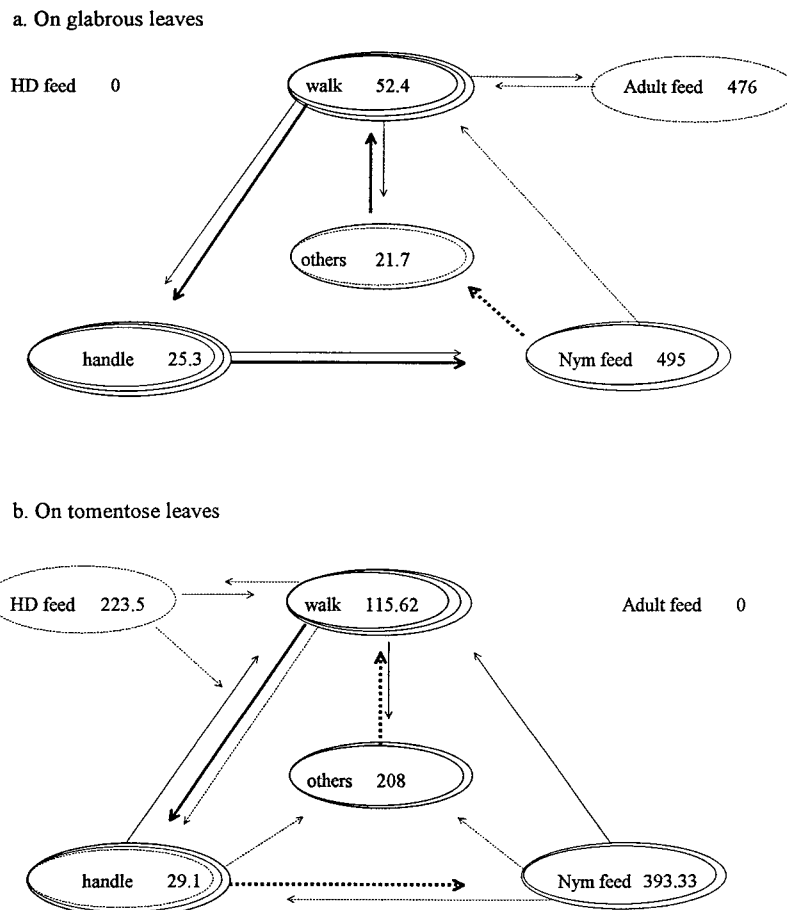


Figure 1. Ethogram of *D. pusillus* preying on *B. tabaci* nymphs on different leaves. Each ellipse represents a relative frequency value: dotted ellipse = 0.05, continuous ellipse = 0.1. The sum of all ellipse values surrounding a specific event represent the relative frequency recorded for that event. For example, 3 continuous ellipses around the event 'walk' represent a proportional frequency of 0.3. The numbers inside the ellipses represent the mean duration of the performance of each specified event (in sec.). The sum of arrows between events indicates proportional frequency of transitions from one event to the other (dotted = 0.05, continuous = 0.1, bold dotted = 0.15, bold continuous = 0.2). Nym feed = feeding on nymphs, HD feed = feeding on honeydew, Adult feed = feeding on *Bemisia* adults.

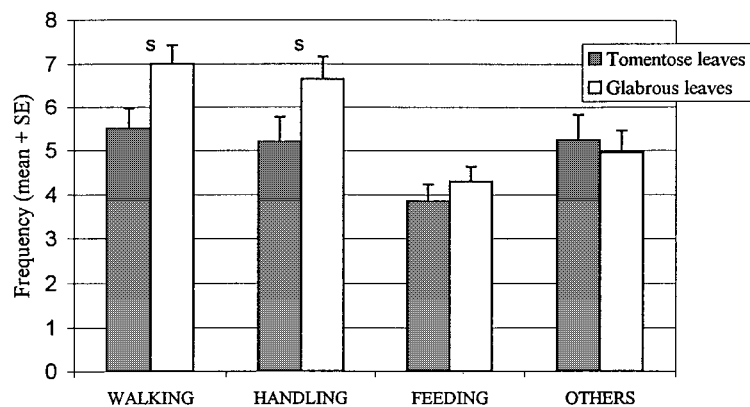


Figure 2. Frequency distribution of events while *D. pusillus* was preying upon *B. tabaci* on different leaves with a naturally growing nymph population. s= significantly different frequency (X^2 analysis, $P < 0.05$).

Table 1. Number of transitions between events performed by *D. pusillus* on glabrous vs. tomentose leaves. Origin = The event from which the beetle starts, Target = the event to which the beetle passes; Nym feed = feeding on nymphs, HD feed = feeding on honeydew; adult feed = feeding on adults; G = Glabrous leaf, T = Tomentose leaf. Total number of transitions (N): Glabrous leaves = 239, Tomentose leaves = 161

Target Origin	Walk		Handle		Nym feed		Others		HD feed		Adult feed	
	G	T	G	T	G	T	G	T	G	T	G	T
Walk			64	33	0	0	19	16	0	4	2	0
X^2			1.403				0.793					
Handle	4	15			55	21	9	4	0	0	0	0
X^2	14.179*				4.889*		0.227					
Nym feed	10	13	3	11			22	7	0	0	0	0
X^2	2.572		8.056*									
Others	44	16	5	6	0	0			0	0	0	0
X^2	4.236*		1.146									
HD feed	0	2	0	0	0	0	0	0			0	0
Adult feed	1	0	0	0	0	0	1	0	0	0		

The marked (*) X^2 values refer to significantly different frequencies ($P < 0.05$; $df = 2$).

Table 1 shows the number of transitions between events for each type of leaf. Differences between leaf types were found for the transitions between handling to walking, handling to feeding on nymphs, feeding on nymphs to handling and for others to walking.

Figure 4a–c depicted the time allocation of the predator while preying upon each whitefly phenotype on different substrates. In all situations, a significantly higher duration of handling behavior was found for beetles preying upon the setose whitefly phenotype. No significant differences were found in time spent on feeding on the different whitefly phenotypes placed on the paper or when on the ‘equivalent’ substrate, (i.e., smooth nymphs on glabrous leaves and setose nymphs on tomentose leaves, Figure 4a, b). However, when the host-leaf combination was inverted, a change occurred in the time devoted to foraging and feeding behaviors (Figure 4c). On tomentose leaves with smooth prey, beetles spent less time foraging and more time feeding than those performing on glabrous leaves with setose prey. These differences resulted in a higher number of attacked prey items for the smooth prey on the tomentose leaf set-up.

Functional response. The responses displayed by the predators are presented in Figure 5a–c. We fitted the type II functional response equation to our data and estimated the parameters a and Th for the different combinations of whitefly phenotypes and substrate. The results can be seen in Table 2.

Although the calculated handling time (Th) values for the setose phenotype were higher than those

estimated for the smooth prey in all situations, these differences were neglectable. Likewise, no significant differences were found in the attack rate (a) for both phenotypes, regardless of the substrate on which the predator-prey encounter took place (NLIN derivative free procedure; SAS Institute Inc., 1988).

Discussion

When comparing predator activity on tomentose vs. glabrous leaves, we found significant differences in the frequency of events and in the transitions between them. These differences indicate that the main behavioral sequence that generally leads to predation (i.e., walking, handling, feeding and others) is less noticeable and more interrupted on the tomentose than on the glabrous leaves. Likewise, the appearance of some events in only one of the leaf types can be attributed to this leaf characteristic. Feeding on honeydew was recorded only from tomentose leaves since excreted honeydew accumulates readily on the leaf trichomes. Attacks and feeding on whitefly adults were not performed on those leaves, probably due to the trichomes inhibiting the predator’s ability to display the necessary ‘fast chase’ and reach the adults. In the patch time allocation observations we found an increase in the effectiveness of searching (defined by the number of prey located per time unit) when preying on smooth prey on the tomentose leaf (Figure 4c). This improvement in the performance of a natural enemy due to specific plant features differs from reported negative

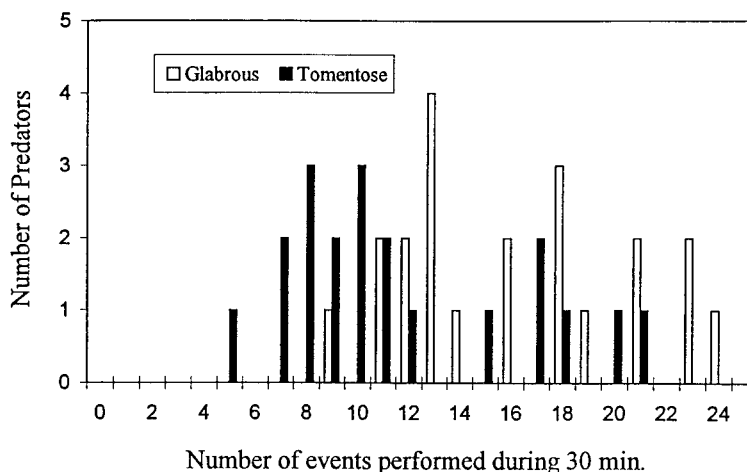


Figure 3. Activity rates of *D. pusillus* preying upon *B. tabaci* on different leaf substrates. Frequencies are significantly different between both leaf types (*t*-test of square root transformed data, $P < 0.05$).

Table 2. Comparison of Holling's type II equation parameters '*a*' and '*Th*' for *D. pusillus* preying on different prey types on different substrates. '*a*' = attack rate, '*Th*' = handling time. Values followed by the same letters are not significantly different ($P > 0.05$, SAS derivative free procedure NLIN)

Substrate	Prey type	<i>a</i> ± 95% C.I.	<i>Th</i> ± 95% C.I. (in hours)
Paper	Smooth nymphs	0.077 ± 0.0268 b	1.008 ± 0.255 c
	Setose nymphs	0.0757 ± 0.0261 b	1.205 ± 0.2685 c
Glabrous leaves	Smooth nymphs	0.0826 ± 0.023 b	1.0421 ± 0.194 c
	Setose nymphs	0.08 ± 0.0313 b	1.229 ± 0.288 c
Tomentose leaves	Smooth nymphs	0.091 ± 0.0215 b	1.116 ± 0.1685 c
	Setose nymphs	0.079 ± 0.0921 b	1.075 ± 0.1999 c

effects of leaf structure on natural enemies, specially to parasitoids (Li et al., 1987; Heinz & Parrella, 1994; van Lenteren et al., 1995; McAuslane et al., 1995). However, it is consistent with results from works dealing with coccinellids, characterized by the detection of prey by contact while randomly searching on the plant (Dixon, 1958; Shah, 1982; Obrycki, 1986). Cases in which a negative effect of leaf characteristics has been reported for coccinellids mainly comprise studies of the larval stages that need to attach their anal disc on the leaf surface for locomotion, which is not the case in the present study in which adult beetles were tested.

Heinz & Zalom (1996) reported an unexpected lack of differences in the performance of *D. pusillus* between tomato cultivars with different trichome densities. These results were explained by longer residence times on pubescent tomatoes, which apparently ameliorate the trichome effects. Our results

describing the diving behavior performed by *D. pusillus* upon tomentose leaves, confirm and may explain these findings. Moreover, this behavior was not observed in another coccinellid, *Clitostethus arcuatus*, which showed poor performance upon tomentose leaves (Guershon, 1997). It is therefore possible that the ability of *D. pusillus* to function on tomentose leaves may confer an advantage over other predator species.

The type II functional response model, typical of predatory insects tested under laboratory conditions (Hassell, 1978; Foglar et al., 1990), was used to describe the response of *D. pusillus* adults to different prey densities and for the comparison between different prey types and different substrates. The estimated values of handling time (*Th*) were expected to be higher for the setose phenotype, since this parameter is partially dependent on host size and/or its morphol-

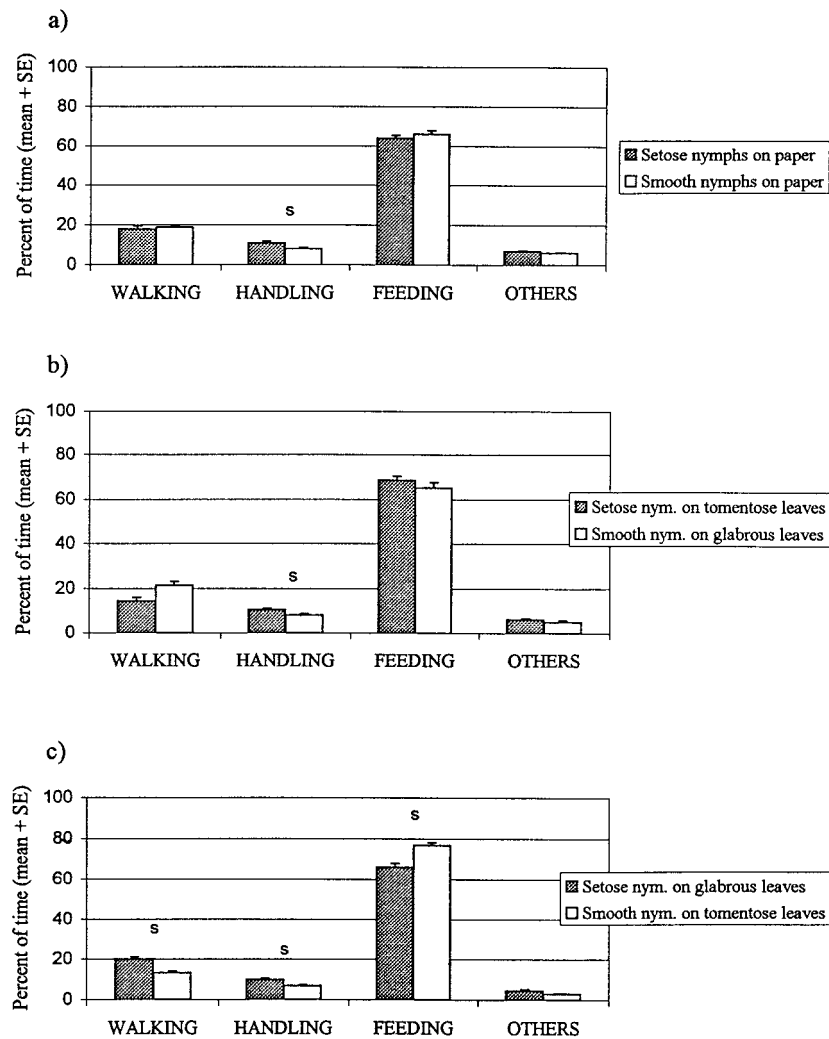


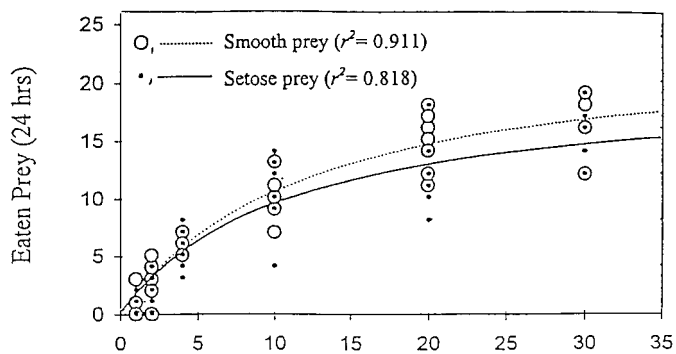
Figure 4. Time allocation of *D. pusillus* preying upon different *B. tabaci* nymphs on different substrates. s = significantly different (ANOVA of the transformed proportions of time, $P < 0.05$).

ogy (Flinn et al., 1985). However, no differences were found when comparing between the values estimated (handling times and attack rates) from the predator's response to each *B. tabaci* type. Moreover, the equation-estimated handling time values were greater than those recorded during the direct observations on patch time allocation. These differences between the estimated and the observational values are explainable by the difference in definition of both 'handling times'. The calculated parameter (Th) includes: (a) the time allocated to behaviors classified as 'others' in the time allocation study (e.g., prey digestion, resting and preening) and, (b) the entire 'dark' period in which this predator is actually inactive and no searching or

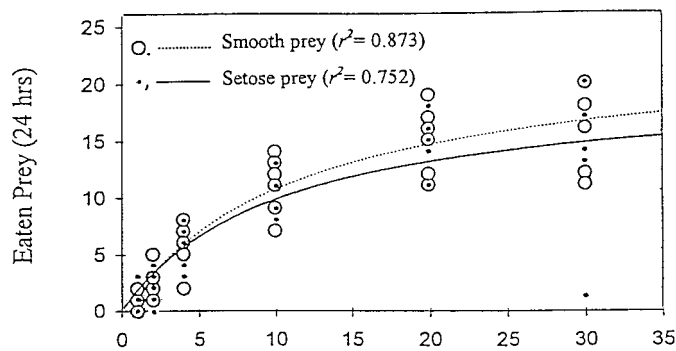
feeding behaviors are performed (Lopez-Avila, 1988; Stern, 1992). On the other hand, the observed handling times included only the time from reaching the prey until the beginning of feeding.

In contrast to the functional response results, the expected differences in handling times between nymph types were found in all combinations examined in the time allocation tests. Nevertheless, these differences did not end in improvement of predatory capacity, which was shown only for one particular case (smooth prey on tomentose leaves). These findings, in addition to the model's results, indicate the dorsal setae's lack of ability to provide an effective defense. It would seem that any direct inhibition of predators that

a. On paper



b. On glabrous leaves



c. On tomentose leaves

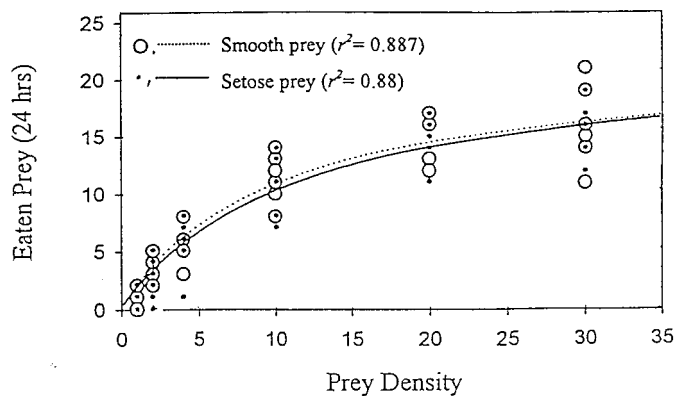


Figure 5. Functional response of *D. pusillus* to different prey densities (*B. tabaci*) while preying upon different nymph types on different substrates.

the setae may confer upon their bearer, can be offset by other predator activities. However, the combined effect of setae and leaf trichomes may be responsible for predator ability to more readily locate smooth prey on the tomentose leaves. Although this specific result might have been influenced by the unnatural conditions of this experiment, including the artificial introduction of only one nymph type upon the leaf surface, this finding could be of major importance since, theoretically, it may indicate a higher survival rate of setose nymphs developing on the same leaves. Indeed, this differential predation has been shown in a preference/rejection test in which the presence of smooth nymphs on a tomentose leaf increased the number of setose nymphs that were rejected by the predator on the same leaf (Guershon, 1997). However, the preference was demonstrated only after the predator had experienced contact with the two types of co-habitant nymphal phenotypes, and not just as the result of differences in search ability. These results indicate an advantage for the setose nymphs, attributable to the phenotypic plasticity that characterizes this species' nymphs when developing on tomentose plants; and suggest the existence of an intraspecific apparent competition. While our current work shows that this would seem to be the situation under field conditions, additional data are necessary for complete corroboration of this hypothesis.

In the last decade greater focus has been placed on insect interactions at more than one trophic level. Nevertheless, as pointed out by several authors (Boethel & Eikenbary, 1986; van Lenteren, 1991; Da Silva et al., 1992; van Lenteren et al., 1995; Bottrell et al., 1998), plant characteristics have not yet received sufficient attention in studies on natural enemy-phytophage relationships. The results of this work, like others dealing with tritrophic level interactions, reinforce awareness of the complexity of ecological systems and the need for a more comprehensive view.

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