

# Effects of plant and prey characteristics on the predatory behavior of *Delphastus catalinae*

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## Abstract

Nymphal setosity of the whitefly *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) has been reported to be induced by mechanical stimuli such as leaf tomentosity, and related to the predatory performance of the coccinellid *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae). In this study, a possible adaptive value of this phenomenon for the whitefly is shown through the combined effects of leaf and prey characteristics on the walking and predatory behaviors of the beetle. Leaf tomentosity significantly affected the walking patterns of the beetle and therefore its searching abilities, thus indirectly increasing the influence of prey distribution upon predator's efficiency. Moreover, while searching on tomentose leaves, the beetles showed preference for the smooth prey phenotype. This behavior was found dependent on the experience of the beetle in previous encounters. These results are pertinent to intraspecific competition between the different nymphal phenotypes and to the predatory efficiency of this beetle, which is utilized in biological control of whiteflies.

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## Introduction

Plant characteristics, such as architecture, leaf texture, morphology, physiology, and secondary metabolites are well known to influence phytophagous insects. This influence may be expressed in a variety of aspects, including the physiology, morphology, development, fecundity, and behavior of the insect (Hopkins & Dixon, 1997; Inbar et al., 1999; but see Inbar et al., 2001). One such case involves the nymphal phenotypes of the whitefly *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) that differ in the occurrence of dorsal setae upon their integument (ranging from zero to six pairs), in a positive correlation with the tomentosity of the leaves upon which they develop (Mound, 1963; Bedford et al., 1994). Guershon & Gerling (2001) showed this nymphal setosity to be directly induced by mechanical stimuli, such as leaf tomentosity, perceived by the sensitive wandering crawler. Several hypotheses concerning the possible costs and benefits of this phenotypic plasticity have been raised. These included the potential adaptive value of shorter developmental time and nymph size vs. the reduced adult size and longevity of the setose nymphs (Guershon & Gerling, 1994, 1999, 2001; Neal, 1997; Neal & Bentz, 1999).

Some of these hypotheses assumed the possibility of reducing exposure to natural enemies in time, by differences in developmental time, in space, by reducing its area, and by possibly conferring crypsis on nymphal whitefly setae within the tomentose leaf environment.

The activity of both herbivores and natural enemies can be influenced by plant characteristics, either directly affecting distribution and foraging behavior or indirectly through the influence on characteristics of their prey (Obrycki, 1986; van Lenteren, 1991; Grevstad & Klepetka, 1992; Gruenhagen & Perring, 1999). In previous work, Guershon & Gerling (1999) reported on the relationship between the plasticity of *B. tabaci* phenotypes and certain predatory behavior characteristics of the coccinellid *Delphastus catalinae* (Horn) (Coleoptera: Coccinellidae) [as *Delphastus pusillus* (LeConte)]. Leaf trichomes were found responsible for changes in duration, frequency, and transitions between the events composing the beetle's behavior. Furthermore, beetles were more prone to locate smooth whitefly nymphs when offered on tomentose than on glabrous leaves. Unexpectedly, these results did not materialize in different prey consumption when exposed to each prey phenotype separately. In fact, the precise manner by which whitefly nymphal setosity and leaf tomentosity influenced this predator's behavior remained unexplained. In order to throw further light on this topic, the present

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work examined additional aspects of the walking behavior of the beetle and its prey preferences on tomentose vs. glabrous leaves inhabited by whitefly nymphs exhibiting differential presence of setae on the integument.

## Methods

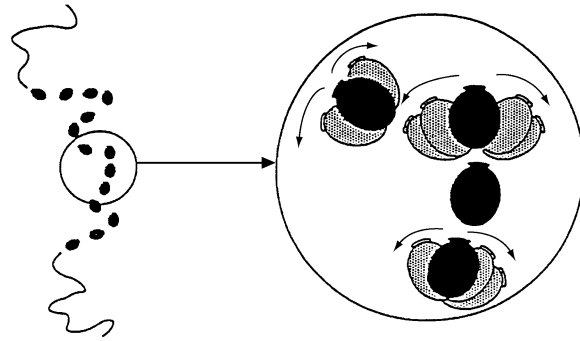
### Insects and plants

All plants used in this study were reared under greenhouse conditions (ca.  $26 \pm 1.5$  °C, 50–60% r.h., and an L14S: D10 photoperiod). Two different varieties of cotton were reared: one with leaves covered with an average of 206.8 hairs/25 mm<sup>2</sup> and another with 2.7 hairs/25 mm<sup>2</sup>, categorized as tomentose and glabrous leaves, respectively. Density of leaf hairs was assessed according to the procedure described in Guershon & Gerling (1999). Whiteflies and predators were reared in laboratory colonies maintained in rearing rooms with environmental conditions similar to those of the greenhouse. The predator colony was established from a commercial culture kept at Bio-Bee, Biological Control Industries at Kibbutz Sede Eliyahu, Israel (the stock originated from Dr. Lance Osborne, Apopka, FL, USA).

The whitefly *B. tabaci* is often considered to encompass a species complex including several biotypes and more than one species. In our paper we refer to all as *B. tabaci* following the recent work of DeBarro et al. (2005).

### Walking behavior study

The walking behavior of the beetles was studied on both glabrous and tomentose leaves. Clean leaves and those that are naturally infested by whitefly were used. Following a starvation period of 24 h, used in order to standardize hunger among the replicates, adult female *D. catalinae* were introduced onto glabrous and tomentose cotton leaves that were either clean or infested by whitefly nymphs. Before introduction, the beetles were cooled for 30–60 s at 4 °C in order to reduce their activity and facilitate manipulation. Observations were recorded with a video camera starting from the moment the beetle began to walk on the leaf (after a short period of ca. 20 s for warming up and acclimatization to the test arena). Each observation lasted 150 s, or until the beetle abandoned the arena (whichever occurred first). Twenty replicates, each using a new beetle and leaf, were performed for each leaf type (making a total of 80 for four combinations: the two leaf types, infested or uninfested). The recorded path of the predator was traced from the video monitor to a transparency fixed on it and marked at 10 s intervals along the resulting line. In order to study the influence of the plant itself, the delineated path was scanned to a computer, enabling the use of a graphic software program (NIHIMAGE 1.44 for Macintosh, NIH, USA) for estimating the following parameters:



**Figure 1** Schematic magnification of the walking pattern of an adult *Delphastus catalinae* on tomentose leaves, showing the trembling behavior that increases the width of the covered track.

- (1) Walking speed, utilizing the 10 s marks on the path line.
- (2) Area covered in the path, calculated as follows:

- (a) Glabrous leaves. Coccinellid adults are believed to locate their prey mostly by contact, although there are also some indications of very close distance attraction to the prey using olfactory and/or visual cues (Dixon, 1958; Hattingh & Samways, 1994; Harmon et al., 1998; Liu & Stansly, 1999). Based on our preliminary observations, which showed mainly contact retrieval of prey, we assumed that the beetle could potentially find any whitefly nymph occurring between the palpi, which are located at the outermost border of its head, plus those whiteflies located in a relatively small additional area adjacent to these palpi. Therefore, the effective prey-finding width of the beetle's walking path is defined by the sum of 'a', the measurable width of the predator's head, and 'b', a small constant value expressing the length of an additional close-distance attraction. Accordingly, the area searched per minute was calculated using the following formula:

$$A = [L \cdot (a + b)] / t$$

where A is the searched area, L the length of the searching path, (a + b) the effective width of the path, and t time in min.

- (b) Tomentose leaves. Preliminary observations showed that the beetle's walking behavior changed from a uniform walk on glabrous leaves to a 'trembling' walk on the tomentose leaves (Figure 1), which at a small scale resembled the 'sweeping walk' reported for some coccinellid larvae (Liu & Stansly, 1999). The trembling caused the body to move in a lateral axis and thus increased the width covered

by the side to side moving head and palpi. Therefore, in order to estimate the searching path width for tomentose leaves, five beetles were recorded under higher magnifications while walking on tomentose leaves. This enabled us to calculate the average distance covered by the trembling beetle's head and define a new 'head width' of this beetles (i.e., a new 'a' value to be applied for all observations). The same small constant ('b') referring to the potential attraction beyond the palpi was added to obtain the new effective width. Only beetles completing 1 min of active walking on the leaves were used for the calculations on both cases.

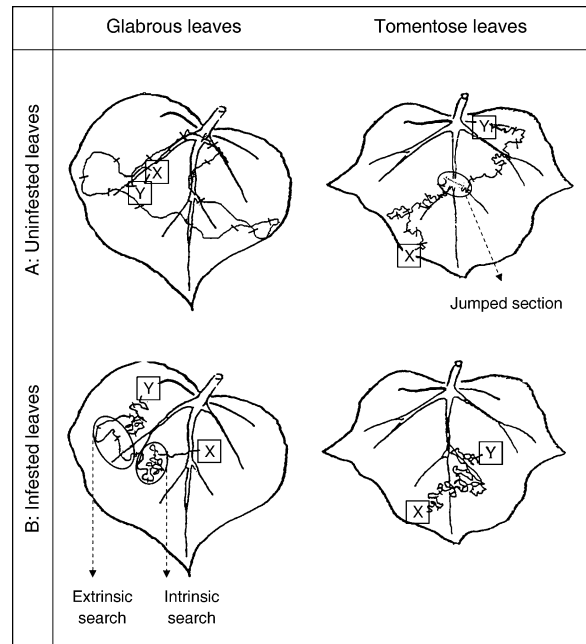
- (3) Number of abandoning attempts. This parameter was divided into two categories (not mutually exclusive):
  - (a) Abandoning the leaf altogether (by flying or walking).
  - (b) Abandoning the local searched site on the leaf, by flying to another spot on the same leaf (recorded as 'jumping').
- (4) Path sinuosity. The sinuosity was calculated by dividing the path length (10 s sections) by the length of the shortest line between the start and finish points of the same path. This parameter is also known as the  $D_b/D_s$  ratio (Nakamuta, 1985) or the index of sinuosity, IS (Dejean et al., 1992). The closer this index approaches to 1, the more rectilinear is the path displayed by the beetle. The index was calculated for 100 of the 10 s paths, randomly selected from all the beetles (five per beetle).

**Prey preference test**

Female beetles (15 per case) were observed for 40 min confronting a constant number of prey on tomentose leaves within a Petri dish in one of the following cases:

- (1) Prey population was composed of 20 setose whitefly nymphs only.
- (2) Prey population was composed of 20 smooth whitefly nymphs only.
- (3) Prey population composed a mixed group of 10 setose and 10 smooth nymphs.

Prey was artificially distributed regularly upon the total leaf area. Throughout the observation, we recorded the number of encounters and whether the prey was eaten or 'ignored' (a term used due to difficulty in distinguishing whether the prey had been really avoided or just un-recognized). In addition, in order to determine whether one encounter influenced the resolution of the next one, a comparison between the rates of accepting (i.e., being eaten) vs. ignoring the prey was performed for pairs of consecutive encounters in the mixed populations.



**Figure 2** Walking paths of *Delphastus catalinae* adults on (A) uninfested and (B) infested, glabrous and tomentose leaves (150 s track with 10 s marks, X = starting point, Y = ending point).

**Statistical analysis**

Description of the statistical tests used for analysis of the data can be found in Sokal & Rohlf (1995) and were performed using STATISTICA 6, Data Analysis Software (Statsoft, Inc., Tulsa, USA) as follows: walking behavior parameters were compared using a t-test for speed and area, a  $\chi^2$  frequency analysis for abandoning, and a Mann-Whitney U-test for the index of sinuosity. For the prey preference study, frequency of eaten prey type in each nymph's combination was compared to the expected frequency using a  $\chi^2$  frequency analysis while the differences between the resolutions for consecutive encounters were analysed using the McNemar test for significance of changes.

**Results**

**Walking behavior**

*On uninfested leaves.* A general view of the walking patterns on tomentose vs. glabrous clean leaves and the comparison between the quantified behavioral parameters on the two leaf surfaces are shown in Figure 2 and Table 1, respectively. The walking speed of the beetle was higher on the glabrous leaf ( $t = 4.602, d.f. = 38, P < 0.05$ ). Magnifications of small path segments of the trembling behavior of the predator, that was observed while walking on the tomentose

**Table 1** Comparison of quantifiable parameters of the walking pattern of *Delphastus catalinae* on uninfested glabrous and tomentose cotton leaves (see text for details on statistical tests). n = number of individuals

Parameter	Glabrous leaf			Tomentose leaf			P-value
	Mean	SD	n	Mean	SD	n	
Speed (mm s <sup>-1</sup> )	1.463	0.7	20	0.739	0.07	20	<0.05
Area (mm <sup>2</sup> )	98.407	27.787	10	116.086	15.441	5	>0.05
Abandonment	30%		(6/20)	75%		(15/20)	<0.05
Jumping	5%		(1/20)	45%		(9/20)	<0.05
Sinuosity index	2.965	0.136	100	4.293	0.375	100	<0.05

leaf, showed this movement to consist of short turns and deviations from the straight path, increasing the searched width (Figure 1). When this increase was added to our calculations, the resulting total area searched on both leaf types was not significantly different ( $t = -1.581$ , d.f. = 13,  $P > 0.05$ ). The number of abandoning attempts was higher on the tomentose leaf for both types, i.e., flying or walking away and 'jumping' within the same leaf ( $\chi^2 = 6.41$ , d.f. = 1,  $P < 0.05$  and  $\chi^2 = 6.533$ , d.f. = 1,  $P < 0.05$ , respectively). The index of sinuosity (IS) was also greater on the tomentose leaf (Mann–Whitney U-test,  $P < 0.05$ ).

*On infested leaves.* An example of the walking pattern performed on the infested leaves of the different types is also shown in Figure 2. The most outstanding difference apparent from these observations is that the pattern on tomentose leaves remains unaltered while on glabrous leaves the path can be subdivided into two different patterns: linear-distance walking vs. sinuous-local walking. As expected, the sinuous-local walking was performed whenever prey items were recognized.

#### Prey preference test

Table 2 shows the results of the preference test that was carried out on tomentose leaves. Only when exposed to mixed prey populations (setose and smooth) the frequency of ignoring setose prey exceeded that of ignoring the smooth prey present ( $\chi^2 = 15.708$ , d.f. = 3,  $P < 0.05$ ). Moreover, preference for the smooth prey in mixed populations exceeded all alternatives, including the acceptance of smooth nymphs in a pure population.

**Table 2** Proportion of *Bemisia tabaci* prey eaten or avoided by *Delphastus catalinae* adults when exposed to different prey type on tomentose cotton leaves holding different prey populations (significance estimated using  $\chi^2$  test). n = number of individuals

Potential prey	Background population	Eaten	Avoided	Expected	n	P-value
Smooth nymphs	Smooth population	0.489	0.511	0.5	15	>0.05
Setose nymphs	Setose population	0.536	0.463	0.5	15	>0.05
Smooth nymphs	Mixed population	0.318	0.161	0.25	30	<0.05
Setose nymphs	Mixed population	0.198	0.322	0.25		

The resolutions for consecutive encounters with mixed prey types on a tomentose leaf are shown in Table 3 and were analyzed using the McNemar test for significance of changes (Sokal & Rohlf, 1995). This procedure allows the determination of any differences between the first and second set of data, in our case the encounter resolution after the beetle's first experience. For example, in 'A' we analyzed the 24 cases in which beetles encountered two smooth nymphs sequentially. In nine of these cases the beetle ate the first and also the following smooth nymph, in four others the predator ignored the second smooth nymph after having eaten one. In eight cases the first smooth nymph was avoided but the next was eaten while in three, both first and second smooth nymphs encountered were ignored. A significant difference between the data sets was found only when a setose nymph followed a smooth one (Table 3B). In that case the frequency of ignoring a setose prey increased significantly once the beetles had previously encountered and eaten a smooth prey. As shown, 25 setose nymphs were ignored when serving as a second encounter following consumption of a smooth nymph ( $\chi^2 = 12.033$ , d.f. = 1,  $P < 0.05$ ).

#### Discussion

While searching for their prey, coccinellids may use two different patterns of movement: 'extensive search', constituting a rapid linear movement from one prey patch to the other, or 'intensive (or area concentrated) search', involving slow and sinuous movement inside each of the patches (Rowlands & Chapin, 1978; Murakami & Tsubaki,

**Table 3** Comparison of the resolution between pairs of sequential encounters. A, B, C, and D represent possible combinations.  $\chi^2$  values followed by an \* represent significant difference at  $\alpha = 0.05$  (McNemar test for significance of changes, see text)

A		Second encounter	
		Smooth nymph	
First encounter		Eat	Ignore
Smooth nymph	Eat	9	4
	Ignore	8	3
$\chi^2$ value		0.75	

B		Second encounter	
		Setose nymph	
First encounter		Eat	Ignore
Smooth nymph	Eat	5	25
	Ignore	5	9
$\chi^2$ value		12.033*	

C		Second encounter	
		Smooth nymph	
First encounter		Eat	Ignore
Setose nymph	Eat	12	10
	Ignore	13	15
$\chi^2$ value		0.174	

D		Second encounter	
		Setose nymph	
First encounter		Eat	Ignore
Setose nymph	Eat	4	6
	Ignore	15	16
$\chi^2$ value		3.04	

1984; Ettifouri & Ferran, 1993; but see also Ferran et al., 1994). The ‘intensive search’ is similar to the arrestment behavior defined and studied mainly for parasitoids (van Alphen & Vet, 1986), which includes a reduction in walking speed (orthokinesis) and an increase in turning rate (klinokinesis) (Shimron et al., 1992). In general, these behaviors are usually induced by perception (or influence) of prey or prey cues (honeydew, feces, etc.). Indeed, switching from extensive to intensive search is the mechanism also predicted by optimal foraging theory in response to prey cues when searching for clustered prey. Accordingly, most research on searching behavior of coccinellids has concentrated on the influences of prey and its by-products (Carter & Dixon, 1982; Nakamura, 1985; Ettifouri & Ferran, 1993; Heidari & Couplan, 1993; Obricky & Kring, 1998).

Our analysis showed that the walking pattern of the predators on the glabrous leaves followed the expected

switching from extensive search to intensive search. In contrast, the pattern on the tomentose surface showed movements typical only to the ‘intensive search’. This searching behavior, recorded on the clean tomentose leaves without any prey cue, was induced by the hairs on the leaf surface, which hampered predator activity, causing it to turn more, rotate, and slow down. Ultimately, it increased the attempts to abandon the leaf. The abundance of obstacles on the leaf thus prevented the beetle on a tomentose leaf from switching between intensive and extensive search patterns or vice versa and therefore from displaying its innate, considered optimal, searching activity. This result is consistent with those of another research showing the behavior of predatory coccinellids being also affected by specific plant characteristics (Eigenbrode et al., 1998).

The similarity in the total areas covered by the beetles on each of the leaf kinds, as shown from the quantified observations performed in the absence of prey, may explain the lack of differences in finding smooth vs. setose prey types that were observed in previously reported time allocation and functional response tests (Guershon & Gerling, 1999). In those tests, prey were distributed randomly on the leaf; thus, there was no expected advantage following the predator’s capacity to switch from one search pattern to another.

Our observations on prey preference suggest that after encountering smooth prey and consuming it, the predator would be more apt to reject setose prey. The setae on the setose nymphs apparently reduced the threshold of prey abandoning (whether by simulating leaf setosity and/or by obstructing the attack). Two explanations may be proposed for understanding the mechanism of this phenomenon. One is that the beetles change their behavior following a specific experience, conforming, although at a primal level, with the definition of the learning process (Robinson, 1990). The second proposes that the predator creates a search image (in a broader sense, including visual and also tactile and olfactory images) after the first or first few encounters (Tinbergen, 1960; Edmunds, 1994). However, such a mechanism is expected to be irreversible and independent of the specific first encountered phenotype (Dukas & Real, 1993), which was not the case in our study. As reported, the beetles returned to feed on setose nymphs after showing an initial avoidance of this phenotype. Moreover, they did not obtain such a search image after initially eating setose nymphs.

The coexisting smooth nymphs reduced predation on setose nymphs (Table 3) while raising the number of consumed smooth nymphs (Table 2). This indirect interaction between the phenotypes resembles a phenomenon known as apparent competition in which two species belonging to the same guild react differentially or provoke a differential

activity of a shared predator and, thus, indirectly compete through the predator's activity (Holt & Lawton, 1994; Eubanks & Denno, 2000). Following this reasoning, prey preference as manifested by *D. catalinae* might increase the relative density of the less preferred phenotype. Therefore, and assuming a genetic basis for the phenotypic plasticity, the more whitefly offspring respond to the stimulus generated by tomentose leaves, the greater their chances of escaping predation (given the presence of a critical relative density of the preferred smooth nymphs). This, in conjunction with the relations found between the two phenotypes and their nymphal and adult sizes and longevity (Guershon & Gerling, 2001), should constitute important considerations in any future analysis of the phenotypic plasticity of *B. tabaci* from selective and increasing fitness viewpoints.

Our results have additional implications for the use of *D. catalinae* as biological control agents. It is reported to have a reproductive capacity similar or higher than that of the whitefly feeding on most vegetable and ornamental crops, indicating it is capable of regulating populations of *B. tabaci* biotype B (= *B. argentifolii* Bellows & Perring) and other whiteflies under greenhouse conditions (Liu, 2005). In fact, this species stands among commonly commercially used natural enemies, being reared for controlling whiteflies on ornamental and vegetable crops under greenhouse conditions (Heinz et al., 1999; Hoelmer & Pickett, 2003; Simmons & Legaspi, 2004). Interestingly, early studies have shown a reduced number of prey eaten by *D. catalinae* when foraging on a hairy strain of poinsettia (Lilo) as compared to a smoother one (Heinz & Parrella, 1994). Additionally, Heinz & Zalom (1996) found that the beetles on a glabrous tomato cultivar had greater lifetime fecundity than beetles on a pubescent tomato cultivar while no significant differences between the adult longevities on the two tomato cultivars was found. Our results show an impediment in performing optimal searching on tomentose leaves, which explains the differential performance of the beetles between the cultivars reported in these studies. Therefore, our results stress the necessity of considering the predatory interactions using a tritrophic level perspective (i.e., the combined effect of plant and prey phenotype) for a better understanding of beetle's performance.

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