Searching and Feeding Behavior of *Nephaspis oculatus* and *Delphastus catalinae* (Coleoptera: Coccinellidae), Predators of *Bemisia argentifolii* (Homoptera: Aleyrodidae)

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ABSTRACT   The coccinellids *Nephaspis oculatus* (Blatchley) and *Delphastus catalinae* (LeConte) [formerly *D. pusillus* (LeConte)] are predators of whiteflies (Homoptera: Aleyrodidae), and have shown potential for biological control of *Bemisia argentifolii* Bellows & Perring in greenhouses. We observed the searching and feeding behavior of *N. oculatus* and *D. catalinae* on hibiscus (*Hibiscus rosa-sinensis* L.). *D. catalinae* larvae maintained the entire body in contact with the substrate while moving, whereas *N. oculatus* larvae planted the uropod on the substrate and swept the body in an arc while searching. Estimated movement rates of all stages of *D. catalinae* were greater than the corresponding stages of *N. oculatus*. However, the searching areas by different larval stages of *D. catalinae* were significantly smaller than those by the corresponding larval stages of *N. oculatus*, which the larvae sweep around while searching. The adults of both coccinellid species traveled in a similar pattern; therefore, *D. catalinae*, moving at a greater rate, searched a greater area than that of *N. oculatus*, moving at a slower rate. Larvae and adults of both coccinellid species responded to prey only after contacting prey with their mouthparts or front legs. Younger larvae took significantly longer to consume prey than older larvae or adults. Larvae and adults of the smaller *N. oculatus* consumed whiteflies at a significantly slower rate than did corresponding stages of *D. catalinae*.

KEY WORDS   Coccinellid, lady beetle, whitefly, predators, biological control, feeding behavior

THE COCCINELLIDS *Nephaspis oculatus* (Blatchley) and *Delphastus catalinae* (LeConte) [formerly known as *D. pusillus* (LeConte)] (Coleoptera: Coccinellidae) are predators of whiteflies (Homoptera: Aleyrodidae), including *Bemisia argentifolii* Bellows & Perring. *N. oculatus* was probably brought from its native Central America on imported plant material, and has been well established in Florida for >25 yr (Gordon 1972, 1985). Under the name of *N. gorhami* Casey, it was introduced to California to control citrus whitefly, *Dialeurodes citri* (Ashmead) (Rose and DeBach 1981). This species also provided effective biological control of the spiraling whitefly *Aleurodicus dispersus* Russell in Hawaii after introduction as *N. amnicola* Wingo (Kumashiro et al. 1983, Yoshida and Mau 1985). It was first reported preying on *B. argentifolii* in Florida by Hoelmer et al. (1994). Biology of *N. oculatus* reared on eggs of *B. argentifolii* and *Trialeurodes variabilis* (Quaintance) was described by Liu et al. (1997).

Delphastus spp. have been extensively studied as a biological control agent for *Aleurocanthus woglumi* Ashby, *Pealius kelloggi* (Bemis), *Trialeurodes floridensis* (Quaintance), *D. citri*, and *D. citrifolii* (Morgan) in citrus in Florida (Muma et al. 1961, Cherry and Dowell 1979), for *Bemisia tabaci* (Gennadius) on tomato in

California (Heinz and Zalom 1996), for *A. woglumi* on citrus in Texas (Meyerdirk et al. 1980), for *A. woglumi* on citrus in Mexico (Smith and Maltby 1994), and for *T. variabilis* on cassava in Colombia (Gold et al. 1989). The genus was recently revised by Gordon (1994). The potential of *D. catalinae* (reported as *D. pusillus*, Pickett et al. 1997) to control *B. argentifolii* on ornamental plants under greenhouse conditions has been recognized (Heinz and Parrella 1994a, b; Heinz et al. 1994; Hoelmer et al. 1994) leading to its present commercialization.

Despite this history of studies and commercial use of the 2 coccinellids, little has been reported on feeding and searching behavior, particularly for *N. oculatus*. Here we provide such information for both species with the hope that better understanding of these characteristics will lead to more efficient utilization of these beetles for biological control of whiteflies.

Materials and Methods

Predator and Prey. *B. argentifolii* was maintained on hibiscus (*Hibiscus rosa-sinensis* L. 'Pink Versicolor') and collards (*Brassica oleracea* L. variety *acephala*, 'Georgia LS') in an air conditioned glass greenhouse at 20–28°C and 60–95% RH. *N. oculatus* appeared spontaneously in the colony in 1994, and was maintained in the greenhouse thereafter. *D. catalinae* pupae and adults originally from Florida were initially provided by J. Nelson (University of California, Davis)

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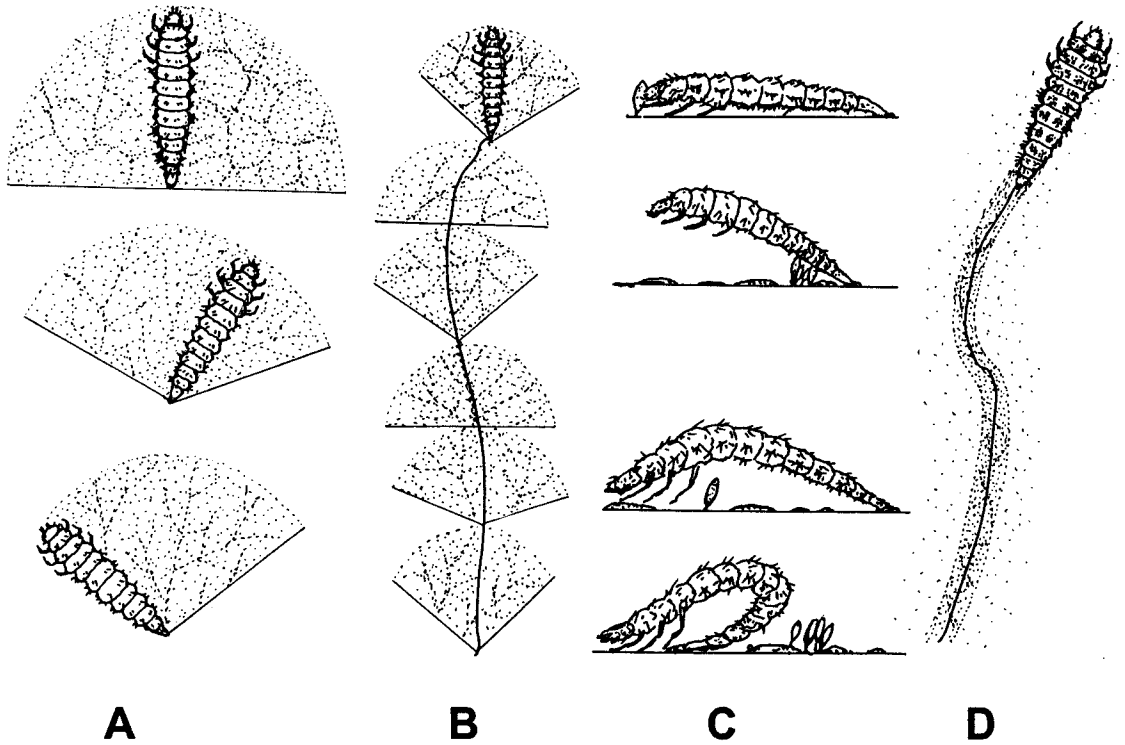
Fig. 1. Traveling and searching patterns of *N. oculatus* (A–C) and *D. catalinae* larvae (D) on a hibiscus leaf.

and were cultured in large cages in an insectary at 25 ± 2°C and 50–60% RH. A mixed culture of *D. catalinae* and *N. oculatus* was initiated in July 1994. Voucher specimens of all developmental stages of *N. oculatus*, *D. catalinae*, and *B. argentifolii* were deposited in the Insect Collection, Texas Agricultural Research & Extension Center, Texas A&M University at Weslaco, and the Insect Collection of Southwest Florida Research and Education Center, University of Florida at Immokalee.

Movement Rate and Searching Behavior. Starved beetles were placed on a whitefly-free hibiscus leaf disk (4 cm diameter) inside a clear plastic petri dish (5.0 cm diameter). The dishes were left uncovered to videotape larvae and were covered to videotape adults. Movement rate and searching and feeding behaviors were viewed on a Sony monitor connected to a video camera mounted on a stereo microscope (Leica, Wild M32, Heerbrugg, Switzerland), and recorded using a Sony EV-C100 videocassette recorder. A ruler scored to the nearest 0.5 mm was placed on each leaf disk and simultaneously recorded to recalibrate whenever the recording magnification was changed. The videotape was replayed, and the track traveled by the beetle traced on translucent paper (36 by 44 cm) held to the television monitor. Length of the track was measured using a swivel handle map measurer (Cat. No. 45240, Forestry Supplier's, Jackson, MS) converted to distance traveled in millimeters.

We assumed that the maximum area (A_{max}) searched by each sweep of the *N. oculatus* larva (Fig. 1) was a half circle described by the expression:

$$A_{max} = 0.5 \ \pi l_b^2,$$

where l_b is the body length of the larva (millimeters) (Liu and Stansly 1996). This provided an overestimate of actual area searched because not all sweeps covered a full 180°. Over a distance D_w the sweep would be repeated D_w/l_b times in T minutes such that SA_{max}, the maximum area searched by an individual in 1 min would be described by the expression

$$SA_{max} = 0.5 \ \pi l_b D_w / T.$$

Larvae of *D. catalinae* and adults of both species did not sweep while searching, so that the expression used to estimate maximum searching rate was simply,

$$A_{max} = D_w B_w / T,$$

where B_w is the body width (millimeters).

Searching distance and area of all larval stages of both *N. oculatus* and *D. catalinae* were subjected to a two-way analysis of variance (ANOVA) (species, stages, and species × stages), and the means were separated using the least significant difference (LSD) test at $\alpha = 0.05$ (SAS Institute 1996) after a significant interaction between the species and the stages was found. A similar two-way ANOVA (species, sex and species × sex) for adults was also conducted.

Table 1. Traveling distance (in centimeters) of *N. oculatus* and *D. catalinae* on hibiscus leaves without prey

Stage	*N. oculatus*		*D. catalinae*		F
	n	cm ± SE	n	cm ± SE	
1st	17	2.2 ± 0.3Ab	19	13.9 ± 3.0Ca	13.58***
2nd	20	5.7 ± 0.4Cb	20	34.6 ± 6.7Ca	18.78***
3rd	19	8.9 ± 0.8Bb	20	65.4 ± 5.9Ba	86.21***
4th	19	12.2 ± 1.3Ab	20	87.8 ± 11.2Aa	43.02***
F		26.64***		19.74***	
Female	20	61.2 ± 11.9Aa	20	86.2 ± 11.1Aa	2.30
Male	20	63.7 ± 12.7Aa	20	129.2 ± 35.3Aa	2.36
F		0.02		1.86	
Adult (overall)	40	61.9 ± 9.0	40	103.39 ± 15.8	5.19*

F-values followed by *, **, or *** indicate the means were significantly different at *P* values of 0.05, 0.01 or 0.0001, respectively. Means in the same subcolumn followed by the same upper case letters and in the same row followed by the same lower case letters did not differ significantly at $\alpha = 0.05$ (LSD, SAS Institute 1996).

Feeding Behavior. Experiments were conducted under ambient laboratory conditions at 23 ± 2°C and 55 ± 5% RH. Larvae of each instar collected from the greenhouse colony were starved for 4 h in petri dishes (5 cm diameter) and adults for 24 h in glass vials (2.0 by 0.5 cm) before use. The 4 larval stadia and male and female adults of *N. oculatus* and *D. catalinae* were separated based on Liu and Stansly (1996). Individual beetles were provided with either eggs (>200), 1st, 2nd, 3rd, and 4th instars or pupae (≈80–100 for each stage) of *B. argentifolii* on a hibiscus leaf disk (4 cm diameter) inside a small petri dish arena (5 cm diameter).

Heinz and Zalom (1996) defined the handling time for *D. catalinae* as the total time spent in assessing and consuming the whitefly prey. We found from preliminary observations that some individuals (mostly larvae) of *N. oculatus* and *D. catalinae* occasionally appeared to initiate an attack on a whitefly egg or nymph, only to move off without causing apparent harm. Therefore, we included data only from attacks resulting in evident damage or destruction of the body or loss of hemolymph.

Feeding behavior of individual whitefly immatures by the beetles was videotaped as described above, and elapsed time was simultaneously monitored with a stopwatch and a timer in the video system from initiation of contact with the mouthparts until the prey was abandoned or consumed. An attack was considered successful if one half of the body was fed or damaged such that eventual death of the prey was most likely. Observations on each individual beetle were made only once. In total, 19–21 individuals for each developmental stage of *N. oculatus* and *D. catalinae* were used in the experiment. Feeding times for *N. oculatus* and *D. catalinae* on *B. argentifolii* were subjected to a three-way ANOVA (species, beetle stages, prey stages, species × beetle stages, species × prey stages, beetle stages × prey stages, species × beetle stages × prey stages), and the means were separated using the LSD test at $\alpha = 0.05$ (SAS Institute 1996) after significant interactions of species × beetle stages, species × prey stages and species × beetle stages × prey stages were found.

Results

Searching Behavior and Movement Rate. The tracks traveled by the larvae of both *N. oculatus* and *D. catalinae* are shown in Fig. 1. Larvae of *N. oculatus* swept the body over a fan-shaped area of variable width up to 180° consisting of a section of leaf described by the body, with the uropod as origin. This movement pattern is more like a measuring worm (geometrid larva), first anchoring the uropod to the substrate, then bringing the anterior body forward to obtain a characteristic looping motion. If no prey were encountered, the larva released its hold and moved on, later repeating the action. The larvae rarely moved 1 body-length without initiating a thorough searching of the reachable leaf area. Therefore, the area searched was considerably wider than the body width. Compared with *N. oculatus, D. catalinae* larvae did not sweep while moving on the plant surface. Therefore, a larva traveled an irregular track with the width of its body. Adults and larvae of both coccinellid species tended to travel on the lower leaf surface and frequently changed directions so that tracts often crossed. In addition, the adults or larvae often follow the midrib, secondary veins, or leaf margins when moving. Thus, even larval paths tended to be relatively straight over short distances as the vein pattern, to some extent, determined lines of attack.

Movement speeds between the 2 coccinellid species, instars and interactions of species and instars were all significantly different (species, F = 128.62; df = 1, 146; P = 0.0001; beetle stages, F = 23.08; df = 3, 146; P = 0.0001; species × stages, F = 13.72; df = 3, 146; P = 0.0001) (Table 1). Among the larval stages, the older instars generally moved faster than the younger instars, fastest for 4th instars, slowest for 1st instars, and 3rd and 2nd in between. In *N. oculatus,* the traveling distance differed significantly among larval stages (F = 26.64; df = 3, 74; P = 0.0001). A 4th-instar larva traveled 1.5-, 2- and 6-fold faster than a 3rd-, a 2nd-, or a 1st-instar larva, respectively. In contrast to *N. oculatus,* a 4th-instar *D. catalinae* moved 1.3-, 2.5-, and 6.3-fold faster than a 3rd-, a 2nd-, and 1st-instar larva. Adult females moved slightly slower than males,

Table 2. Searching area (in square centimeters) of *N. oculatus* and *D. catalinae* on hibiscus leaves without prey

Stage	*N. oculatus*		*D. catalinae*		F
	n	cm^2 ± SE	n	cm^2 ± SE	
1st	17	6.4 ± 3.4Db	19	2.4 ± 0.5Ca	1.53
2nd	20	12.8 ± 1.0Cb	20	6.6 ± 1.3Ca	15.14**
3rd	19	25.0 ± 2.4Bb	20	16.4 ± 1.5Ba	9.76**
4th	19	45.3 ± 4.7Ab	20	28.0 ± 3.6Aa	8.83**
F		29.89***		30.41***	
Female	20	59.3 ± 11.6Ab	20	94.0 ± 12.1Aa	4.25*
Male	20	61.8 ± 12.4Aa	20	140.8 ± 38.5Aa	2.93
F		0.02		1.86	
Adult (overall)	40	60.08 ± 8.7	40	112.7 ± 17.2	7.42**

F-values followed by *, **, or *** indicate the means were significantly different at *P* values of 0.05, 0.01 or 0.0001, respectively. Means in the same subcolumn followed by the same upper case letters and in the same row followed by the same lower case letters did not differ significantly at α = 0.05 (LSD, SAS Institute 1996).

but the difference was not significantly different (*F* = 1.86; df = 1, 19; *P* = 0.1899).

Movement distance between the adults of the 2 coccinellid species was significantly different (*F* = 5.19; df = 1, 39; *P* = 0.0229), but not between the sex (*F* = 1.43; df = 1, 39; *P* = 0.2393) and species × sex (*F* = 1.13; df = 1, 39; *P* = 0.2949). Females traveled almost the same as the males (*F* = 0.02; df = 1, 19; *P* = 0.901).

The leaf areas searched by larval stages of the 2 coccinellid species were significantly different (species (*F* = 23.88; df = 1, 146; *P* = 0.0001; beetle larval stages, *F* = 58.92; df = 3, 146; *P* = 0.0001; and species × beetle larval stages, *F* = 3.45; df = 3, 146; *P* = 0.0461) (Table 2). Generally, *N. oculatus* larvae searched greater areas than did *D. catalinae,* but not the adults. The areas searched by *N. oculatus* larvae were 1.5- to 2.7-fold greater than *D. catalinae*. The comparison between adults of the 2 species greatly favored *D. catalinae* than *N. oculatus* (*F* = 7.59; df = 1, 39; *P* = 0.0091), and *D. catalinae* adults searched 1.9-fold larger areas than *N. oculatus* adults because of its greater head width (28%) as well as the faster movement rate (Tables 1 and 2). Searching areas were not significantly different between males and females of both coccinellid species (*F* = 1.69; df = 1, 39; *P* = 0.2021) and the interaction of species and sex (*F* = 1.21; df = 1, 39; *P* = 0.2783).

Feeding Behavior. After eclosing from the egg, the 1st instar of both coccinellid species remained motionless for a few minutes, and then began to move over the leaf surface. Although prey were occasionally abandoned before being consumed or even significantly damaged, most were not left until the carcass was empty.

The three-way ANOVA results indicated that the time to consume an immature stages of *B. argentifolii* was slightly significant between the 2 species (*F* = 6.21; df = 1, 2,390; *P* = 0.0489), strongly different among beetle stages (*F* = 179.27; df = 4, 2,390; *P* = 0.0001), and remarkably different among prey stages (*F* = 392.77; df = 5, 2,390; *P* = 0.0001). There were strong interactions of species × beetle stages (*F* = 45.18; df = 4, 2,390; *P* = 0.0001), species × prey stages (*F* = 112.35; df = 5, 2,390; *P* = 0.0001), and beetle stages × prey stages (*F* = 86.57; df = 20, 2,390; *P* = 0.0001). However, the 3-way interactions of species × beetle stages × prey stages were only minor (*F* = 8.11; df = 20, 2,390; *P* = 0.0481).

Generally, *D. catalinae* took less time to consume an immature whitefly than did *N. oculatus,* although differences among some larval stages and adults were not always significant (Table 3). Although similar patterns were observed among stages of the 2 coccinellid species, *D. catalinae,* the larger species, spent less time consuming a prey than corresponding stages of *N. oculatus.* A *D. catalinae* adult spent 18-fold less time consuming a whitefly egg than did a 1st-instar larva. Similarly, consumption of a whitefly pupa by an adult was ≈9-fold shorter than a 1st-instar larva. In both species, a larva or an adult took significantly more time to consume a larger or older prey, and the time of each

Table 3. Mean time (mean minutes ± SE) spent by different developmental stages of *N. oculatus* (NO) and bdit*D. catalinae* (DC) to consume an immature stage of *B. argentifolii*

Prey stage	1st instar[a]		2nd instar		3rd instar		4th instar		Adult	
	NO	DC	NO	DC	NO	DC	NO	DC	NO	DC
Egg	22.3 ± 2.2	17.4 ± 2.1	8.2 ± 0.6	6.5 ± 0.8*	5.5 ± 0.3	4.2 ± 1.0*	2.5 ± 0.5	1.9 ± 0.2	0.4 ± 0.0	0.3 ± 0.0*
First	18.1 ± 6.0	14.3 ± 3.2	5.1 ± 0.5	4.3 ± 0.7*	3.6 ± 0.3	2.6 ± 0.2*	1.9 ± 0.1	1.6 ± 0.1*	0.9 ± 0.1	0.8 ± 0.1
Second	50.0 ± 6.7	20.6 ± 3.5*	10.8 ± 1.6	9.6 ± 2.1	6.0 ± 0.6	4.5 ± 0.5*	4.3 ± 0.1	3.4 ± 0.3*	1.3 ± 0.1	1.0 ± 0.2
Third	62.9 ± 7.0	49.8 ± 6.1*	31.0 ± 3.7	21.1 ± 5.1*	25.9 ± 4.3	18.9 ± 2.2*	6.8 ± 0.4	5.9 ± 1.1	3.7 ± 0.2	2.6 ± 0.1*
Fourth	79.1 ± 15.1	63.8 ± 9.8*	99.4 ± 11.8	76.1 ± 8.4*	39.1 ± 6.6	33.9 ± 3.1*	38.4 ± 0.6	18.4 ± 1.8*	7.2 ± 0.8	5.1 ± 0.6*
Pupa	194.8 ± 75.7	149.4 ± 3.1*	104.7 ± 12.0	86.9 ± 11.3*	61.2 ± 8.0	48.5 ± 5.3*	46.4 ± 10.3	31.7 ± 4.3*	21.8 ± 3.4	16.5 ± 1.7*
F	154.74***	168.11***	14.55***	36.35***	98.44***	65.21***	35.91***	28.85***	14.01***	11.24**

F-values followed by *** indicate *P* < 0.0001.
[a] Mean times of each larval or adult stage between *N. oculatus* and *D. catalinae* with an * differed significantly at α = 0.05.

developmental stage of the coccinellids spent feeding on individual prey of different stages decreased with each successive predator stage. These differences could be very significant. In *N. oculatus*, for instance, the time for an adult to consume a whitefly egg and pupa could be as much as 53- and 9-fold faster than those of a 1st-instar larvae, respectively.

Discussion

The greenhouse ornamental industry is extremely intolerant of any sign or presence of pests. On hibiscus, for instance, the mere presence of whitefly exuviae is considered unacceptable (Liu and Stansly 1998). Therefore, whiteflies must be managed to extremely low densities in ornamentals. Given such stringent requirements, any characteristics that might assist a potential biological control agent to survive under low density conditions would be advantageous.

The searching and feeding behaviors of *N. oculatus* and *D. catalinae* were characterized by many similarities but also a few important differences. Adults of both coccinellid species consumed more whitefly eggs than other whitefly immature stages (Hoelmer et al. 1993, Liu et al. 1997). Eggs of *Bemisia* are attached to the leaf surface by a pedicel inserted into the leaf surface and stand upright, possibly facilitating detection and feeding by the beetle. Also, eggs may provide essential nutrients not available from nymphs (Hagen 1962, Hoelmer et al. 1993).

Larvae of both species seemed to respond to prey only after making contact with the mouthparts or front legs, as is typical among most coccinellids (Fleschner 1950, Dixon 1959, Wratten 1973, Hoelmer et al. 1993) with few exceptions (Nakamuta 1984). *D. catalinae* forged ahead in conformance with the model of Fleschner (1950) who also calculated the area effectively searched by a larva as the width of the head times the length of the track. In contrast, *N. oculatus* larvae swept from side to side with each step while anchored on the plant surface with its uropod. For instance, some coccinellid species exhibit similar behavior, such as *Propylea quatuordecempunctatat* (L.), although swaying in a more intermittent manner (Banks 1957). Frazer et al. (1981) commented that the larvae of fast moving coccinellid species rarely capture the 1st prey (aphid) they encounter, whereas slow moving species rarely miss a prey item. Both *N. oculatus* and *D. catalinae* are relatively slow runners, especially the former, which could enhance their ability to control whiteflies under confined conditions. However, the smaller *N. oculatus* larvae searched significantly larger plant surface per unit time than did *D. catalinae*. The apparently more efficient search behavior of *N. oculatus* might impart a further advantage under conditions of relatively low prey density.

Early instars would be expected to spend more time between encounters with prey because of their relatively slow movement, a pattern typical among predators (Dixon 1959, 1970; Brown 1972; Evans 1976). Time spent handling a captured prey appeared to increase with the state of food deprivation. We have noticed that some larvae fed on honeydew and dew drops, even when abundant whiteflies were available. Availability of this and other alternate foods might allow the coccinellids to survive periods of low prey density.

Greenhouse grown crops, including vegetables, might be better able to use coccinellids for whitefly control. However, not all plants may be favorable to efficient searching by the beetles. Heinz and Parrella (1994a) observed 10-fold lower fecundity of *D. catalinae* (=*D. pusillus*) and lower longevity on a poinsettia cultivar with approximately twice the density of trichomes as the more favorable cultivar. The tendency of the beetles to follow veins on leaves or leaf margins might somewhat mitigate against the aversion to hairiness by providing a route that could lead to whitefly immatures that typically favor close proximately to veins (Ohnesorge et al. 1980, Liu et al. 1993). However, crawling on the leaf edge could eventually become a prelude to flight when the search has been fruitless.

Delphastus catalinae has been mass reared and commercialized for whitefly management for many years. Our results and experience with both coccinellid species studied here would indicate a role for *N. oculatus* as well, due, in part, to its apparent ability to survive under different sets of conditions. Perhaps in some future time, improved rearing techniques and market conditions would make inundative release of 1 or both of these coccinellids a viable option in certain situations. However, it is unlikely that coccinellids alone would ever provide sufficient or satisfactory whitefly control. Their ability to reduce high populations quickly might be combined with the superior searching ability of parasitoides (Heinz and Parrella 1994b) and other compatible management strategies to provide a functional management system for whiteflies in field and greenhouse crops.

Acknowledgments

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