FUNCTIONAL RESPONSE AND PLANT PREFERENCE OF NEPHASPIS OCULATUS (COLEOPTERA: COCCINELLIDAE), PREYING ON BEMISIA ARGENTIFOLII (HOMOPTERA: ALEYRODIDAE) IN THE LABORATORY

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The predatory behavior and functional response of all larval stages and adults of Nephaspis oculatus Abstract (Blatchley), a predacious coccinellid, on various egg densities of Bemisia argentifolii Bellows & Perring, and prey preference of adult N. oculatus, were studied in the laboratory. Daily consumption of eggs of B. argentifolii by N. oculatus was evaluated at six different densities to obtain functional response curves for all active stages of the coccinellid. Bemisia argentifolii eggs were offered to N. oculatus on collard leaf disks in Petri dish arenas over a 24-h period at 26.7 ¥ 2℃ and a photoperiod of 14:10 (L:D) h. Linear relationships were observed between percentage prey consumed and prey density, with r^2 values between 0.82 - 0.99 for all stages except for the fourth instar that had a smaller r^2 value (0.64). Functional response curves of prey consumption by N. oculatus against density of B. argentifolii eggs fitted the type II model of Holling's disc equation for all larval stages and both the male and female adults. Adult females consumed more prey than adult males. The maximum theoretical number of prey consumed per day increased with larval development. The fourth instar was the most effective larval predator, followed by the third instar, the second instar, and finally, the first instar. Based on the functional response parameters, a maximum of 321, 312, 237, 229, 73, and 34 B. argentifolii eggs could be attacked by an adult female, a fourth instar, an adult male, a third instar, a second instar, and a first instar of N. oculatus, respectively. Nephaspis oculatus adults strongly preferred collard to tomato, soybean, eggplant or sweetpotato for oviposition and foraging. Nephaspis oculatus did not deposit any eggs on soybean and tomato.

Key words biological control, coccinellid, functional response, predation, whiteflie

1 INTRODUCTION

The silverleaf whitefly, Bemisia argentifolii Bellows & Perring, is one of the most important insect pests of vegetables, broadleaf field crops, and ornamentals in the southern United States. The rapid rise of B. argentifolii to key pest status has been attributed, in part, to insecticide resistance and the decimation of natural enemies by broad-spectrum insecticides (Henneberry *et al.* 2000). Biological control might offer an attractive management alternative for B. argentifolii if natural enemy populations could be maintained at sufficiently high levelOs to hold the whitefly in check. The consumption rate of predators and their capacity to respond to prey availability are important parameters in evaluating their ability to regulate pest populations.

Nephaspis oculatus (Blatchley) is considered as a specialized predator of whiteflies (Homoptera; Aleyrodidae), and it has shown potential for biological control of B. argentifolii under greenhouse conditions (Hoelmer et al. 1993, 1994; Liu et al. 1997; Liu and Stansly 1999). Nephaspis oculatus, probably arrived from its native Central America on imported plant material, and has been well established in Florida for > 25 years (Gordon 1972, 1985). The

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coccinellid also occurs in California where it was introduced from Central America to control citrus whitefly, *Dialeurodes citri* (Ashmead) (Rose and DeBach 1981). It was introduced from Honduras, Trinidad and West Indies to Hawaii in 1979 – 1980 where it became effective in biological control of the spiraling whitefly, *Aleurodicus dispersus* Russell (Kumashiro *et al.* 1983, Yoshida and Mau 1985). The capacity of *N. oculatus* to prey on eggs of *B. argentifolii* and thereby contribute to biological control in greenhouses has been previously recognized previously (Hoelmer *et al.* 1993, 1994; Liu and Stansly 1996a, b; Liu *et al.* 1997).

The number of resources (prey or host) that an insect finds is generally proportional to the number available in time and space. Prey consumption by a predator depends on a number of factors including the length of time the prey is exposed, the handling time required for each prey item, and the rate of successful attack (Holling 1959a, 1963, Fujii *et al*. 1986). Interrelationships between these three parameters are specified by Holling's disc equation used to describe the functional response, i.e. the change in prey consumption in response to changes in prey density (Holling 1959b). Thus evaluated, the functional response has been used to describe and predict the impact of predation on prey populations at different relative densities (Sabelis 1986).

Liu and Stansly (1999) studied the feeding and walking behavior of N. oculatus, as well as Delphastus catalinae (Horn) [formerly known as D. pusillus (LeConte)], another important predator of whiteflies under greenhouse conditions. While N. oculatus has shown great potential for biological control of B. argentifolii, little is known about its predatory behavior and functional response. Generally, the amount of time available for searching varies among larval instars, being relatively short in the first instar and progressively longer in older instars and adults. Study of the functional response represents an important first step in building a comprehensive understanding of predator-prey interaction in nature. Evaluation of the functional response of N. oculatus to eggs of B. argentifolii should provide an estimate of the capacity of this predator to respond to various prey densities and thus aid in realizing the biological control potential of this coccinellid.

Host plants can significantly affect the searching and feeding behavior of coccinellids (Shah 1982, Carter 1984, Ponsonby and Copland 1995, Vohland 1996), their consumption of food and effectiveness in biological control (Marinoni and Ribeiro 1987, Copland *et al*. 1993), development and survival (Marinoni and Ribeiro 1987), and their longevity (Legaspi *et al*. 1996).

Here we report results on the functional response of N. oculatus to various densities of eggs and nymphs of B. argentifolii, and the preference of N. oculatus for five species of plants.

2 MATERIALS AND METHODS

2.1 Predator and prey

Bemisia argentifolii was obtained in 1990 from D. J. Schuster (University of Florida at Bradenton) was maintained in an air-conditioned greenhouse on collard (Brassica oleracea L. var. acephala, variety 'Georgia LS') and other host species. Nephaspis oculatus appeared spontaneously in the colony in 1994. Voucher specimens of N. oculatus and B. argentifolii have been deposited in the Insect collection at the Texas Agricultural Experiment Station, Texas A&M University at Weslaco, and the Southwest Florida Research and Education Center, University of Florida at Immokalee.

Collard plants were exposed in a whitefly colony for 24 h to allow whiteflies to oviposit on leaves. Leaf disks were cut from the egg-bearing leaves and excess eggs removed with a probe under a stereomicroscope to obtain the desired egg density. The size of the leaf disks and egg densities tested varied with life stage of the coccinellids being evaluated (see below). The leaf disks were placed ventral-side-up on water-saturated filter paper in clear plastic Petri dishes into which the coccinellids were introduced singly.

Experiments were conducted in an air-conditioned insectary at 26.7 \forall 2EC, and 55 \forall 5% RH. Photoperiod was set at 14:10 (L:D) h with light intensities measured as photosynthetically active radiation at 39 - 44: mol⁻² s⁻¹ inside cages (LI-COR, Steady State Porometer, Model LI-1600, Lincoln, NE).

2.2 B. argentifolii egg consumption by N. oculatus adults and Larvae

Sexed N. oculatus adults collected from the greenhouse culture were starved for 24 h in glass vials (6 H 0.5 cm) before introducing them singly into 5×1.5 cm Petri dishes containing an infested collard leaf disk 5 cm in diameter (19.6 cm²). The 6 prey densities tested were 20, 50, 100, 200, 300, and 400 eggs per leaf disk with! 20 replicates for each density and sex. Beetles were removed from the leaf disk after 24 h and the number of eggs attacked (completely or partially eaten and damaged) was determined under a stereomicroscope. A replicate was discarded if the beetle died or did not eat any B. argentifolii eggs.

After a large number of B. argentifolii eggs (>3000 per leaf) were obtained as described above, N. oculatus adults (male and female) were introduced onto the plants in a wood-frame screen cage $(60 \times 60 \times 60 \text{ cm})$. Newly laid N. oculatus eggs were coded with date and number using an India ink pen, and were allowed to hatch. The larvae of the beetles were monitored daily for development. The larvae of N. oculatus were gently transferred to observation arenas using a No. 00 camel hair brush where they developed to the desired instar (Liu and Stansly 1996a). Larvae were starved in small Petri dishes (2.5H 0.5 cm) for 4 h before the experiments. The size of the collard leaf disks varied according to the larval instars, $0.79 \text{ cm}^2(1$ cm diam.) for first instar, $3.14 \text{ cm}^2(2\text{-cm diam.})$ for second instar, and 7.0 cm² (3-cm diam.) for third and fourth instars. Nephaspis oculatus larvae were singly introduced onto leaf disk bearing various densities of B. argentifolii eggs based on our preliminary observation. The densities of B. argentifolii eggs offered to each larva were: 5, 10, 15, 20, 30 and 40 for first instar; 20, 40, 60, 80, 100, and 150 for second instar; 20, 50, 100, 150, 200, and 300 for third and fourth instars.

Smaller Petri dishes $(2.5 \times 1.0 \text{ cm})$ were used for first instar, and larger $(5 \times 1.5 \text{ cm})$ for older instars. Each prey density had 20 replicates for each larval instar.

2.3 Plant Preference

Responses of N. oculatus adults to five species of plants of B. argentifolii, collard, sweetpotato, eggplants, tomato and soybean were tested. Collard and sweetpotato have glabrous leaves, and eggplant, tomato and soybean have pubescent leaves. The plants were maintained in an air-conditioned greenhouse. When plants were 50 - 60 cm high, the third and fourth fully expanded leaves from the terminal were selected for use. Forty whitefly adults were collected from a greenhouse colony, and introduced to clip-on cages (2 cm top covered with 60 mesh screen, 4 cm bottom attached on leaf surface, and 1.4 cm high) for oviposition. The whitefly adults were removed 48 h later, and the leaf disks $(12.56 \text{ cm}^2 \text{ or } 4 \text{ cm in diameter})$ were trimmed off from the whole leaf. Each leaf disk had > 300 B. argentifolii eggs. Five leaf disks, one from each of the five plant species, were randomly arranged in a circle in a large Petri dish $(15 \times 1.5 \text{ cm})$. A piece of filter paper disk (15 cm in diameter) was placed on the bottom, and a few drops of water were added for moisture. Adults of N. oculatus (5 males and 5 females) were collected from the greenhouse colony and placed in the center of each Petri dish. The number of beetles present on each leaf disk was monitored at 4 and 24 h. The experiment was terminated after 24 h and the numbers of eggs laid by females on each leaf disk were recorded. The experiment had 5 treatments with 6 replicates each.

2.4 Data Analysis

The relationship between mean percentage of prey consumed versus prey density [(prey consumed/prey offered) H 100] for all larval stages and adults of N. oculatus was analyzed using the general regression procedure (PROC REG, SAS Institute 2000). Holling's curvilinear Type II model (Holling 1959a, Fujii et al. 1986) was used to fit

the functional response, and Table CurveTM Version 1.0 (Jandel Scientific 1994, San Rafael, CA) was used to fit the model. In this model, the number of prey consumed (N_a) is a function of prey density (N), as described by Holling (1959a):

 $N_a = (a' T_t N) / (1 + a' T_h N),$

where a' is the predator's rate of discovery of prey, T_i is the total time available (24 h, or 1 day in this study), and T_h is the handling time. For plant preference data, the numbers of beetles observed and eggs laid on the leaf disks were analyzed using PROC GLM procedure, followed by Tukey's studentized range test at P = 0.05 (SAS Institute 2000) for separation of means.

3 RESULTS

3.1 Consumption of B. argentifolii eggs by N. oculatus adults and larvae

Predation rates by each larval instar and adults of N. oculatus were negatively correlated with the prey offered, with r^2 ranging from 0.83 to 0.94 for the first three instars, and a lower r^2 for the fourth instar (0.63) (Fig. 1). However, for the third and fourth instars, the larvae only consumed 74.1 and 92.5% eggs, respectively, when they were offered as few as 5 eggs. Similarly, only 85.6% eggs were consumed by adult females at the same prey density.

The numbers of prey consumed by each larval instar of N. oculatus were well correlated with prey density, r^2 ranging from 0.83 to 0.94 for the first three instars, and a lower r^2 for the fourth instar (0.63) (Fig. 2). The numbers of prey consumed by adult females and males were identical, and well correlated with prey density.

A good fit was observed between the functional response curves for all larval stages and the type II model of the Holling's disc equation (Fig. 2). The model would predict a maximum of 34, 106, 229, and 312 *B*. argentifolii eggs per day by a first, a second, a third, and a fourth instar larva, respectively (Table 1).

Table 1 Rate of successful attack, handling time(day[minutes]), and predicted maximum prey consumable by N. oculatus feeding *B*. argentifolii eggs on collard leaf disks estimated using Holling's disc equation.

Stage	Attack rate (a')	Handling time, T_h (minutes)	T_i / T_h^a	r^2 First instar
	0.97	0.0295(42.5)	34	0.98
Second instar	0.91	0.0094(13.5)	106	0.97
Third instar	0.93	0.0044(6.3)	229	0.98
Fourth instar	1.27	0.0032(4.6)	312	0.97
Adult female	1.29	0.0031(4.5)	321	0.99
Adult male	1.24	0.0042(6.0)	237	0.99

^a $T_i = 1$ day; $T_i/T_h = a$ maximum numbers of prey that a predator could attack per day.

3.2 Plant preference

Numbers of N. oculatus adults on the leaf disks of the 5 species of host plants were significantly different at 4 h and 24 h (F = 4.37; df = 4, 145; P = 0.023 for 4 h. F = 13.47; df = 4, 145;

P = 0.0001 for 24 h. F = 15.98; df = 4, 290; P = 0.0001 for overall). Adults of N. oculatus strongly preferred collards to the other plants (Table 2), whereas there was no preference expressed for any of the other four species. Female N. oculatus

Table 2 Effect of host plants on Nephaspis oculatus adults and oviposition.

II l	Mean number of beetles/leaf disk ∀ SE ^a				
Host plant	4 h	24 h	Overall	Eggs laid	
Collard	1.03 ∀ 0.14a	1.43 ∀ 0.19a	1.23 ∀ 0.14a	6.90∀1.74a	
Eggplant	0.37 ¥ 0.12b	0.53 ¥0.13b	0.45 ¥ 0.09b	0.20 ¥ 0.13b	
Tomato	0.33 ¥ 0.10b	0.30 ¥ 0.09b	0.32 ¥ 0.07b	0.00 ¥ 0.00b	
Sovbean	0.47 ¥ 0.16b	0.47 ¥0.15b	0.47 ¥ 0.11b	0.00 ¥ 0.00b	
Sweet potato	0.30 ¥ 0.11b	0.23 ¥0.08b	0.27 ¥ 0.07b	0.10 ¥ 0.10b	
$F_{4,145}$	4.16	7.17	5.64	12.53	
P	0.0378	0.0211	0.0312	0.0001	

^a Means in the same column followed by the same letters are not significantly different at P = 0.05 (Tukey's studentized range test, SAS, Institute 2000).



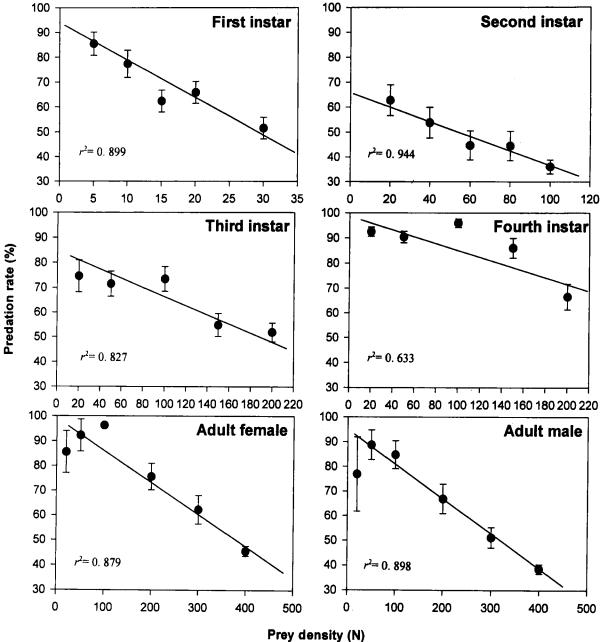


Fig.1 Relationship between prey density (*Bemisia argentifolii* eggs) and predation rate (%) by *Nephaspis oculatus* on collard leaf disks.

also laid significantly more eggs on collard leaf disks than on other plant lead disks (F = 12.53; df = 4, 145; P = 0.0001). The numbers of adult beetles observed on leaf disks for each of the five plant species were not significantly different between 4 and 24 h (F = 0.12 - 1.02; df = 1, 19; P = 0. 2822 - 0.7103). The beetles did not oviposit any eggs on soybean or tomato leaf disks.

4 DISCUSSION

Results from this study indicated that both larvae and adults of N. *oculatus* show a type II functional response to increases in prey density until the beetle is satiated. This is typical of most coccinel-

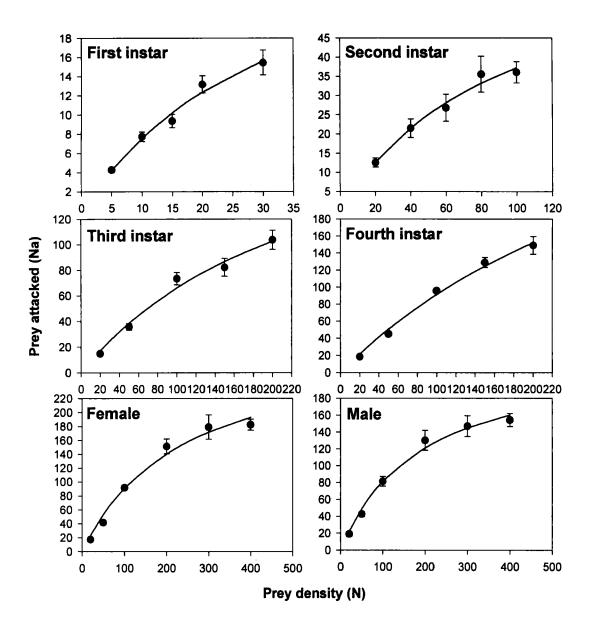


Fig.2 Functional response of Nephaspic oculatus predation on various densities of Bemisia argentifolii eggs on collard leaf disks.

lids with few exceptions (i. e. Hodek *et al*. 1984). Most larvae and adults attacked all or most of the prey provided at lower densities, but were less thorough and exhibited more variable consumption when prey density was high. Our results also indicate that these beetles, especially the third and fourth instars and the adult females, failed to consume all available prey no matter how low the prey density was. Although all larval stages of N. *oculatus* are functionally capable of preying on all developmental stages of B. *argentifolii*, we have ob-

served that ca. 30% of *B*. argentifolii eggs were incompletely consumed by both larvae and adults of *N*. oculatus if the egg density was greater than 100 for each individual beetle. This phenomenon indicates two promising advantages when the beetles are used as biological control agents: they destroy more prey than they could consume when prey density is high, and can improve their efficiency by consuming prey completely when food is less abundant.

Handling time can be defined as the time that a predator requires to kill and eat its prey. Based on the result from this study, the beetles could consume 237 B. argentifolii eggs for males and 321 eggs for females in 24 h (Table 1). However, functional response parameters obtained from the small arena under laboratory conditions may not always reflect those under field conditions. Searching behavior, plant size (leaf areas), and prey distribution will affect the searching success and, ultimately, prey consumption. O' Neil (1989) observed that Podisus maculiventris (Say) showed a consistent rate of predation on Epilachna varivestis Mulsant in the field attacking 0.42 larvae per day, while at the same prey density in the laboratory the predator exhibited a typical type II functional response with a maximum attack rate of 4.4 per day, a 10-fold difference. Furthermore, the existence of a plateu for predation rate suggests that once the prey density on the plant exceeds a critical threshold, the beetles would not attack sufficient prey to prevent a pest outbreak.

Data from the plant preference study reveal a clear preference for collard by adult N. oculatus among the five plant species tested. However, more studies are needed to explain the nature of sensory cues mediating the preference. The searching behavior of a predator can be affected by plants pubescence. Banks (1957) found that Coccinella quatuordecimpunctata L. moves more slowly on the pubescence leaves of potato than on the glabrous leaves of bean. Leaf pubescence not only directly influences the searching efficiency of coccinellids, but has also been implicated as a characteristic of whitefly resistance of plants. Generally, glabrous leaves in many field and vegetable crops, i.e. cotton, eggplant and cantaloupe, have significantly lower whitefly populations than do moderately or heavily pubescent leaves (Wilson et al. 1993, Rilev et al. 1998). However, host plant volatiles may also affect the searching and feeding behavior of coccinellids. Ponsonby and Copland (1995) found that Chilocorus nigritus (F.), a coccidophagous coccinellid, was attracted to a combination of Solanum tuberosum L. and Abgrallaspis cyanophylli (Sign.) odors.

The present study provides additional information to advance our understanding of the predatorprey relationship between N. oculatus and B. argentifolii, and plant preference by the predator. We feel that this information can be useful to develop a predictive model for using N. oculatus as a biological control agent against B. argentifolii in the greenhouse or in other controlled-environmental settings.

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粉虱小毛瓢虫 Nephaspis oculatus (鞘翅目,瓢虫科) 捕食功能反应与寄主植物选择

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Nephaspis oculatus (Blatchley)属毛瓢虫亚科的小毛瓢虫族,专食粉虱。它源于中美洲,自七十年代初就在美国佛州被发现,是柑橘和蔬菜上白粉虱的重要天敌。本研究确定了该瓢虫各幼虫龄期和雌雄成虫在青菜(collard)叶上捕食银叶白粉虱 Bemisia argentifolii Bellows & Perring 卵在 6 个密度的捕食功能反应及其成虫对 5 种寄 主植物的选择。结果表明,该瓢虫捕食率与白粉虱卵的密度呈线性相关。除第四龄幼虫其相关系数(r²)仅为 0.633 外,其它各虫态的相关系数高达 0.827 ~ 0.944。根据该瓢虫各龄幼虫和雌雄成虫捕食量和白粉虱卵密度 的关系,其捕食功能反应符合 Holling 圆盘方程的第二种反应模式。随着龄期的增加,幼虫捕食白粉虱卵的量也 随之增加。第四龄幼虫捕食白粉虱卵量最多可达 312 粒,其次为第三龄幼虫 229 粒,第二龄幼虫 73 粒,而第一 龄幼虫捕食量仅为 34 粒。雌成虫捕食白粉虱卵量(321 粒)明显高于雄成虫(237 粒)。雌成虫特别喜欢在青菜 上活动、取食和产卵,而不喜欢番茄,大豆,茄子和甘薯。有 44.9%的雌成虫在青菜上活动,只有 9.9% - 17.1% 的雌成虫在其它植物上活动。雌成虫在青菜,甘薯和茄子上的产卵量占总产卵量的比率依次为 95.8%,2.8%

关键词 生物防治 飘虫 功能反应 捕食 白粉虱

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