Comparison of Searching Behavior of Parasitoid, *Toxoneuron nigriceps* Vierick, for Three Tobacco Herbivores[1]

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Abstract Host searching behavior of females of the endoparasitoid *Toxoneuron nigriceps* Vierick (Hymenoptera: Braconidae) was observed in the field for three tobacco herbivores, *Heliothis virescens* (F.), *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), and *Manduca sexta* L. (Lepidoptera: Sphingidae). The only developmentally suitable host for the parasitoid was *H. virescens*. Hovering, searching, and oviposition (for plants with herbivores) by *T. nigriceps* were observed for a combination of two plant types, plants with only herbivore-induced plant volatiles or damaged plants with herbivores, and three insect species. The six treatments were as follows: (1) plants with only *H. virescens*-induced plant volatiles, (2) plants with only *H. zea*-induced plant volatiles, (3) plants with only *M. sexta*-induced plant volatiles, (4) plants damaged by *H. virescens*, (5) plants damaged by *H. zea*, and (6) plants damaged by *M. sexta*. Parasitoid females readily hovered around and searched on plants of both types. However, females spent more time foraging for *H. virescens* than for the nonhosts, *H. zea* and *M. sexta*. For plants with only herbivore-induced plant volatiles, *T. nigriceps* females spent more time searching on *H. virescens* plants than on *H. zea* and *M. sexta* plants. For damaged plants, parasitoid females visited more *H. virescens* plants than *M. sexta* plants and spent more time searching for *H. virescens* larvae than for *M. sexta* and *H. zea* larvae. Even though *T. nigriceps* females laid eggs in *M. sexta* and *H. zea* larvae, oviposition was higher for *H. virescens* than for the nonhosts. In conclusion, *T. nigriceps* females utilized more of their energy searching for and parasitizing *H. virescens* over the nonhosts on tobacco.

Key Words *Heliothis virescens*, *Helicoverpa zea*, *Manduca sexta*, herbivore-induced plant volatiles, damaged plants, hovering, oviposition

Larvae of the tobacco budworm, *Heliothis virescens* (F.), the corn earworm, *Helicoverpa zea* (Boddie), and the tobacco hornworm, *Manduca sexta* L., can be found on tobacco, *Nicotiana tabacum* L., in very high numbers (Thurston 1955, Neunzig 1969, Manley et al. 1991). The solitary endoparasitoid *Toxoneuron nigriceps* (formerly *Cardiochiles nigriceps*) Viereck can contribute substantially (50-100% mortality) to the biological control of *H. virescens* on tobacco (Lewis et al. 1972, Roach 1976, Tingle and Mitchell 1982, Johnson and Manley 1983, Jackson et al. 1996). This parasitoid also parasitizes *Heliothis subflexa* (Guenée) on ground cherry, *Physalis* spp. (Lewis et al. 1967), and larvae of the beet armyworm, *Spodoptera exigua* (Hübner) (Ruberson et al. 1994). However, *T. nigriceps* basically is host specific for *H.*

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virescens because parasitization of *H. subflexa* by this parasitoid is relatively low (4.5%), and *S. exigua* is a rare host (0.02% parasitization) for this wasp. In nature, *T. nigriceps* females also will oviposit in *H. zea* (Lewis and Brazzel 1966), but the larvae are unsuitable for development of this parasitoid (Lewis and Vinson 1968). Chamberlin and Tenhet (1926) reported that *T. nigriceps* attempted oviposition in 1st-instar *M. sexta*, but parasitoids did not emerge from the insect larvae.

Hovering-searching-oviposition is the most common ovipositional behavior sequence for *T. nigriceps* searching for *H. virescens* on tobacco (Tillman and Mullinix 2003). When a foraging female locates a host plant, she begins hovering around the plant. When she lands on the plant, she follows a “trail” to a host larva while antennating the plant (Vinson and Lewis 1965). A substance from the mandibular glands of the host larva elicits this searching response (Vinson 1968). Upon locating a host, the *T. nigriceps* female deposits an egg into it.

Plant volatiles can affect the host searching behavior of *T. nigriceps* females. Tobacco volatiles are highly attractive to females of this parasitoid because the females will hover and land on tobacco plants even in the absence of their hosts (Vinson 1975). Herbivory causes plants to release volatiles that differ from volatiles associated with artificial damage, and production and release of these volatiles can be triggered at least in part by an interaction of elicitors in the oral secretion of herbivores with damaged plant tissues (Turlings et al. 1990). In addition to the release of volatiles at the site of herbivore feeding, there is also a systemic response (Turlings and Tumlinson 1992). Female *T. nigriceps* can detect these plant volatiles and use them to locate their hosts. In field choice tests, *T. nigriceps* females preferred plant volatiles released from tobacco plants damaged by *H. virescens* in comparison with those released by undamaged tobacco (Vinson 1975, De Moraes and Lewis 1999, Oppenheim and Gould 2003). In other field trials, the occurrence of total visits, or directed searches of the plant, by *T. nigriceps* females was higher for plants releasing *H. virescens*-induced plant volatiles over plants releasing *H. zea*-induced plant volatiles, demonstrating that herbivore-induced plant volatiles can transmit herbivore specific information (De Moraes et al. 1998).

Potentially, tobacco can be a refuge and natural insectary for *T. nigriceps* in cotton, *Gossypium hirsutum* L. However, female *T. nigriceps* have been observed attacking the two nonhosts *H. zea* and *M. sexta* on tobacco in the field. Thus, a field test was conducted to compare searching behavior and oviposition by *T. nigriceps* for each of the three tobacco herbivores, *H. virescens*, *H. zea*, and *M. sexta*.

Materials and Methods

Plants. All experiments were conducted using tobacco (strain K-326) 7-9 wks old (vegetative stage). The plants were grown in 2.8-L plastic nursery pots (one plant/pot) in a greenhouse held at 25-30°C, 50-70% RH, and a 16:8 L:D photoperiod. Osmocote™ 14-14-14 (Scotts-Sierra Horticulture Products Co., Marysville, OH) was used as a time-release fertilizer.

Insects. Eggs of *H. virescens* and *H. zea* were obtained from the USDA, ARS, Crop Protection and Management Research Laboratory in Tifton, GA. *Manduca sexta* eggs were obtained from the North Carolina State University Rearing Laboratory in Raleigh, NC. All insect larvae were fed a laboratory bean diet (Perkins et al. 1973) and held in a climatic-controlled room at 25°C and 14:10 L:D photoperiod. To acclimate laboratory-fed insect larvae to feed on tobacco, 236.6 ml of tobacco pulverized by a blender were added to every batch (3.8 L) of diet. The behavioral studies were conducted in the field with feral females because *T. nigriceps* females spend most of their time trying to escape from enclosed test arenas.

Experimental procedure. Searching behavior of *T. nigriceps* was observed for a combination of two plant types, plants with only herbivore-induced plant volatiles or damaged plants with herbivores, and three insect species, *H. virescens*, *H. zea*, or *M. sexta*, in June 2000. The six treatments were as follows: (1) plants with only *H. virescens*-induced plant volatiles, (2) plants with only *H. zea*-induced plant volatiles, (3) plants with only *M. sexta*-induced plant volatiles, (4) plants damaged by *H. virescens*, (5) plants damaged by *H. zea*, and (6) plants damaged by *M. sexta*. Each treatment was replicated 3 times. For each of the six treatments, three 3rd instars of an insect species were allowed to feed individually for 48 h in 6.4 cm^2 cages on individual fully-extended leaves near the middle of the plant in the greenhouse. During this time period, all insect larvae, regardless of species, consumed all the tobacco within the feeding cages so the amount of tobacco eaten by each insect was similar.

After the 48 h feeding period, the 18 plants (6 treatments × 3 replicates) were transferred to the middle of a 5-ha cotton field with feral *T. nigriceps* females. All feeding cages and insects were removed from the plants. For plants with only herbivore-induced plant volatiles, damaged leaves were also removed, and cut areas were covered with aluminum foil. For herbivore-damaged plants, insect larvae that had fed on the plants in the greenhouse were replaced with fresh larvae that were positioned at the site of herbivore damage. In the field, newly-ecdysed 2nd-instar *H. virescens* and *H. zea* were used as herbivores because they could be observed and handled easily. First-instar *M. sexta* were used because they were about the same size as the early 2nd-instar noctuids. Plants were arranged randomly in a row with 60 cm between pots. Then hovering, searching, and oviposition by *T. nigriceps* females was observed and recorded using a Psion Organizer II™, Model LZ64 (Psion PLC, London, England) with Observer™ software (Noldus Information Technology, Inc., Sterling, VA). The test was conducted on 4 days (8, 9, 29, and 30 June) around 0,900 - 1500 because ovipositional activity is much greater during that time of day (Chamberlin and Tenhet 1926). A single female was observed until she flew away from the test (gone for 5 min), and then another female was observed. Occurrence of total visits (directed searches of the plant) by all *T. nigriceps* females during this time period was not determined. Once an insect larva was stung, it was removed, and an unparasitized larva was placed in the same position that the stung insect larva had occupied. Stung insect larvae were dissected under a dissecting microscope to verify oviposition.

Statistical analyses. Hovering, searching, and oviposition data were combined to make the experimental unit the plant for the whole time a *T. nigriceps* female was in the arena of the test. Preliminary analyses of hovering and searching showed that variances between volatile and damaged plants were unequal. Therefore, these data were analyzed separately for type of plant using PROC MIXED (SAS Institute 2003). The fixed effect was insect species. Random effects were female within date and residual error. Least squares means were separated by least significant difference (LSD) (SAS Institute 2003) where appropriate. For each of the six treatments, means for occurrence of hovering and searching per plant were compared using Student's *t*-tests. Means for occurrence of ovipositions by *T. nigriceps* per damaged plant searched were compared between insect species using Student's *t*-tests.

Results and Discussion

Seventy-four females (19, 13, 19, and 23 females on day 1, 2, 3, and 4, respectively) visited a total of 686 plants over 4 days (1.2, 1.7, 3.2 and 1.9 h on day 1, 2, 3, and 4, respectively). The average number of plants visited per female per date was 11.2.

For plants with only herbivore-induced plant volatiles, *T. nigriceps* females were observed not only hovering around the plants, but also searching on the plants regardless of herbivore species. A statistically significant difference was not detected among herbivore species for occurrence of hovering (F = 0.62; df = 2, 206; P = 0.5392) and searching (F = 1.52; df = 2, 20; P = 0.2425) per plant by *T. nigriceps* females (Table 1). However, time *T. nigriceps* females searched plants was significantly higher for plants with *H. virescens*-induced plant volatiles than for those plants emitting volatiles induced by the two nonhosts, *H. zea* and *M. sexta* (F = 5.29; df = 2, 57; P = 0.0078) (Table 1). Occurrence of searching appears to be directly related to the occurrence of hovering because there was no significant difference between occurrence of hovering and searching for each herbivore species. This phenomenon was not unexpected, because hovering always precedes searching when *T. nigriceps* females are host-searching (Tillman and Mullinix 2003). Numerical values for host-searching behavioral data suggest that there was a progressive increase in occurrence of hovering and searching and time searching by *T. nigriceps* females from *M. sexta* to *H. zea* to *H. virescens* plants.

Systemic volatiles appeared to elicit a host-specific response from *T. nigriceps* females to search tobacco plants previously fed upon by *H. virescens* over plants fed upon by *H. zea* and *M. sexta*. In previous field studies, *T. nigriceps* landed more often on plants releasing systemic volatiles induced by *H. virescens* feeding than on plants releasing *H. zea*-induced plant volatiles (De Moraes et al. 1998). Recent field observations (Oppenheim and Gould 2003) have confirmed that this preferential attraction by *T. nigriceps* extends to *H. subflexa*-induced systemic volatiles when compared with *H. zea*-induced systemic volatiles.

Toxoneuron nigriceps females readily hovered around and searched on plants on which any of the three species of herbivores were feeding. Similar to results for volatile plants, there was no significant difference between occurrence of hovering and occurrence of searching for each herbivore species on damaged plants (Table 1). Occurrence of hovering by *T. nigriceps* per plant was significantly higher (F = 7.66; df = 2, 338; P = 0.0006) and occurrence of searching by *T. nigriceps* per plant was significantly higher (F = 6.11; df = 2, 178; P = 0.0027) for *H. virescens* compared with *M. sexta* (Table 1). In addition, time *T. nigriceps* females searched plants was significantly higher for *H. virescens* than for *M. sexta* and *H. zea* and significantly higher for *H. zea* compared with *M. sexta* (F = 10.91; df = 2, 240; P = 0.0001) (Table 1). Again, results on searching time along with the numerical values for occurrence of hovering and searching strongly suggest that there was a progressive increase in host-searching by *T. nigriceps* females from *M. sexta* to *H. zea* to *H. virescens* damaged plants.

Based on dissections of stung insect larvae, all “stings” by *T. nigriceps* females resulted in oviposition. The total number of ovipositions was 13 for *M. sexta*, 36 for *H. zea*, and 51 for *H. virescens*, for a total of 100 ovipositions over all insect species (Table 2). Occurrence of oviposition by *T. nigriceps* females searching herbivore-damaged plants was significantly higher for *H. virescens* compared with the two

Table 1. Occurrence of hovering and searching and time of searching by *T. nigriceps* per plant for tobacco plants with only herbivore-induced volatiles (HIPV) and damaged tobacco plants with herbivores for *H. virescens*, *H. zea*, and *M. sexta*

		Occurrence of hovering per plant		Occurrence of searching per plant		Time (s) searching per plant
Plant type	Insect species	n	Mean ± SE	n	Mean ± SE	Mean ± SE
HIPV	*H. virescens*	118	1.53 ± 0.11 a1	27	2.30 ± 0.30 a1	6.70 ± 0.89 a
	H. zea	80	1.40 ± 0.13 a1	16	1.88 ± 0.38 a1	3.06 ± 1.13 b
	M. sexta	76	1.36 ± 0.13 a1	17	1.47 ± 0.38 a1	2.56 ± 1.16 b
Damaged	*H. virescens*	120	3.80 ± 0.31 a1	76	4.36 ± 0.41 a1	42.68 ± 4.63 a
	H. zea	159	3.31 ± 0.27 a1	99	3.69 ± 0.37 a1	29.83 ± 4.09 b
	M. sexta	133	2.34 ± 0.30 b1	73	2.51 ± 0.42 b1	13.12 ± 4.74 c

Within a column, least squares means followed by the same letter are not significantly different among insect species for a single plant type (PROC MIXED, LSD, $P < 0.05$). Within a row, least squares means followed by the same number are not significantly different between occurrence of hovering and occurrence of searching for a single species (t-test, $P < 0.05$).

Table 2. Occurrence of oviposition by *T. nigriceps* per searched tobacco plant damaged by *H. virescens, H. zea,* and *M. sexta*

Insect species	No. plants searched	No. ovipositions	Mean ± SE proportion of searches with oviposition
H. virescens	76	51	0.67 ± 0.06 a
H. zea	99	36	0.37 ± 0.05 b
M. sexta	73	13	0.18 ± 0.05 c

Within a column, means followed by the same letter are not significantly different (*t*-tests, $P < 0.05$).

nonhost insect species, and also higher for *H. zea* than for *M. sexta* (Table 2). Similarly, Vinson (1975) reported that percentage egg deposition for *T. nigriceps* females was 100% for *H. virescens*, 81% for *H. zea*, and 50% for *M. sexta*.

Eggs oviposited in *H. zea* larvae are always encapsulated in the hemolymph of these larvae (Lewis and Vinson 1968). All *T. nigriceps* eggs in tobacco hornworm larvae collected during this experiment were encapsulated. Since both *H. zea* and *M. sexta* are unsuitable hosts for *T. nigriceps*, the question is why would these females seemingly waste eggs in these insect species? Perhaps, the strong adaptation of *T. nigriceps* to tobacco may provide the parasitoid species some evolutionary advantage in trying to develop in these nonhosts on this plant. Maybe the urge of *T. nigriceps* females to reproduce for continuance of the species overrides the placement of eggs in developmentally unsuitable insect species especially since egg number is not a limiting factor for reproduction by this parasitoid. In studying the suitability of various lepidopteran larvae as hosts for *T. nigriceps*, Lewis and Vinson (1971) determined that *T. nigriceps* eggs were always encapsulated in 2nd-instar *Heliothis phloxiphaga* Grote & Robinson, but 18% of the parasitoids escaped encapsulation in 1st instars of this insect. As for *H. zea*, encapsulation occurred while *T. nigriceps* was in the egg stage except when oviposition occurred in 1st instars, in which case the parasitoid reached the 1st instar before encapsulation occurred. Thus, there is a remote possibility that *T. nigriceps* may be able to adapt and develop in 1st instars of *H. zea* and *M. sexta*.

Results on searching time on volatile and damaged plants and occurrence of oviposition for the three insect species demonstrate that *T. nigriceps* females preferred their host, *H. virescens*, to nonhosts. In addition, the greater occurrence of hovering around *H. virescens* damaged plants compared with *M. sexta* damaged plants demonstrates that this parasitoid preferred *H. virescens* to *M. sexta* before even landing on the plants. This observed trend for host preference is consistent with evolutionary relationships for these three insect species, for *H. virescens* and *H. zea* are both noctuids and are more closely related to each other than they are to *M. sexta*. Our observations on host preference are supported by Lewis and Vinson's (1971) report that the antennal response (4 was maximum response) of *T. nigriceps* to herbivore salivary material was 1.3, 2.2, and 3.9 for *M. sexta*, *H. zea*, and *H. virescens*, respectively. Similarly, in field experiments De Moraes et al. (1998) showed that occurrence of landings of *T. nigriceps* was higher for plants fed upon by *H. virescens* than those fed upon by *H. zea* for both plants with systemic volatiles alone and damaged plants. Oppenheim and Gould (2003) also reported that the number of visits to treated plants was higher for *H. virescens* than for *H. zea* for damaged plants with herbivore larvae and herbivore-induced systemic plants. The fact that a significant difference was not detected in occurrence of hovering and searching per plant between *H. virescens* and *H. zea* in this paper does not refute the earlier work of these authors because in this research occurrences of these searching behaviors were not equivalent to the directed landings or visits reported by De Moraes et al. (1998) and Oppenheim and Gould (2003) for *T. nigriceps*.

The relationship between the three tropic levels—tobacco plants, *H. virescens* feeding on tobacco, and *T. nigriceps* parasitizing *H. virescens* on tobacco—probably evolved so that chemical compounds associated with the plant and host are used by *T. nigriceps* females to search for hosts. Interestingly, oral secretions from the host indirectly (through host-induced plant volatiles) and directly (through host-searching cues) elicit host-specific responses for *T. nigriceps* females in both host habitat finding and host location. Thus, as *H. virescens* adapted to feeding on tobacco, the plant adapted to using herbivore-related products, such as oral secretions, to stimulate production and emission of plant volatiles, and the parasitoid *T. nigriceps* adapted to using these volatiles and oral secretions for host-habitat finding and host-location.

In conclusion, *T. nigriceps* females used more of their energy searching for and parasitizing *H. virescens* larvae over larvae of the nonhosts *H. zea* and *M. sexta* on tobacco. Therefore, tobacco, which can harbor very high numbers of *H. virescens* larvae, has the potential to be a refuge and natural insectary for *T. nigriceps* in cotton.

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