Effect of Host Plants on Successful Parasitism by *Haeckeliania sperata* (Hymenoptera: Trichogrammatidae) on *Diaprepes abbreviatus* (Coleoptera: Curculionidae) Eggs

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Effect of Host Plants on Successful Parasitism by *Haeckeliania sperata* (Hymenoptera: Trichogrammatidae) on *Diaprepes abbreviatus* (Coleoptera: Curculionidae) Eggs

**DANIEL CARRILLO,¹ ² JORGE E. PEÑA,¹ AND JOHN L. CAPINERA³**


**ABSTRACT** *Diaprepes abbreviatus* L. is a highly polyphagous root weevil that causes damage to several fruit crops, ornamental plants, and other naturally occurring plants in Florida. *Haeckeliania sperata* Pinto is a gregarious endoparasitoid that attacks *D. abbreviatus* eggs. We hypothesized that the reproductive success of *H. sperata* is affected by the host plant of *D. abbreviatus*. Six host plants with varying degrees of pubescence were used to determine the effect of leaf trichomes on the searching behavior and success of parasitism by *H. sperata*. No-choice tests showed that *H. sperata* was able to parasitize *Diaprepes* eggs laid on the six host plants. However, the plants with a high trichome density on their leaves had a lower percent of parasitism than the plants with smoother leaves. Removing trichomes from a host plant showed that the presence of some leaf trichomes had a negative effect on the overall searching efficiency of *H. sperata*. The presence of trichomes decreased the total distance traveled and increased the total search time of *H. sperata* females, resulting in a lower searching speed. Multiple regression analysis was used to establish the relationship between percent parasitism and leaf trichome density, leaf thickness, and the searching speed of *H. sperata*. Searching speed was the best predictor of percent parasitism; this parameter could be used to predict the suitability of host plants for the establishment of *H. sperata*. Our findings suggest that the reproductive success of *H. sperata* is affected by the host plant of *D. abbreviatus*.

**KEY WORDS** *Diaprepes* root weevil, egg parasitoid, host plants, trichomes, searching speed

*Diaprepes abbreviatus* L. is a highly polyphagous root weevil that is native to the Lesser Antilles and was unintentionally introduced to Florida in the mid-1960s (Woodruff 1985). Since its first detection in Apopka (Orange County) in 1964, this weevil has spread throughout the central and southern part of the Florida peninsula. *Diaprepes* is now considered established in 23 counties, infesting >100,000 acres of citrus groves and many other agricultural, ornamental, and wild plants (Nguyen et al. 2003, Weissling et al. 2004). Estimates show that this pest has increased production costs >70 million dollars annually for the citrus industry in Florida (Stanley 1996, Muraro 2000). Moreover, the infestation of this weevil has spread to Texas and California (Grafton-Cardwell et al. 2004, CDFA 2006), resulting in drastic measures to restrict the introduction of ornamental plants from Florida (TDA 2001).

The pest status of *D. abbreviatus* is partly attributable to its polyphagy. The list of host plants of *D. abbreviatus* includes >270 plant species from 60 plant families (Simpson et al. 1996, Mannion et al. 2003). Many *Diaprepes* host plants are important agricultural crops such as citrus (all varieties), papaya, sugarcane, peanut, sorghum, sweet potato, cassava, loquat, guava, mango, avocado, banana, and corn. Some of the other reported hosts are widely used by the ornamental plant industry, and they include native plants and invasive species, all of great ecological significance (Simpson et al. 1996). The broad host range of *D. abbreviatus* represents a significant challenge for developing efficient and sustainable management tactics.

Classical biological control of *Diaprepes abbreviatus* is viewed as one of the components of integrated pest management (IPM) programs with potential to effectively reduce weevil numbers (Peña et al. 2001, 2004). Several efforts have been made to identify and introduce classical biological control agents of *D. abbreviatus* in an attempt to reduce weevil populations to tolerable levels. Three species of egg parasitoids have been introduced to Florida. As a result of these introductions, two eulophid parasitoids [Quadrastichus haitiensis (Gahan) and Aprostocetus vaquitarum (Wollcott)] have successfully established in the southern...
portion of the Florida peninsula where they have become an important mortality factor of Diaprepes eggs (Peña et al. 2004, 2006). Another promising biocontrol agent against D. abbreviatus is Haeckeliania sperata (Hymenoptera: Trichogrammatidae), a gregarious, egg-endoparasitoid that was collected in Dominica in 2003 (Peña et al. 2006). This species was found as a primary parasitoid parasitizing >50% of egg masses found in citrus groves and citrus nurseries in Dominica (Peña et al. 2006). Jacas et al. (2005) studied the thermal requirements of H. sperata and found that this parasitoid has a greater thermal plasticity than the parasitoids already established in south Florida, which could increase their chances of establishment in the central portion of the state. Furthermore, H. sperata was collected in areas of high altitude (509 m), which suggests that it could have more cold hardiness than other imported parasitoids. In addition to the adaptability of this parasitoid to Florida’s climate, other important factors could influence its fitness in its new environment.

An array of factors of the host plant can affect the colonization, phenotype, and effectiveness of natural enemies used in biological control (Bottrell and Barbosa 1998). Plants use many physical and chemical defenses against insect herbivores that are not necessarily compatible with natural enemies. Physical defenses may include structural traits such as surface waxes, leaf trichomes, and/or spines, whereas chemical defenses are often secondary metabolites that act as repellents, toxins, and/or digestibility reducers (Jeffree 1986, Southwood 1986). Plant defense mechanisms may directly or indirectly inhibit natural enemies.

Direct plant effects on parasitoids may involve simple mechanisms such as reduced parasitoid searching efficiency caused by trichomes (Bottrell and Barbosa 1998). An interesting case is the negative effect of glandular trichomes of some alfalfa cultivars on the parasitism of Empoasca fabae (Harris) (Hemiptera: Cicadellidae) by Anagrus nigriventris Girault (Hymenoptera: Mymaridae) (Lovingier et al. 2000). In another study, Mulatu et al. (2006) found that the presence of trichomes on tomato leaves had a direct adverse effect on the parasitoid Diadegma pulchripes (Kokujev) (Hymenoptera: Ichneumonidae). In contrast, Styrsky et al. (2006) found that the presence of trichomes in soybean plants did not inhibit fire ants [Solenopsis invicta Buren (Hymenoptera: Formicidae)] from foraging on plants and that predation of herbivores was greater in pubescent plants when compared with glabrous plants.

The effects of host plants have proven to be especially important for relatively small parasitoids (Rabb and Bradley 1965, Jeffree 1986, Lukianchuk and Smith 1997, Sütterlin and Van Lenteren 1997, 1998, 2000, Romeis et al. 1998, 1999, 2005, Styrsky et al. 2006). Because of the small size of H. sperata, trichomes and trichome exudates could inhibit the parasitoid’s movements. As with many other trichogrammatids (Schmidt 1994, Romeis et al. 2005), H. sperata searches for weevil eggs by walking on the leaf surface (D.C., unpublished data). Thus, physical and chemical leaf surface characters can alter parasitoid searching and host encounter rates.

Another factor that can affect the ability of H. sperata to parasitize D. abbreviatus eggs is the leaf thickness of the host plant. H. sperata inserts its ovipositor through the leaf to reach the weevil egg mass cemented between two leaves (Peña et al. 2004). This aspect of H. sperata’s behavior suggests that the relationship between the length of the ovipositor and leaf thickness could be critical to the successful parasitism of D. abbreviatus in certain host plants. Given the wide range of host plants of D. abbreviatus, knowledge of the potential antagonism between the host plants and H. sperata is particularly important.

The study presented here hypothesizes that the reproductive success of H. sperata is affected by the host plant of D. abbreviatus. The objectives of this study were to (1) determine the successful parasitism of D. abbreviatus eggs by H. sperata on different host plants, (2) determine the effect of leaf trichomes on the searching behavior of H. sperata, and (3) determine the relationship between searching speed, trichome density and leaf thickness to parasitism of H. sperata on Diaprepes eggs.

Materials and Methods

Stock Colonies

Haeckeliania sperata used in each of the experiments described below were collected in Dominica in 2003 and reared for several generations at the Tropical Research and Education Center (TREC) insectary (L:D: 12:12 h, 26.5 ± 1°C, and 75% RH). Parasitoids were reared on D. abbreviatus eggs from adult weevils that were collected from a pesticide-free commercial nursery in Homestead, FL. The weevils were placed randomly in groups of 300 in Plexiglas cages (30 by 30 cm) and fed on green buttonwood, Conocarpus erectus L. (Combretaceae), 2 wk before the beginning of the experiments. Several collections of weevils were made during the course of all the experiments. The parasitoids used in the experiments were presumably mated, fed, naïve with respect to hosts, and were 1 d old at the time of testing.

Plant Material

Six host plants with different trichome densities and leaf thickness were chosen (Table 1). The fruit crops selected for this study were lime, Citrus aurantifolia, a many-branched, spiny shrub with elliptic ovate glabrous leaves (Bayley and Bayley 1976); and loquat, Eriobotrya japonica, a small tree with alternate, short-petioled leaves with a high density of long, unicellular, nonglandular trichomes (Bayley and Bayley 1976). Ornamental host plants selected were pygmy palm, Phoenix roebelini, a sometimes clustered slender palm with pinnate narrow pinnae with sparse unicellular, nonglandular trichomes; button mangrove, C. erectus, a native erect shrub or tree, with elliptic to ovate

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nearly glabrous leaves; and silver buttonwood, C. erectus variety. sericeus Fors ex. DC with silky-hairy leaves (Bayley and Bayley 1976). The sixth host plant selected for this study was elephant grass, Pennisetum purpureum, an invasive grass with often branched stems and elongate blades with a high density of long, unicellular trichomes.

### Successful Parasitism by H. sperata on D. abbreviatus Eggs on Six Host Plants

**No-Choice Tests.** Leaves free of any damage were removed from each host plant, leaving a 10-cm petiole, stem, or other plant structure to hold the cutting firmly upright when formed into bouquets with exposed leaves (≈1,500 cm² of leaf surface). The bouquets were formed by inserting the stems into wet florist foam covered with aluminum foil, leaving the leaves exposed. The bouquets were placed separately into Plexiglas oviposition cages (30 by 30 by 30 cm) along with 250 adult weevils (50:50 D. abbreviatus : H. sperata) on the sides of a weevil cage during the oviposition period. The egg-infested bouquets were removed from the cages and checked under a microscope to make sure that no parasitoids were left in the bouquets. Seven days later, the leaves were torn open, and parasitized eggs were identified by the presence of four nearly glabrous leaves; and silver buttonwood, C. erectus variety. sericeus Fors ex. DC with silky-hairy leaves (Bayley and Bayley 1976). The sixth host plant selected for this study was elephant grass, Pennisetum purpureum, an invasive grass with often branched stems and elongate blades with a high density of long, unicellular trichomes.

### Statistical Analysis

**Effect of Leaf Trichomes on the Searching Behavior of H. sperata**

This experiment was designed to determine the effect of leaf trichomes in two host plants on the walking speed of H. sperata. Only the two biotypes of C. erectus were used in this experiment. The searching speed of H. sperata females was measured on leaves kept intact or leaves where the trichomes were removed by two methods. A set of leaves of each C. erectus biotype was washed with a 0.1% Triton X-100 solution, a nonphytotoxic detergent that helps removing trichomes and leaf-surface linked chemicals. Trichomes were removed from another set of leaves of C. erectus variety sericeus by shaving them with a razor blade under a microscope. We included wax paper (Cut-Rite; Reynolds, Richmond, VA) as a nonleaf surface without the potential confounding effects from chemicals and epicuticular waxes. The mean searching speed on each substrate was measured for 10 mated, 1-d-old and honey-fed H. sperata females. Leaf disks (6.3 cm²) of each surface (abaxial and adaxial) were excised and tightly placed in the bottom of a petri dish of the same size. Female wasps were individualized in similar petri dishes 30 min before each observation. Females were placed on the middle of each surface, and the petri dish was left uncovered, which allowed ventilation and the females to leave the surface freely. The walking patterns were monitored using a video camera (Video Flex 7000 series; Ken-a-vision, Inc., Kansas City, MO), equipped with a macro lens mounted 5 cm above the plane of the surface. Walking patterns were traced onto acetate sheets attached to a television screen. The path and location were recorded every 10 s until the wasp left the surface or after 2 min had passed. The acetate sheets were scanned to convert the walking traces into digital images. The traces were processed using the image processing and analyzing software Scion Image. This procedure allowed us to calculate the total search time (s), the time spent motionless (s), the total distance traveled (mm), the walking speed (mm/s), and the searching speed of each female on each surface (mm/s). Searching speed is the average velocity of H. sperata during the whole observational period (considering the time spent walking and immobile). Walking speed refers to the average velocity only while walking. Searching speed is usually the variable of interest because it is a quantitative measure of how far a parasitoid searches in a given time (Van Hezewijk et al. 2000).

**Statistical Analysis.** This experiment was replicated 13 times, each time with new parasitoids and leaves. It was analyzed using Student's t-test for independent samples. Pairwise comparisons were done with Fisher's least significant difference (LSD) procedure. All tests were performed using StatView (SAS Institute 1999) at the 0.05 level of significance. A significant difference in mean searching speed was observed between the host plants C. erectus and E. japonica (ANOVA: F = 2.49, P = 0.05). Significant differences were also found between C. erectus and P. purpureum (F = 8.86, P = 0.05). However, no significant difference was found between C. erectus and S. sericeus (F = 0.27, P = 0.60), indicating that the effect of leaf trichomes is similar in these two biotypes. The mean searching speed of H. sperata on C. erectus was significantly lower than on P. purpureum (ANOVA: F = 12.11, P = 0.005). The mean searching speed of H. sperata on C. erectus was also lower than on S. sericeus (F = 14.11, P = 0.005), indicating that the effect of leaf trichomes is higher on P. purpureum than on S. sericeus.

**Table 1. Trichome density and leaf thickness of six host plants of D. abbreviatus (N = 10, means ± SEM)**

<table>
<thead>
<tr>
<th>Plant</th>
<th>No. trichomes/cm²</th>
<th>Leaf thickness (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Citrus aurantifolia</em> (Christm.) (Rutaceae)</td>
<td>0</td>
<td>0.14 ± 0.0013</td>
</tr>
<tr>
<td><em>Conocarpus erectus</em> L. (Combretaceae)</td>
<td>22 ± 2.5</td>
<td>0.25 ± 0.021</td>
</tr>
<tr>
<td><em>Phoenix roebelii</em> O'Brien (Arecaceae)</td>
<td>29 ± 0.7</td>
<td>0.21 ± 0.011</td>
</tr>
<tr>
<td><em>Pennisetum purpureum</em> Schmuck (Poaceae)</td>
<td>92.4 ± 2.7</td>
<td>0.07 ± 0.006</td>
</tr>
<tr>
<td><em>Erigeron japonica</em> Lindl. (Rosaceae)</td>
<td>429.6 ± 17.5</td>
<td>0.22 ± 0.011</td>
</tr>
<tr>
<td><em>C. erectus</em> var. <em>sericeus</em> Fors ex. DC (Combretaceae)</td>
<td>39,030 ± 3,457</td>
<td>0.17 ± 0.013</td>
</tr>
</tbody>
</table>

Statistical Analysis. Analysis of covariance (ANCOVA; SAS Institute 1999) was used to detect the effects of host plants on the level of parasitism by H. sperata in the no-choice tests. Egg mass size (number of *Dia-prepess* eggs per egg mass) was used as a covariate to control variation associated with host abundance. Means were compared using Tukey's honest significance test (P < 0.05).
ANOVA (SAS Institute 1999) were used to detect the
effect of trichomes on the total search time, the time
spent motionless, the total distance traveled, the walk-
ing speed, and the searching speed of *H. sperata*
males on *C. erectus* leaves kept intact or leaves where
the trichomes were removed. Means were compared
using Tukey’s honest significance test (*P* < 0.05).

**Relationship of Searching Speed, Trichome Density,
and Leaf Thickness to Parasitism**

This experiment was designed to measure the
degree to which variation in searching speed,
trichome density, and leaf thickness explained the
variation in parasitism. The six host plants used in
the first experiment were included. All observations
were made between 1300 and 1700 hours. Leaves
from each plant were collected and divided in three
groups. The first group was used to test the propor-
tion of hosts parasitized on each plant, the second
group was used to determine the searching speed on
each leaf surface, and the third group was used to
measure the trichome density and leaf thickness of
each plant biotype.

The proportion of parasitized hosts was determined
in an experiment similar to the no-choice tests. Bou-
quets of each host plant bearing five egg masses were
introduced in 2-liter square jars (17 by 10 by 10 cm)
provisioned with a drop of honey as food source for
the parasitoids. Ten 1-d-old females of *H. sperata*
were introduced into each cage. After the parasitism period,
the bouquets were removed from the cages and
checked under a microscope to make sure that no
parasitoids were on the bouquets. Seven days later,
parasitized eggs were counted and percent parasitism
was determined by dividing the number of parasitized
eggs by the total number of eggs on each egg mass of
each host plant. Searching speed of *H. sperata* on the
different host plant leaves was measured in the same
way as in the previous experiment. This experiment
was replicated 10 times, each time with new paras-
toids and plants.

Trichome density and leaf thickness were mea-
ured on 10 newly expanded leaves of the same plant
material used in the previous experiments. Two
squares (1 cm² each) from the middle part of the
leaves were excised; one square was used to deter-
mine the leaf thickness, and the other one was used
for the trichome density for each leaf surface (ab-
axial and adaxial). Leaf thickness was determined by
placing the excised square standing on a piece of
clay and measuring its thickness under a microscope
(40×) equipped with a reticle. Trichome density
was established by counting the total number of
trichomes on each surface (abaxial and adaxial) and
making an average of the two values. Because of the
high density of trichomes on *C. erectus* variety seri-
ceus leaves, the 1-cm² squares were divided in four
equal 0.25-cm² sections and trichomes counted in
one of the four sections.

**Statistical Analysis.** Multiple regression (PROG
REG) analysis was used to establish the relationship
between three explanatory variables (searching
speed, trichome density, and leaf thickness) and the
response variable level of parasitism (SAS Institute
1999).

### Results

**Successful Parasitism by *H. sperata* on *D. abbreviatus* Eggs on Six Host Plants**

The no-choice test showed that *H. sperata* is able to
parasitize *D. abbreviatus* eggs laid on all six host plants
but failed to parasitize egg masses on wax paper (Fig.
1). The size of egg masses did not vary significantly
among the plants (*F* = 1.08; df = 6.47; *P* = 0.29).
However, eggs on leaves with higher densities of
trichomes had significantly lower parasitism com-
pared with those on glabrous leaves (*C. aurantifolia*)
or a low density of trichomes (*P. roebelinii* and *C.
erectus*; *F* = 17.22; df = 6.47; *P* < 0.01; Fig. 1; Table 1).
Furthermore, percent parasitism was >10 times
greater in the glabrous morph of *C. erectus* compared with the pubescent biotype.

**Effect of Leaf Trichomes on the Searching Behavior of *H. sperata***

The overall results of this experiment show that the presence of trichomes has a significant negative effect in the searching efficiency of *H. sperata*. There was no effect of the leaf surface orientation (abaxial and adaxial) on any of the variables measured ($F = 0.03; \text{df} = 1,141; P = 0.86$). The total distance traveled by *H. sperata* females was three-fold greater on any of the surfaces that had no trichomes than on the pubescent surface (Table 2). When the trichomes were removed from the pubescent morph by shaving them or treating the leaf with Triton X-100, the traveled distance increased to levels similar to the glabrous green morph (Table 2; $F = 23.07; \text{df} = 5,141; P < 0.001$). In contrast, *H. sperata* females spent more time on the pubescent surface and less on the smooth leaf surfaces. When the trichomes were shaved from the pubescent morph, the total time spent on the surface decreased (Table 2; $F = 4.55; P < 0.01$). The walking speed was significantly higher on all the surfaces with no trichomes compared with the pubescent surfaces. When the trichomes were removed by any method, the walking speed increased to levels similar to the smooth surfaces ($F = 22.9; P < 0.001$). A similar pattern was observed in the searching speed analysis; however, the searching speed on surfaces treated with Triton was significantly lower, which could suggest a confounding effect of this detergent that made the parasitoids stay longer on the surface ($F = 4.93; P < 0.01$).

**Relationship of Searching Speed, Trichome Density, and Leaf Thickness to Parasitism**

Multiple regression analyses showed an association between the response variable (percent of parasitism) and the full set of explanatory variables (Mean Square Error = 708.41; $P < 0.001$). However, when testing for association between percent of parasitism and the individual explanatory variables, we found that searching speed was useful in predicting parasitism, but neither trichome density nor leaf thickness explained the variation on parasitism (Table 3). It is likely that the type of trichomes and the exudates associated with them are more important than the number per unit of area.

**Discussion**

*Haeckeliania sperata* was able to parasitize eggs laid on the leaves of all the host plants. However, the levels of parasitism were affected by variations in the leaf surface structures of the host plants. We tested six host plants with various degrees of pubescence and found that the reproductive success of *H. sperata* is much higher in plants with smooth surfaces, like *C. erectus* or *C. aurantifolia*, than on those with pubescence (*C. erectus* variety *sericeus* and *E. japonica*). Considering that *H. sperata* was originally collected from citrus groves and nurseries where it acted as a primary parasitoid, we could expect better chances of control and establishment in citrus plants which are one of the major hosts of *D. abbreviatus* in central and south Florida. *Conocarpus erectus* is used for rearing *H. sperata*; our results reaffirm that this plant is the best known option for rearing this parasitoid. Besides being available throughout the year in south Florida, a high parasitism rate was found on this plant in all the experiments. In contrast, parasitism was lowest on the pubescent morph of *C. erectus*. These results are similar to those obtained by Amalin et al. (2005) working with another trichogrammatid parasitoid of *D. abbreviatus*, *Ceratogramma etiennei* Delavare. In a no-choice experiment with four of the same host plants that we used, *C. etiennei* showed a high parasitism of *D. abbreviatus* eggs on *C. aurantifolia*, *P. roebelini*, and *C.*

### Table 2. Effect of leaf trichomes on the searching behavior of *H. sperata* (means ± SEM)

<table>
<thead>
<tr>
<th>Leaf surface</th>
<th>Total distance traveled (mm)</th>
<th>Total time on surface (s)</th>
<th>Walking speed (mm/s)</th>
<th>Searching speed (mm/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wax paper</td>
<td>70.0 ± 7.8 a</td>
<td>59.2 ± 5.5 c</td>
<td>7.8 ± 3.9 a</td>
<td>1.9 ± 0.3 a</td>
</tr>
<tr>
<td><em>C. erectus</em></td>
<td>59.0 ± 4.3 b</td>
<td>72.3 ± 4.7 b</td>
<td>5.7 ± 0.6 b</td>
<td>1.0 ± 0.2 b</td>
</tr>
<tr>
<td><em>C. erectus</em> var. <em>sericeus</em></td>
<td>17.9 ± 1.2 c</td>
<td>94.2 ± 6.3 a</td>
<td>1.9 ± 0.2 c</td>
<td>0.2 ± 0.04 c</td>
</tr>
<tr>
<td><em>C. erectus</em> var. <em>sericeus</em> shaved</td>
<td>54.9 ± 3.8 b</td>
<td>61.2 ± 6.1 c</td>
<td>5.1 ± 0.5 b</td>
<td>1.5 ± 0.4 ab</td>
</tr>
<tr>
<td><em>C. erectus</em> + Triton X-100</td>
<td>76.0 ± 5.1 ab</td>
<td>70.9 ± 5.1 ab</td>
<td>5.5 ± 0.5 b</td>
<td>0.9 ± 0.2 bc</td>
</tr>
<tr>
<td><em>C. erectus</em> var. <em>sericeus</em> + Triton X-100</td>
<td>50.8 ± 3.2 b</td>
<td>82.7 ± 6.2 ab</td>
<td>5.2 ± 0.5 b</td>
<td>0.8 ± 0.1 bc</td>
</tr>
</tbody>
</table>

Means within a column followed by the same letter are not significantly different ($P < 0.05$; ANOVA, Tukey’s studentized range test).

### Table 3. Relationship of searching speed, trichome density, and leaf thickness to parasitism

<table>
<thead>
<tr>
<th></th>
<th>Model</th>
<th>Slope</th>
<th>SE</th>
<th>$P^a$</th>
<th>$R^2b$</th>
<th>$P^c$ (overall)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parasitism</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Searching speed</td>
<td>2.8</td>
<td>0.16</td>
<td>&lt;0.01</td>
<td>0.59</td>
<td>&lt;0.01</td>
<td></td>
</tr>
<tr>
<td>Trichome density</td>
<td>$1.2 \times 10^{-6}$</td>
<td>$2.1 \times 10^{-5}$</td>
<td>0.53</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf thickness</td>
<td>12.02</td>
<td>7.16</td>
<td>0.016</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Multiple regression analysis of the effect of searching speed, trichome density, and leaf thickness on mean percent of parasitism of *H. sperata* on *D. abbreviatus* eggs laid on six host plants.

$^a P$ values associated with each parameter and significance of the variable in the predicted response.

$^b R^2$, proportion of the variance explained by the model.

$^c P$(overall) is for the test of significance of the model using GLM.
erectus and a low parasitism on the pubescent C. erectus variety sericeus.

Schoener (1987) suggested that the presence of trichomes on C. erectus represents a putative defense against defoliation by herbivores. He also suggested that trichomes are costly, occurring differentially where the threat of defoliation is greater. Interestingly, Mannion et al. (2003) found that D. abbreviatus, when given a choice, prefers to oviposit on C. erectus variety sericeus, where it has better larval survivorship. This suggests that the presence of trichomes in C. erectus variety sericeus has no adverse effects on the fitness of D. abbreviatus. Moreover, results presented here and those reported by Amalin et al. (2005) suggest that the presence of trichomes in C. erectus could be beneficial for D. abbreviatus in terms of avoiding parasitism by H. sperata and C. etiennei, respectively.

The presence of trichomes on C. erectus variety sericeus has a negative effect on the searching efficiency and therefore on the fitness of H. sperata. Trichomes can alter the walking patterns of many parasitoids by changing the distribution of turning angles, reducing their searching speed, and ultimately affecting their host finding ability (Price et al. 1980, Sütterlin and Van Lenteren 1997, Mulatu et al. 2006, Olson and Andow 2006). In theory, faster-walking females have a higher chance of finding hosts because they can search a larger surface area per unit of time (Olson and Andow 2005). In fact, searching speed has been adopted by the IOBC working group on “quality control of mass reared organisms” as an important criterion for preintroductory selection of suitable strains of Trichogramma spp. parasitoids (Limburg and Pak 1991). Searching speed has been used to select strains and/or releasing sites of several trichogrammatid species (i.e., Trichogramma brassicae Bezdenerko, Trichogramma nubilale Ertle and Davis, Trichogramma exiguum Pinto and Platner, and Trichogramma chilonis Ishii) (Keller 1987). However, Van Hezewijk et al. (2000) reported that the level of parasitism in Trichogramma minutum Riley was positively affected by host acceptance but was not related to the parasite’s searching speed. Thus, searching speed cannot always be used to predict parasitoid quality or to select plants or release sites. However, our results suggest that searching speed is a parameter tightly linked to parasitism and that it is feasible to use this parameter to predict the suitability of host plants for releasing H. sperata.

Diaprepes has many host plants in Florida that represent an array of leaf structures and types of trichomes that could hinder the reproductive success of H. sperata. The degree of control of Diaprepes populations by H. sperata may depend on, among other factors, the interaction of the parasitoids with the microenvironment created by the plants on the leaves surfaces. Other factors such as the total leaf area, host plant foliage structural complexity (Gingras and Boivin 2002, Gingras et al. 2003), and surface-associated chemicals could also have an effect on Haecckeli-

Our study underlines the importance of habitat selection on the success of inoculative and augmentative biological control programs. To increase the chances of establishment of H. sperata, releases should be done where suitable host plant species exist. As seen in other trichogrammatids (Flanders 1937), it is possible that H. sperata will become more prevalent in certain habitats or on specific plants. Also, parasitism levels of D. abbreviatus can vary widely, depending on the plants on which the eggs are found. In addition, parasitism by H. sperata may vary with the plant structure on which the host eggs are located. For instance, most of the Florida fields that are known to be infested with Diaprepes are either citrus monocultures or open nurseries. Citrus monocultures seem to be suitable scenarios for releasing H. sperata. However, citrus groves also have weeds that could serve as reservoirs of Diaprepes eggs were a low parasitism by H. sperata could be expected, such as P. purpureum. The situation in open nurseries could be more complex. South Florida’s open nurseries are often composed of a mosaic of plants that are randomly placed in the fields. Under these conditions, we could expect a highly variable parasitism by H. sperata depending on the plant composition of the nursery. Our results suggest that differences in the establishment and levels of control by H. sperata in different habitats with varying plant composition can be expected.

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