FIELD OBSERVATIONS QUANTIFYING ATTRACTION OF THE PARASITIC WASP, *DIACHASMA ALLOEUM* (HYMENOPTERA: BRACONIDAE) TO BLUEBERRY FRUIT INFESTED BY THE BLUEBERRY MAGGOT FLY, *RHAGOLETIS MENDAX* (DIPTERA: TEPHRITIDAE)

L. L. Stelinski[1], K. S. Pelz[1] and O. E. Liburd[2]

[1]Department of Entomology, Michigan State University, East Lansing, MI 48824

[2]Entomology & Nematology Department, University of Florida, Gainesville, FL 32611

Abstract

The host foraging behavior of the larval parasitoid *Diachasma alloeum* (Muesebeck) (Hymenoptera: Braconidae) from natural populations was directly observed in a highbush blueberry, *Vaccinium corymbosum* L., plantation. More *D. alloeum* were observed alighting on blueberry fruit clusters infested with *Rhagoletis mendax* Curran larvae than were observed alighting on uninfested blueberry fruit clusters 80 cm away. Approximately equal numbers of *D. alloeum* alighted on uninfested blueberries that were mechanically damaged versus undamaged. The majority of *D. alloeum* females were attracted to host-infested blueberries 15 to 21 days after *R. mendax* females had oviposited into fruit. Female *D. alloeum* spent more time alighting on *R. mendax*-infested blueberry fruit clusters than on uninfested blueberry clusters 80 cm away. There was no difference in the duration of time spent by *D. alloeum* on mechanically damaged versus undamaged uninfested blueberries. The data herein are an initial step toward elucidating the cues mediating microhabitat selection by *D. alloeum* in blueberries.

Key Words: Conservation biological control, alighting behavior, *Diachasma alloeum*, *Rhagoletis mendax*

Resumen

El comportamiento del parasitoide larval *Diachasma alloeum* (Muesebeck) (Hymenoptera: Braconidae) por la busqueda del hospedero para alimentarse en poblaciones naturales fue observado directamente en plantaciones de mora azul, *Vaccinium corymbosum* L. Se observaron un mayor número de *D. alloeum* posando sobre los racimos de la fruta de la mora azul infestados con larvas de *Rhagoletis mendax* Curran de los que fueron observados posando sobre los racimos de fruta de mora azul no infestados separados por 80 cm de distancia. Aproximadamente números iguales de *D. alloeum* posaron sobre las moras azules no infestadas que fueron dañadas por la maquinaria agrícola versus las no dañadas. La mayoría de las hembras de *D. alloeum* fueron atraidas a las moras azules infestadas con el hospedero 15 a 21 días después que las hembras de *R. mendax* ovipositaron en la fruta. Las hembras de *D. alloeum* pasaron más tiempo posando sobre racimos de fruta de la mora azul infestados con *R. mendax* que en los racimos de la mora azul no infestadas separados por 80 cm de distancia. No habia una diferencia en la duración del tiempo que paso el *D. alloeum* sobre las moras azules dañadas por la maquinaria agricola versus las moras azules no dañadas o no infestadas. Los datos presentados aqui son un paso inicial hacia el aclaramento de las señales mediadoras para la selección del microhabitat hecho por el *D. alloeum* en la mora azul.

Hosts of insect parasitoids are often characterized by complex and patchy distributions making successful host location a major challenge for insect natural enemies (Hoffmeister & Gienapp 1999). Exploitation of chemical or visual cues associated with plants utilized by herbivorous hosts is known to increase host-searching efficiency of insect parasitoids (Vet & Dicke 1992; Godfray 1994; Vet et al. 1995). In addition, parasitoids are often attracted to damaged plants with cases of heightened attraction to plant damage created specifically by the herbivore host (Turlings et al. 1991; McAuslane et al. 1991, Henneman et al.

2002). The chemical cues released by herbivore-damaged plants and exploited by parasitoids include systemically released plant-volatile compounds (Dicke et al. 1993; Röse et al. 1996).

Several braconid species from the subfamily Opiinae are known to parasitize larval stages of Tephritidae (Wharton & March 1978). *Diachasma alloeum* (Muesebeck) occurs on hawthorn, *Crataegus mollis*, and apple, *Malus domestica* Borkhausen, in the northeastern U.S.A. and bordering regions of Canada and was thought to specifically attack the apple maggot fly, *Rhagoletis pomonella* (Walsh) (Glas & Vet 1983). Recently, *D.*

alloeum has also been reported attacking another member of the *Rhagoletis* sibling species complex, the blueberry maggot fly, *Rhagoletis mendax* Curran (Liburd & Finn 2003). Parasitization percentages of *R. mendax* larvae by *D. alloeum* collected from abandoned blueberry plantings in Michigan were extremely high, ranging from 30-50%. These rates of parasitization are higher than those known for *R. pomonella*, which range from 0.1 to 20.1% (Rivard 1967; Cameron & Morrison 1977; Maier 1982).

Only three detailed studies have been published on the behavior of *D. alloeum* attacking *R. pomonella* in hawthorns or apples. Boush & Baerwald (1967) reported on the courtship behavior and suggested the presence of a female-produced sex pheromone. Prokopy & Webster (1978) and later Glas & Vet (1983) analyzed the oviposition behavior of *D. alloeum* with specific interest in elucidating the stimuli involved in host-searching behavior. Visual orientation was found to play an important role for location of picked hawthorn fruit in laboratory assays and no difference in attractiveness was found between uninfested and *R. pomonella*-infested hawthorn fruit (Glas & Vet 1983). However, ovipositor probing activity and duration of stay were strongly influenced by the presence and movement of *R. pomonella* larvae feeding inside hawthorn fruit. The authors concluded that host movement within hawthorns was the prime stimulus for the location of host-infested fruit by *D. alloeum* (Glas & Vet 1983).

Recent studies with *Diachasmimorpha juglandis* (Muesebeck) have shown that females can distinguish between host-infested and uninfested walnut fruits before alighting (Henneman 1996, 1998). As they approach fruit, females hover close to the fruit surface for up to 1 sec before they alight or fly away, possibly assessing volatiles in order to decide whether to land (Henneman et al. 2002). Presence of fruit damage, however, rather than presence of larval infestation by *R. juglandis* larvae appears to produce the necessary cues for fruit choice by *D. juglandis* females (Henneman et al. 2002). Furthermore, both olfactory and visual cues are used by *D. juglandis* females to distinguish between infested and uninfested walnuts (Henneman et al. 2002).

To our knowledge, nothing has been published about the biology of *D. alloeum* in blueberry plantings. The current communication describes observations of the behavioral interactions of *D. alloeum* females with uninfested, mechanically damaged, and *R. mendax*-infested blueberries in an abandoned blueberry plantation. The specific objectives were to 1) determine whether blueberries infested with *R. mendax* larvae are more attractive to *D. alloeum* females than uninfested fruit, 2) determine whether mechanically damaged and uninfested blueberries are more attractive to *D. alloeum* females than undamaged

and uninfested fruit, 3) document duration of visits and associated behaviors of *D. alloeum* on *R. mendax*-infested and uninfested blueberries in the field.

MATERIALS AND METHODS

Research Site

Observational studies were conducted in the summer of 2001 in an abandoned plantation of highbush blueberry, *Vaccinium corymbosum* L. in Fennville, MI. The abandoned plantation was highly infested by *R. mendax* with approximately 45% of picked berries containing developing larvae in 1999 and 2000. In addition, this plantation was known to harbor a substantial population of *D. alloeum*. Parasitization rates of *R. mendax* collected from this plantation were above 50% in 1999 and 2000.

Insect Source

Rhagoletis mendax were reared from larvae collected from fruit of unsprayed blueberries (var. Jersey) from the plantation described above and from an organically managed plantation 3.2 km away. Flies were reared according to the protocol outlined in Liburd et al. (2003). Prior to testing, flies were maintained in aluminum screen-Plexiglas cages (30 × 30 × 30 cm) (BioQuip, Gardenia, CA) and supplied with water and food (enzymatic yeast hydrolysate and sucrose) (ICN Biomedicals, Inc., Costa Mesa, CA). Adults were kept at 24°C, 55-60% RH, under a 16:8 (L:D) photocycle.

Three weeks after removal of *R. mendax* puparia from 4°C (diapause), *D. alloeum* began emerging from more than 50 and 2% of puparia collected from the abandoned and organically managed sites, respectively. The parasitoids were identified by R. A. Wharton (Texas A&M University) and voucher specimens were deposited at Michigan State University (A. J. Cook Arthropod Research Collection).

Observational Study

Forty pairs of blueberry fruit clusters were selected for observation on 12 June before *R. mendax* emergence. Each pair of clusters was approximately 80 cm apart and each individual cluster contained 20-35 blueberries. All clusters were approximately 15-cm from the uppermost bush; this location within the blueberry bush canopy has been found to be the most effective position for trapping blueberry maggot (Liburd et al. 2000). At this stage of the season, blueberry fruit was still green and unripe. Experimental bushes were flagged and selected clusters were individually enveloped with 1 L translucent plastic bags that had been punctured with a pin multiple

times. Bags were positioned around blueberry fruit clusters such that berries did not directly contact the bag surface. The purpose of this bagging was to prevent native *R. mendax* from ovipositing into the selected berry clusters. On 19 June, we captured the first *R. mendax* on monitoring traps in the abandoned plantation. Twenty of the 40 bagged berry clusters were monitored from 25 June until 15 July to determine whether this bagging method interfered with normal berry development and to determine whether this technique successfully prevented *R. mendax* from ovipositing into berries. On each day, a single bagged cluster was randomly chosen for inspection. All fruit within that cluster were dissected and inspected for *R. mendax* larvae. In addition, on each day, two randomly selected clusters (15-20 berries) that had not been previously enveloped with a plastic bag were dissected for *R. mendax* larvae. No *R. mendax* larvae were found in berries that were enveloped by our plastic bags. In addition, berry size and color did not differ between bagged and unbagged berries. Among the unbagged clusters that were dissected, *R. mendax* infestation was first detected on 14 July.

The remaining 20 pairs of bagged clusters were used for the observational study. On 16 July, 10 of the 20 pairs of bagged blueberry clusters were randomly chosen for *R. mendax* infestation. Ten laboratory-reared and mated *R. mendax* females (10-15 days old) were introduced into one of the bagged blueberry clusters from each pair at 1200 hours. Introduced *R. mendax* were left in the bags for 24 h and then removed. Four of the 10 bags containing introduced *R. mendax* were observed for 1 h to confirm that flies were ovipositing into berries.

The other 10 pairs of bagged blueberry clusters were chosen for mechanical damage. The blueberries on one cluster of each bagged pair were mechanically damaged by making three equally spaced punctures in the skin of the berries with a 0-size insect pin. These manipulations resulted in 10 replicates of two paired treatments: 1) uninfested and undamaged berries versus *R. mendax*-infested berries, and 2) uninfested and undamaged berries versus uninfested and mechanically damaged berries. All other blueberries within a 1.5 m radius of each experimental pair were removed from bushes. The paired treatment clusters were 80 cm apart in a two-by-two design with the two treatments placed in alternate positions; each pair of treatment clusters was separated by at least 4 m.

Direct visual observations began 24 h after initial treatment manipulations were made and continued thereafter on every second day. Observations were conducted between 1230 and 1530 h. Two or more observers rotated among the ten replicates of each treatment pair conducting approximately 20-min observational bouts per location. Observations were terminated 31 days after the treatment manipulations were conducted.

During each period of observation, the plastic bags enveloping blueberry fruit clusters were removed and replaced immediately after observations were terminated. Also, native *R. mendax* were prevented from alighting on experimental clusters during observations. Observed events were spoken into a hand-held microcassette audio recorder by an investigator sitting or standing 0.75 m from the paired treatment clusters. Data recorded were: 1) landing by *D. alloeum* on berry clusters, 2) duration of visits on berry clusters, 3) oviposition into berries by *D. alloeum*. We attempted to collect observed *D. alloeum* with an aspirator after they oviposited and before they left experimental berry clusters. We estimate to have captured 70% of all visitors. The captured *D. alloeum* were taken to the laboratory and their identity was confirmed.

Statistical Analysis

Results of all dual-choice tests were analyzed by paired *t* tests (SAS Institute 2000). In all cases, significance level was $P < 0.05$. All ± values are SEM.

Results

Significantly more *D. alloeum* alighted per day on blueberry clusters that were infested with *R. mendax* larvae than on blueberry clusters that were uninfested (2.6 ± 0.5 and 0.3 ± 0.09, respectively). There was no significant difference between the number of *D. alloeum* alighting per day on blueberry clusters containing mechanically damaged and uninfested fruit compared with the number alighting on clusters containing undamaged and uninfested fruit (0.5 ± 0.8 and 0.5 ± 0.9, respectively). Blueberries that were infested with *R. mendax* larvae attracted the majority (64%) of *D. alloeum* females between 15 and 21 days after *R. mendax* females had oviposited into fruit (Fig. 1). There was no noticeable difference in attractiveness of mechanically damaged and undamaged fruit over time.

Female *D. alloeum* spent significantly more time alighting on *R. mendax*-infested blueberry clusters than on uninfested blueberry clusters (10.0 ± 1.1 min and 2.3 ± 1.2 min, respectively). There was no significant difference in the duration of time spent by *D. alloeum* on mechanically damaged and uninfested blueberries compared with undamaged and uninfested blueberries (1.1 ± 0.1 min and 0.9 ± 0.2 min, respectively). Of the 41 *D. alloeum* observed alighting on *R. mendax*-infested blueberry clusters, 34 were observed making a single ovipositional probe into blueberries. All of the *D. alloeum* that were observed ovipositing into berries performed "excreting"
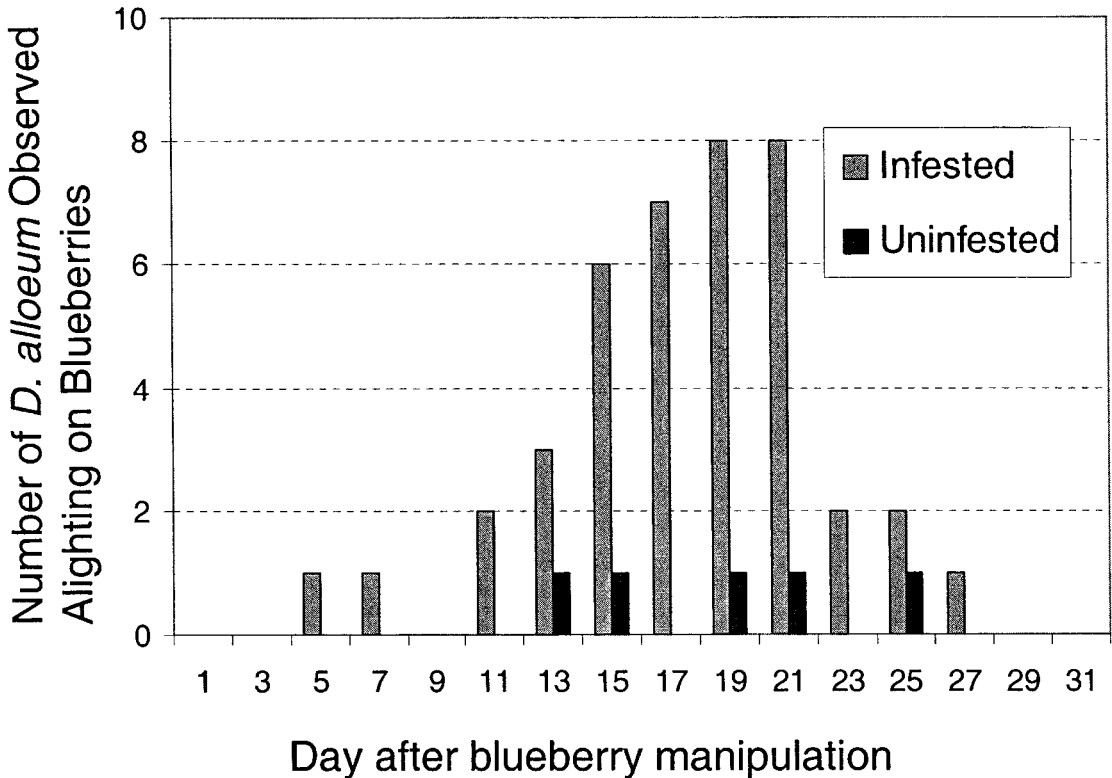
R. mendax-infested versus uninfested berries

Fig. 1. Numbers of *D. alloeum* observed alighting on *R. mendax*-infested and uninfested blueberries spaced 80 cm apart every other day after *R. mendax* oviposition.

behavior directly thereafter as previously described by Glas & Vet (1983). Specifically, after ovipositing, these females walked on the blueberry dragging and dabbing their ovipositors on the fruit surface and excreting a clear fluid. None of the *D. alloeum* observed alighting on uninfested fruit attempted to oviposit.

DISCUSSION

More host-infested blueberry fruit were visited by female *D. alloeum* than uninfested fruit suggesting that females have the capability of distinguishing *R. mendax*-infested berries prior to alighting. *D. juglandis* have also been shown to distinguish host-infested from uninfested fruits prior to alighting (Henneman 1996, 1998), relying on both visual and olfactory cues to make their decision (Henneman et al. 2002). *D. juglandis* distinguish host-infested fruit in the early stages of infestation (3-4 d after fly oviposition) as eggs are beginning to hatch (Henneman et al. 2002). In contrast to our results, previous laboratory studies comparing the attractiveness of *R. pomonella*-infested hawthorn fruit with uninfested fruit, showed that *D. alloeum* did not exhibit a preference and landed equally on both types of fruit (Glas & Vet 1983). However, the hawthorn fruit used in that study were field collected and infested by *R. pomonella* under laboratory conditions following a period of cold storage (Glas & Vet 1983). Thus, it is possible that the volatile profiles released by such picked and stored fruits may have differed from those of unpicked and *R. pomonella*-infested hawthorn fruit. It will be informative to determine whether *D. alloeum* distinguishes between *R. pomonella*-infested and uninfested hawthorn fruit under field conditions using unpicked fruit as was done in this study.

The behavior of *D. alloeum* documented in the current study varied in some respects from that previously reported in hawthorns. The majority of *D. alloeum* visits and ovipositions into *R. mendax*-infested blueberries occurred 15-21 days after female *R. mendax* had oviposited into the fruit. At this stage, the majority of *R. mendax* were likely in the second instar (Lathrop & Nickels 1932; Neunzig & Sorensen 1976). After the twenty-first day,

there was a dramatic reduction in the number of *D. alloeum* approaching and alighting on *R. mendax*-infested blueberries (Fig. 1). At this point, the majority of *R. mendax* larvae should have reached the third instar and were likely beginning to exit drying fruit to pupariate in the soil (Lathrop & Nickels 1932). In hawthorns, *D. alloeum* is known to attack the third (final) instar of *R. pomonella* (Glas & Vet 1983). In addition, *D. alloeum* spent less total time on blueberries during oviposition compared with hawthorns. On average, *D. alloeum* spent approximately 10 min on blueberries after alighting, while they spent anywhere from 18 to 140 min on hawthorn fruit during probing and oviposition bouts (Glas & Vet 1983). Furthermore, *D. alloeum* were observed making only one ovipositional probe per blueberry, while 1 to 5 ovipositional probes have been observed per individual *R. pomonella*-infested hawthorn fruit (Glas & Vet 1983). These differences in behavior of *D. alloeum* in blueberries versus hawthorns are possibly due to the differences in size and skin rigidity between blueberries and hawthorns. Given the smaller size and comparatively less rigid fruit skin of blueberries, it may be easier for *D. alloeum* to find and oviposit into a younger *R. mendax* larva in less time in blueberries than a comparably sized *R. pomonella* larva in hawthorns.

In the current study, more *D. alloeum* females landed on *R. mendax*-infested blueberries compared with uninfested berries, but not on mechanically damaged blueberries compared with the undamaged ones. This activity peaked 15-21 d after *R. mendax* had oviposited into blueberries. In contrast, *D. juglandis* females chose walnuts based on the presence of fruit damage rather than the presence of *R. juglandis* larvae inside the fruit (Henneman et al. 2002). However, in that study, mechanically damaged walnuts took on a distinctly different appearance (darkened) compared with undamaged walnuts, which was shown to influence fruit selection by *D. juglandis*. Color of host-infested walnuts is known to be an important visual cue mediating searching behavior of *D. juglandis* (Henneman 1998). In the current study, mechanically damaged blueberries did not appear different from undamaged berries. Furthermore, *R. mendax*-infested blueberries remained morphologically indistinguishable from uninfested berries for more than 20 days after *R. mendax* oviposition. It has been documented that certain female parasitic wasps exhibit an innate attraction to plant-released volatiles (Geervliet et al. 1996). Also, parasitic wasps are known to exhibit attraction to the host marking pheromone of tephritid fruit flies (Hoffmeister & Gienapp 1999). Based on the current results, we postulate that plant volatile compounds released by *R. mendax*-infested blueberries, but not mechanically-damaged fruit, provide an olfactory cue that attracts female *D. alloeum*. However, it is also possible that acoustic signals given off by chewing and tunneling *R. mendax* larvae within infested blueberries provide *D. alloeum* with an ovipositional stimulus.

Although labor intensive, our approach of conducting direct visual observations of *D. alloeum* responding to *R. mendax*-infested blueberries under authentic field conditions was indeed possible. Moreover, the data produced are an initial step toward elucidating the cues mediating microhabitat selection by *D. alloeum* in blueberries. The next step will be to determine whether *R. mendax*-infested blueberries release volatile profiles that differ quantitatively or qualitatively from those released by uninfested fruit. Finally, we hope to identify the relevant volatiles that may be involved in mediating attraction of *D. alloeum* to *R. mendax*-infested blueberries as has been done for other parasitoids (Turlings et al. 1991). Identification of plant volatiles attractive to *D. alloeum* may allow for recruitment of these beneficial insects in blueberry plantations, thereby improving biologically based management tactics for *R. mendax*.

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