Host-marking by female pepper weevils, Anthonomus eugenii

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Abstract

Pepper weevils, Anthonomus eugenii Cano (Coleoptera: Curculionidae), feed and oviposit in flower buds and small fruits of plants in the genus Capsicum, as well as several species of Solanum (Solanaceae). Females chew a small hole into the fruit, deposit a single egg within the cavity, and seal the hole with a clear anal secretion that hardens into an 'oviposition plug'. Female oviposition behavior was studied in a series of small-arena bioassays to determine whether previous oviposition in Jalapeño pepper fruit deterred subsequent oviposition and to determine what specific cues from an infested fruit influence female behavior. In choice and no-choice tests, females preferred clean fruit to fruit that had received four eggs 24 h previously (i.e., infested fruit), whether the fruit was infested with conspecific eggs or their own eggs. Further bioassays demonstrated that the presence of female frass, or oviposition plugs alone, in the absence of eggs or any fruit damage, was sufficient to deter oviposition. In addition, females given the choice between an infested fruit with the oviposition plug removed or an unaltered infested fruit preferred the fruit with no plugs, even when eggs, frass, and feeding damage were still present. To determine whether females would avoid infested peppers under more natural conditions, we quantified oviposition on infested and uninfested sentinel pepper fruit within individually caged plants and on clean and infested plants caged together. Females consistently laid more eggs on clean fruit than on infested fruits and moved within and among pepper plants to search for more acceptable oviposition sites. We conclude that oviposition plugs, along with contaminated female, but not male, frass contain a deterrent that, in the absence of any other cue, is enough to alert a female that a patch is occupied.

Introduction

Insect oviposition behavior can be modified by cues and signals associated with the presence of conspecific immature stages. Cues associated with the presence of immatures can come directly from eggs, larvae, or the response of hosts to infestation (Rausher, 1979; Blaakmeer et al., 1994; Fatouros et al., 2005; Schröder et al., 2005). In addition to broodassociated cues, many insect herbivores and parasitoids have evolved specific pheromone signals to convey information about host quality (Nufio & Papaj, 2001). These signals, referred to as marking pheromones, may be used by females to reduce offspring competition (Prokopy, 1981).

Currently, more than 100 species in the orders Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Neuroptera are known to produce marking pheromones (Anderson, 2002). Many of these species oviposit on discrete hosts that must support complete larval development. Marking pheromones may be produced by female insects or by larvae that co-occur with them. Female marks may be applied externally or internally, as in the case with some parasitoids. Deposition may be simultaneous with or following oviposition. For example, in the genus Ostrinia, extracts of egg masses contain a marking pheromone (Li & Ishikawa, 2005) while female Rhagoletis flies deposit marking pheromones by dragging their ovipositor over the fruit following oviposition (Prokopy, 1972; Prokopy et al., 1976). Trissolcus basalis (Wollaston), an egg parasitoid of the southern green stink bug, Nezara viridula (L.), marks its hosts on the surface (Rosi et al., 2001) while the aphid parasitoid, Ephedrus cerasicola Stary, uses both an internal and external marker (Hofsvang, 1988).

A marking pheromone will only be selected for when it increases the relative fitness of marking individuals.

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Marking can improve the search efficiency of an individual by allowing the female to avoid previously infested patches in addition to decreasing competition with conspecifics. In some cases, females may choose to ignore the marking pheromone. Reasons for ignoring the pheromone may include a lack of unexploited patches (Messina & Renwick, 1985) or differences in female egg load (Höller & Hörmann, 1993). Marking pheromones may also differ between individuals within a species, allowing females to discriminate between self and conspecific marks (van Dijken et al., 1992; Ueno, 1994; Agboka et al., 2002; McKay & Broce, 2004).

The pepper weevil, Anthonomus eugenii Cano (Coleoptera: Curculionidae), is a Neotropical pest of cultivated pepper, Capsicum spp. and also reproduces on wild American black nightshade (Solanum americanum Mill.), silverleaf nightshade (Solanum elaeagnifolium Cav.), and eggplant (Solanum melongena L.) (all Solanaceae) (Tejada & Reyes, 1986; Wilson, 1986; Diaz et al., 2004). Females oviposit preferentially in young fruit but will also utilize mature fruit or flower buds for oviposition. They deposit eggs individually in feeding punctures and then cover the hole with a clear anal secretion often mixed with frass that hardens into a plug. Similar oviposition behavior has been observed in the boll weevil, Anthonomus grandis Boheman, and their oviposition plugs were found to deter other females from reusing staminate Hampea nutricia Fryxell flower buds (Stansly & Cate, 1984). Prior to this study, other authors noted the deterrent properties of previously infested cotton squares, female frass, and anal secretions (Everett & Earle, 1964; Mitchell & Cross, 1969; Hedin et al., 1974).

Pepper fruit and flower buds are discrete hosts, highly susceptible to overcrowding. An examination of boll weevil oviposition found that females offered 10, 15, and 20 cotton squares per day had a greater estimated percent of egg hatch and survival of offspring to adulthood than females offered 5 or 1 square per day, presumably due to larval competition for host resources (Greenberg et al., 2003). It is not clear if competition or cannibalism plays a role in pepper weevil offspring success. If it does, female pepper weevils would benefit from avoiding previously exploited hosts.

Nufio & Papaj (2001) outlined four categories of evidence required to document the presence of marking pheromones. The first category includes behavioral assays demonstrating a response to the marking pheromone. These studies quantify rejection patterns of marked hosts, distinguish between responses to the mark and other potential cues, and determine the chemical nature and composition of the pheromone. The second category is the observation and description of a distinct host-marking behavior. The third category of evidence involves identifying the mechanisms of marking pheromone production and detection, and the final category is documentation of the ecological consequences of the marking pheromone, assessed under natural conditions.

A putative host-marking behavior has already been described in the pepper weevil: the deposition of an anal secretion that hardens into a plug (Elmore et al., 1934). This article will address the behavioral response of pepper weevil to infested pepper fruit in order to confirm the presence of a marking pheromone. Through the use of naturally infested and artificially manipulated hosts, we will answer the following three questions: (i) Are female pepper weevils deterred by previous oviposition? (ii) What components of oviposition confer deterrence? and (iii) Are the deterrent effects observed in small scale arena experiments also seen when insects are forced to search larger patches within and among plants?

Materials and methods

Insects and plants

Pepper weevils were collected in south Florida near the city of Clewiston (26°45'12"N, 80°56'1"W) in the spring of 2004, and a laboratory colony was established at the University of Florida, Gainesville, FL, USA. Additional field collections were made in Immokalee, Bradenton, and Wimauma, FL, USA, in the fall of 2005 and 2006 to maintain colony health. Insects were maintained in the laboratory (L14:D10, approximately 27 °C, and 30% r.h.) on excised greenhouse-grown 'Jalapeño' peppers [Capsicum annuum L. (Solanaceae)] with water and honey supplements. Gravid females were removed from the colony cage 10 days after emergence and transferred singly into oviposition containers made from waxed cardboard cans with screened lids of 250 ml, 8.5 cm in diameter (The Fonda Group, Inc., Union, NJ, USA). Gravid females were provided with a single pepper, which was replaced every 2 days with a new one. Infested fruit were held in plastic emergence boxes (1.5-1 Tupperware® containers, Orlando, FL, USA) for 3 weeks or until all weevils emerged.

Weevils were assayed on immature 'Jalapeño' peppers (4–5 cm in length) collected from pepper plants grown in a glass greenhouse in Gainesville, FL, USA. Peppers were collected from plants the day prior to bioassay to ensure freshness. Infested fruit used in the bioassays were prepared by presenting a single pepper to a gravid female in an oviposition container. The female was permitted to oviposit overnight and the following morning the pepper was collected. Oviposition scars were counted on the collected fruit and only those fruit containing 3–4 eggs, as indicated by oviposition plugs, were used in the assays as this represents the average number of eggs deposited by one weevil per day. Gravid females, at least 10 days old, used in the following assays were isolated from the colony 24 h prior to the assay and allowed to feed and oviposit on a single clean pepper fruit during that period.

Small arena experiments

Female weevils were placed individually in $10 \times 10 \times 8$ cm plastic boxes with screen lids for all experiments (20 replicates for each experiment). In no-choice tests, a single pepper was offered to a female. In choice tests, one pepper of each treatment was offered to a female. Peppers were laid in the containers on their sides. Eggs were counted after a 12-h oviposition period during the light phase.

Influence of maternal source of eggs in infested peppers on oviposition preference. In the first choice and no-choice experiments, females were presented with clean peppers and/or peppers containing eggs laid during the previous night by a different female. In the second experiments, females were presented in choice and no-choice experiments with clean peppers and/or peppers containing eggs they had laid during the previous night. In a third experiment, females were offered a choice between two infested peppers, one containing their own eggs and the second containing the eggs of a different female. In this choice assay, both peppers contained the same number of eggs (either three or four).

Effects of potential cues associated with oviposition on oviposition preference. All bioassays performed for this series of experiments were conducted under choice situations only. Stimuli associated with oviposition were either added to clean fruit or removed from infested fruit to determine their importance in oviposition deterrence. In the first experiment, fruits were punctured with a sterilized metal probe to mimic the mechanical damage that would be associated with oviposition. Females were given a choice between a clean fruit and a fruit with four mechanical punctures around the calyx, the preferred oviposition site. The punctures were made in the fruit moments before being placed in the arena.

In a second experiment, females were presented with peppers contaminated with male or female frass, as might occur naturally during feeding and oviposition. Separate 1.5-l square plastic boxes ($18 \times 18 \times 6$ cm) with screen lids were set up containing either male or female weevils. Weevils were permitted to feed on pepper fruit for 7 days before frass was collected from the cages. Frass was collected by first lightly scraping the container with a sterilized metal probe to loosen the fecal spots. A small paintbrush (2/0, 1 cm bristle length) was dipped in deionized water and rolled in the frass. Frass was then smeared around the calyx of the pepper fruit. Approximately 0.30 mg of frass was applied to each fruit. Females were presented with choices of fruit contaminated with male frass vs. clean fruit, fruit contaminated with female frass vs. clean fruit, or fruit contaminated with male frass vs. contaminated with female frass.

In a third experiment, females were presented with clean peppers and clean peppers to which ovipositon plugs were attached with deionized water. Oviposition plugs were dissected from infested peppers using an insect pin and paintbrush (2/0, 1 cm bristle length). Plugs were taken from fruit that had been infested the previous night. Four plugs were applied around the calyx of the fruit using deionized water.

In the fourth and fifth experiments, components of the oviposited fruit were removed with cotton swabs moistened with deionized water and the effect of their removal on oviposition quantified. In the fourth experiment, females were presented with infested fruit and one of the following: (i) an infested pepper with plugs removed, (ii) an infested pepper with frass removed, or (iii) an infested pepper with both plugs and frass removed. In the fifth experiment, females were given a choice of a clean fruit and an infested fruit with both frass and plugs removed.

Whole plant cage experiments

The purpose of the two whole plant cage experiments was to determine how females distribute their eggs within and between plants with different levels of initial infestation. In the first experiment, single 'Jalapeño' plants at the flowering stage (2-3 months old) were contained in plastic cylinder cages (60 cm tall × 15 cm in diameter) with screen lids and three 10×10 cm screen windows to provide ventilation. Artificial branches were constructed from a 45-cm green bamboo stake capped by two 12-cm wooden craft sticks crossed at right angles to each other. Four 'Jalapeño' peppers were hung from the ends of the wooden stick 'branches' with green twist ties. Two treatments were tested; the clean treatment had four clean fruit and the mixed treatment had three clean fruit and one infested fruit containing 3-4 eggs. The infested fruit were placed systematically in each of the four positions (front, back, left, and right) to control for position effects. Two females were added to each enclosure through a corked hole just above the base of the cylinder and were held in a rearing room under L14:D10 regime at 27 °C. Eggs were counted in each fruit after 48 h. Twenty-two replications were performed.

In a second experiment, two 'Jalapeño' plants at the flowering stage were placed in a chiffon mesh cage $(30 \times 30 \times 30 \text{ cm})$ in a glass greenhouse (L11:D13, average temperature 24 °C, and 60% r.h.). Artificial branches as described above held four clean fruits on one plant and four infested fruits containing 3–4 eggs on the second plant in

Comparisons	Mean eggs laid per pepper \pm SE						
	Choice test			No-choice test			
	Clean	Infested	Р	Clean	Infested	Р	
Clean vs. other infested	1.35 ± 0.28	0.30 ± 0.11	0.0007	1.20 ± 0.26	0.32 ± 0.14	0.0031	
Clean vs. self-infested	1.82 ± 0.21	0.23 ± 0.09	< 0.0001	2.30 ± 0.37	1.05 ± 0.32	0.0008	
	Other	Self	Р				
Other infested vs. self-infested	1.05 ± 0.26	0.85 ± 0.15	0.4706	_	_		

 Table 1
 The average number of eggs laid by female pepper weevils in choice and no-choice tests in clean peppers or peppers oviposited in by themselves or other females

the cage. Two females were placed in each cage. Eggs in each fruit were counted 48 h later. Twenty replications were performed.

Analysis

Egg counts were analyzed using the normal approximation of a one-sided Wilcoxon rank sum analysis for choice tests with two treatments and the Kruskal–Wallis test for multiple treatments (SAS Institute, 2006). No-choice data were analyzed by Mann–Whitney U-test (Conover, 1980). Data are presented as means \pm SE.

Results

Small arena experiments

Influence of maternal source of eggs in infested peppers on oviposition preference. Females laid more eggs in clean fruit than in fruit previously infested by conspecifics in both no-choice (U = -3.06, P = 0.0031) and choice tests (Z = -3.21, P = 0.0007) (Table 1). They also laid more eggs in clean fruit than in their own previously infested fruit in both no-choice (U = -3.33, P = 0.0008) and choice tests (Z = -5.15, P<0.0001). Females did not discriminate between peppers containing their own or conspecific eggs, laying equivalent numbers of eggs in both treatments (Z = 0.07, P = 0.4706).

Table 2 The average number of eggs laid by female pepper

 weevils in choice tests with uninfested pepper fruit contaminated

 with male and female frass

	Mean eggs laid per pepper \pm SE			
Comparisons	Clean	Frass	Р	
Clean vs. male frass Clean vs. female frass	$\begin{array}{c} 1.20 \pm 0.31 \\ 1.95 \pm 0.29 \end{array}$	$\begin{array}{c} 1.00 \pm 0.27 \\ 0.55 \pm 0.15 \end{array}$	0.3061 0.0002	
Male frass vs. female frass	Male 1.45 ± 0.26	Female 0.60 ± 0.20	P 0.0065	

Effects of potential cues associated with oviposition on oviposition preference. Mechanical punctures did not deter oviposition (Z = -0.56, P = 0.2867). Females laid equivalent numbers of eggs when given a choice of clean peppers and peppers containing mechanical punctures (clean = $0.90 \pm$ 0.18; mechanical damage = 0.80 ± 0.21). In addition, two females laid eggs within the artificial punctures and covered the punctures with oviposition plugs.

Male frass added to clean fruit did not deter oviposition (Z = 0.51, P = 0.3061), but female frass was deterrent (Z = -3.61, P = 0.0002) (Table 2). Females chose to lay more eggs on peppers with male frass than female frass when given a choice between the two (Z = 2.49, P = 0.0065), indicating that deterrent compounds present in the weevil frass are female specific in origin. The source of frass did not influence the total number of eggs laid in the three-choice experiments ($\chi^2 = 1.14$, P = 0.5660).

Females laid fewer eggs on clean peppers to which oviposition plugs were added than on uninfested peppers $(Z = -2.04, P = 0.0209; clean = 1.25 \pm 0.20; plugs = 0.65 \pm$ 0.20). The tiny amount of plug material (four plugs) required to decrease oviposition marginally compared to the amount of frass used in these experiments (0.30 mg of frass = ~150 plugs) suggested that the active compound(s) in the plug were more concentrated than in the frass.

Females laid more eggs in infested peppers with frass removed (Z = -1.86, P = 0.0311), plugs removed (Z = -3.30, P = 0.0005), and frass and plugs removed (Z = -2.41, P = 0.0080) than in infested fruit contaminated with all female-deposited material (Table 3). In addition, females preferred clean peppers over peppers with plugs and frass removed (Z = 4.36, P<0.0001; clean = 1.6 ± 0.15 ; removed = 0.40 ± 0.13).

Whole plant cage experiments

There were no branch position effects observed in the clean $(\chi^2 = 3.12, \text{ d.f.} = 3, P = 0.7749)$ and mixed treatments $(\chi^2 = 0.96, \text{ d.f.} = 3, P = 0.8096)$ (Table 4). There was no difference in total eggs laid in the clean and mixed

Table 3 The average number of eggs laidby female pepper weevils in choice testsbetween infested peppers and peppers withfrass and/or oviposition plugs removed

	Mean eggs laid per pepper \pm SE			
Comparisons	Female-produced Infested material removed		Р	
Infested vs. frass removed	0.75 ± 0.19	1.35 ± 0.24	0.0311	
Infested vs. plugs removed	0.50 ± 0.17	1.30 ± 0.18	0.0005	
Infested vs. frass and plugs removed	0.63 ± 0.17	1.42 ± 0.24	0.0080	

treatments (Z = -1.35, P = 0.0875). Females laid more eggs per clean fruit in the mixed treatment than in the clean treatment (Z = -1.75, P = 0.0399). In the mixed treatment, females laid more eggs per fruit in the clean pepper than in the infested peppers (Z = 2.96, P = 0.0015), indicating a shift in the distribution of new egg deposition rather than a decrease in overall eggs laid. In the second cage experiment, where females were caged with two plants, one with infested peppers and one with clean peppers, females moved between plants, laying more eggs on plants with clean peppers than on plants with infested peppers (Z = 2.41, P = 0.0081).

Discussion

Our study clearly shows that oviposition plugs are involved in deterrence. The deterrent effect of plugs was extremely high given that they covered only 0.01–0.04% of the pepper surface area. Female frass was also deterrent, but much more frass was required to observe deterrent activity, suggesting the frass may be contaminated by the anal secretion and that frass alone is not the source of the marking pheromone. Male frass, on the other hand, showed no deterrent or stimulatory properties. Males are known to produce an aggregation pheromone, one that is excreted in the frass (Eller et al., 1994). The potential presence of this pheromone on peppers contaminated with male frass did not appear to influence female oviposition.

In addition to the female-specific deterrent, pepper fruit damage and eggs may also have some deterrent effects, although the deterrence in fruit with plugs and frass removed could have been due to incomplete removal of these materials. Females do not normally come into direct contact with eggs as they are laid in cavities below the fruit surface. However, the presence of eggs may itself alter the chemistry of the fruit providing additional cues to the presence of brood (see review by Hilker & Meiners, 2006).

The production of host-marking pheromones is known to occur in closely related species. Some well-studied genera include *Rhagoletis* (15 spp.), *Telenomus* (6 spp.), *Anastrepha* (5 spp.), *Callosobruchus* (4 spp.), *Chrysopa* (4 spp.), *Ephestia* (3 spp.), and *Anaphes* (3 spp.) (Agboka et al., 2002; Anderson, 2002; Aluja & Diaz-Fleischer, 2006). The only other species of *Anthonomus* known to possess an oviposition deterrent is another member of the *mexicanus* group, the cotton boll weevil, *A. grandis* (Stansly & Cate, 1984). Other well-known pest species within the genus include the strawberry blossom weevil (*Anthonomus rubi* Herbst) and the apple blossom weevil [*Anthonomus pomorum* (L.)] both found primarily in Eurasia, and the North American cranberry weevil (*Anthonomus musculus* Say). *Anthonomus rubi* and *A. pomorum* do not exhibit the

Table 4 The average number of eggs laid by female pepper weevils in peppers in whole plant experiments

	Mean eggs laid per pepper ± SE			
Comparisons	Clean treatment	Mixed treatment	Р	
Experiment 1 ¹ – Clean treatment vs. mixed treatment (overall eggs laid)	2.16 ± 0.31	2.77 ± 0.34	0.0879	
Experiment 1 – Clean treatment vs. mixed treatment (clean fruit only)	2.16 ± 0.31	3.21 ± 0.40	0.0399	
	Clean peppers	Infested peppers	Р	
Experiment 1 – Clean peppers vs. infested peppers (mixed treatment)	3.21 ± 0.40	1.45 ± 0.36	0.0015	
	Clean plant	Infested plant	Р	
Experiment 2 ² – Clean plant vs. infested plant	4.50 ± 0.89	1.45 ± 0.36	0.0081	

¹In Experiment 1, females were presented with a single plant with four clean peppers (clean treatment) or a single plant with one infested pepper and three clean peppers (mixed treatment).

²In Experiment 2, females were presented a choice between two plants, one with all four peppers infested and one with no peppers infested.

same plugging behavior as the boll weevil and pepper weevil (J Cross, pers. comm.). The cranberry weevil does cover its oviposition scars with a plug (A Averill, pers. comm.), but whether the plug contains an oviposition deterrent is unknown. In addition to pest species, *Anthonomus tenebrosus* Boheman, a potential biological control agent of the tropical soda apple (*Solanum viarum* Dunal), also exhibits plugging behavior (BJ Davis, pers. comm.). It is currently unclear how widespread 'plugging' behavior is within the genus, whether it occurs randomly throughout *Anthonomus*, or if it is a characteristic of particular species groups. More research is needed to determine if other 'plugging' species within *Anthonomus* also deposit marking pheromones with their plugs.

It is important to note that pepper weevils did lay eggs in the presence of oviposition plugs and female frass, though in smaller numbers. One major question of interest when studying marking pheromones is: When should females ignore the signal? Some possible reasons why females lay eggs in the presence of a deterrent include genetic variation in detecting the deterrent, differences in egg load, and habituation. Egg load may have affected female decision-making. Females laid anywhere from 1-7 eggs during the 12-h assay period (no females laid no eggs in any of the replicates). It is quite possible that females with higher egg loads were less discriminating in their choice of oviposition sites. In the aphid hyperparasitoid, Dendrocerus carpenteri (Curtis), females with low egg loads spent less time in previously explored patches as compared to females with large egg loads (Höller & Hörmann, 1993). In addition, females with low egg load continuously applied the marking pheromone while walking, presumably in an attempt to increase its deterrent effect.

It is also important to point out that the mechanical damage, frass, and plugs were applied solely around the calyx of the fruit, where the majority of oviposition takes place. If a female decided to oviposit elsewhere on the fruit, it may never have encountered the deterrent. It is also possible that rather than assessing the presence or absence of eggs, pepper weevils may be measuring the level of competition their offspring will encounter in a given host patch, altering the number of eggs deposited based on pepper infestation level. The seed bruchid, Callosobruchus maculatus laid more eggs in seeds with small egg loads and fewer eggs in seeds with high egg loads, maintaining a uniform egg distribution within the seeds, as well as indicating that females can detect small differences in egg density (Messina & Renwick, 1985). The walnut fly, Rhagoletis juglandis, known for reusing oviposition sites, determines the level of competition in a fruit by the amount of pheromone detected (Nufio & Papaj, 2004). Another reason why female weevils might ignore the marking pheromone is that they may become insensitive to the deterrent after repeated exposure as seen in *Rhagoletis cerasi* (Boller & Aluja, 1992). For all fruit assays, females were confined to one or two fruits for 12 h. Females who deposited eggs on infested fruit may have lost sensitivity to the deterrent after being exposed to the marking pheromone for such a long period of time.

In some species, particularly parasitoids, females have been shown to discriminate between their own marks and those of conspecifics (van Dijken et al., 1992; Ueno, 1994; McKay & Broce, 2004). Discrimination is expected if superparasitism of their own offspring decreases female fitness, while depositing additional eggs in conspecificparasitized hosts may increase fitness. The pepper weevil does not appear capable of discriminating between self and conspecific marks, suggesting that the fitness consequences of reusing a particular host are independent of the identity of developing larvae.

One major danger of using host marking pheromones is eavesdropping by predators and parasitoids. Previous studies have demonstrated that insect pheromones can be used by predators and parasitoids to locate potential hosts (Prokopy & Webster, 1978; Roitberg & Lalonde, 1991; Wiskerke et al., 1993; Aldrich, 1995; Hoffmeister & Gienapp, 1999; Hoffmeister et al., 2000; Kumazaki et al., 2000; Onodera et al., 2002). A recent study of the pepper weevil egg–larval parasitoid, *Triaspis eugenii* Wharton and Lopez-Martinez, showed parasitism success decreased by 2.5–3 times when weevil oviposition plugs were removed (Rodríguez-Leyva, 2006). Further studies are required to determine whether the same compounds involved in weevil oviposition deterrence are used by *T. eugenii* to identify hosts.

Information on pepper weevil oviposition deterrents adds to the small but growing body of evidence that intraspecific chemical communication is a vital part of female decision-making during the host selection process. Such knowledge may lead us to new and targeted ways of controlling or suppressing weevil pest populations by augmenting current chemical, behavioral, and cultural control methods. In order for practical use of the pepper weevil oviposition deterring pheromone to be possible, it must first be isolated and identified from female frass and oviposition plugs. We will then have a better understanding of the nature of the pheromone and whether it can be a useful tool in integrated pest-management programs.

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