Does Prior Feeding Behavior by Previous Generations of the Maize Weevil (Coleoptera: Curculionidae) Determine Future Descendants Feeding Preference and Ovipositional Suitability?

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Does prior feeding behavior by previous generations of the maize weevil (Coleoptera: Curculionidae) determine future descendants feeding preference and ovipositional suitability?

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Abstract

The maize weevil *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae) is an important pest of stored grains, predominantly corn (*Zea mays*), wheat (*Triticum* spp.), rice (*Oryza* spp.), and sorghum (*Sorghum bicolor*) (all Poaceae). In Africa, post-harvest grain losses of maize amounts to about US $4 billion annually, with an estimate of 10 to 88% loss of maize due to stored grain pests (FAO 2010; Ojo & Omoloye 2012). Current control methods are the application of an insecticide, cultural practices, and the development of resistant grain. Unfortunately, there is no effective trapping system for control of the maize weevil. Previous studies have indicated that the odors associated with the grains upon which the weevils feed, mate, and oviposit are known to be attractive. To better understand this behavior, a study was developed to investigate the weevil's attraction to dry grains with and without the presence of the commercial pheromone lure. The weevil's ability to develop on specific grains also was investigated. The weevils were reared on 4 types of grain to determine, if presented a choice, whether they would prefer the grain upon which their parents and they themselves fed as larvae. This research demonstrates that previous feeding did not influence the weevil's attraction to a certain grain. The isolation of key corn semiochemicals should be the focus in the development of an attractant for *S. zeamais*. These findings eliminate the need to develop individualized attractants that would have to be tailored to weevils feeding upon specific hosts.

Key Words: stored grain pests; pest management; insect behavior

Resumen

El gorgojo del maíz, *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae), es una plaga importante de los granos almacenados, predominantemente de maíz (*Zea mays*), trigo (*Triticum* spp.), arroz (*Oryza* spp.) y sorgo (*Sorghum bicolor*) (todos Poaceae). En África, las pérdidas de granos de maíz pos-cosechados representan alrededor de US $4 billones anuales de pérdida de granos, con un estimado de 10 a 88% de pérdida de maíz debido a plagas de granos almacenados (FAO 2010, Ojo y Omoloye 2012). Los métodos de control actuales son la aplicación de un insecticida, las prácticas culturales y el desarrollo de granos resistentes. Desafortunadamente, no existe un sistema efectivo de captura para controlar el gorgojo del maíz. Estudios previos han indicado que los olores asociados con los granos sobre los cuales los gorgojos se alimentan, se aparean y ovipositan son atractivos. Para comprender mejor este comportamiento, se desarrolló un estudio para investigar la atracción del gorgojo por los granos secos con y sin la presencia del cebo comercial con feromonas. También se investigó la capacidad del gorgojo para desarrollarse en granos específicos. Los gorgojos se criaron en 4 tipos de grano para determinar si presentaban una opción, ellos preferirían el grano sobre el cual sus parientes y ellos mismos se alimentaron previamente como larvas. Los resultados de estos experimentos facilitarán una comprensión de cual clase de grano inició la mayor atracción. Los semioquímicos de los olores de grano específicos del hospedero se aislarán para desarrollar un atrayente efectivo. El efecto sinérgico de una feromona en conjunción con un hospedero específico volátil (alimento u oviposición) puede aumentar considerablemente la atracción. La mayor preocupación al desarrollar un sistema de trampeo para los gorgojos del maíz es el impacto de la alimentación previa y la tendencia del gorgojo a un grano determinado. La información obtenida de este estudio conducirá al aislamiento de semioquímicos específicos del sustrato de alimentación más atractivo.

Palabras Clave: plagas de granos almacenados; manejo de plagas; comportamiento de los insectos

Sitophilus zeamais (Motschulsky) (Coleoptera: Curculionidae), known as the maize weevil, are serious pests of stored grains worldwide, with the association between weevils and human food dating back about 10,500 yr (Obata et al. 2011). Both adults and larvae can survive on a wide variety of food substances but are known as a pest species primarily from their infestations of corn (*Zea mays* L.; Poaceae), wheat (*Triticum* spp.; Poaceae), rice (*Oryza* spp.; Poaceae), and sorghum (*Sorghum bicolor* [L.] Moench; Poaceae). These pests not only affect stored grains, but also infest grains prior to harvest (Ni et al. 2011; Vyavhare & Pendleton 2011). As such, new infestations in storage facilities occur after each harvest. In grain storage facilities, control of these weevils usually is done by application of insecticides when loaded into silos, or as a surface treatment after storage (Arthur & Throne 2003). The female weevil chews a hole in the grain and lays an egg inside the kernel. The hole is then sealed with a waxy secretion that creates a plug. This hardens, sealing the hole in the seed

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to protect the egg. The egg hatches and the larva consumes the valuable commodity. At the end of the life cycle, an adult weevil emerges from the grain. Control of this pest must be directed at the adult due to the immature's development within the grain, protected from pesticide exposure (Walgenbach et al. 1983). However, consumer preference, pesticide deregulation, and resistance have reduced the use of such treatments, making alternatives to chemical pesticides necessary (Vyavhare et al. 2018).

The attraction of insects to plants and other host organisms involves detection of specific semiochemicals, more notably specific ratios of semiochemicals. The isolation of these odors can be used as attractants for the control and monitoring of pest populations (Norin 2007). Male- and female-produced insect pheromones have been successfully isolated and are used for mating, aggregation, defense, and host recognition (El-Sayed et al. 2006). Male-produced sex attractants are referred to as aggregation pheromones, because they typically attract both sexes and have been reported in many species of Coleoptera, Dictyoptera, Hemiptera, and Orthoptera (Landolt 1997). The aggregation pheromone for the rice weevil, *Sitophilus oryzae* Schoenherr (Coleoptera: Dryophthoridae) and maize weevil, (4S, 5R)-5-hydroxy-4-methylheptan-3-one, has been identified (Phillips et al. 1985) and is currently used as the attractant for traps in indoor applications, particularly in household pantries. However, there is little information on the use of the pheromone for monitoring and control in large grain storage facilities or in the field. Additionally, little is known about the host produced volatiles that attract the maize and rice weevils. Therefore, there is a need to develop more effective semiochemical based attractants for these pests. For instance, the identification of the sex and aggregation pheromones for the boll weevil, *Anthonomus grandis* (Boheman) (Coleoptera: Curculionidae), played a crucial role in successful implementation of the boll weevil eradication program (Tumlinson et al. 1969). It has been shown that the pheromone, in combination with the green leaf volatile trans-2-hexen-1-ol, enhanced pheromone trap captures. It also increased trap capture by extending the longevity of attractiveness of pheromone-baited traps. (Dickens 1989). This dynamic has been shown in many trapping systems for Coleoptera, such as the boll weevil. The synergistic effect of a sex or aggregation pheromone in conjunction with a host volatile (food or oviposition) greatly enhances attraction (Bartelt & Dowd 1991). Insect produced pheromones and host plant odors assist conspecifics for mating and locating feeding and oviposition sites. Aggregation pheromones for trapping are useful because both sexes may be captured in the trapping device (Burkholder 1990; Sato & Touhara 2008). The male boll weevils locate their host plant, feed, and then release an aggregation pheromone in their frass (Tumilson et al. 1969).

In insects, the location of a mate or a food source is dependent upon olfactory information. Their highly specialized structures can detect compounds with a high sensitivity, and initiate a behavioral response to the olfactory message received (Martin et al. 2011). These specialized structures allow phytophagous insects to selectively feed only on a limited number of plant species or generalist feeding on a diverse range of plants in many families (Bruce et al. 2005). It is not known whether weevils that feed on a certain host grain will be attracted to a host plant odor that it has never encountered. It is also unknown if this naïvety is passed to future generations. The maize weevil is primarily a maize specialist, but is found infesting several other stored grains. This research explores the behavioral responses of the weevil to specific host grains on which they were not reared. This investigation allows for the potential isolation of specific semiochemicals from a single host grain. If prior feeding changes preference, multiple attractants would be needed to attract weevils feeding on a wide range of hosts. Additionally, the response to a host grain when paired with a pheromone lure was investigated. This information is invaluable in the development of a semiochemical-based monitoring and management system that employs the isolated odors that will synergistically enhance the aggregation pheromone. The development of a novel, inexpensive method for monitoring and control would help reduce losses due to this pest (Walgenbach et al. 1983).

Materials and Methods

SOURCE OF WEEVILS

Maize weevils were obtained from colonies reared at the USDA-ARS, Center for Medical, Agricultural, and Veterinary Entomology (USDA-ARS, CMAVE), Gainesville, Florida, USA. Weevils were collected from dried intact ears of corn purchased from a commercial animal feed retailer in Gainesville, Florida. Specimen insects were sent to the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, for positive taxonomy using a morphological key for identification. Weevils were reared on 4 different cereal grains for 10 generations. To test for any conditioning on host selection behavior, weevils were reared on corn (Yellow Corn, Flint River Mills, Bainbridge, Georgia, USA), barley (Rolled Barley, La Crosse Milling Co., Cochrane, Wisconsin, USA), brown rice (Nishiki Premium Brown Rice, JFC International, Inc., Los Angeles, California, USA), and white rice (Nishiki Premium Grade Rice, JFC International, Inc., Los Angeles, California). Weevils were reared in 950 mL glass canning jars (Jarden Home Brands, Daleville, Indiana, USA) containing 1 of the 4 grains. Jars were sealed with copper mesh to allow for ventilation, held in place with a metal screw band. This method allowed for the rearing of several thousand weevils per jar. Weevils were sexed using dimorphic rostrum characteristics as stated in Halstead (1962). Insects were reared in a temperature-controlled chamber at 23 ± 5 °C, 60% RH, and photoperiod of 12:12 h (L:D).

CHOICE ASSAY

To determine the response of the maize weevil to various grains, 200 unsexed weevils were aspirated from the rearing substrate and released in an escape-proof clear container with lid measuring 60 × 45 × 28 cm (Ziplock Weathertight Box, Iris USA, Pleasant Prairie, Wisconsin). Four treatments containing corn, barley, brown rice, and white rice (150 mg) were offered in separate square glass jars (8.5 cm high and measuring 8.5 cm at the opening, tapering to 8 cm at the base; #5475 Libby Glass Inc., Toledo, Ohio, USA) that held the 4 treatments within the assay container. The jars contained 150 mg of either corn, barley, brown rice, or white rice, respectively. The assay was run for 24 h, after which the inside of the container was checked for insects that did not respond. The weevil's presence within the grain was then counted for each treatment. Insects collected from the treatments were placed in a vial and labeled to be sexed. One repetition consisted of a clockwise rotation of each treatment to all 4 sides within the container to account for positional bias. Assay containers were rotated to 4 different locations within the environmental chamber to account for positional bias within the chamber. Ten repetitions from each weevil rearing substrate were assayed, for a total of 40 observations (n = 8,000 weevils per substrate). Assays were performed in a temperature-controlled chamber at 23 ± 5 °C, 60% RH, and photoperiod of 12:12 h (L:D). Comparisons of treatments were made through Analysis of Variance (ANOVA) with subsequent mean comparisons by Waller's test (SAS Institute 2009).

CHOICE ASSAY WITH PHEROMONE LURE

This choice assay was performed in the same manner as previously described, except a commercial pheromone lure was placed within 1 of the grain treatments. The commercial 4 component lure (Alpha Scents, West Linn, Orego, USA) contained an aggregation pheromone ((4S,5R)-5-hydroxy-4-methylheptan-3-one) and 3 food odor compounds (3-methoxy-4-hydroxy-benzaldehyde, valeraldehyde, and 3-methoxy-2-methyl-4-pyrone) in a 200 µL Eppendorf tube. A headspace volatile collection was performed on the lure before the assay to determine the abundance of the 4 compounds (Heath & Manukian 1992). Due to its potency, the lure was uncapped for a period of 4 wk prior to being used in the experiment, and another headspace volatile collection was performed to confirm the reduction in strength. The Eppendorf tube was concealed within the treatment grain. Ten repetitions from each weevil rearing substrate were assayed, for a total of 40 observations (n = 8,000 weevils per substrate). Assays were performed in a temperature-controlled chamber at 23 ± 5 °C, 60% RH, and photoperiod of 12:12 h (L:D). Comparisons of treatments were made through ANOVA with subsequent mean comparisons by Waller's test (SAS Institute 2009).

EMERGENCE FROM CORN KERNEL

Due to the large size of a kernel of corn, it is not known if more than 1 weevil can develop in a single grain. To establish if a kernel of corn was able to support the development of more than 1 weevil, an assay was developed to observe this occurrence. This information was used to determine if corn can be compared to other grains where only a single weevil develops. Corn-reared colony weevils (10 males, 10 females) were placed in a 950 mL glass canning jar (Jarden Home Brands, Daleville, Indiana) containing 200 corn kernels (Yellow Corn, Flint River Mills, Bainbridge, Georgia). Weevils could freely oviposit for 8 d. After the 8-d period, the contents of the jar were spread on a tray and 200 kernels selected. A single kernel was placed in a 1 mL Eppendorf® tube. A small hole was placed in the lid of the tube with a #5 insect pin to allow for air exchange. The tubes were capped and placed in a temperature-controlled chamber at 23 ± 5 °C, 60% RH, and photoperiod of 12:12 h (L:D) for about 40 d for development. After the 40-d period, tubes were checked for emergence. The number and sex of the emerged weevils was recorded. Statistical analysis was through ANOVA (SAS Institute 2009).

OVIPOSITION ASSAY

To determine the suitability of 4 cereal grains, corn-reared weevils were provided with grains and allowed to freely oviposit. Ten pairs of weevils about 2 wk old were placed in a 950 mL glass canning jar (Jarden Home Brands, Daleville, Indiana). The solid lid was replaced with fine copper mesh to allow for ventilation held in place with a metal screw band. To ensure that the weevils had the same amount of substrate from each grain assayed, 1,000 pieces of each grain were counted and weighed: corn 325 g, barley 40 g, white rice 36 g, and brown rice 20 g. Weevils were placed in jars with grain and allowed to oviposit for 10 d, after which the weevils were removed. The assay was observed beginning at 30 d for emergence. There were 10 repetitions for each grain, and emerged weevils were counted and sexed. Jars were held and observed for 7 d after the emergence reached 0 to ensure that all weevils were collected. Assays were performed in a temperature-controlled chamber at 23 ± 5 °C, 60% RH, and photoperiod of 12:12 h (L:D). Statistical analysis was through ANOVA with subsequent mean comparisons by Waller's test (SAS Institute 2009).

Results

CHOICE ASSAY

When provided with a choice of grains, male (F = 82.71; df = 4; P < 0.0001) and female (F = 98.69; df = 4; P < 0.0001) weevils were predominantly located in corn, regardless of rearing substrate (Fig. 1). Corn-reared males and females preferred white rice over barley and brown rice. All others selected barley, brown rice, and white rice, respectively.

CHOICE ASSAY WITH LURE

Corn containing the pheromone lure resulted in males (F = 35; df = 4; P < 0.0001) and females (F = 22.97; df = 4; P < 0.0001) preferentially located in corn (Fig. 2). Male and female response to barley was greater than that of brown rice, white rice, and those that did not make a choice. White rice exhibited the least attractiveness for males and females. The lure placed in barley demonstrated that most of the male (F = 100.43; df = 4; P < 0.0001) and female (F = 54.93; df = 4; P < 0.0001) weevils from all substrates were in barley, whereas barley-reared males chose corn (Fig. 3). Brown rice containing the lure attracted male and female weevils reared on barley. Females reared on white rice preferred barley, and all other males (F = 116.62; df = 4; P < 0.0001) and females selected corn (F = 57.08; df = 4; P < 0.0001) (Fig. 5). Corn- and brown rice-reared males selected corn (F = 51.75; df = 4; P < 0.0001) when the lure was placed in white rice. Barley- and brown rice-reared females also selected corn (F = 72.30; df = 4; P < 0.0001). All other weevils selected barley (Fig. 4). There was no significant difference dependent on the rearing substrate for males (F = 46; df = 3; P = 0.7086) or females (F = 52; df = 3; P = 0.6707).

EMERGENCE FROM CORN KERNEL

There were only 2 instances out of 200 where more than 1 weevil emerged from a single kernel of corn. In both cases, the kernels each contained 1 male and 1 female. Therefore, results indicate that there is a 0.01% chance that a female will oviposit more than 1 egg per corn kernel.

OVIPOSITION ASSAY

There was significantly greater emergence of males and females from barley and brown rice (Fig. 6). On average for 1,000 grains, 15.71 males and 10.58 females emerged from barley, whereas 7.81 males and 9.59 females emerged from brown rice. The average number from corn was 3.77 males and 6.74 females, whereas white rice averaged 4.33 males and 3.89 females per 1,000 grains. There was no significant sex difference in emergence from any of the grains.

Discussion

Host-produced volatiles that initiate behavioral responses in the maize weevil are essential for development of an attractant. Maize weevils can infest a wide variety of stored products, but prefer corn. Being a generalist, it was hypothesized that the weevil would not be partial to a specific grain selected for the assay. By using weevils reared on multiple substrates over multiple generations, it was demonstrated that the rearing substrate of previous feeding has limited effect on host grain selection.

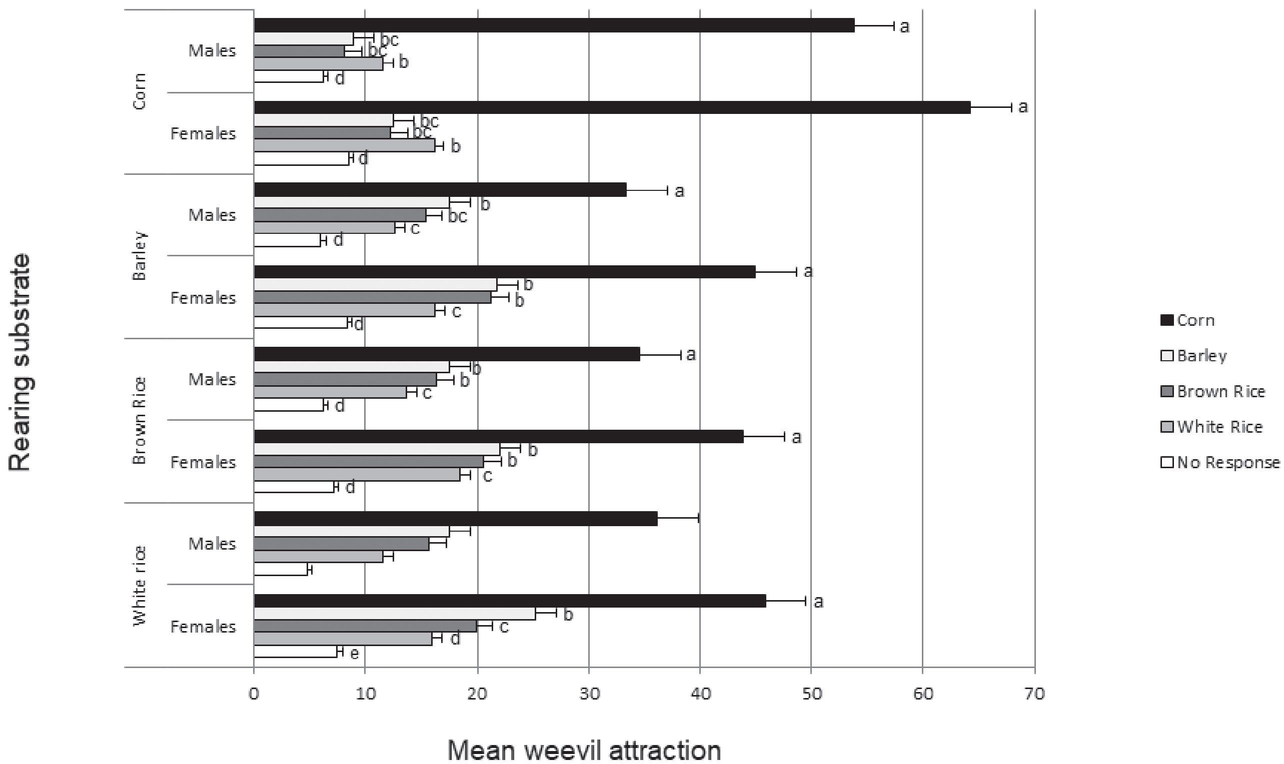

Fig. 1. Mean (SE) number of *S. zeamais* (n = 8,000) attracted to corn, barley, brown rice, and white rice. Weevils were reared on corn, barley, brown rice, and white rice, then presented with a choice of 4 host grains. Means with the same letter are not significantly different.

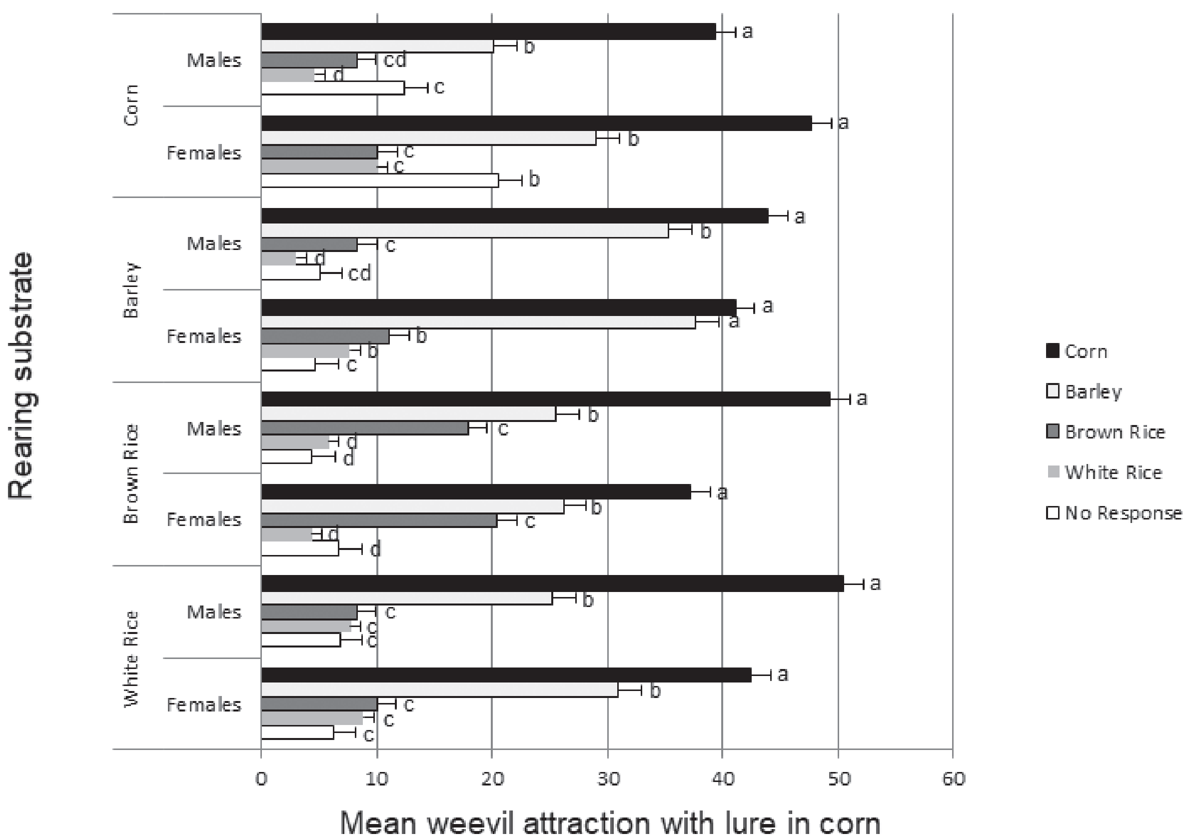

Fig. 2. Mean (SE) number of *S. zeamais* (n = 8,000) attracted to corn, barley, brown rice, and white rice, with a 200 µL Eppendorf tube containing the pheromone lure placed in corn. Weevils were reared on corn, barley, brown rice, and white rice, then presented with a choice of 4 host grains. Means with the same letter are not significantly different.

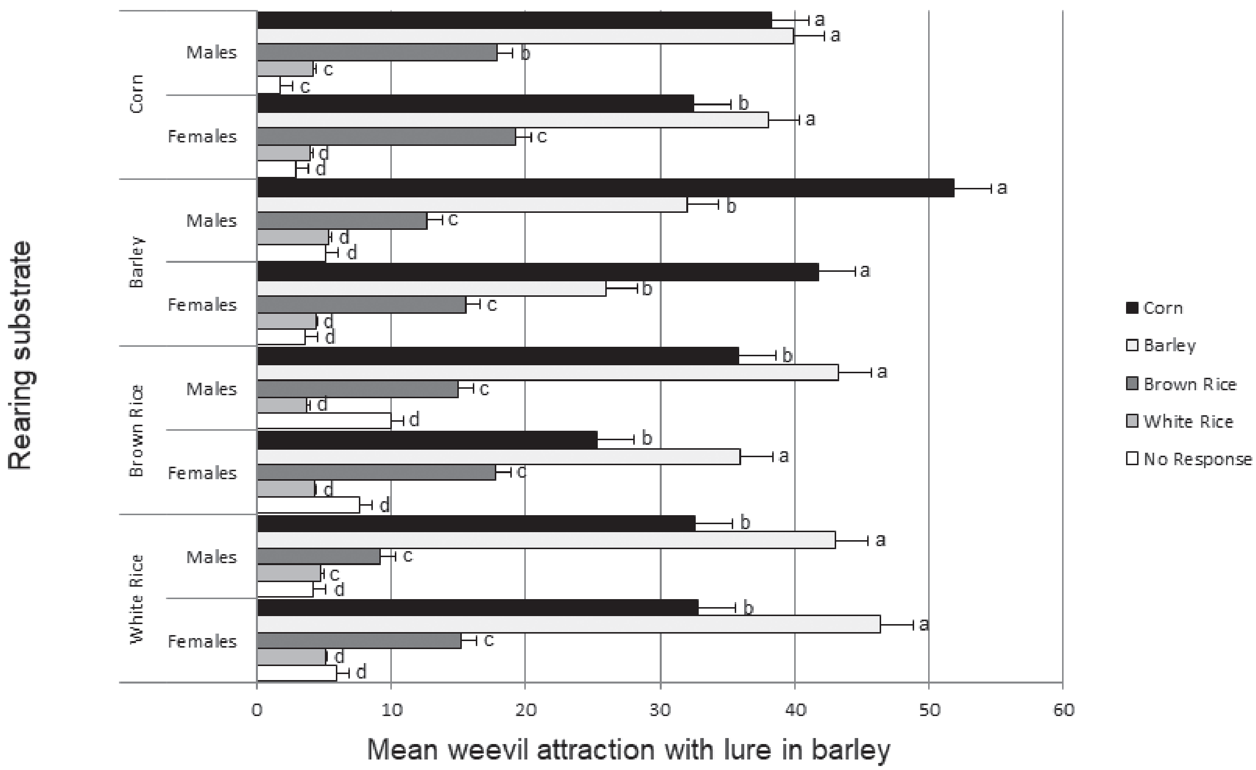

Fig. 3. Mean (SE) number of *S. zeamais* (n = 8,000) attracted to corn, barley, brown rice, and white rice, with a 200 µL Eppendorf tube containing the pheromone lure placed in barley. Means with the same letter are not significantly different.

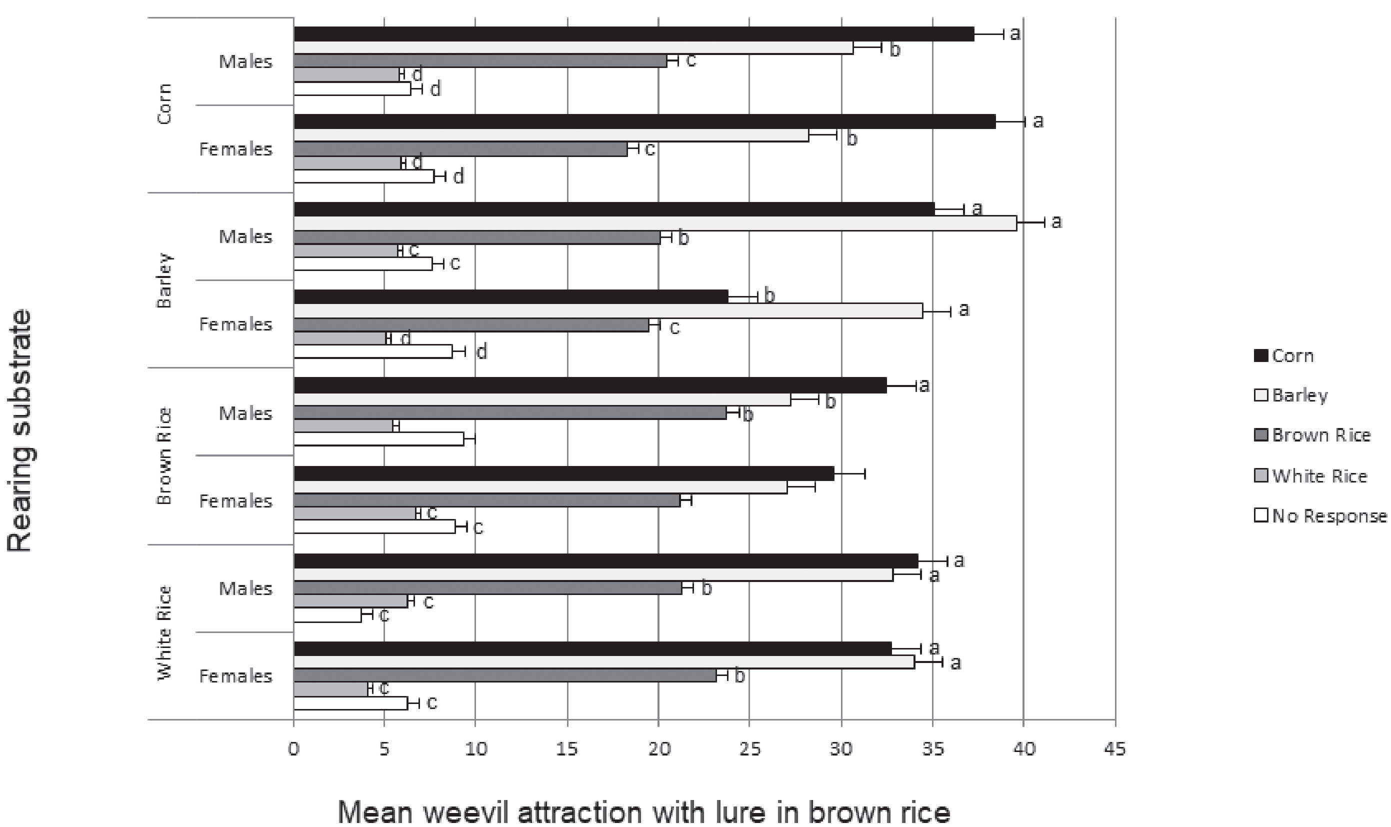

Fig. 4. Mean (SE) number of *S. zeamais* (n = 8,000) attracted to corn, barley, brown rice, and white rice, with a 200 µL Eppendorf tube containing the pheromone lure placed in white rice. Means with the same letter are not significantly different.

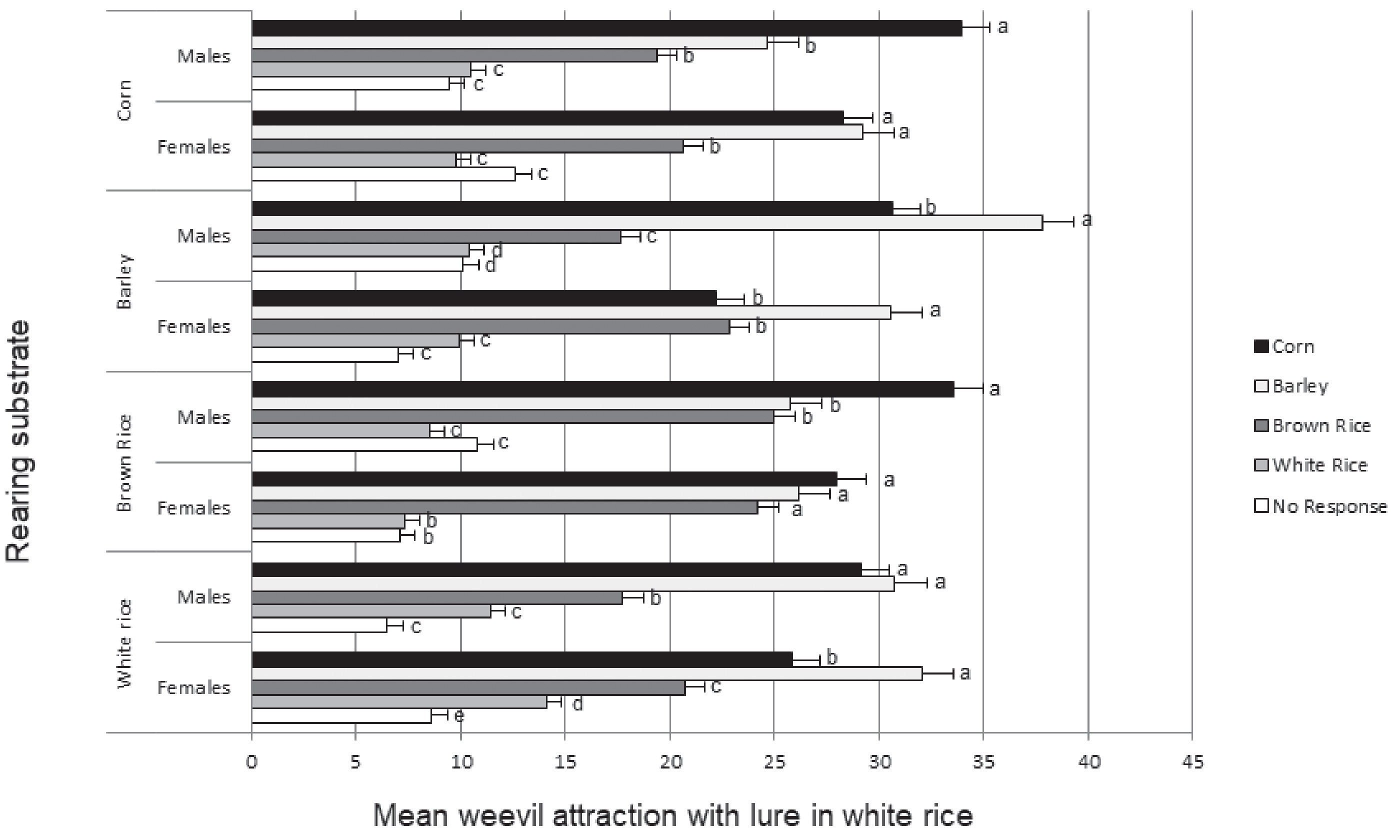

Fig. 5. Mean (SE) number of *S. zeamais* (n = 8,000) attracted to corn, barley, brown rice, and white rice, with a 200 µL Eppendorf tube containing the pheromone lure placed in brown rice. Means with the same letter are not significantly different.

When weevils were provided with a choice of corn, barley, white rice, or brown rice, males and females were significantly more likely to be attracted to corn. The male response to barley, brown rice, and white rice was equal. The female response to brown rice was greater than that of barley, with little attraction to white rice. There was no significant difference dependent on the substrate on which the weevils were reared. These results indicate that the volatile emissions from corn appear to be most attractive to the maize weevil when presented with other grains. The weevil's evolutionary history with corn appears to dominate in the presence of other host grains.

The placement of the commercial lure in the host grains delivered varying results. When provided with a choice of corn containing a pheromone lure, males and females were significantly more likely to be attracted to the corn. The responses for males and females to barley were greater than that of brown rice and white rice. However, the treatment that had the least response for males and females was white rice. The continued aversion to white rice may be due to the grain's lack of husk, bran, and germ. It was demonstrated that white rice can be used as a reproductive substrate, although it may lack semiochemicals found in the husk, bran, and germ that are necessary for attraction. When the lure was placed in barley, male and female weevils were more likely to be found visiting barley. However, males that were reared on barley chose corn. For attraction to brown rice containing the lure, male and female weevils reared on barley, and females reared on white rice preferred barley, whereas all other males and females selected corn. These results are the only instance where males and females selected according to their rearing substrate. Males reared on corn and brown rice selected corn when the lure was placed in white rice. Female weevils reared on barley and brown rice also selected corn; all other weevils selected barley.

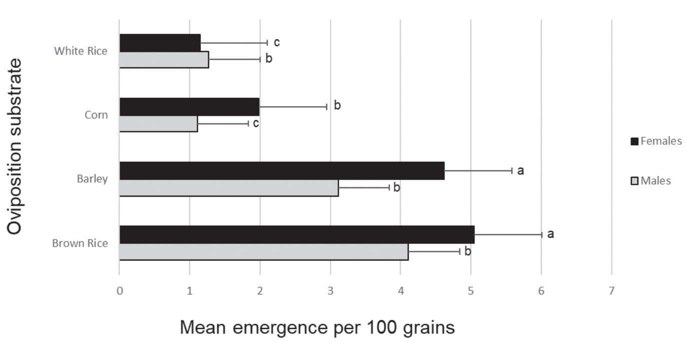

Fig. 6. Number (SE) of *S. zeamais* male and female (n = 200) emergence when reared on the individual host grains: corn, barley, brown rice, and white rice. Means with the same letter are not significantly different.

The large size of the corn grain, as compared to the other grains, presented the question of the ability of more than 1 weevil developing within the kernel. Visual inspection of barley, white rice, and brown rice verified that only 1 larva was feeding within. The emergence assay indicated that there is an extremely low incidence (0.01%) that multiple weevils emerge from a single kernel of corn. This verified that a grain of corn would only produce a single individual. This supported the decision to use a known number of grains (1,000 pieces) to determine oviposition and emergence. This assay showed significantly greater emergence of males and females from barley and brown rice. The attraction results indicated the greatest attraction to corn, which should have had the greatest oviposition. The type, size, texture, and age of grain may play a significant role in the weevil's decision to oviposit. Although corn is the preferred oviposition site, the hard exterior of the kernel may require more time to penetrate, allowing for fewer grain visits. An advantage is that the hard exterior of the corn kernel may provide the greatest protection for the developing larva. There was significantly greater emergence of males and females from barley and brown rice (Fig. 6). On average for 1,000 grains, 15.71 males and 10.58 females emerged from barley, and 7.81 males and 9.59 females from brown rice. The average number from corn was 3.77 males and 6.74 females, whereas white rice averaged 4.33 males and 3.89 females per 1,000 grains.

This research suggests that previous feeding does not make the weevil biased to a certain grain. The importance of this discovery allows for the conclusion that the isolation of key corn semiochemicals will be the most attractive host odors for the development of an attractant for *S. zeamais*. Otherwise, the feeding attractant would have to be tailored to weevils feeding upon specific hosts.

Volatile profiles will be developed from corn, barley, and brown rice for comparison to identify similar compounds that may be present. The host grain attraction assay illustrates that males and females are more likely to be found on corn, but surprisingly there is greater emergence from barley and brown rice. This gives greater support of the attractiveness of corn to the maize weevil even when a better host for development is available.

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