

Response of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) to its Aggregation Pheromone and Wheat Volatiles

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ABSTRACT The attraction of adult *Rhyzopertha dominica* (F.) to its aggregation pheromone and to volatiles of infested wheat was examined in relation to age, sex, and female mating status. Male and female beetles did not differ in their response to pheromone or wheat volatiles regardless of insect age. Virgin and mated females did not differ in their response to the pheromone or wheat volatiles. *R. dominica* was more responsive to wheat that was infested than to clean wheat, and the response was proportional to the density of insects in the wheat. This suggests a strong attraction to the insect pheromone in infested grain. The implications of these findings for the attraction and migration of *R. dominica* to stored wheat are discussed.

KEY WORDS *Rhyzopertha dominica*, wheat grain volatiles, insect pheromones

MANY STORED PRODUCT insects use sex and aggregation pheromones to attract conspecifics and increase densities to a point where mates can be readily located (Burkholder & Ma 1985). The aggregation pheromone of the lesser grain borer, *Rhyzopertha dominica* (F.), is a two-component blend called Dominicalure 1 and 2 (Williams et al. 1981) that is effective in attracting male and female *R. dominica* to traps placed inside and outside feed and seed warehouses (Leos-Martinez et al. 1986, 1987) and around metal farm bins containing stored rice (Cogburn et al. 1984). Several stored product insects, including *R. dominica*, are also known to orient to stored grain odors (Barrer & Jay 1980, Freedman et al. 1982, Barrer 1983), and such odors may be important in helping females locate ovipositional sites (Crombie 1941). The synergistic effects of host odors and pheromone have been documented for some insect pest species (Dickens et al. 1990). Little work, however, has been published on how stored-product insect pheromones and host odors might interact, or how the life history traits of a species might affect their response to stored grain.

The rate at which insects invade a grain storage facility is likely to depend on the ability of each species to use stimuli originating from this facility and on critical life history parameters such as age, sex, and mating status. In the case of *R. dominica*, the presence of an existing or prior infestation with its presumed release of aggrega-

tion pheromones may, in combination with grain volatiles, attract lesser grain borers in some density-dependent manner. The three objectives of this study were (1) to examine whether the attraction of *R. dominica* to pheromone and food is influenced by age, sex, or female mating status; (2) to determine the attraction of *R. dominica* adults to pheromone in wheat previously infested for varying lengths of time with different densities of *R. dominica*; and (3) to estimate the amount of pheromone present in cultures of *R. dominica* at varying densities and durations of infestation.

Materials and Methods

A series of experiments was conducted with *R. dominica* adults from cultures established with feral adults collected from wheat bins in central Kansas in July 1989. Voucher specimens (No. 050) have been deposited in the Entomology Museum at Kansas State University, Manhattan.

Culturing Beetles and Bioassay Conditions. Beetles to be tested were reared individually from eggs in tissue culture plates on cleaned cracked wheat incubated at 26 ± 1°C and 60 ± 5% RH. Within 24 h of emergence, adults were transferred to individual 35-ml plastic diet cups with additional cracked grain and the dates of emergence were recorded. Sex of beetles of desired age was determined, and the beetles were placed individually in plastic boxes (4.8 by 4.8 by 2.0 cm) with filter paper bottoms and starved 24 h before testing. Sex was determined under white fluorescent lights using color characteris-

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tics on the venter of the fifth abdominal segment (Stemley & Wilbur 1966).

To obtain mated females, emerging females were placed in 35-ml plastic diet cups containing cracked grain and an equal number of males for 3, 7, or 14 d. We assumed that all females exposed to males were mated because males copulate readily (Crombie 1941). Virgin females were kept isolated in 35-ml cups before testing.

Rhyzopertha dominica exhibits a variation in response to pheromone stimuli throughout the day (Obeng-Ofori & Coaker 1990) and tends to be attracted to light (A.K.D., personal observation). To minimize these effects and to standardize responses, beetles were maintained with a 0:24 (L:D) h photoperiod throughout development and bioassays were conducted under dim red light to simulate darkness. Bioassays were conducted between 0700 and 1200 hours (CST) and each beetle was used in only one bioassay.

Volatile Sources. The sources of volatiles in all experiments were 1.9-liter glass jars containing one of the following five (1) 1 kg of uninfested 'Victory' wheat (12.0% moisture, 755 g/liter); (2) different numbers of *R. dominica* only; (3) a rubber pheromone septum impregnated with synthetic aggregation pheromone of the beetle (1-methyl-(E)-2-methyl-1-pentanoate and 1-methyl-(E)-2,4-dimethyl-2-pentanoate in a 1:1 ratio) (Trece, Salinas, CA [pheromone dose not available]); (4) wheat plus a pheromone septum; or (5) wheat that had been incubated with 1, 10, 100, or 1,000 beetles for 1, 7, or 21 d at $26 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH and a 0:24 h photoperiod. Beetles used as pheromone sources were >2 wk old and were reared and maintained on whole wheat before the experiments were done. The response of beetles to pure extracts of wheat volatiles was not examined because the insects are exposed to the entire grain odor profile in applied farm storage situations. Additionally, there is insufficient research on the overall chemistry of grain odors to effectively select pure extracts for testing (Seitz & Sauer 1992).

Bioassay and Olfactometer. Charcoal-filtered air was pumped through jars containing the volatile sources and into a choice arena constructed of sheet metal with a filter paper bottom and a glass top. The arena was Y-shaped with arms 3.5 cm long by 1.0 cm wide by 1.2 cm deep. It had two inlet ports for a different odor source on each arm and a single exhaust port on the stem. The ports were covered with fine brass screen (50 mesh) to contain the insects in the arena. The air flow rate from each volatile source into the Y-tube choice arena was $300 \text{ cm}^3/\text{min}$. After 5 min, location of the beetle in the arena was recorded. The choice arena was cleaned with acetone and air-dried between runs to eliminate cross-contamination.

Statistical Analysis. In all experiments, response frequencies of beetle choices (left port,

right port, or no movement out of the central stem) were calculated from the resulting data (SAS Institute 1985). Categorical data modeling was used to detect significant differences in the response functions among treatments within each experiment using the CATMOD procedure (SAS Institute 1985). By weighting each choice in the response arena as +1, -1, or 0, CATMOD fits a log-linear model to the response function. This results in a linear relationship in which a response mean value approaching -1 indicates preference for one choice of a pair and a response mean value approaching +1 indicates preference for the other choice of a pair. A response mean value close to 0 indicates that no preference was exhibited for the volatiles from either culture. Although it can be argued whether or not to retain in the analysis any insects that did not respond to either volatile source, we believe that there may be some physiological or behavioral reason for the beetles not choosing to move, and we have accordingly considered "no response" to be a valid trait.

Effects of Sex, Age, and Mating Status on Beetle Response. The first experiment was a split plot design for comparing the ability of male ($n = 161$) and female ($n = 167$) beetles 2-21 d after eclosion to distinguish between volatiles from wheat only or wheat plus synthetic pheromone. Beetles were grouped into four age classes; 2-5, 6-9, 10-13, and 18-21 d after eclosion. The next experiment examined the orientation response to wheat volatiles and synthetic pheromone by virgin females and females that had been mated for 3, 7, or 14 d ($n = 101$).

Responses of Beetles to Insect and Wheat Volatiles and Synthetic Pheromone. The purpose of the second series of experiments was to determine the responses of mixed-sex beetles to volatiles from several different sources: clean air (empty jar); uninfested wheat; wheat infested for 1, 7, or 21 d (incubated as previously described); and wheat infested with 1 (male), 10 (5 males and 5 females), 100 (mixed sex), or 1,000 (mixed sex) beetles. Because the Y-tube olfactometer could accommodate only two choices, the volatiles were presented pairwise: beetles only versus clean air ($n = 255$), beetles only versus wheat only ($n = 298$), beetles only versus beetles plus wheat ($n = 210$), and beetles plus wheat versus wheat only ($n = 754$). A synthetic pheromone septum alone or in combination with wheat was also used as a positive control treatment in all experiments.

Effect of Beetle Density on Pheromone Production. The amount of aggregation pheromone produced by beetles was determined by sampling grain from jars with densities of 0, 1 (male), 10 (5 males and 5 females), 100 (mixed sex) or 1,000 (mixed sex) adults and incubated at $26 \pm 1^\circ\text{C}$ and $60 \pm 5\%$ RH for 1, 7, or 21 d. Three replicates of each treatment were frozen to kill

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the beetles and stop pheromone production. Pheromones and headspace volatiles were collected from 31-g samples in Tekmar sample tubes and concentrated by using a model LSC 2000 purge and trap instrument (Tekmar, Cincinnati, OH) equipped with a sample heater and a capillary interface module (model 2530). The sample was heated to 60°C and purged with helium for 10 min to transfer volatiles to a Tenax trap (Alltech Associates, Deerfield, IL) (3.18 by 305 mm). Excess water was removed by purging the trap with helium for 6 min. Collected volatiles were thermally desorbed at 200°C and transferred via a heated fused silica tube to the capillary interface module where they were cryofocused (-130°C) at the top of the gas chromatography column. Rapid heating released the cryofocused components in a narrow band for separation on a BPX 5 column (50 m long, 0.32 mm inside diameter, 0.25 mm film thickness) (SGE, Austin, TX) in a model 5890 gas chromatograph (Hewlett Packard, Palo Alto, CA). Column temperature was held at 50°C for 2 min, then increased at 10°C per min to 170°C and finally increased at 20°C per min to 230°C. Separated components were detected and identified with a model 5970 mass selective detector (Hewlett Packard) with a mass range set at 30-230. Dominicalures 1 and 2 were eluted at 13.16 and 13.52 min, respectively. For selective detection of the pheromones, extracted ion chromatograms were generated for ions m/z 97 and 115 from dominicalure 1 and for ions m/z 111 and 128 for dominicalure 2. After integrating the extracted ion chromatograms, the four peak areas representing the pheromones were summed. A standard curve was developed from wheat samples treated with known concentrations of synthetic aggregation pheromone (source: W. E. Burkholder, USDA-ARS) in hexane injected into pheromone-free wheat just before the sample was purged with helium on the purge and trap instrument. Calibration samples were run each day that samples were analyzed, making sure that the calibration range adequately covered the range of pheromone detected in the insect-infested samples.

Results

Sex, Age, and Mating Status. Orientation responses to volatiles from pheromone plus wheat versus wheat only were similar for males and females ($\chi^2 = 1.52$, $df = 2$, $P = 0.4668$, $n = 328$) (Table 1) with a strong preference by both sexes for volatiles emanating from jars containing synthetic pheromone plus wheat. Male response to the volatiles of pheromone plus wheat averaged 73.3% compared with 9.3% to the volatiles from wheat only (Table 1). Female response to the volatiles of pheromone plus wheat averaged 68.3% versus 13.2% to wheat only. The re-

Table 1. Comparison of orientation responses by male and female *R. dominica* of different ages to volatiles from synthetic *R. dominica* pheromone plus wheat versus wheat only

Age, d	Pheromone plus wheat ^a	Wheat only ^a	n	Response means ^b
Males				
2-5	14 (73.7)	3 (15.8)	19	0.58
6-9	26 (74.3)	4 (11.4)	35	0.63
10-13	27 (69.2)	5 (12.8)	39	0.56
14-17	36 (75.0)	2 (4.2)	48	0.71
18-21	15 (75.0)	1 (5.0)	20	0.70
Females				
2-5	12 (57.1)	6 (28.6)	21	0.29
6-9	20 (64.5)	6 (19.4)	31	0.45
10-13	27 (67.5)	6 (15.0)	40	0.53
14-17	35 (76.1)	2 (4.4)	46	0.72
18-21	20 (69.0)	2 (6.9)	29	0.62

^a Values are the observed number (percentage of beetles) responding to a particular stimulus.

^b Values approaching +1 indicate response toward pheromone plus wheat, values approaching -1 indicate response toward wheat only, values near 0 indicate no clear preference.

sponses did not differ significantly among any of the age groups ($\chi^2 = 6.24$, $df = 4$, $P = 0.1821$), nor was the interaction between age and sex significant ($\chi^2 = 1.63$, $df = 4$, $P = 0.8028$).

The mating status of females also had no significant effect on their orientation responses to volatiles from pheromone plus wheat or wheat only ($\chi^2 = 0.45$, $df = 3$, $P = 0.9292$, $n = 101$) (Table 2). The response means were similar for mated and unmated females and averaged 0.46, indicating a consistent preference for the volatiles from jars containing pheromone plus wheat. An average of 57.4% of the females responded to the volatiles from the pheromone plus wheat combination compared with a response of only 11.9% to volatiles from wheat only (Table 2).

Comparative Responses of Beetles to Volatiles from Insects, Wheat, and Synthetic Pheromone. *Response of Adults to Other Beetles.* The weak orientation response toward the volatiles from beetles only versus an empty jar was similar (Table 3). This suggests that beetles may not release

Table 2. Comparison of orientation responses by mated and unmated female *R. dominica* to volatiles from synthetic *R. dominica* pheromone plus wheat versus wheat only

Mating period, d	Pheromone plus wheat ^a	Wheat only ^a	n	Response means ^b
Virgin ^c	15 (60.0)	3 (12.0)	25	0.50
3	16 (66.7)	4 (16.7)	24	0.45
7	13 (54.2)	2 (8.3)	24	0.49
21	14 (50.0)	3 (10.7)	28	0.39

^a Values are the observed number (percentage) of beetles responding to a particular stimulus.

^b Values approaching +1 indicate response toward pheromone plus wheat, values approaching -1 indicate response toward wheat only, values near 0 indicate no clear preference.

^c Pooled across ages of 3, 7, and 21 d.

Table 3. Comparison of orientation responses by adult *R. dominica* to volatiles from *R. dominica* and wheat both singly and in combination, clean air, and synthetic aggregation pheromone

No. beetles ^a	Choice 1 ^b	Choice 2 ^b	n	Response mean ^c
	Beetles only	Empty jar (control)		
0	15 (29.4)	23 (45.1)	51	-0.16
1	14 (27.5)	15 (29.4)	51	-0.02
10	15 (31.3)	13 (27.1)	51	0.04
100	18 (35.3)	18 (35.3)	51	0.00
Control	31 (60.8)	2 (3.9)	51	0.57
	Beetles only	Wheat only		
0	21 (22.3)	31 (33.0)	94	-0.11
1	12 (23.5)	25 (49.0)	51	-0.25
10	17 (33.3)	13 (25.5)	51	0.08
100	20 (39.2)	14 (27.5)	51	0.12
Control	33 (64.7)	5 (9.8)	51	0.55
	Beetles only	Beetles plus wheat		
1	22 (44.0)	15 (30.0)	50	0.14
10	10 (20.0)	26 (52.0)	50	-0.32
100	4 (8.0)	42 (84.0)	50	-0.76
Control	26 (43.3)	10 (16.7)	60	-0.27
	Beetles plus wheat	Wheat only		
1	66 (42.9)	40 (26.0)	154 ^d	0.17
10	78 (52.0)	45 (30.0)	150 ^d	0.22
100	93 (62.0)	17 (11.3)	150 ^d	0.51
1,000	105 (70.0)	17 (11.3)	150 ^d	0.59
Control	72 (48.0)	29 (19.3)	150 ^d	0.29

^a In all experiments, beetles were replaced with pheromone septa to act as control standards.

^b Values are the observed number (percentage) of beetles responding to a particular stimulus.

^c Values approaching +1 indicate response toward choice 1, values approaching -1 indicate response toward choice 2, values near 0 indicate no clear preference.

^d Numbers of beetles pooled over three durations of infestation.

pheromone without host food. When presented with a choice of synthetic pheromone from a septum versus air only, 60.8% of the test insects responded toward the pheromone source compared with only 3.9% toward the clean air stream, thus ruling out the possibility of nonresponsiveness by the test beetles. This high level of response to pheromone was significantly greater ($\chi^2 = 39.27$, $df = 4$, $P = 0.0001$, $n = 255$) than the response to all levels of beetles.

Beetles Only Versus Wheat Only. The weak orientation response to volatiles from jars containing insects only or wheat only was similar (Table 3). This also suggests the possibility that beetles may not release pheromone in the absence of food. A control comparison between volatiles of wheat only versus synthetic pheromone resulted in 64.7% responding to pheromone compared with 9.8% responding to the volatiles of wheat. The response to pheromone was significantly greater ($\chi^2 = 40.08$, $df = 4$, $P < 0.0001$, $n = 298$) than that to volatiles from beetles only.

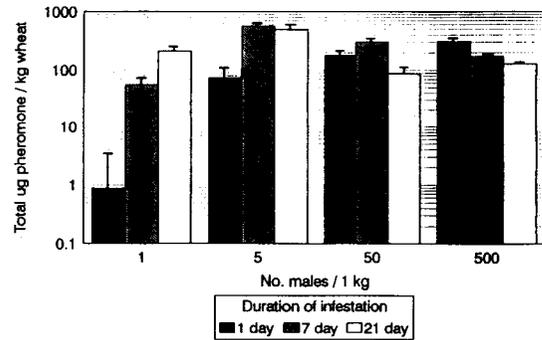


Fig. 1. Amount of male-produced aggregation pheromone in wheat cultures containing *R. dominica* at varying densities for three lengths of infestation.

Beetles Only Versus Beetles Plus Wheat. The orientation response to volatiles from beetles plus wheat was significantly greater than to beetles only, particularly at a density of 100 per kg ($\chi^2 = 79.14$, $df = 3$, $P < 0.0001$, $n = 210$) (Table 3). The response differential increased as the number of beetles in the wheat increased. Neither volatile source was consistently chosen at a density of 1 male per kg, but at densities of 10 and 100, the volatiles from the beetles plus wheat were consistently chosen. There was possibly insufficient pheromone emanating from the one male beetle plus wheat jar to enhance attractiveness relative to volatiles from the single male without wheat.

Beetles Plus Wheat Versus Wheat Only. The orientation response was significantly greater to beetles plus wheat than to wheat alone, and the response differential was proportional to the beetle density in the wheat ($\chi^2 = 37.32$, $df = 4$, $P < 0.0001$, $n = 754$) (Table 3). However, neither the duration of infestation ($\chi^2 = 2.62$, $df = 2$, $P = 0.2702$) nor the density by duration interaction were significant ($\chi^2 = 13.30$, $df = 8$, $P = 0.1019$). This suggests that the pheromones might not persist but rather that a continuous production of an unstable material may occur. The data in the right hand columns of Table 3 are the numbers of *R. dominica* in the cultures pooled over the three lengths of infestation (1, 7, and 21 d). There was little preference exhibited for volatiles either from 1 or 10 *R. dominica* plus wheat compared with those from wheat only. There was a clear preference for volatiles from cultures containing 100 or 1,000 *R. dominica* plus wheat, as indicated by response mean values being larger for these treatments compared with the other treatments.

Pheromone Concentration. Significantly higher pheromone concentrations were present in cultures containing five male beetles than in the other cultures ($F = 6.35$; $df = 3, 16$; $P = 0.0048$) (Fig. 1). There was no significant difference ($F = 2.32$; $df = 2, 4$; $P = 0.2139$) in the amount of

Fig. 2. Pheromone concentration in wheat cultures containing *R. dominica* at varying densities for three lengths of infestation.

pheromone concentrations in wheat cultures containing *R. dominica* at varying densities for three lengths of infestation.

Although wheat cultures containing *R. dominica* correlated with the number of male beetles ($F = 12.38$; $df = 3, 16$; $P = 0.0001$), the amount of pheromone produced was not significantly different ($F = 0.00$; $df = 3, 16$; $P = 0.9999$) between the three durations of infestation.

An important parameter in the study of aggregation is the accuracy of the response to the pheromone. The parameters of the response to the pheromone are always present in the absence of grain volatiles. These parameters were always present in the attractive response to the pheromone. The addition of *tella* (Wa

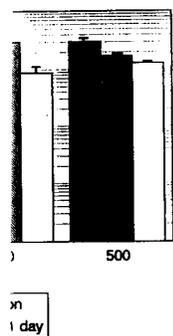


Fig. 2. Amount of male-produced aggregation pheromone per male in wheat cultures containing *R. dominica* at varying densities for three lengths of infestation.

pheromone present in cultures because of differences in length of infestation. Interaction between the numbers of males per kg and length of infestation was significant ($F = 3.63$; $df = 6, 16$; $P = 0.0182$).

Although the amount of pheromone in a jar of wheat containing beetles was not significantly correlated ($r = 0.06$; $P = 0.74$; $n = 34$) with the number of males, the amount of pheromone per male was significantly negatively correlated ($r = -0.38$; $P = 0.0253$; $n = 34$) with the number of males (Fig. 2). There was a comparably higher ($F = 12.28$; $df = 3, 16$; $P = 0.0002$) amount of aggregation pheromone produced per male when insect densities were low but substantially less per male was produced at higher densities. Additionally, there was significantly less ($F = 21.62$; $df = 2, 4$; $P = 0.0072$) pheromone present in cultures infested for only 1 d than in the cultures infested for 7 and 21 d. Again, interaction between the length of infestation and the number of males was significant ($F = 6.47$; $df = 6, 16$; $P = 0.0013$).

Discussion

An important component of any model that attempts to quantify the early population dynamics of stored grain insect pest populations is an accurate knowledge of the factors regulating migration into and out of bins. Such factors are undoubtedly complex and to some extent site-specific. It is likely, however, that life history parameters such as age, sex, and mating status are always important, as may be the presence or absence of aggregation pheromones and host grain volatiles. However, the relationship of these variables to a predictable impact on insect movement is not obvious. In the laboratory, the attractiveness of a host food in combination with other insects of the same species was shown to be additive for the almond moth, *Ephesia cautella* (Walker) (Barrar 1977). The rice and maize

weevils, *Sitophilus oryzae* (L.) and *S. zeamais* Motschulsky, are also attracted to aggregation pheromone and volatiles from cracked corn, rice, or wheat, and their response to pheromone-host plant odor is synergistic rather than additive (Trematerra & Girginti 1989, Walgenbach & Burkholder 1986, Walgenbach et al. 1987). A similar synergistic response was found for the macrolide aggregation pheromone of five cucujid grain beetles presented with food baits (Oehlschlager et al. 1988).

Our studies on the movement of *R. dominica* to volatiles from conspecifics, wheat only, wheat infested with lesser grain borer, and synthetic pheromone sources have shown a complex pattern of results. Air passed over either insects alone or wheat alone elicited little, if any, oriented movement by the beetles toward the odor sources. This was true irrespective of the responding insect's age, sex, or mating status. The addition of synthetic lesser grain borer pheromone to the air stream, however, resulted in a significant proportion of the test insects responding with upwind orientation. Unlike the studies mentioned above, addition of wheat volatiles to the pheromone source did not result in either a simple additive or synergistic behavioral response by the beetles. Instead, an ill-defined but positive density-dependent relationship was found for the mixture of odors. The density-dependent response to volatile sources was positive, even though aggregation pheromone concentration increased initially but reached a plateau at densities greater than five males per kg. This might indicate that a compound or compounds in the wheat or beetle feces, other than the pheromone itself, may be important in eliciting the observed response.

Of prime importance from the perspective of understanding population dynamics in field situations is our finding that only a few pheromone-releasing insects in the presence of wheat is enough to cause a significant upwind orientation. If one assumes that grain bins are free of insects when filled with newly harvested wheat in summer (June to August in most of the wheat-growing regions of the midwestern United States), and that a low rate of infestation by lesser grain borers is the normal situation (one per kg wheat/d), the initial population density of beetles in the grain will be very low (substantially less than 0.5 per kg), which is the lowest level detectable with reasonable sampling effort (Hagstrum et al. 1985) for at least 3 mo. By autumn when lesser grain borer populations are detectable by sampling, resident populations in the bins will be approaching levels of 50,000 or more and any additional immigrants attracted into the grain mass by the aggregation pheromone-grain volatile combination will make only negligible impact on the population dynamics of the resident population (Flinn & Hagstrum 1990, Hag-

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strum & Flinn 1990). Given these realities, the influence of aggregation pheromones and host volatile interactions are most likely to be of greatest biological importance very early in the grain storage period or perhaps again in the spring of the following year when populations have been reduced by low winter temperatures, or during reinfestation of a commodity when pest populations have been reduced or eliminated by fumigation.

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