Behavioral Response of *Podisus maculiventris* (Hemiptera: Pentatomidae) to its Synthetic Pheromone[1]

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Abstract A wind-tunnel bioassay was used to determine the effect of age and feeding history (starvation) on the response of *Podisus maculiventris* (Say) to its synthetic pheromone. Starved male and female adults showed positive anemotaxis toward the pheromone source; well-fed insects did not. This supports the hypothesis that *P. maculiventris* adults use the pheromone as a cue indicating presence of prey, in addition to a mating cue, although a physiological explanation for the lack of response by well-fed insects is also possible. In the presence of the pheromone, fed as well as starved insects increased activities such as extending antennae upwind; fluttering wings; and rubbing antennae, proboscis, forelegs, hindlegs, and abdomen. These activities may indicate stimulation of olfactory receptors on antennae and contact chemoreceptors elsewhere on the body. First- to third-generation offspring of field-collected *P. maculiventris* showed greater response to the synthetic pheromone compared with individuals from a 2-year-old laboratory colony, indicating the importance of using field-collected insects in behavioral studies. Fifth instars did not respond to the synthetic pheromone in the wind tunnel.

Key Words *Podisus maculiventris,* pheromone, anemotaxis, wind tunnel, behavior.

Podisus maculiventris (Say) is a generalist predator that feeds on many different insect species (McPherson 1980). Adult male *P. maculiventris* release a pheromone from large, paired dorsal abdominal glands located under their wings (Aldrich et al. 1978). Immature *P. maculiventris* have dorsal abdominal glands between tergites 3-4, 4-5, and 5-6, but the 4-5 and 5-6 dorsal abdominal glands are inactive in adults. The 3-4 dorsal abdominal glands are retained in both adult males and females, but are much larger in males (Aldrich et al. 1978).

The major components of the pheromone blend produced in the male glands are (E)-2-hexenal, alpha-terpineol, and benzyl alcohol; at least three other components are present in smaller amounts (Aldrich et al., 1978, 1984a). The pheromone is a long-range attractant of conspecific adults especially in the early spring as adults emerge from overwintering sites. Both males and females responded equally in initial field tests (Aldrich et al. 1984b), but in subsequent tests significantly more males than females were attracted to baited traps (Aldrich 1988). Only alpha-terpineol and (E)-2-hexenal are essential for attractancy (Aldrich 1988). A synthetic attractant containing these two compounds is commercially available ("Soldier Bug Attractor", Anon. 1992).

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Male *P. maculiventris* secrete from their dorsal abdominal glands during courtship; thus, the pheromone may be a short-range mating stimulant as well as a long-range attractant (Aldrich et al. 1984a, Aldrich 1985). In addition, *P. maculiventris* immatures are at least moderately attracted to the pheromone (Aldrich et al. 1984a, Aldrich 1985, 1988). Males produce the pheromone sporadically, falling "silent" at times, probably to avoid detection by parasitoids attracted to the pheromone (Aldrich et al. 1984a,b, Aldrich 1985, Shetty 1995).

Overwintered males emerge in early spring and begin pheromone calling without feeding (Aldrich 1995). Subsequent generations of males may initially search for food, then call females using the pheromone (Aldrich et al. 1984a,b, Aldrich 1995). Thus, both males and females may use the pheromone as a cue for the presence of prey in addition to mates. One might expect, then, that starved males and females would be more responsive to the pheromone than well-fed bugs. Food limitation and prey-finding are crucial factors in the life history of *P. maculiventris* (O'Neil and Wiedenmann 1987, 1990).

Our objective here was to determine the effect of age and feeding history (starvation) on the response of *P. maculiventris* to its synthetic phermone. We used a wind-tunnel bioassay to compare the response to the synthetic pheromone by newly-molted adult *P. maculiventris* males and females, and by adult males and females that had been held either without food or with ample prey for a period of 2 to 6 days. Fifth instars (starved for 2 d) were also tested. Anemotaxis (movement upwind) as well as other behaviors in the presence/absence of the pheromone were compared.

Materials and Methods

Field-collected *P. maculiventris* adults were obtained from pheromone-baited traps similar to those described by Aldrich et al. (1984b), placed at the edges of woodlots near Newark, Middletown and Dover, DE, in March 1993 (Shetty 1995). The offspring of these adults were used in bioassays, over a period of several months. Thus, insects from the "field colony" were one to three generations removed from the field. Additional test insects were from a 2-year-old laboratory colony originally purchased from Gardens Alive (Lawrenceburg, IN) in 1992. Field-colony and laboratory-colony insects were assigned randomly to all trials, with the origin of the individuals noted during data collection.

Both colonies were fed various lepidopteran larvae, including *Trichoplusia ni* (Hübner), *Spodoptera frugiperda* (J. E. Smith), *S. exigua* (Hübner), and *Heliothis virescens* (F.). Larvae were obtained from the DuPont Co. Stine-Haskell Research Center (Newark, DE) where they had been reared on artificial diet. *Podisus maculiventris* were kept in plastic boxes (17 × 12 × 6 cm) with screened lids, containing moist dental wicks, in an incubator at 26 ± 1°C and a photoperiod of 16:8 (L:D). Cages were cleaned and *P. maculiventris* fed every other day.

A wind tunnel made from a glass aquarium (50 × 25 × 30 cm) was used to observe movement upwind and other behavioral responses of *P. maculiventris* to the synthetic pheromone. A sheet of plexiglass was used as the bottom of the wind tunnel, with strips of white paper placed diagonally across its width to mimic flight over a greater distance than the length of the tunnel and to help guide and orient the insects during movement upwind (Baker and Linn 1984). The glass was removed from the two ends of the tunnel and replaced with fine cotton mesh fastened with velcro tape. A 25-cm three-speed box fan (Paragon Industries, Malvern, PA) was placed at the upwind end

outside the cotton mesh, 30 cm away from the wind tunnel. This distance was selected by observing the airflow inside the wind tunnel using a powdered airflow checker ("Flowchecker," Lab Safety Supply, Janesville, WI) and adjusting the position of the fan so that the airflow appeared laminar.

Laminar flow was verified by determined the Reynolds number. A flow is said to be laminar if the Reynolds number ranges from 0 to 2000 and turbulent if the number is in the range of 2000 to 4000 (Currie 1993, Cheremisinoff 1993). Here, the Reynolds number was 24 (Shetty 1995). The velocity of the airflow was determined using an anemometer (Kurz 1440 digital portable air velocity and temperature meter, Kurz Instruments, Monterary, CA). The average wind flow in the tunnel was 1.56 cubic m/min. The temperature in the room with the wind tunnel was 26 ± 1°C.

The synthetic pheromone used in the wind tunnel was purchased from Sterling International Inc. (Liberty Lake, WA) in yellow cone-shaped "attractors." The outer plastic cone was cut open and the vial containing the pheromone blend was removed. The vial was attached to a hook on the inside of the upwind end of the wind tunnel about 15 cm from the bottom of the tunnel.

The following ages and physiological conditions were tested for both male and female *P. maculiventris:* newly-molted adults; adults that had been starved (given water only) for 2, 4, or 6 or more days; and adults that were fed *ad lib* for 2, 4 (females only), or 6 or more days. Fifth instars, starved for 2 days, were also tested. For each experiment, the response of insects in the wind tunnel to the presence of pheromone was compared with the response of similar insects in the tunnel without pheromone. Sample sizes ranged from 30 to 92 individuals for each experiment, about half exposed to pheromone and half to air alone. Each physiological condition (starved or fed), age, and gender was examined (with and without pheromone) as a separate experiment, as insects became available. Although not all trials for each experiment were run on a single day, approximately the same number of controls as pheromone-exposed insects for each experiment were run each day.

For experiments using adults, late fifth instars were individually isolated in Petri dishes containing a moist dental wick. When the adults emerged their sex was determined and they were then assigned to a test treatment. Males and females were kept isolated from each other to prevent contact between them or their scents. Depending on availability of insects, some individuals were used for the control and then the test (pheromone) treatment, while others were used only for the control or only for the test runs. The insects to be tested each day were chosen randomly. Each day that trials were run, controls were done first, so the wind tunnel would not be contaminated by the presence of residual pheromone. The wind tunnel was thoroughly cleaned at the end of each set of trials.

The experiments were conducted about 4 h after the beginning of photophase. The insects were placed in the test area about half an hour before each experiment to acclimate them to room conditions and to eliminate disturbance due to transport. For each trial, one insect was placed at the downwind end of the flight tunnel and observed for 10 min. Movement toward the pheromone was scored on a scale of 1 to 4, with 1 = no movement, 2 = activity at the release point or movement of up to one-fourth the distance to the pheromone vial, 3 = movement one-fourth to one-half the distance to the pheromone vial; and 4 = movement more than halfway to the pheromone vial. Specific behavioral activities and the number of times each activity was repeated during the 10-min observation also were recorded. The behavioral activities observed (and codes used in Tables) were as follows: "alert" stance, with antennae

Table 1. Comparison of movement upwind (on a scale of 1-4) by *P. maculiventris* in wind tunnel trials with and without a synthetic pheromone

Test insects	N	Movement score* (SEM)		P**
		Pheromone	Control	
Females				
Newly molted	61	1.91 (0.13)	1.93 (0.13)	0.8591
Starved 2-d	69	2.09 (0.19)	1.36 (0.08)	0.0025**
4-d	61	2.26 (0.18)	2.03 (0.15)	0.4719
6-d	42	3.05 (0.20)	1.90 (0.17)	0.0003**
Fed 2-d	79	1.69 (0.08)	1.68 (0.07)	0.9555
4-d	54	1.86 (0.08)	1.88 (0.06)	0.8310
6-d	69	1.86 (0.15)	1.88 (0.12)	0.2903
Males				
Newly molted	54	1.40 (0.09)	1.71 (0.15)	0.1249
Starved 2-d	43	1.86 (0.08)	1.68 (0.10)	0.1842
4-d	68	2.36 (0.17)	1.69 (0.15)	0.0042**
6-d	59	2.70 (0.21)	1.69 (0.12)	0.0005**
Fed 2-d	69	1.72 (0.13)	1.65 (0.10)	0.8744
6-d	92	1.88 (0.13)	1.65 (0.08)	0.6267
Nymphs				
Starved 2-d	30	1.80 (0.13)	1.80 (0.16)	0.7621

* 1—no movement, 2—activity at release point or movement up to ¼ distance to pheromone vial, 3—movement ¼-½ distance to vial, 4—movement >½ distance to vial.

** Based on Wilcoxon 2-sample test; differences significant at $P \leq 0.05$ are indicated by **.

extended toward the flow of air (Alert); rubbing antennae with forelegs (Antennae); flight or fluttering of wings (Flutter); extension of proboscis or rubbing proboscis with forelegs (Proboscis); walking "on stilts", i.e., on the tips of tarsi (Stilts); rubbing forelegs against each other (Forelegs); rubbing hindlegs against each other (Hindlegs); and rubbing wings and hindlegs against abdomen (Rub Abd.).

Movement scores and numbers of times that different behavior activities were observed for insects exposed to pheromone were compared with those same parameters for control insects (those exposed to airflow in the wind tunnel but without the pheromone). Visual inspection of normal plots showed that data were not normally distributed, which was not surprising given the discrete nature of the response data. Therefore, data were analyzed using Wilcoxon 2-sample tests (proc npar1way of SAS [SAS Institute 1990]) for each behavioral parameter, and for each gender, age, and condition (starved or fed) of test insect. Because laboratory and field insects were assigned randomly to all experimental insects, we also conducted Wilcoxon tests directly comparing laboratory and field insects over all trials.

Table 2. Comparison of behavioral responses by *P. maculiventris* adult females in wind tunnel trials with and without a synthetic pheromone

Test insects	N	Behavior*	No. responses (SEM)		P**
			Pheromone	Control	
Newly molted	61	Alert	0.63 (0.16)	0.00 (0.00)	0.0003
		(Antennae)+	0.09 (0.07)	0.48 (0.15)	(0.0073)+
Starved 2-d	69	Antennae	0.42 (0.12)	0.11 (0.05)	0.0371
		Alert	0.33 (0.10)	0.00 (0.00)	0.0009
		Forelegs	0.24 (0.07)	0.00 (0.00)	0.0019
Starved 4-d	61	Stilts	0.68 (0.26)	0.07 (0.05)	0.0363
Starved 6-d	42	Flutter	1.29 (0.41)	0.38 (0.23)	0.0156
		Rub abd.	1.19 (0.41)	0.24 (0.12)	0.0362
		Alert	0.52 (0.15)	0.38 (0.23)	0.0211
Fed 2-d	79	Flutter	0.13 (0.06)	0.00 (0.00)	0.0139
Fed 4-d	54	Alert	0.86 (0.19)	0.36 (0.11)	0.0223
		Hindlegs	0.57 (0.19)	0.00 (0.00)	0.0005
		Proboscis	0.57 (0.11)	0.09 (0.05)	0.0001
		Flutter	0.29 (0.10)	0.00 (0.00)	0.0013
		(Rub abd.)+	0.00 (0.00)	0.67 (0.15)	(0.0007)+
Fed 6-d	69	Hindlegs	0.19 (0.06)	0.00 (0.00)	0.0208

* Alert—antennae extended toward source of airflow, Antennae—rubbing antennae with forelegs, Flutter—flight or wing fluttering, Forelegs—rubbing forelegs together, Hindlegs—rubbing hindlegs together, Proboscis—extension of or rubbing proboscis, Rub abd.—rubbing wings and hindlegs against abdomen, Stilts—walking on tips of tarsi.

** Based on Wilcoxon 2-sample test; only behaviors with significant differences ($P \leq 0.05$) are shown.

\+ Indicates greater response in control than in pheromone-exposed insects.

Results

Newly-molted adults showed no significant difference in movement upwind in the pheromone plume compared with movement in the control air plume (Table 1). Significant movement in the pheromone plume was shown by 2-day and 6-day-old starved females and by 4-day and 6-day-old starved males (Table 1). Neither fed females, fed males, nor nymphs responded to the pheromone (Table 1).

Significantly greater frequency of various behaviors was recorded for insects exposed to the pheromone than for those exposed to air only for both starved and fed females (Table 2) and starved and fed males (Table 3), but not for fifth-instar nymphs. Significant positive responses in *P. maculiventris* adults occurred most often for "alert" stance with antennae extended upwind, flight or wing-fluttering, and rubbing antennae. Positive responses to pheromone also were observed for proboscis extension or rubbing, bugs walking "on stilts", and rubbing forelegs, hindlegs, and

Table 3. Comparison of behavioral responses by *P. maculiventris* adult males in wind tunnel trials with and without a synthetic pheromone

Test insects	N	Behavior*	No. responses (SEM)		P**
			Pheromone	Control	
Newly molted	54	Alert	0.63 (0.15)	0.25 (0.11)	0.0474
		(Antennae)+	0.00 (0.00)	0.38 (0.13)	(0.0018)+
Starved 2-d	43	Proboscis	1.19 (0.18)	0.64 (0.14)	0.0233
		Forelegs	0.57 (0.18)	0.00 (0.00)	0.0017
		Antennae	0.52 (0.18)	0.00 (0.00)	0.0038
Starved 4-d	68	Flutter	0.95 (0.24)	0.00 (0.00)	0.0003
		Stilts	0.30 (0.12)	0.00 (0.00)	0.0100
		(Antennae)+	0.00 (0.00)	0.52 (0.18)	(0.0070)+
Starved 6-d	59	Flutter	0.63 (0.24)	0.00 (0.00)	0.0032
		Alert	0.57 (0.16)	0.00 (0.00)	0.0004
Fed 2-d	69	Rub abd.	0.25 (0.10)	0.03 (0.03)	0.0282
		Antennae	0.25 (0.09)	0.05 (0.04)	0.0434
		Proboscis	0.19 (0.07)	0.03 (0.03)	0.0297
Fed 6-d	92	Antennae	0.35 (0.08)	0.15 (0.08)	0.0314
		Flutter	0.35 (0.15)	0.00 (0.00)	0.0279
		Stilts	0.12 (0.04)	0.0 (0.00)	0.0278

* Alert—antennae extended toward source of airflow, Antennae—rubbing antennae with forelegs, Flutter—flight or wing fluttering, Forelegs—rubbing forelegs together, Proboscis—extension of or rubbing proboscis, Rub abd.—rubbing wings and hindlegs against abdomen, Stilts—walking on tips of tarsi.

** Based on Wilcoxon 2-sample test; only behaviors with significant differences ($P \leq 0.05$) are shown.

\+ Indicates greater response in control than in pheromone-exposed insects.

abdomen (Tables 2 and 3). There were no clear-cut behavioral differences between starved and fed insects or between male and female insects (Tables 2 and 3). Antenna-rubbing by newly-molted females, males, and 4-d starved males, and rubbing abdomen by 4-d fed females were observed more frequently in the control insects than in the pheromone-exposed insects (Tables 2 and 3).

Over all tests, insects from the "field colony" showed a greater response to the pheromone than those from the laboratory colony in terms of movement scores (Table 4) and behavioral activities (Table 5). Field colony insects moved toward the pheromone significantly more than toward the control air flow ($P = 0.0045$); the response by laboratory insects was not significant ($P = 0.0905$; Table 4A). In addition, a direct comparison of field and laboratory-reared insects showed greater activity by field colony insects both in the presence of the pheromone and under control conditions (Table 4B). Similarly, both field and laboratory insects showed various behavioral responses to the pheromone (Table 5A), but in a direct comparison between the

Table 4. Comparison of movement upwind (on a scale of 1-4) by all field-colony and all laboratory-colony *P. maculiventris* in wind tunnel trials with and without a synthetic pheromone

		Movement score* (SEM)		
A. Test insects	N	Pheromone	Control	*P***
Field	468	2.15 (0.06)	1.84 (0.05)	0.0045**
Laboratory	402	1.84 (0.06)	1.65 (0.04)	0.0905
		Movement score* (SEM)		
B. Test condition	N	Field	Laboratory	*P***
Pheromone	427	2.15 (0.06)	1.84 (0.06)	0.0018**
Control	443	1.84 (0.05)	1.65 (0.04)	0.0054**

* 1—no movement, 2—activity at release point or movement up to ¼ distance to pheromone vial, 3—movement ¼-½ distance to vial, 4—movement > ½ distance to vial.

** Based on Wilcoxon 2-sample test; differences significant at $P \leq 0.05$ are indicated by **.

two, behaviors with significant differences were always greater in field than in laboratory insects (Table 5B).

Discussion

Starved female and male *P. maculiventris* showed positive anemotaxis toward a synthetic pheromone in the wind tunnel; well-fed males and females did not. This supports the hypothesis that *P. maculiventris* adults use the pheromone as a cue indicating presence of prey, in addition to a mating cue. However, there may also be a physiological explanation for the lack of response by well-fed insects; for example, well-fed insects may use their energy to digest food rather than fly in search of additional prey. Newly-molted and 2-d-old starved *P. maculiventris* males did not respond to the pheromone in terms of movement; 4 and 6-d starved males did. The premating period of the adult is about 5 d (Mukerji and LeRoux 1965); thus, as adults become sexually mature, they may respond more to the pheromone as a means of finding a mate. Starved adults probably respond more as they become hungrier as well.

Fed and starved insects showed increased incidence of various activities, especially extending their antennae upwind ("alert" stance), flight or fluttering of wings, and rubbing their antennae in the presence of the pheromone. Although detailed investigations of odor or taste receptors have not been done for *P. maculiventris,* insect olfactory receptors are usually found on the antennae (Schneider 1986). Recent studies of another heteropteran (*Lygus lineolaris,* Family Miridae) indicated olfactory sensillae present on the second and third antennal segments of adult bugs but not fifth instars (Dickens et al. 1995). A putative odorant-binding protein was also found in this species, localized to the antennae. Thus, behavior such as extending antennae upwind and rubbing antennae may reflect stimulation of olfactory sensillae by the pheromone. Nymphs in our study did not respond to the synthetic pheromone, either

Table 5. Comparison of behavioral responses by all field-colony and all laboratory-colony *P. maculiventris* in wind tunnel trials with and without a synthetic pheromone

			No. responses (SEM)		
A. Test insects	N	Behavior**	Pheromone	Control	P^+
Field	468	Proboscis	0.51 (0.06)	0.25 (0.04)	0.0013
		Alert	0.41 (0.05)	0.21 (0.03)	0.0042
		Flutter	0.27 (0.06)	0.15 (0.04)	0.0084
		Stilts	0.09 (0.03)	0.03 (0.02)	0.0242
Laboratory	402	Alert	0.48 (0.06)	0.31 (0.04)	0.0068
		Flutter	0.24 (0.05)	0.02 (0.01)	0.0001
		Hindlegs	0.11 (0.03)	0.06 (0.02)	0.0431
			No. responses (SEM)		
B. Test condition	N	Behavior**	Field	Laboratory	P^+
Pheromone	427	Proboscis	0.51 (0.06)	0.30 (0.05)	0.0205
		Antennae	0.43 (0.06)	0.25 (0.05)	0.0070
		Forelegs	0.28 (0.04)	0.09 (0.02)	0.0019
Control	443	Forelegs	0.27 (0.05)	0.11 (0.03)	0.0176
		Flutter	0.15 (0.04)	0.02 (0.01)	0.0033

** Alert—antennae extended toward source of airflow, Antennae—rubbing antennae with forelegs, Flutter—flight or wing fluttering, Forelegs—rubbing forelegs together, Hindlegs—rubbing hindlegs together, Proboscis—extension of or rubbing proboscis, Stilts—walking on tips of tarsi.

+ Based on Wilcoxon 2-sample tests; only behaviors with significant differences are shown.

through movement upwind or increased activity, despite evidence of nymphal responsiveness in other studies (Aldrich 1988). Morphological studies would indicate if nymphs as well as adults in this species have olfactory sensillae capable of responding to the pheromone.

The division between contact chemoreception and olfaction is not always clearcut, especially at short range (as in our small wind tunnel); contact chemoreceptors in insects are usually found on the proboscis, tarsi, and palpi (Städler 1984). Thus, behaviors such as proboscis extension and rubbing of forelegs and hindlegs (also observed in some insects in our study in the presence of the pheromone) may reflect stimulation of contact chemoreceptors by high concentrations of the pheromone.

The four cases in which insects responded significantly more to the control air stream than to the pheromone may be due to Type II statistical error, likely here because of the large number of Wilcoxon 2-sample tests that were done (Snedecor and Cochran 1980). Indeed, some of the specific significant positive responses to the pheromone were likely also spurious; however, the preponderance of positive significant responses validates the overall pattern.

Insects one to three generations removed from the field showed greater response

to the synthetic pheromone than adults from a 2-year-old laboratory colony. Insects reared in the laboratory have a much smaller arena to search than insects in the field. With diminished need for pheromone due to the easy availability of prey and mates, the genetically determined response to the pheromone may not be selected for and hence may decline in laboratory populations. These results indicate the importance of using field-collected rather than laboratory-reared insects in studies where behavioral response to pheromones is of interest.

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