Active Spaces of Pheromone Traps for *Plodia interpunctella* (Lepidoptera: Pyralidae) in Enclosed Environments

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ABSTRACT Pheromone traps of different types vary considerably in their attractive ranges and trapping efficiency. This report examines physical and behavioral factors that affect the attractive range of pheromone traps for *Plodia interpunctella* (Hübner) in enclosed areas. The lures in a trap used to target infestations in department stores emitted (*Z*,*E*)–9,12-tetradecadien-1-ol acetate at ≈2.3 ng/h, or 10% of typical rates for field-trap lures. Males exhibited flight or wing-fanning responses at distances up to ≈4 m from the traps, which is in good agreement with predictions of previous pheromone dispersal models. At distances of ≈0.5 m, the sound pressure level of wing beats (and thus the wing aerodynamic power output) by males responding to pheromone was significantly higher than the sound pressure level of wing beats in the absence of pheromone. Responsiveness to pheromone habituated rapidly after initial exposure (≈3 min half-life), and the aerodynamic power output declined quickly to levels measured without pheromone. The habituation response may be reproductively advantageous by allowing moths to conserve energy when a mate is not located quickly. It contributes to the ability of short–range pheromone traps to spatially target infestations of *P. interpunctella* in department stores by decreasing the attractive ranges from 4 m to 2–3 m within 5–10 min after the moth's initial exposure to pheromone.

KEY WORDS *Plodia interpunctella*, meal moth, sex pheromone, stored products, habituation, spatial targeting

PHEROMONE TRAPS ARE used routinely to monitor infestations in large stored product facilities and to pinpoint infestations (e.g., Vick et al. 1986, Bowditch and Madden 1996, Plarre 1998). Precision targeting is possible partly because the range of attraction of a pheromone trap, its active space (Bossert and Wilson 1963), is usually smaller in a typical storage environment than in the field. Three factors are known to contribute to this reduced range. First, orientational cues are reduced in an enclosed environment with no consistent wind speed and direction (Murlis et al. 1992, Mankin et al. 1980a). Second, storage areas and department stores usually contain numerous surfaces that adsorb and then re-emit pheromone, competing with the trap lure (Mankin et al. 1980a). Third, habituation can reduce the effective active space still further if the insect does not locate a trap soon after it detects the pheromone (Shorey and Gaston 1964; Bartell and Lawrence 1973, 1977; Mafra–Neto and Baker 1996). A limited trapping range enables the pinpointing of localized infestations, however, and short-range traps have been developed specifically to assist in precision targeting efforts.

Short-range traps that target infestations have recently become even more useful with the introduction of spatial analyses into insect pest management programs (e.g., Arbogast et al. 1998, Brenner et al. 1998). A pheromone-baited trap for *Plodia interpunctella* (Hübner), for example, has been successfully used in spatial targeting surveys of department stores and warehouses (Arbogast and Mankin 1997).

To improve the effectiveness of monitoring techniques, we conducted a study to quantify physical and behavioral factors affecting the attractive range of the *P. interpunctella* spatial survey traps. We measured the attractive range of the traps and compared the observed behavior with the predictions of pheromone dispersal equations.

Materials and Methods

Insects. The *P. interpunctella* in this study were taken from a colony established with field-collected insects from Alachua and Levy Counties, FL. The larvae were reared on a cereal diet (Silhacek and Miller 1972) and maintained at 27 ± 1°C, 60 ± 2% RH, and a photoperiod of 12:12 (L:D) h. In preparation for bioassays, pupae were removed from the colony and sorted by sex. Adult males were placed in a separate cage on the day they emerged.

Observation Arenas. The enclosed environment was a shed (3.25 by 8.84 by 2.44 m) maintained at the same temperature and relative humidity as the rearing incubator. A door and an air conditioner were at opposite sides of the shed. Reference points were marked relative to a central axis from the door to the air conditioner (1.2 m above the floor).

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To characterize the pheromone dispersal patterns as precisely as possible, the shed was isolated from external airflow patterns, and the internal airflow convection patterns were monitored. The shed had no windows and all openings were sealed to eliminate drafts. Plume movement and airflow were checked at different positions in the shed with a hot wire anemometer (model 8470, TSI, St. Paul, MN) and a smoke generator (model FVSP003, TEM Engineering, Crawley, England). The measurements included tests under bioassay conditions and tests to simulate typical department store conditions. During bioassays, observers remained stationary and air conditioning was turned off 10 min before testing. For simulation of department store conditions, observers walked on a tangent that passed within 30 cm of the release point of a smoke plume and the tip of the anemometer.

A bank of six 40 W fluorescent bulbs operated during the light phase. A 15-W tungsten bulb operated during the dark phase. Light levels ranged from ≈0.5 lux at either end of the shed to ≈2 lux at the center during the dark phase, as measured with a light meter (model 403125, Extech Instruments, Waltham, MA) near the central axis. In the light phase, the corresponding levels were ≈80 and ≈200 lux, respectively.

The Plexiglas wind tunnel (61 by 61 by 152 cm) had a mesh filter inlet and outlet. Air conditioned laboratory room air at 25°C was pulled at 5 cm/s from the inlet, passing through the tunnel into a vacuum at the outlet. Tests were done during the dark phase at a level of ≈1 lux.

Pheromone Traps. Two types of sticky trap, SP-Locator (AgriSense, Mid Glamorgan, UK) and Pherocon II (Trécé, Salinas, CA), were tested in the wind tunnel, each with 2 different *P. interpunctella* lures, Minimoth (AgriSense) and IMM+4 (Trécé). The SP-Locator traps with Minimoth lures were selected for further bioassays in the research shed. To enable comparisons with the predictions of pheromone dispersal models, the emission rates of 5 Minimoth lures (septa) were measured by procedures described in Mayer and Mitchell (1998). The lures were placed in a hood for 10 d at 22–28°C and the emissions were passed through an adsorbent for 3.5 h at 96 h and at 240 h. The amounts collected were quantified by gas chromatography, calibrated against 200 ng of a n-tetradecane internal standard.

Bioassays. For wind tunnel bioassays, individual 0- to 1–d–old males were released 85 cm downwind of a pheromone trap and observed for 5 min. The total number of flying and trapped males was recorded.

Two different bioassays were done in the shed. For tests of initial activity, simulating when a moth first enters the active space of a pheromone trap, 10 moths (2–4–d after emergence) were placed in each of 4 screened cages (45.7 by 38.1 by 38.7 cm) suspended 1.2 m above the floor in a linear array, 1 m apart. Cage 1 was 2.4 m from the door and cage 4 was 3.4 m from the air conditioner. An unbaited trap was suspended midway between cages 1 and 2. Moths were left undisturbed for at least 1 h before testing to allow acclimation.

The beginning of a trial, $t_T = 0$, was specified as the time when a Minimoth lure was removed from its sealed package and positioned at the SP-Locator station. For 3 min, observers at each cage recorded the number of moths active at the beginning of each 30-s interval. Positive readings included moths in flight and those actively wing fanning and walking about on the screen. The 11 replicates were >48 h apart to reduce background pheromone levels.

Tests of longer duration were done to observe temporal patterns and compare observed attraction distances with predictions of pheromone dispersal models (Mankin et al. 1980a). The tests were identical to those measuring initial activity except for the following. A 5th cage was set 1 m beyond cage 4 (farthest from the door). The pheromone trap was removed from its position between cages 1 and 2 and, to control for positional effects, was stationed either 1.5 m in front of cage 1 or 1.5 m past cage 5. The 3-d-old males in each cage were observed for 15 min. There were 10 replicates at each pheromone station.

Acoustic System. Sounds of male *P. interpunctella* in flight were recorded with a microphone (Brüel and Kjær [B&K] model 4145, Nærum, Denmark) suspended inside an insect cage, with and without a pheromone trap adjacent to the cage. Cages in tests with pheromone exposure held 10 insects each, but cages in tests without pheromone held 70 to ensure that enough insects flew into a 3- to 8-cm radius within which the wing beats could be recorded at the microphone. The signals were amplified (B&K model 2610) by a factor of 10^4 (80 dB, where $dB = 20 \log_{10}(P/P_{ref})$, P is the sound pressure, and P_{ref} is a reference sound pressure, Beranek 1988). The recorded signals were digitized at 25 kHz and analyzed using a personal computer with the DAVIS spectral analysis system described in Mankin et al. (1994, 1996). Low-pass filtering at 10 kHz was used to eliminate aliasing artifacts. Calibrations of sound pressure level in decibels referenced to 20 μPa was performed by procedures described in Mankin et al. (1996). Spectrograms were constructed from 0.5- to 1.0-s intervals of 5 individual moth flights with pheromone and 5 without pheromone exposure. Individual spectra contained 4096 points covering a 0.1638–s interval, and the spectra were spaced 0.1 s apart.

Statistical Analysis. Comparisons of numbers of active moths and analyses of the temporal patterns of responses in different cages were performed using SAS PROC GLM and PROC NLIN (SAS Institute 1988). For analysis of tests that measured initial activity, the *Activity Level* was the sum of the numbers of insects flying or wing fanning at all seven 30-s intervals. Analyses of variance (SAS Institute 1988) were performed on fundamental (wing beat) frequencies, a sound pressure level. Chi-square tests (Box et al. 1978) were performed on the proportions of flying and captured males in the wind tunnel bioassays.

Table 1. Numbers of male *P. interpunctella* taking flight in wind tunnel and numbers captured with different combinations of pheromone traps and lures

Trap	Lure	No.		
		Tested	Flying[a]	Captured[b]
Pherocon II	IMM+4	31	27	23
Pherocon II	Minilure	38	26	15
SP-Locator	Minilure	32	29	23
SP-Locator	IMM+4	33	30	28

[a] $\chi^2 = 9.10$, df = 3, $P < 0.05$.
[b] $\chi^2 = 21.9$, df = 3, $P < 0.05$.

Results and Discussion

Wind Tunnel Bioassays. The wind tunnel bioassays of flight activity and trap capture revealed significant differences among 4 combinations of AgriSense and Trécé traps and lures (Table 1). The major differences were reductions in the numbers of males taking flight and captured with the Minilure septa, possibly because Minilure emission rates were lower than the IMM+4 emission rates.

Gas chromatography measurements confirmed that the Minilure had a low emission rate of (*Z,E*)-9,12-tetradecadien-1-ol acetate (ZETA), the primary pheromone component of *P. interpunctella.* There were no significant differences between measurements at 4 d and 10 d, so all measurements were pooled to obtain an average rate of 2.3 ± 0.26 ng per septum per hour at 24°C. This rate is approximately the same as the emission rate of ZETA from a female *P. interpunctella* (Sower and Fish 1975), and is much lower than the 10–100 ng/h levels typically used for monitoring in the field (e.g., Sanders 1981, Mitchell and Heath 1986, Hendricks et al. 1987). Because of the low emission rate, the Minilure was expected to have a short attractive range, and the SP–Locator with Minilure combination was tested further for its potential to pinpoint the locations of infestations in a department store or storage environment.

Bioassays of Initial Activity. Male *P. interpunctella* in cages 0.5 m from a SP–Locator trap with a Minilure exhibited flight and wing-fanning activity within 30 s after beginning a trial. The observed amplitudes of wing beats appeared elevated relative to their levels in the absence of pheromone. Thus, it was expected that the aerodynamic power output, P_O, which is proportional to the cube of the wing beat frequency times the cube of the wing beat amplitude (Sotavalta 1963, Wilkin 1985), also would be increased relative to its levels in the absence of pheromone unless it was counteracted by a change in the orientation of the wings. An increase in power output was confirmed by signal analysis of the acoustic recordings, examples of which are shown in Fig. 1. The power output is proportional to the square of the sound pressure (e.g., Beranek 1988). In this case, the mean sound pressure level increased from 51.2 ± 3.7–79.2 ± 0.8 dB over 0–500 Hz ($t = 16.4$, df = 10, $P < 0.01$). It should be noted that the sound pressure level at closest approach, next to the cage, could be 6–8 dB higher than the sound pressure level at 5–8 cm distances, but the observed differences in decibels greatly exceed these levels. The increase in power output was due primarily to the increased wing beat amplitude because the frequency increased only slightly from 64 ± 1.3–65.5 ± 1.0 ($t = 0.88$, df = 10, $P < 0.39$; not significant).

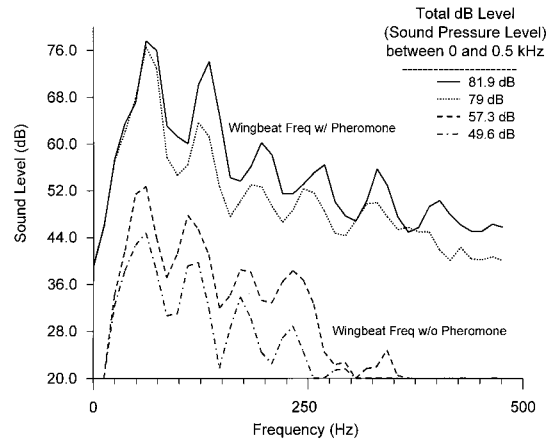

Fig. 1. Comparisons of wing beat power spectra and sound pressure levels of male *P. interpunctella* in the presence and absence of pheromone (frequency range, 0–500 Hz; sound pressure level reference, 20 μPa).

An increase in power output after exposure to pheromone is not surprising because ultrasonic communication has been implicated in *P. interpunctella* courtship. The reproductive performance decreases when the tegulae that produce ultrasonic pulses are removed from the male antennae or if the female tympanums are pierced (Trematerra and Pavan 1995).

No significant positional effects (cages 1 and 2 at 0.5 m) were expected, and none were detected (Table 2). However, the initial *Activity Level* was significantly lower at 1.5 and 2.5 m than for cages 1 and 2 at 0.5 m (Table 2), and the amplitudes of wing beats were similar to those observed in the absence of pheromone. This is to be expected if, on average, the pheromone concentration decreases at greater distances from the trap (Mankin et al. 1980a, Murlis et al. 1992, and see below).

Bioassays of Long-Term Activity. The temporal patterns of mean response to pheromone by *P. interpunctella* males in cages 1.5–5.5 m from the trap are shown

Table 2. Activity Level (mean ± SE) of male *P. interpunctella* in cages at different distances from trap during the first 3 min after exposure to lure

Cage No.	Distance from trap, m	Activity level
1	0.5	19.22a ± 2.75
2	0.5	16.89a ± 3.76
3	1.5	4.67b ± 1.96
4	2.5	1.78b ± 1.28

Mean values of activity level followed by same letter are not significantly different by Waller–Duncan *K*-ratio *t*-test (*K*-ratio = 100, $P < 0.05$, df = 32, residual mean standard error = 69.4).

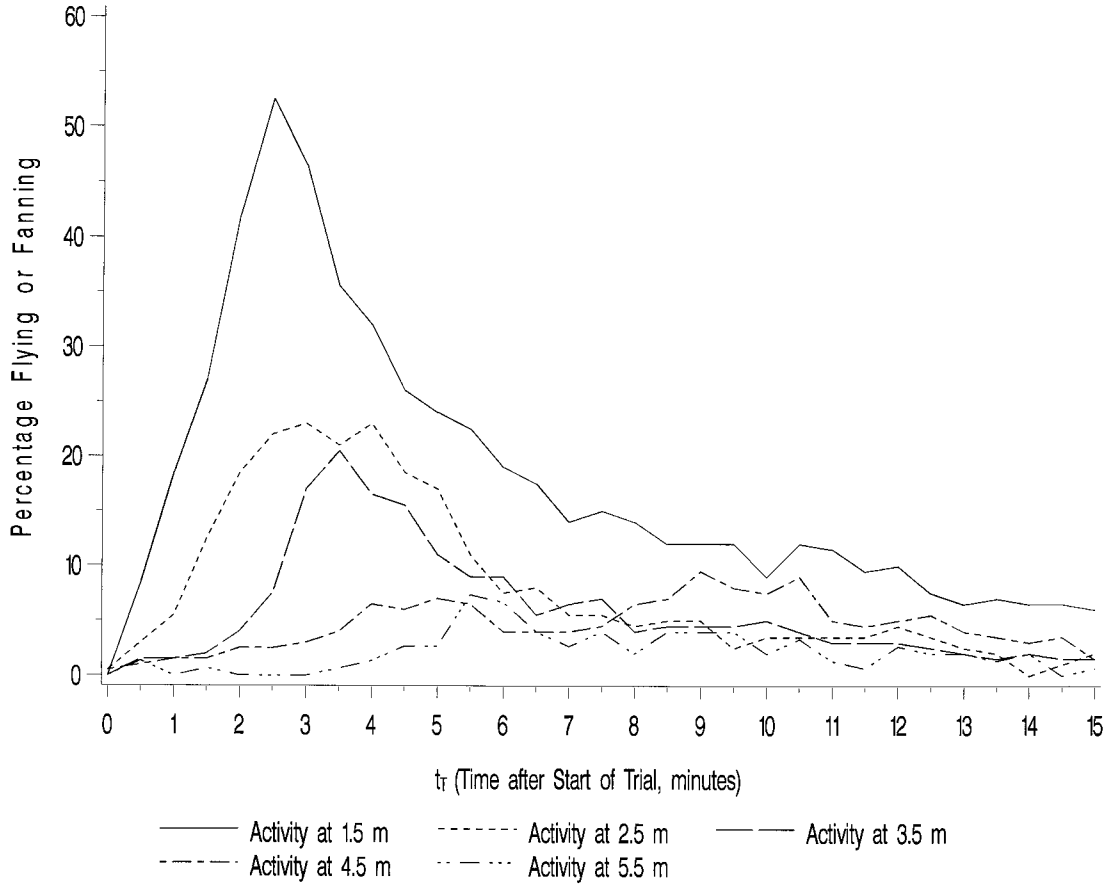

Fig. 2. Temporal pattern of mean response by *P. interpunctella* males in cages at different distances from pheromone trap: t_T (time after start of trial), minutes; *Percentage Flying or Fanning* (10× number flying or wing-fanning in cage at specified 0.5-min interval).

in Fig. 2. Analysis of variance (ANOVA) revealed no differences among counts in different 30–s intervals at either 4.5 m (mean = 4.58 ± 8.82; $F = 1.42$; df = 30, 589; $P > 0.075$) or 5.5 m (mean = 2.13 ± 6.25; $F = 1.35$; df = 30, 434; $P > 0.10$), although slight peaks in the mean response can be seen near $t_T = 5$ min in both cases. F values for observations at 3.5, 2.5, and 1.5 m were 4.48, 6, and 10.42 (df = 30, 589 and $P < 0.0001$), respectively. By this measure, responses are clearly present in observations of cages up to 3.5 m from the trap, but not in observations of cages at greater distances.

Pheromone Active Space. An objective of this study was to determine the attractive range of the short-range pheromone traps for *P. interpunctella* in enclosed environments and compare the observed behavior with the predictions of pheromone dispersal equations. Mankin et al. (1980a) derived methods to predict the range of behavioral response over time in a spherical enclosure with a boundary at distance, d_b. The pheromone concentration, C, at distance from the source, r, at time, t, is predicted from the equation:

$$C = Q(2\pi d_b r D)^{-1}\{\Sigma^{\infty}_{n=1}[(d_b h - 1)^2 + d_b^2\theta^2 n][d_b^2\theta^2_n + d_b h\,(d_b h - 1)]^{-1}\}[\sin(r\theta_n)/\theta_n][1 - \exp(-D\theta^2_n t)], \quad [1]$$

where θ_n is the nth positive root of the equation:

$$d_b \cot(d_b\theta_n) + d_b h = 1, \quad [2]$$

Q is the emission rate of the pheromone source, D is a diffusion coefficient that estimates the rate of pheromone dispersal, V_d, is a deposition velocity that estimates the rate at which pheromone deposits onto the boundary, and h is the ratio V_d/D. According to equation 1, the pheromone concentration is directly proportional to the rate and duration of emission and inversely proportional to the distance from the source and the diffusion coefficient, but the exact proportionality depends on the position of the boundary and the rate of deposition to the boundary surface.

The pheromone dispersal equation can be adapted for prediction of behavioral responses in the shed bioassays by making some assumptions about the boundaries of the shed, the pheromone diffusion co-

efficient, and the relationship between the behavioral response and the pheromone concentration. We consider first the estimates for these parameters and the assumptions on which they were based, and then consider the resultant predictions of the dispersal equation.

Pheromone Deposition Velocity and Distance to Shed Wall. Calculations with different values for V_d and d_b (Mankin et al. 1980a) demonstrated that these 2 parameters do not significantly affect the pheromone concentration except for positions near a boundary. Consequently, the concentrations near the cages and away from the shed walls can be calculated by approximating the shed as a sphere of large radius, e.g., setting $d_b = 10$ m, and setting the deposition velocity to a representative value typical of pheromone-wood or pheromone-vegetation interfaces, e.g., $V_d = 1$ cm/s (Mankin et al. 1980a).

Pheromone Diffusion Coefficient. The diffusion coefficient for pheromone dispersal can vary over a wide range from $\approx$0.03 cm^2/s in completely still air to >0.5 cm^2/s under turbulent conditions (Bossert and Wilson 1963, Mankin et al. 1980a). In these bioassays, the conditions were approximately those of still air. Within 5 min after turning off the air conditioner, plumes emitted from the smoke generator expanded slowly and did not move horizontally. Air velocity varied between 0.5 and 2 cm/s. However, these conditions are rarely encountered in a department store, and were not continuously present in the shed. In 10 tests where an observer walked past a hot wire anemometer probe, the air speed increased temporarily to 4.12 ± 0.17 cm/s and the wake created by the passage took 13 ± 0.37 s to dissipate. In tests where the anemometer was replaced with a smoke generator probe, the plume first drifted away from the observer during the approach, and then was sucked into a turbulent wake and dispersed as the observer passed. The diffusion coefficient would be large within the wake and smaller outside it. Operation of the air conditioner also caused the plume to move and disperse rapidly. The air velocity increased rapidly to 20 ± 5 cm/s within 30 s after starting the air conditioner. Because the dispersal equation does not directly incorporate the effects of variation in the diffusion coefficient over time, we estimated a value of D in equation 1 based on average conditions, intermediate between still air and turbulent convection extremes, $\approx$1 cm^2/s. The actual value could have been as low as 0.1 cm^2/s during much of the bioassay because the air conditioner was not in operation and the observers remained stationary.

Behavioral Threshold. The pheromone behavioral threshold, T_B, was defined by Bossert and Wilson (1963) as a minimum detectable concentration. Its magnitude depends somewhat on the type of bioassay and the specification of the criterion used to distinguish the pheromonal response from background. Mankin et al. (1980b) measured the *P. interpunctella* behavioral threshold by conducting wind tunnel bioassays at several different concentrations and 2 temperatures, specifying T_B as the concentration at which 50% flew upwind during a 3-min period. Those measurements can be used as a basis for estimating a behavioral threshold in the shed bioassay, but the thresholds cannot be specified with the same operational definition in both cases. The pheromone concentration was constant during the wind tunnel testing periods, but it increased continuously during the shed bioassay testing periods.

One way to relate the response measurements in the 2 *P. interpunctella* bioassays is to set $C = T_B$ and solve for t in equation 1. The solution for t then provides an estimate of the initial time at which $C \geq T_B$ at a specified distance from the source. The initial time can be measured in the shed bioassay as the time at which the moths first begin to respond in cages at different distances from the pheromone trap. The background activity level was 2–4% (see discussion of Fig. 2 above), so we chose a level of 5–10% flight activity in a test cage as an indicator that the concentration had risen above the behavioral threshold.

The behavioral threshold is dependent on many different environmental variables, including temperature. To account for this variation, we considered 2 different representative values for T_B in equation 1. Mankin et al. (1980b) measured the *P. interpunctella* upwind anemotaxis threshold as 5.6×10^{-7} ng/cm^3 at 23°C and 6.7×10^{-9} ng/cm^3 at 34°C. The 27°C temperature in the shed bioassays lies within the range of test temperatures.

Pheromone Lure Emission Rate. An estimate for the emission rate of the pheromone traps is provided by the measurements of the Minilure average emission rate (see wind tunnel bioassay section above), 2.3 ng/h = 6.39×10^{-4} ng/s. There may be an initial flush of high pheromone emission when a fresh lure is opened, so the actual emission rate could be greater than this value for a brief period when a new lure is 1st opened.

Predicted Initial Time of Response. Fig. 3 shows the predicted values for initial time of response at different distances from the pheromone trap at 23 and 34°C. We checked these predictions by plotting the observed times for 5 and 10% behavioral response on the same graph. Although there is some uncertainty in the estimates for Q, D, and T_B, the observed timing of initial response is in good agreement with the calculated values. The pheromone dispersal equation thus has considerable predictive validity over a 15-min period in an enclosure with restricted air movement.

In Fig. 3, the predicted and observed times of initial response first increase slowly and then rapidly with distance from the trap. Based on the distances at which the response times at 23 and 34°C begin to increase asymptotically, we estimate the active space of the traps in the shed at 27°C to be 4–5 m within 3–6 min after the start of a trial. After this initial phase of responsiveness, however, the active space decreases in size as discussed in the next section.

Habituation of Response. The percentage of flying or wing-fanning *P. interpunctella* rose to maximum levels within 2–5 min after initial exposure to pheromone (Fig. 2) and then declined in an exponential pattern in cages at 1.5, 2.5, and 3.5 m from the trap. The

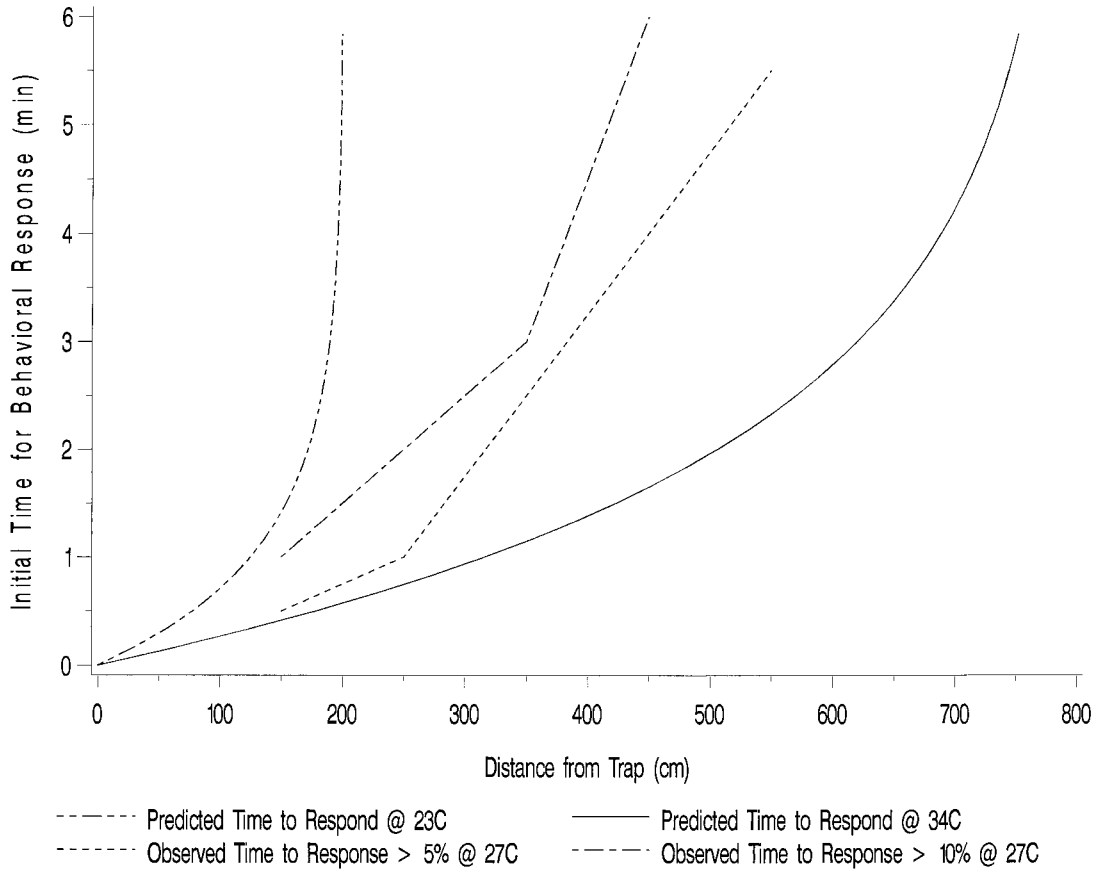

Fig. 3. Predicted time for pheromone concentration to reach behavioral response threshold levels at 23 and 34°C, and observed times for 5 and 10% of *P. interpunctella* males at 27°C to respond in cages at different distances from pheromone trap: *Distance from Trap*, centimeters; *Initial Time for Behavioral Response* (time when predicted concentration initially exceeds threshold or time when percentage response initially exceeds specified level), minutes.

essential characteristics of an exponential decline pattern are described by its half–life τ_H, or time for decline to 50% of maximal activity. To calculate the half–life for habituation, the behavioral responses were fitted to the equation:

$$\text{Activity} = A_M \exp(-t_N/t_R), \qquad [3]$$

where t_N and t_R are mathematically dimensionless parameters describing the time course of the behavioral response. Specifically, t_T is time after start of trial in min, *Activity* is the mean number responding at t_T/mean number responding at t_m, t_m is the time of maximum response, t_f is the total duration of the trial (in this test, 15 min), $t_N = [t_T - t_m]/[t_f - t_m]$, A_M is the maximum activity level, and t_R is a regression coefficient called the relaxation time. The half life and the relaxation time are related by equation: $\tau_H = \ln(2)$ (t_R) $(t_f - t_m)$. Parameters estimated by PROC NLIN (SAS Institute 1988) are listed in Table 3 for activity levels 1.5–3.5 m from the trap, and the resultant habituation curves are shown in Fig. 4.

The regression estimates for maximum activity and relaxation time overlapped, and the half lives of the pheromone responses were similar for all 3 cages, 2.25–3.25 min. Because these patterns of decline were similar, the activities in the closer cages to the trap always remained higher than in cages farther from the trap. It thus can be argued that the sooner a moth passes close to a trap, the more likely it is to search long enough to enter the trap.

Table 3. Estimated parameters (mean ± SE) in equations describing the decrease in activity of male *P. interpunctella* after initial exposure to lure

Distance from trap, m	Max activity, A_M	1/Relaxation, $1/t_R$	Half-life, τ_H	No. of reps.	Resid mean SE
1.5	0.89 ± 0.03	2.67 ± 0.16	3.25	23	0.003
2.5	0.93 ± 0.05	3.81 ± 0.33	2.25	23	0.005
3.5	0.91 ± 0.01	3.12 ± 0.20	2.57	23	0.003

Regression equation: activity = $A_M \exp(-t_N/t_R)$; with t_T (time after start of trial), minutes; activity (normalized as [mean number flying at t_T]/[mean number flying at t_m], where t_m is the time of maximum response), dimensionless; t_f (total duration of trial), 15 min; t_N (normalized time = $[t_T - t_m]/[t_f - t_m]$), dimensionless; A_M (maximum activity level), dimensionless; t_R (normalized relaxation time), dimensionless; τ_H (half-life, i.e., interval needed for relaxation to 50% of maximal activity), minutes.

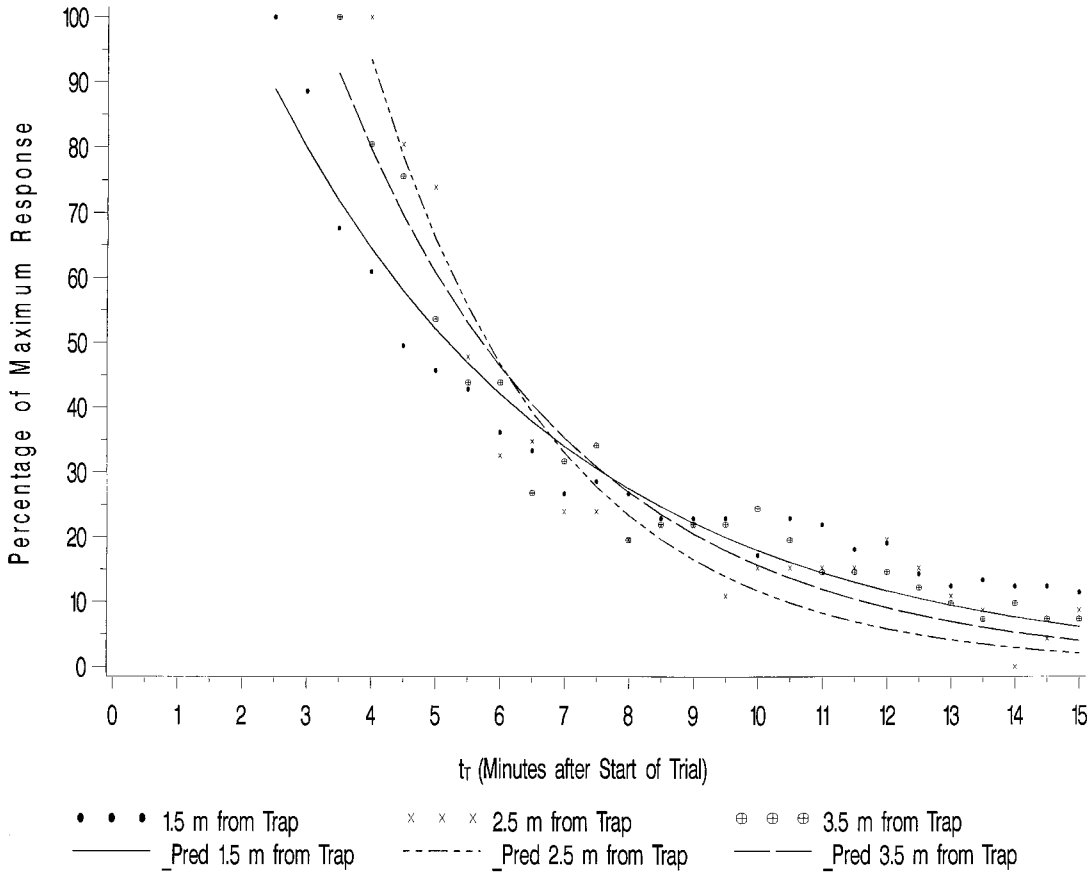

Fig. 4. Regression equation predictions and observed values for decline from peak mean response by *P. interpunctella* males in cages at different distances from pheromone trap: t_T (time after start of trial), minutes; *Percentage of Maximum Response* ([100× mean number responding at t_T]/[mean number responding at t_m], where t_m is the time of maximum response), minutes.

Incorporation of Habituation into the Pheromone Dispersal Equation. The original derivation of the pheromone dispersal equation in Mankin et al. (1980a) did not take into account the effects of habituation, but the results of this and other studies suggest how the habituation of responsiveness could be incorporated into equation 1. The initial part of the response pattern in Fig. 2 is clearly consistent with equation 1, which predicts that the pheromone concentration is highest at cages closest to the trap. The responses in the nearest cages to the trap are always greater than the responses farther from the trap. Equation 1 does not predict that the response in each cage will decline after an initial peak, but such results are consistent with the hypothesis of Mafra-Neto and Baker (1996) that brief exposure to pheromone temporarily raises the behavioral threshold but does not reduce the overall responsiveness. If we change T_B from a constant to a slowly increasing function of time after the beginning of pheromone stimulation, equation 1 predicts the following sequence of changes in pheromone concentrations and behavioral responses. At all cages, the concentration rises steadily after the start of pheromone emission. Behavioral responses appear after the concentration first rises above the behavioral threshold. At first, the number of insects responding in the cage increases as the pheromone concentration increases, but after a τ_H of 2–3 min, the behavioral threshold also begins to increase. The number of responding insects begins to decrease when the behavioral threshold rises past the pheromone concentration level at the cage. Note also that on average, the time for the threshold to rise above the higher concentrations present at the closest cages will be longer than the time to rise above the lower concentrations at the farthest cages, so the response will decline to background levels at the farthest cages 1st. This is the same pattern seen in Fig. 2.

Behavioral Basis for Effectiveness at Spatial Targeting. A goal of this study was to gain some insight into the behavioral basis for the observed effectiveness of pheromone traps in targeting moth infestations in department stores (Arbogast and Mankin 1997), factories (Bowditch and Madden 1996), and warehouses

(Vick et al. 1986, Pierce 1994). In these and other studies, traps spaced as closely as 2–3 m apart captured different numbers of moths consistently, and the numbers correlated with observed centers of infestation.

The results in this report help to quantify the factors that contribute to the effectiveness of these traps. First, the low emission rate of lures in commercially available stored–product insect traps results in an initially reduced active space of ≈4 m. Then, because of the low rate and high directional variability of air movement in enclosed facilities, the searching moth is not usually able to take advantage of well-defined pheromone filaments and wind direction cues that extend the length of the active space in field conditions (e.g., Mafra–Neto and Cardé 1994, Fadamiro and Baker 1997). If, because of these reduced orientational cues, the moth is unsuccessful in finding the source within a few minutes, the response to pheromone begins to habituate. This reduces the active space further down to 2–3 m.

Habituation can be a reproductively advantageous behavior because the flight patterns of mate seeking male moths are energetically expensive. The aerodynamic power expended in level flight has been estimated to be ≈10% of the total metabolic rate in the locust (Wilkin 1985). The relative power output during periods when the wing beat amplitude is large is greater than in flight where the insect is not rapidly changing direction or height. Consider also that in related stored product insects (Mankin and Hagstrum 1995), high levels of pheromone stimulation can trigger a pattern of intensive, restricted search during which less area is covered per unit time than in the absence of pheromone. If the stimulated moth does not pass into a region of even higher concentration closer to the pheromone source within a 5- to 10-min period, there is a strong likelihood that it is not near the source, and it would be advantageous to reduce energy expenditure and extend the search pattern to cover more territory.

Because of the reproductive advantages of such behavior, this pattern of increase in the behavioral threshold over time may occur for other insects in addition to *P. interpunctella* and *C. cautella* (Mafra-Neto and Baker 1996). The time courses of habituation in *Anagasta kuehniella* (Zeller) (Traynier 1970) and *Trichoplusia ni* (Hübner) (Shorey et al. 1967) were similar to the pattern in this report, so the neurophysiological mechanisms underlying the habituation behavior may have evolved similarly in all of these insects. Habituation is a generally observed phenomenon that has been proposed as one of the mechanisms of pheromone disruption (Cardé 1990, Cardé and Minks 1995).

The practical result of this combination of a low emission rate and habituation response pattern is that pheromone traps can often be used successfully in storage facilities and department stores to target aggregated insect infestations. This makes them easy to incorporate into spatial targeting techniques that are becoming important tools of integrated pest management (Brenner et al. 1998).

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