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# Effects of Pheromone Concentration and Photoperiod on the Behavioral Response Sequence to Sex Pheromone in the Male Brown-Banded Cockroach, *Supella longipalpa*

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*The effects of female sex pheromone concentration and time of day on behavioral responses of male brown-banded cockroaches were monitored with a two-choice olfactometer. The duration of each behavior or behavioral event in a deterministic response sequence and the probabilities of behavioral transitions were analyzed. Pheromone concentration had a significant effect on all behaviors in the response sequence. The time of testing, relative to the entrainment photoperiodic regime, significantly affected behavioral events early in the sequence but not later-occuring behaviors. Although the probability of males choosing the pheromone rather than the solvent control was a function of the pheromone concentration, it was independent of the time of testing. By affecting the probability of behavioral transitions, the pheromone concentration and time of testing determined the number of insects exhibiting specific behaviors in the response sequence. The behavioral response sequence can be characterized by probabilities of behavioral transitions along with latencies of early behavioral acts.*

**KEY WORDS:** brown-banded cockroach; *Supella longipalpa*; sex pheromone; male response; behavioral sequence.

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## INTRODUCTION

Male insects respond to volatile female sex pheromones with species-specific behavioral sequences (Shorey, 1973; Roelofs and Cardé, 1977). The sequence is comprised of various spatially and temporally organized behaviors which usually include activation of the insect from a quiescent state, upwind orientation, and ultimately, location of the pheromone source. In many insects, the response sequence is affected by the ratio of the various components in the pheromone blend (Cardé *et al.*, 1975; Baker *et al.*, 1981; Linn and Roelofs, 1983) and different components may elicit different behaviors in the sequence (Roelofs and Cardé, 1977; Bradshaw *et al.*, 1983). Neuroactive compounds (e.g., carbaryl, octopamine, and yohimbine) were also found to exert their stimulating or inhibiting effects on different behaviors of the sequence (Linn and Roelofs, 1984).

The response to sex pheromones, measured as the percentage of insects exhibiting a particular behavior in the response sequence, is affected by physiological and environmental factors such as pheromone concentration, light intensity, portion of the entrained light/dark cycle, and ambient temperature (Shorey, 1976). Surprisingly, little is known about how such factors modulate the behavioral response sequence. In male gypsy moths, *Lymantria dispar* (L.), the probability and latency of wing-fanning, as well as the number of preflight behaviors preceding wing-fanning, were affected by pheromone concentration (Hagaman and Cardé, 1984) and by ambient temperature (Cardé and Hagaman, 1983). Ambient temperature has also been shown to affect orientation to the pheromone plume, initiation of upwind flight, and arrestment of upwind flight in male Oriental fruit moths, *Grapholitha molesta* (Busck), and pink bollworm moths, *Pectinophora gossypiella* (Sanders), in a flight tunnel assay (Linn *et al.*, 1988). In response to sex pheromone at different times of the day, the percentage of male codling moths (*Laspeyresia pomonella*) showing wing-fanning and upwind orientation was much higher in scotophase than in photophase, but the percentage of males showing nonanemotactic movement, such as hopping and walking, remained the same throughout the whole photoperiodic cycle (Castrovillo and Cardé, 1979).

Rust (1976) showed that in response to low pheromone concentrations, few males of the American cockroach, *Periplaneta americana* L., exhibited behaviors late in the response sequence (i.e., courtship wing-raising), while high concentrations elicited wing-raising in a large percentage of males. Moreover, older males showed a higher probability of exhibiting the late behaviors than young males (Silverman, 1977). It is unknown, however, what specific behavior(s) in the response sequence of the male American cockroach is most affected by age and pheromone concentration.

The female brown-banded cockroach, *Supella longipalpa* (F.) (Dictyop-

tera: Blattellidae) produces a volatile sex pheromone. Hales and Breed (1983) described a calling behavior during which the pheromone is released (Smith, 1988). Males respond to pheromone adsorbed onto filter paper with increased locomotor activity (Wright, 1977) and exhibit rapid antennal movement, running, and courtship wing-raising behavior in response to mature virgin females (Hales and Breed, 1983). In this investigation, we used a two-choice olfactometer to study the behavioral response sequence of males to female sex pheromone and to examine how the pheromone concentration and the time of testing relative to the entrainment photoperiodic regime affected the sequence.

## MATERIALS AND METHODS

### Insects

Large nymphs were collected from *S. longipalpa* colonies and transferred into incubators under controlled photoperiodic (12L:12D) and temperature (27°C) conditions. Newly emerged adult males and females were separated daily and the two groups were placed in separate vented rooms under the same light and temperature conditions. Water and dog food were provided ad libitum.

### Pheromone

The concentration of the female sex pheromone was measured by female-equivalents (FE): one FE is the extract of one 8-day-old virgin female. A stock solution of pheromone was obtained by extracting multiple groups of 8-day-old virgin females twice in 1 ml hexane for 5 min each. The crude extract was concentrated under nitrogen to 1 FE/50 $\mu$l, which was used to make a concentration series of 1, 0.1, 0.01, 0.001, and 0.0001 FE/50 $\mu$l. A concentration of 10 FE/50 $\mu$l was obtained by further concentrating the crude extract under nitrogen. All solutions were stored at −20°C.

Fifty microliters of pheromone solution were applied to a 50-mm$^2$ triangular filter paper (Whatman No. 1) and the solvent was allowed to evaporate. A control dispenser was treated with 50 $\mu$l of hexane. Each dispenser was attached to a cork with an insect pin and kept inside a glass vial until use (maximum, 30 min). Each treated dispenser was used in four tests only to minimize variation in the pheromone release rate.

### Behavioral Assays

Eight two-choice olfactometers each consisted of a Plexiglas tube (115 cm long × 4.5-cm ID) with a 45 × 4.5-cm Plexiglas divider sealed vertically in its upwind end. The pheromone and control dispensers were introduced into the

tubes at the upwind end through two holes (0.7-mm ID) which were equally spaced from the vertical divider. A cage made of a 20-cm-long tube with a metal screen gate was placed in the downwind (undivided) end and used to release males into the olfactometer. Eight olfactometers were connected symmetrically to a vacuum pump, which was set to provide a wind velocity of 20 cm/s in each tube during assays and about 250 cm/s at other times to minimize contamination of the tubes with pheromone. The tubes were rinsed weekly with hexane. Fluorescent lights ensheathed in red photographic filters were placed 60 cm below the olfactometers to facilitate observations during scotophase.

A single 25- to 30-day-old male was placed into each of eight cages and allowed to acclimate to the airflow for 30 min. The assay was initiated by opening the gate and positioning the pheromone and control dispensers at the upwind end. The behaviors of each insect were observed through the transparent tube wall and recorded with a microcomputer-based time-event recorder. Males were allowed 120 s to initiate movement and a maximum of 240 s to complete the sequence. Each male was used once and discarded.

### Experimental Design and Data Analysis

In order to test for differences within either the photophase or the scotophase, the 24-h L:D cycle was divided into eight equal intervals of 3 h each, and six concentrations of pheromone were tested in the middle of each interval. Since there were no significant differences in the response sequence within either photophase or scotophase, data were combined from the middle 6 h of each, respectively. Thus, 12 concentration-time treatment combinations were obtained. For each treatment combination, 32 males were tested.

The probabilities of five conditional transitions and the latencies, durations, and intervals of behavioral events were calculated. The probabilities were then analyzed by the *G*- test (Sokal and Rohlf, 1981). Durations of behavioral events were analyzed by two-way ANOVA and Duncan's multiple-range test for mean separation after log $(x + 1)$ transformation (SAS Institute, 1985).

## RESULTS

The percentages of males completing each of the six successive behaviors, in response to different pheromone concentrations in both scotophase and photophase, are shown in Fig. 1. For any concentration of pheromone, the responses in scotophase (Fig. 1B) were higher than in photophase (Fig. 1A). For both periods, higher pheromone concentrations elicited greater responses. However, whereas in the scotophase the greatest increase in response occurred when the pheromone concentration increased from 0.001 to 0.01 FE, a similar increase

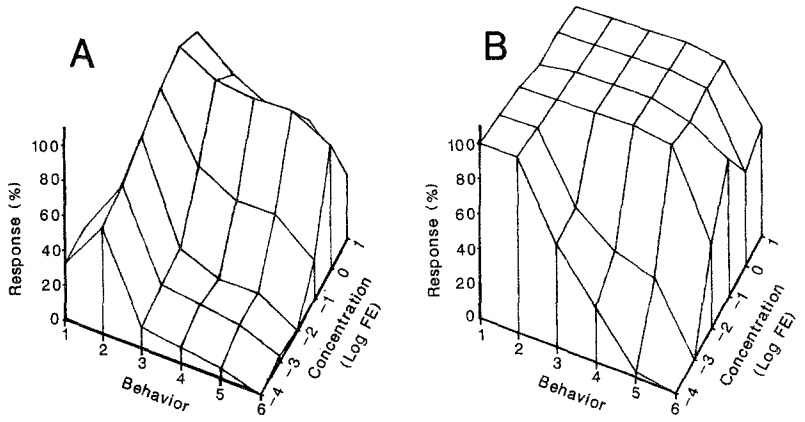


**Fig. 1.** The behavioral response of *Supella longipalpa* males to various concentrations of pheromone in the photophase (A) and scotophase (B). The behaviors are (1) antennae waving before introducing pheromone, (2) antennae waving after introducing pheromone, (3) insect moving within cage, (4) running 70 cm from gate to divider (binary choice), (5) running 35 cm from binary choice to pheromone dispenser, and (6) mounting pheromone dispenser.

in response in the photophase required about 100 times higher concentrations of pheromone.

Pheromone concentration significantly affected all of the behavioral transitions ($P < 0.005$, three-way $G$ test, response x concentration x time of testing); higher concentrations generally resulted in higher probabilities of transition between successive behaviors (Fig. 2). For all the conditional probabilities, except for the transition from reaching the divider (binary choice) to choosing the pheromone, the interactions between pheromone concentration and time of testing were significant, indicating that concentration affected the transitions differently in the scotophase than in the photophase (Fig. 2). For the early portions of the response sequence (until males exited the cage), the probabilities of transitions between successive behaviors were significantly higher in scotophase than in photophase (Figs. 2B and C; $P < 0.005$, three-way $G$ test). Probabilities of the two behavioral transitions later in the response sequence (percentage choosing the pheromone at the binary choice and percentage mounting the pheromone dispenser) were independent of the time of testing (Figs. 2D and E; $P > 0.1$, three-way $G$ test).

In the scotophase, almost all (99.4%) of the acclimated test males and control males waved their antennae before the test dispensers were introduced (Fig. 1B, behavior 1), thus precluding analysis of this behavior. On the other hand, in the photophase, only 22.3% (range, 16.7–35.7%) of the males waved

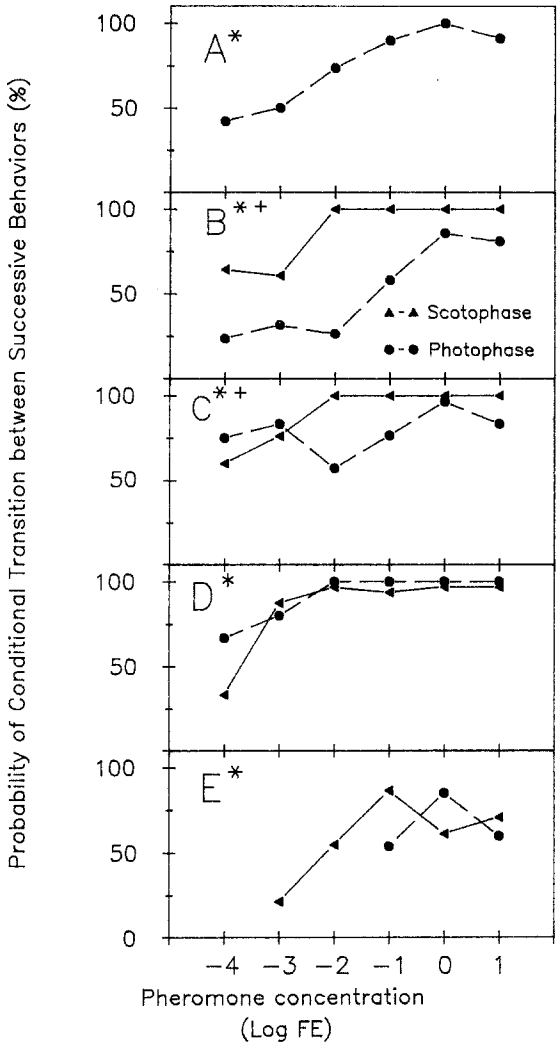


**Fig. 2.** Probability of conditional transitions of the behavioral response sequence of *Supella longipalpa* males at various pheromone concentrations in photophase (dashed line) and scotophase (solid line). (*) A significant effect of pheromone concentration on transition probability ($P < 0.05$, 3-way $G$ test). (+) A significant effect of time of testing on the transition probability ($P < 0.05$, 3-way $G$ test). The transitions are (A) percentage of insects that waved their antennae upon pheromone introduction, of all quiescent insects (antennal activation); (B) percentage of insects that ran within the cage, of all insects which exhibited antennal movement; (C) percentage of running insects which exited the cage; (D) percentage of insects that chose the pheromone dispenser, of all insects which made a binary choice; and (E) percentage of insects that mounted the pheromone dispenser, of all insects that reached the pheromone dispenser. All males which exited the cage reached the divider and males that chose the pheromone arm of the olfactometer reached the dispenser.

their antennae spontaneously (Fig. 1A, behavior 1, line hidden). The percentage of males with quiescent antennae being activated was a function of pheromone concentration: it increased from about 40 to 100% as the pheromone concentration was increased from $10^{-4}$ to 1 FE (Fig. 2A).

Higher pheromone concentrations also resulted in higher probabilities of all the other behavioral transitions (Figs. 2B–E). Thus, the effect of concentration on the percentage of males mounting the pheromone dispenser (Fig. 1, behavior 6) was realized through the combined effects on the probabilities of all preceding behavioral transitions. In contrast, although the time of testing affected most of the behavioral transitions, it did not influence the conditional probability of males choosing the pheromone and the conditional probability of males mounting the pheromone dispenser. For example, the percentage of males choosing the pheromone (of those making a choice) in scotophase was not different from that in photophase for any given pheromone concentration ($P > 0.1$, three-way $G$ test) (Fig. 2D). However, pheromone concentration affected this transition significantly ($P < 0.001$, three-way $G$ test). At concentrations greater than $10^{-2}$ FE, close to 100% of the males reaching the divider chose the pheromone (Fig. 2D). The probability decreased as the pheromone concentration decreased from $10^{-2}$ to $10^{-4}$ FE. At the lowest concentration ($10^{-4}$ FE), the probability of transition for this behavior was low (40%; $N = 15$, pooled from both light and dark periods) and not different from 50% random choice ($P > 0.15$, binomial test).

The temporal parameters measured were all affected significantly by the pheromone concentration ($P < 0.05$, ANOVA); higher pheromone concentrations resulted in longer durations of mounting the pheromone dispenser (arrestment) and shorter latencies and durations of all activation and upwind orientation behaviors (Fig. 3). Again, similar to its effect on conditional probabilities of behavioral transitions, the time of testing (relative to the L:D cycle to which the males were entrained) significantly affected the latencies and durations of early events, including the latency of running (Fig. 3B), the duration of running within the cage (Fig. 3C) and the time interval taken to reach the divider (Fig. 3D; $P < 0.05$, ANOVA). However, the time of testing did not affect later events in the response sequence including the duration of running along the divider to the pheromone dispenser (Fig. 3E) and the duration of mounting the pheromone dispenser (Fig. 3F; $P > 0.1$, ANOVA).

Running speeds along equal distances but in different portions of the olfactometer tube were different (Fig. 4). They were higher in the first 70 cm of the tube after the males exited the cage and significantly slower in the divided portion of the tube in both the light and the dark periods. Generally, running speeds in all portions of the tube increased with pheromone concentration, in both photophase and scotophase. However, during the photophase running speeds decreased in response to the highest pheromone concentration (10 FE) (Fig. 4A).

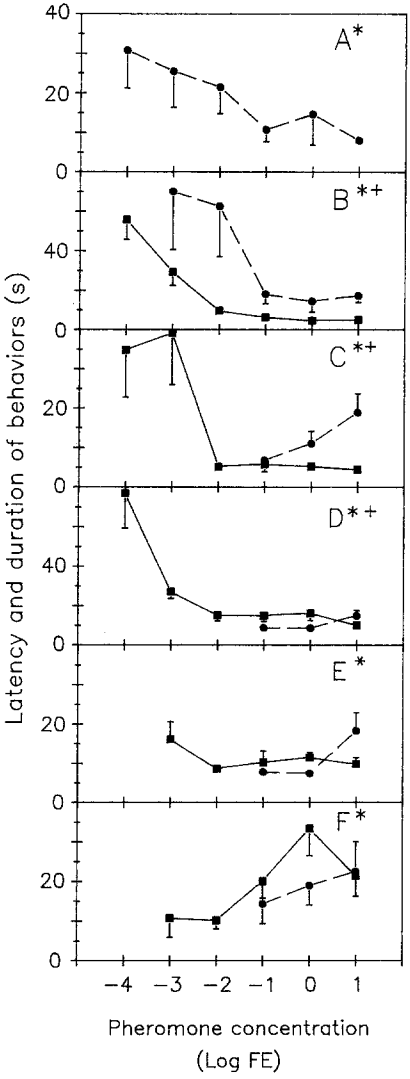


**Fig. 3.** Latencies, intervals, and durations (seconds) of behaviors in response to various concentrations of pheromone in the photophase (dashed line) and the scotophase (solid line). (*) A significant effect of pheromone concentration on transition probability ($P < 0.05$, 2-way ANOVA). (+) A significant effect of time of testing on the transition probability ($P < 0.05$, 2-way ANOVA). The latencies and durations are for (A) introduction of pheromone until activation of antennae, (B) antennal activation until onset of running, (C) interval between onset of running and exiting the cage, (D) duration of running from the gate to the binary choice, (E) duration of running from the binary choice to the pheromone dispenser, and (F) duration of mounting the pheromone dispenser.

## DISCUSSION

This study examines the temporal and sequential relations among the behavioral events that comprise the response sequence of the male brown-banded cockroach to female sex pheromone. The structure of the female's volatile pheromone has not been elucidated; therefore, we extracted whole females and related pheromone concentrations to female equivalents (FE). Preliminary data

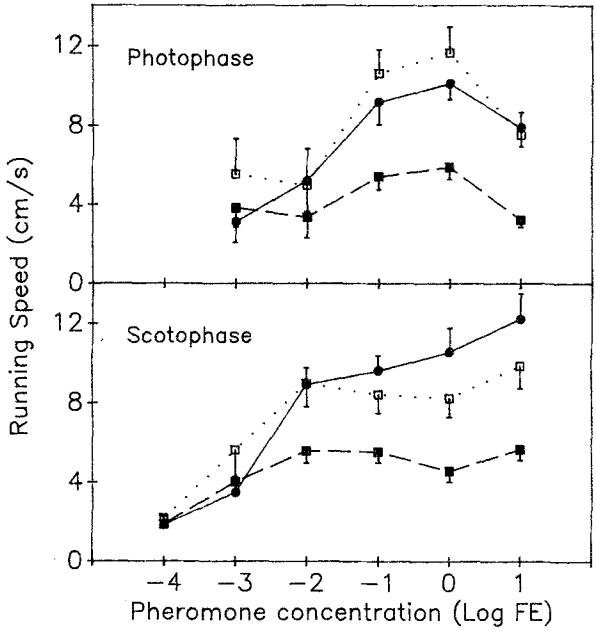


**Fig. 4.** Running speeds (cm/s) of males running in three portions of the olfactometer tube in response to various concentrations of pheromone. Solid line is for the first 35 cm; dotted line is for the second 35 cm; dashed line is for the last 35 cm in the divided portion of the tube.

indicate that hexane extracts and pheromone adsorbed onto Tenax-GC and Porapak Q in a flow-through system elicit identical responses.

Our results show that, by affecting the probabilities of conditional transitions (Fig. 2), the pheromone concentration and the time of testing relative to the entrainment conditions determined the number of insects exhibiting specific behaviors in the response sequence (Fig. 1). Pheromone concentration significantly affects latencies, durations, and transitions of all behavioral events in the response sequence of *S. longipalpa*. By examining the number of *P. americana* males exhibiting various behavioral components of the response sequence, Rust (1976) showed that higher pheromone concentrations were required to elicit later behaviors of the response sequence. He noted that wing-raising, which is a final step in courtship, occurred after a latency which decreased as the pheromone concentration increased. In our olfactometer, this latency would be composed of the latency of antennal activation, latency of running, duration of running within the cage, and duration of running in the tube (Fig. 3). Pheromone concentration influenced the total latency of the terminal behavior by affecting latencies and durations of these earlier occuring behaviors. No wing-

raising behavior was observed in any of our tests, all of which used single males. However, the wing-raising behavior was observed in preliminary tests when two or more males were released simultaneously in a single trial. This suggests that tactile stimulation, possibly involving contact chemoreception, is required to elicit wing-raising.

The behavioral response of males was highest in the scotophase, as was calling behavior in females (Hales and Breed, 1983). Spontaneous antennal waving and running also were more common in the scotophase. The time of testing affected the probabilities of transitions early in the sequence (Fig. 2B and 2C). However, once orientation to pheromone was elicited, at any given concentration, the conditional probabilities of progressing to the next event were similar in both photophase and scotophase (Figs. 2D and E). These results suggest that differences in behavioral responses between the scotophase and the photophase may be due to differences in internal states of "arousal" which, in response to low and high pheromone concentrations, respectively, lower central thresholds for subsequent stimuli. The time of testing also affected the latencies and durations of behaviors in the early phase of the response sequence (Fig. 3), and as expected, after the insect was excited, the time of testing did not affect the durations of later behaviors (i.e., duration of running through the last 35-cm portion of the tube and the duration of mounting the pheromone dispenser) (Fig. 3). Since all tested males were of the same age, it is unlikely that these differences reflect changes in sensitivity of the peripheral nervous system, but rather in the state of "arousal" of the central nervous system which has a diel periodicity (Payne *et al.*, 1970; Hall, 1980).

Hales and Breed (1983) showed that calling in female *S. longipalpa* followed a diel periodicity, with peak calling occurring in the scotophase. Smith (1988) established that this periodicity has a circadian component which may be modulated by shifts in the photoperiodic regime. Our data indicate that the periodicity of the orientation response of males mirrors the periodicity of calling in females. We have shown that in *S. longipalpa*, as in other species (e.g., Hawkins and Rust, 1977; Turgeon *et al.*, 1983), high concentrations of pheromone can obscure the periodicity of male response. Recently we established that an underlying circadian clock is also involved in regulating the periodicity of male response and that this behavior persists rhythmically in constant environmental conditions (Liang and Schal, 1990).

In our assays, a pheromone concentration of $10^{-2}$ FE oriented almost 100% of the males that reached the binary choice to the pheromone dispenser; increasing the concentration did not change this probability (Fig. 2D). However, the probability decreased at concentrations lower than $10^{-2}$ FE: in response to $10^{-4}$ FE, 40% of males which made a choice chose the pheromone, and this was not significantly different from random choice. Since the choice is made after the males are stimulated to initiate upwind orientation, when the central excitatory state is high, it is reasonable to expect that in both photophase and scotophase,

any pheromone concentration that stimulates upwind running, results in proper orientation to the pheromone source (Fig. 2D).

Running activity of males is generally used to bioassay sex pheromone activity in cockroaches (Bell, 1982). Typically, the numbers of times that a group of receptive males crosses a line and performs courtship wing-raising before and after stimulation with pheromone are compared. The line-crossing assay is less reliable for *S. longipalpa*. In a closed cage, males tend to orient toward the pheromone source and movement is arrested near the source (Smith and Schal, unpublished). Moreover, as shown for *P. americana* (Seelinger, 1985), groups of *Supella* males readily court each other when exposed to female pheromone, but individual males in our assays were never observed to court. Bell *et al.* (1974) speculated that the relationship of line-crossing with pheromone concentration was due to prolonged running and participation by more males as concentration increased. In *P. americana*, more males were activated by higher concentrations of pheromone (Rust, 1976), as in our results with *S. longipalpa*, and running speeds were similar among treatments of different pheromone concentrations (Seelinger, 1985). It thus appears that the number of participating males contributes the most to the line-crossing assay and running speed may add little to the separation of treatments. Although the overall running speeds were different at different concentrations in *S. longipalpa* (Fig. 4), we have not excluded qualitative differences among treatments, such as the frequency of stopping and the linearity of the running patterns.

Generally, the response to sex pheromones is quantified as the percentage of insects exhibiting a chosen behavioral act of a response sequence, which is usually easy to observe. However, since most insect sex pheromones are composed of several components, each possibly eliciting different behaviors in the responder (Roelofs and Cardé, 1977; Bradshaw *et al.*, 1983), it is necessary to examine the whole behavioral sequence. The commonly used approach to examine treatment effects on the behavioral sequence is to compare the percentage of insects exhibiting successive behaviors in the sequence. Using this method, various factors such as ratio and release rate of components and ambient temperature have been shown to exhibit quantitative and qualitative effects on behavioral components of the sequence (e.g., Linn and Roelofs, 1983). However, this method may be insensitive to some potentially important treatment effects on late phases of the response sequence. For example, a transition from behavior A to behavior B resulting in a 50% reduction of the total number of insects may be considered important. However, using this procedure, the same 50% reduction between behavior B and behavior C is considered less important because it results in only a 25% reduction in the total number of insects. Thus, significant effects of the treatment on later components of the sequence may be underestimated due to the low numbers of test insects entering later phases of the sequence.

Conditional probabilities have been used to show that insecticides affect

various transitions of the response sequence to sex pheromone in the male pink bollworm moth, *Pectinophora gossypiella* (Haynes and Baker, 1985; Haynes *et al.*, 1986). We have shown that, in *S. longipalpa*, the probability of conditional transitions between successive behaviors provides an excellent measure of the influence of various factors on the behavioral response sequence. For example, in response to $10^{-1}$ FE in the photophase (Fig. 1A), only 58% of the males that wave their antennae (behavior 2) initiate running within the cage (behavior 3) (Fig. 2B). The net result is a dramatic decline (42%) in the number of males proceeding to other behaviors; this transition is therefore considered a "key" transition, or a "sensitive" portion of the response sequence. Although a similar decline (46%) occurs between behavior 5 (reaching the pheromone dispenser) and behavior 6 (mountingthe dispenser) (Fig. 2E), fewer males enter this transition and therefore it contributes less to the total decline in the number of males completing the sequence (Fig. 1A). The probability of conditional transitions thus provides a more objective comparison of the relative contribution of each behavioral transition to the total decline in the number of insects completing the sequence. It also provides an objective assessment of the effects of specific factors (e.g., temperature, humidity, insecticides) on specific behavioral transitions.

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