

RESPONSE OF MALE POTATO STEM BORER MOTHS,
Hydraecia micacea (ESPER) TO CONSPECIFIC
FEMALES AND SYNTHETIC PHEROMONE
BLENDS IN THE LABORATORY AND FIELD

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(Received March 25, 1988; accepted June 30, 1988)

Abstract—Behavior of males of *Hydraecia micacea* (Esper) responding to virgin females and to synthetic pheromone blends were investigated in a laboratory wind tunnel. The synthetic blend consisted of saturated 14:Ac (68.9%), Z9-14:Ac (3.4%), E11-14:Ac (14.6%), and Z11-14:Ac (13.1%). Virgin females were significantly better lures than the four-component synthetic blend for most behaviors. By deleting components individually from the four-component blend, Z9-14:Ac, Z11-14:Ac, and saturated 14:Ac were found to be necessary for communication but E11-14:Ac was found to have no effect on typical pheromone-mediated reproductive behaviors. Close-range studies suggested that chemicals of low volatility, released from moths, were important in eliciting copulation attempts. Field studies reinforced laboratory findings regarding the effectiveness of different lures and indicated that *Heliothis* traps were the most effective for monitoring.

Key Words—*Hydraecia micacea*, Lepidoptera, Noctuidae, potato stem borer, sex pheromones, field trapping, reproductive behavior, tetradecenyl acetate, (Z)-9-tetradecenyl acetate, (E)-11-tetradecenyl acetate, (Z)-11-tetradecenyl acetate.

INTRODUCTION

The potato stem borer moth, *Hydraecia micacea* (Esper), is a periodic pest of numerous crops (Deedat et al., 1983). In the northeastern United States and

southern Canada, the major impact of this insect is on corn, which suffers from wilting of the axial leaves due to larvae feeding within the corn stalk. Although eggs are laid on leaves of weed grasses that surround fields, larvae migrate into fields, and consequently the incidence of damage caused by the insect is correlated directly with the presence of suitable grass oviposition sites (Deedat and Ellis, 1983). Population levels are variable between fields, and, while damage is usually restricted to the outer 20 rows, crop loss in some fields can be as high as 80% (Tetor, 1980).

Synthetic sex pheromones of Lepidoptera are used widely as lures for population monitoring and have potential for use in pest control, particularly when the pest species is distributed in isolated, low-density populations (Plimmer, 1982). We felt that the potato stem borer (PSB) was a good candidate for studies aimed at the development of pheromone-based control programs because reports of PSB infestations fit the criteria outlined above. However, prior to the development of control methods, it is necessary that the pheromone-mediated behavior be thoroughly understood. Consequently, we undertook laboratory study on aspects of the reproductive biology that are regulated by semiochemicals for this insect. Here we report the results of studies of the responses of PSB males to females and to various synthetic blends of pheromone components identified in earlier studies (Teal et al., 1983).

METHODS AND MATERIALS

General. Potato stem borers were reared at 25°C as described by West et al. (1985) using a diet modified from Hinks and Byers (1976). The insects were from a laboratory stock into which field-collected males were introduced each year. Insects were sexed as pupae and transferred to separate rooms that had reversed light cycles. The conditions were 14 hr: 10 hr (light-dark) with temperature at 26°C and 24°C (photophase-scotophase) and relative humidity of 55%. Emergence was checked 30 min prior to scotophase, and adults were transferred to nylon screen cages measuring 30 × 30 × 30 cm, which contained cotton wicks soaked with 10% sucrose solution. Insects used for all laboratory trials were 2 to 5 days old.

Chemical Solutions and Lure Formulations. All chemicals used for formulation of synthetic lures were purchased from Sigma Chemical Co. (St. Louis, Missouri) and were purified by high-performance liquid chromatography using a 25 × 2.5-cm (OD) 5- μ m silica column coated in situ with 15% AgNO₃ (Heath and Sonnet, 1980). The compounds were eluted with toluene. All chemicals were at least 99% pure as determined by capillary gas chromatographic (GC) analysis.

Analyses of pheromone component purity were conducted using 30 m ×

0.25 mm ID SPB-1 and Supelcowax 10 columns (Supelco, Bellefonte, Pennsylvania). Ratios of blend components were verified using both columns. Samples were run isothermally in the split mode at 165°C. Hydrogen was used as the carrier gas at a linear flow velocity of 38 cm/sec. A Hewlett-Packard (Avondale, Pennsylvania) 5790 GC equipped with a flame ionization detector and interfaced with a Hewlett-Packard 3390A integrator was used for all analyses.

White rubber septa (Sigma Chemical Co., St. Louis, Missouri, catalog No. S5509), used as pheromone dispensers, were Soxhlet extracted with methylene chloride for 24 hr and air dried prior to loading. Blends of synthetic compounds (see Table 1) loaded into lures included 500 μg of the four-component blend identified by Teal et al. (1983), which included tetradecenyl acetate (14:Ac) (68.9%), (*Z*)-9-tetradecenyl acetate (*Z*9-14:Ac) (3.4%), (*E*)-11-tetradecenyl acetate (*E*11-14:Ac) (14.6%), (*Z*)-11-tetradecenyl acetate (*Z*11-14:Ac) (13.1%), and blends from which one of the above components had been deleted. Blends were applied in 200 μl of isooctane to the large well of the septum, and septa were allowed to stand in a fume hood for two days to allow for solvent evaporation.

Bioassays. All laboratory studies were conducted 5–8 hr into the scotophase, which coincided with the peak period of pheromone release by females (West et al., 1984). Tests were conducted in a 2.0 \times 1.0 \times 0.5-m Plexiglas flight tunnel housed in a room with the same photoperiod, temperatures, and humidity maintained in rooms used to house adults. The excurrent end of the flight tunnel was fitted to a fume hood controlled by a variable transformer. Air was pulled through the tunnel at 0.5 m/sec and expelled outside the building.

Lures for all studies, including females, and synthetic blends, were housed in an 8 \times 10 \times 10-cm Plexiglas holding cage with aluminum screen on two opposing sides to allow for air flow through the cage. The holding cage for all trials was positioned in the center of the tunnel about 30 cm from the upwind end. All males used were quiescent before the trial. Males were transferred individually to a 2 \times 2 \times 8-cm Plexiglas cage suspended in the center of the tunnel about 15 cm from the downwind end. Males were used once, then discarded, with the exception of males flown to blanks. These insects were flown to a lure that contained pheromone 24 hr after exposure to blank lures. Males were allowed 1 min for activation, a behavior identified by ambulation and wing fanning. If activation did not occur within this time, the moth was discarded. Otherwise, the trial lasted 5 min. Behaviors were recorded on audiocassette tape and later transcribed.

Male response to females was established by using five to six virgin females that had been observed calling for at least 5 min in the holding cage. When the male behavioral repertoire was established, observed behavior frequencies were tabulated in first order, preceding–following transition matrices from which ethograms were derived as outlined by Stevenson and Poole (1976) and Fagen and

Young (1978). To determine if individual transitions occurred greater than chance, $(\text{observed} - \text{expected})/\text{expected}^{0.5}$ must have been greater than chi-square value at $0.05/(dF)^2$ [when the degrees of freedom (dF) equaled 72 as determined from the transition matrix]. The most probable sequence of behaviors was determined using standard normal deviates calculated from significant chi-square values using the binomial test (Siegel, 1956).

When synthetic blends were tested, two rubber septa were enclosed in aluminum screen and suspended on the downwind screen of the cage used to hold lures or females in earlier studies. The role of individual pheromone components was studied by eliminating a single compound from the four-compound blend (Table 1). The percentages of moths exhibiting each behavior to each lure were calculated. Responses to each of the three-component blends, the four-component blend, and to virgin females were compared using a chi-square test of independence with Yates' correction at $P = 0.05$ (Steel and Torrie, 1980).

Field Studies. Six different lures were used in three different traps in a 6×3 factorial design for field studies. The five synthetic lures were the same as those used in flight tunnel studies, and the sixth was a pair of caged virgin females. Synthetic blends were tested using one rubber septum. The trap designs used were *Heliothis* Trap (Albany International, Needham Heights, Massachusetts), Pherocon 1-C (Zoecon corp., Palo Alto, California), and a cone-orifice trap (Struble, 1983) that had the rubber septa suspended centrally. Traps were set with all lures standardized at 1 m high.

Trap catches were counted and trap positions were rerandomized every other day from August 8 to 25, 1985, in a field near Alma, Ontario. Traps were positioned in two adjacent fields where the highest PSB infestation occurred

TABLE 1. COMPARISON OF RESPONSES OF MALE POTATO STEM BORERS TO FEMALES AND SYNTHETIC BLENDS IN WIND TUNNEL USING CHI-SQUARE TEST OF INDEPENDENCE WITH YATES' CORRECTION^a

Treatment	N	Percent behavioral response						
		Flight	Orient	Approach	Land	Search	Copulate	Reorient
Females	67	100.0 a	82.1 a	70.1 a	71.6 a	67.2 a	34.3 a	52.2 a
Four-component	41	95.1 a	41.5 b	26.8 bc	17.1 bc	4.8 b	0.0 b	24.4 bc
No 14:Ac	38	86.8 b	42.1 b	13.2 c	0.0 d	0.0 c	0.0 b	10.5 cd
No Z9-14:ac	37	97.3 a	37.8 b	21.6 bc	5.4 c	0.0 c	0.0 b	23.3 bc
No E11-14:Ac	36	94.4 ab	55.6 b	36.1 b	25.0 b	13.9 b	0.0 b	41.7 ab
No Z11-14:Ac	40	100.0 a	37.5 b	2.5 d	2.5 c	0.0 c	0.0 b	10.0 d
Blank	41	84.9 b	0.0 c	0.0 d	0.0 d	0.0 c	0.0 b	0.0 d

^aNumbers in the same column followed by the same letter are not significantly different at $P = 0.05$.

along the common hedgerow and extended to a grassy L-shaped strip through one of the fields. Traps were positioned 30 m apart. Septa were not changed, but females were replaced after counts were taken. No traps were filled to capacity when counts were taken. Both lure and trap-catch data were transformed by $(X + 1)^{0.5}$ before being subjected to analysis of variance and Duncan's new multiple-range test (Anonymous, 1982).

Close-Range Behavior. The roles of chemical cues and vision in eliciting copulation attempts were tested using wind-tunnel bioassays. Virgin females were used as the pheromone source to satisfy the assumption that the sex pheromone blend was correct.

Two distances were used to test chemical cues in eliciting copulation attempts. Virgin females were placed in screen tubes, measuring 2 cm in diameter, which were placed inside the holding cage at two distances from the downwind screen of the holding cage. At the farthest position, the females were 2–4 cm from the downwind screen of the holding cage, while they were less than 2 cm from the screen at the closer distance. The holding cage was placed in the flight tunnel as described earlier.

The two conditions to test vision were the presence or absence of a model. The model was a dead male rinsed with acetone, impaled on a fine wire and positioned inside the same holding cage used previously. The wings of the model were spread to simulate the outline of a calling female.

Only responses from males that landed on the holding cage were recorded. Four comparisons were made. Two comparisons tested the effect of the model at each distance, and two tested the effect of distance with and without the model. New models were used with each pheromone source. A test of proportion with the Z statistic was used for statistical analysis (Steel and Torrie, 1980).

RESULTS AND DISCUSSION

Male Behavior to Virgin Females. The behavioral repertoire of males responding to calling females included activation, random flight, upwind orientation, hovering, landing, searching the site, attempted copulation, casting downwind, reorientation, and stopping (Figure 1). Activation included ambulation, wing fanning, and antennal grooming. Random flight involved movement through the entire volume of the tunnel and included short bouts (< 1 min) of sitting or walking on the tunnel walls. Orientation was identified as wide horizontal and vertical sweeps in the downwind half of the tunnel with slow upwind movement and progressively narrower sweeps closer to the pheromone source. Hovering was indicated by stationary flight within 10 cm downwind of the holding cage, and landing indicated that the male had contacted the holding cage. Searching consisted of a combination of behaviors performed while on

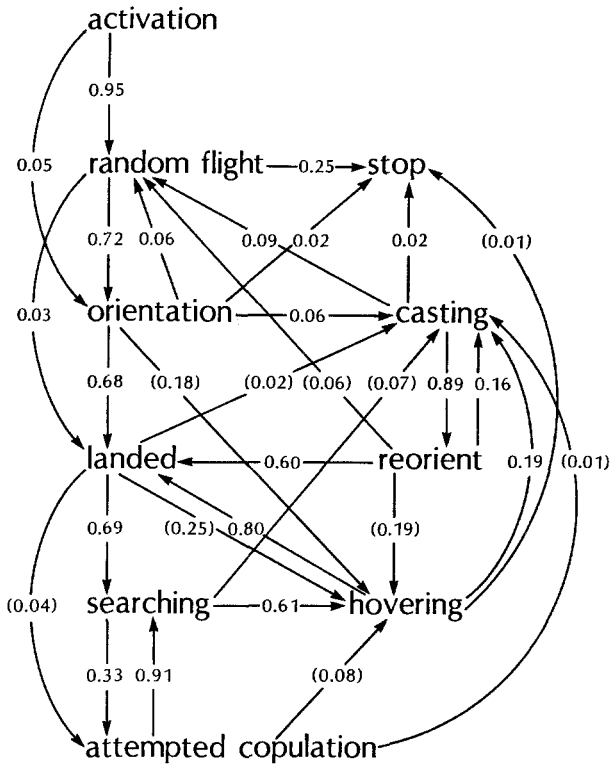


FIG. 1. Ethogram of response of male PSB to calling virgin female PSB in wind-tunnel bioassays. Numbers represent the conditional probability of a moth performing a behavior after exhibiting the previous behavior. Numbers in parentheses represent transitions occurring at a frequency not greater than chance ($N = 67$).

the holding cage that included walking vertically and horizontally and turning both clockwise and counterclockwise. Searching was always accompanied by rapid wing-fanning. Attempted copulation was typically a lateral curving of the abdomen to either left or right. Casting was direct downwind flight, usually in an upward arc, after the male had oriented to the lure. Reorientation was upwind flight to the pheromone source after having oriented previously. Males were regarded as stopped when they sat on a wall for at least 1 min.

Behavioral responses of males to calling females were highly variable (Figure 1), but use of the binomial test allowed for the identification of the most probable sequence of behaviors (Figure 2). PSB males typically oriented to the females within ca. 1 min, with landing on the source usually initiating a cyclic series of behaviors. Landing led to searching, which was interspersed with

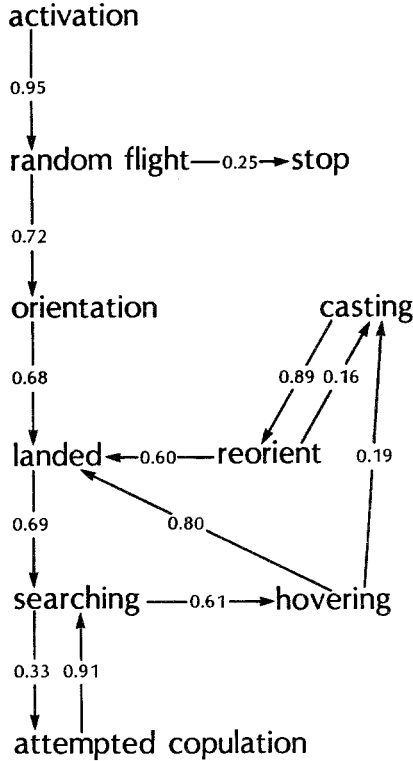


FIG. 2. Ethogram of the most probable sequence of response of male PSB in the wind tunnel. Numbers represent the most probable sequence of behaviors from the comprehensive ethogram of Figure 1 ($N = 67$).

attempted copulations. Copulation attempts were made only when the female was opposite the male on the downwind screen of the holding cage. Subsequent hovering was followed by a return to landing. This cycling could last the duration of the trial. Some males had a larger cycle of behaviors that included casting after hovering and then reorienting back to the source. Male PSB were usually active through the end of the trial. Blank lures elicited only random flight in the wind tunnel, indicating that upwind orientation behavior was induced by pheromones.

Response to Synthetic Blends in the Wind Tunnel. No blend of synthetic components was as effective as females in eliciting behaviors (i.e., orientation, landing, copulation) necessary for successful mating in a single attempt (Table 1). This reduction in response was not due solely to the significant decreases in the number of males orienting upwind but due also to combined reductions in

the numbers of males orienting, landing, and attempting to copulate. Studies with other noctuid species, for example, *Heliothis phloxiphaga* Grote and Robinson (Raina et al., 1986) and *H. virescens* (Teal et al., 1986), have shown that synthetic blends of pheromone components are capable of reproducing or surpassing virgin females in attractiveness and ability to elicit reproductive behaviors. Consequently, the four-component pheromone blend used in this study and identified by Teal et al. (1983) does not accurately represent the complete sex pheromone released by as many as five to six females of the potato stem borer.

Differences in behavioral response between the synthetic lures and calling females could be due to components missing from the blend and/or inaccurate component ratios and release rates. Reevaluations of sex pheromone blends of other species have often resulted in the addition of components which, although present in small quantities, were important for either maximizing pheromone-induced behaviors in the wind tunnel or for increasing trap catch (Bjostad et al., 1984; Sparks et al., 1979).

Subsequent studies by Teal and Tumlinson (1987) indicated the presence of picogram amounts of a series of 14-carbon alcohols in ethyl ether extracts of the pheromone gland of calling female PSB. These alcohols are the immediate precursors of the acetates identified for the PSB by Teal et al. (1983) and may be released in the pheromone blend by female PSB in minute amounts. Consequently, these compounds could be critical for effective signaling, while still being precursors for the acetate compounds. This supposition is supported by a study of *H. phloxiphaga* conducted by Raina et al. (1986) in which minute amounts of (*Z*)-11-hexadecen-1-ol, a compound known to be the immediate precursor of the aldehyde present in the greatest amount in the volatile pheromone blends of *Heliothis* spp. (Teal and Tumlinson, 1987), is critical for effective communication. Other unidentified components also may be present in the pheromone blend of PSB females.

Ratios of components have been reported to differ between gland extracts and volatile blends in other Noctuidae (Bjostad et al., 1980; Teal et al., 1985, 1986) and in other lepidopteran families (Hill et al., 1975; Roelofs et al., 1975; Hill and Roelofs, 1981). Evaluation of the volatile pheromone blend released by calling PSB females will allow for the elucidation of the actual components, ratios, and release rates of the pheromone.

Although none of the synthetic blends tested was as effective as females in inducing males to perform behaviors associated with pheromone communication (i.e., orientation, landing, etc.), most blends were as effective as females in causing males to enter flight (Table 1). No behaviors were affected when *E*11-14:Ac was deleted from the four-component blend. This suggests that *E*11-14:Ac does not play a role in chemical communication by this species. However, we cannot exclude the possibility that this compound affects as yet

undefined behaviors of conspecific males or that it may play a role in reproductive isolation between the PSB and other closely related species. Fewer males approached to within 10 cm of lures that did not contain Z11-14:Ac than when either the four- or three-component blend that lacked E11-14:Ac was tested. The decrease in the number of approaches also resulted in fewer males landing when Z11-14:Ac was deleted with respect to the blend lacking E11-14:Ac. Consequently, Z11-14:Ac appears to affect close range orientation by males. Deletion of 14:Ac resulted in significant reductions, with respect to either the four-component or three-component blend lacking E11-14:Ac, in the number of males that landed on the holding cage. Similarly, the blend lacking Z9-14:Ac was less effective than the blend lacking E11-14:Ac in inducing males to land. However, no single compound appeared to be responsible for the release of a specific behavior and, consequently, the totality of the blend may be as important as the blend constituents in stimulating pheromone-mediated reproductive behavior.

Field Trapping Studies. Results of field trapping studies that employed different lures and trap types are given in Table 2. Trap design accounted for the greatest variation in catch as is indicated by the fact that *Heliothis* traps always caught some males when baited with any lure, whereas males were captured in double-cone traps only when these traps were baited with females. The success of the *Heliothis* trap was probably the result of the large lower aperture. After approaching or landing on lures in flight-tunnel studies, males commonly cast back downwind. Therefore, moths that flew up and away from the lures positioned beneath these traps would fly into the trap. Once inside, the lower rim probably prevented most moths from crawling down and out of the trap. The Pherocon trap requires insects to land in order to be captured. Consequently, lures that did not induce landing or close-range approach in the flight

TABLE 2. MEAN NUMBER OF MALE PSB CAPTURED PER SAMPLING PERIOD IN DIFFERENT TRAP TYPES BAITED WITH VARIOUS PHEROMONE LURES

Lure	Trap type ^a		
	Heliothis	Pherocon 1-C	Double cone
Female	47.0 a	3.4 c	1.8 d
Four-component	36.7 a	2.6 c	0.0 d
Minus E11-14:Ac	44.6 a	2.6 c	0.0 d
Minus Z9-14:Ac	10.4 b	0.0 d	0.0 d
Minus 14:Ac	2.0 c	0.0 d	0.0 d
Minus Z11-14:Ac	3.0 c	0.0 d	0.0 d

^aValues followed by the same letter are not significantly different by Duncan's multiple-range test.

tunnel (i.e., those that lacked either Z11-14:Ac or 14:Ac) were ineffective in these traps. Pherocon traps baited with lures lacking Z9-14:Ac also did not capture males in field studies. This may be explained by the low incidence of landing in the flight-tunnel study, coupled with the chance of escape from the trap glue by these large moths.

It was expected that cone-orifice traps would catch moths only when baited with females for two reasons: first because males would spend considerable time searching and crawling into these traps, and second because the levels of activity to the synthetic blends were significantly lower for all behavioral criteria examined in the flight tunnel than those recorded when females were tested. The relatively low number of insects caught in cone-orifice traps when females were used as lures may be explained by plume shape. *Heliothis* traps and Pherocon 1-C traps probably had the least plume disruption because their exposed lures probably produced an omnidirectional effect with respect to wind. Cone-orifice traps were unidirectional with respect to wind, however, and probably had poor flow through the trap most of the time because of variable wind direction. Struble (1983) found cone-orifice type traps generally had lower catches of Lepidoptera than omnidirectional designs.

There was also a good correlation between the capture of males in *Heliothis* traps with different lures and the ability of those lures to elicit reproductive behaviors from males in wind-tunnel bioassays. Numbers of males caught using the four-component blend or the blend missing E11-14:Ac were not significantly different. The fact that neither of these synthetic lures was different from females suggests an inconsistency between these field data and wind-tunnel studies. However, wind-tunnel studies employed groups of five to six females caged in a relatively large container that enabled females to call undisturbed, while field studies employed only two females housed in small cages, which increased contact between insects. Consequently, the difference between the laboratory and field may be the result of much smaller amounts of pheromone released by females used in field studies. Deletion of Z11-14:Ac from lures used in the field caused a reduction in captures that is correlated with the fact that this compound affected both the approach and landing of insects in flight-tunnel studies. Similarly, deletion of 14:Ac resulted in reduced capture. The intermediate numbers captured in *Heliothis* Traps baited with lures that did not contain Z9-14:Ac reflect the fact that while the number of males that both approached and landed on these lures in the flight tunnel was reduced with respect to more effective blends, the reduction was not significant.

Close-Range Reproductive Behavior. The fact that few insects landed or performed subsequent searching and that none attempted to copulate in response to any of the synthetic blends in the wind tunnel, coupled with the results of field studies that indicated the four-component blend and three-component blend lacking E11-14:Ac were as effective as females in traps, suggested that factors

other than the compounds identified from the gland extracts played a role in the reproductive behavior of these insects. Therefore, we conducted studies on the close-range reproductive behaviors of these moths. There were few attempted copulations when caged females were farther than 2 cm from the downwind screen of the holding cage and no behavioral differences between presence or absence of the model at that distance (Figure 3). Copulation attempts increased when the female was less than 2 cm from the downwind screen, but the increase was significant only when the model was absent (Figure 3).

Clearly, factors associated with proximity of the sexes were important in eliciting copulation attempts. These factors were probably chemical, since tactile cues were eliminated by the two layers of aluminum screen that separated the sexes. Since three pairs of males were observed attempting male-male copulations in preliminary trials when females were positioned greater than 2 cm from the downwind holding cage screen, these chemical cues do not appear to be restricted to the female sex pheromone blend. Chemicals of low volatility released from moth scales may be a cue. Acetone-washed males used as models may have been stripped of these chemical cues.

Grant et al. (1987) reported contact pheromones found in scale extracts of white-marked tussock moth females, *Orgyia leucostigma* (J.E. Smith), that released copulatory behavior from the males. Similarly, Ono (1981) found the presence of scales could induce interspecific copulation attempts in three species

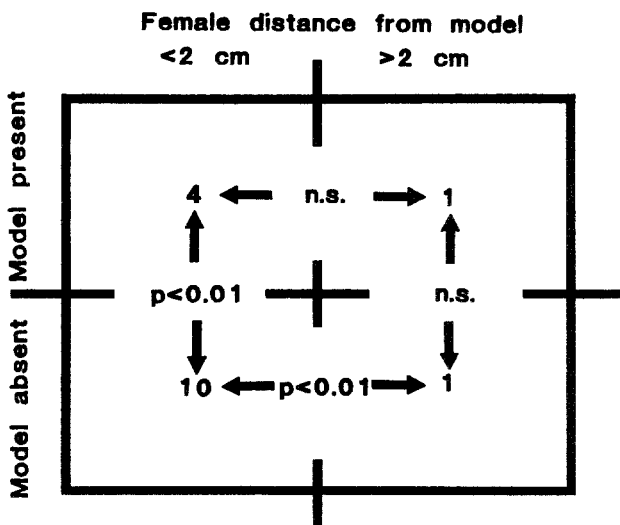


FIG. 3. Number of male PSB attempting to copulate with caged female PSB both with and without the model, and at two distances, in the wind tunnel. Arrows indicate pairwise comparisons made using the Z statistic at $P = 0.05$ ($N = 10$ in each cell).

of phycitid moths. Male PSB may require similar compounds to release the copulatory response. If so, present studies indicated that for the PSB, chemicals can be perceived at short distances and that male contact with the female is not necessary to elicit a copulatory response.

Visual stimuli played a secondary role to chemical cues in eliciting copulation attempts because any factor that decreased copulation attempts with the model present was more important than vision. It was expected that the model with females less than 2 cm distant would elicit the same behaviors as males responding to unrestricted females. However, the reverse occurred. Inhibition in response to the model at close range may be the result of either chemicals from the model that inhibited behavior, or because close-range chemicals from a female less than 2 cm away were not perceived due to disrupted air flow around the model. It is not possible to determine from these data, however, what role visual cues do play in eliciting copulation attempts from male PSB. The role of visual cues is variable in the Noctuidae, but for most, it is secondary to an accurate sex pheromone blend in eliciting close-range behaviors (Shorey, 1964; Shorey and Gaston, 1970; Carpenter and Sparks, 1982).

In conclusion, our studies suggest that the four compounds identified from extracts of the pheromone gland of females of *H. micacea* are of importance in semiochemical communication. However, disparities observed in flight-tunnel studies between synthetic lures and females suggest that this blend does not accurately represent the one released by females. This could be the result of the lack of as yet unidentified compounds important for communication, inappropriate release rate, or incorrect ratios, or all of these factors.

Acknowledgments—The authors wish to thank Drs. T.C. Baker, P.J. Landolt, and E.R. Mitchell for their constructive reviews of this manuscript.

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