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CHEMICAL IDENTIFICATION AND BEHAVIORAL CHARACTERIZATION OF MALE WING PHEROMONE OF *Ephestia elutella* (PYRALIDAE)

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Abstract—Behavioral and chemical evidence is presented for the identity of the male wing pheromone of *Ephestia elutella* (Hübner) and the role of this pheromone in courtship success is evaluated. Males with the forewing removed experienced a mating success rate less than half of that of either intact males or males that had only the wing gland area remaining of their forewings. GC-MS analysis and microchemical reactions indicated the presence of (*E*)-phytol and a series of saturated γ-lactones in a methylene chloride extract of the wings. Using an assay of female courtship behavioral response, (*E*)-phytol was found to evoke an intermediate level of response in females when presented alone, while the complete array of insect-derived γ-lactones produced no significant response. The combination of either γ-decalactone or γ-undecalactone with (*E*)-phytol in a 1 : 2 ratio, however, elicited a female response equivalent to that produced by the unfractionated wing extract.

Key Words—courtship pheromone, wing pheromone, male pheromone, *Ephestia elutella*, Pyralidae, phytol, γ-decalactone, γ-undecalactone.

INTRODUCTION

Behavioral studies of members of the stored-product complex of phycitine moths have revealed relatively complex courtship sequences. In addition to the long-range sex pheromone of the female, males of most species have been found to possess pheromone glands on the costal margin of the forewings (Barth, 1937;

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Grant, 1978) and/or the dorsal surface of the eighth abdominal segment (Dickens, 1936; Corbet and Lai-Fook, 1977). Female behavioral responses to conspecific wing pheromones have been demonstrated in three species: *Plodia interpunctella* (Grant and Brady, 1975; McLaughlin, 1982), *Vitula edmandsae* (Grant, 1976), and *Ephestia elutella* (Krasnoff and Vick, 1984). To date, however, no chemicals from these glands have been identified. We report here behavioral and chemical evidence for the identity of the male wing pheromone of the tobacco moth, *Ephestia elutella* (Hübner) and evaluate the importance of this pheromone on courtship success.

METHODS AND MATERIALS

Wing Pheromone Collection. *Ephestia elutella* were reared on a honey–bran–glycerol diet according to the procedure of Strong et al. (1968). Males and females were separated at the pupal stage, and adults were maintained in separate chambers on 14 : 10 light–dark cycles at 22–24°C. The wing pheromone was collected from 2- to 5-day-old males by excising the forewings during the period of peak sexual activity (3–6 hr into scotophase) and extracting them with methlene chloride for several hours. Wing extracts were filtered with glass wool, concentrated to 200–300 μl under a gentle flow of N_2, and stored at −15°C.

Chemical Identification. The wing gland extract was fractionated using a Waters Assoc. high-performance liquid chromatograph (HPLC), comprised of two model 6000A solvent delivery pumps, a No. 660 solvent programmer, a RCM-100 radial compression separation module, a No. 450 variable wavelength detector (190–700 nm), and a series R-400 differential refractometer. The extract was chromatographed on a silica gel RCM column using either an isocratic mobile phase of 1% methanol–99% methylene chloride or a linear solvent program of 100% methylene chloride to 10% methanol–90% methylene chloride in 10 min with a flow rate of 1 ml/min. The eluant was collected in 1-ml fractions. The mobile phases were "distilled in glass" spectral grade from Burdick & Jackson (Muskegon, Michigan). Analysis and further fractionation of the extract was carried out on a Varian model 3700 gas chromatograph with two hydrogen flame ionization detectors. A range of polarities in columns was used: 10% Silar 10C (cyanopropyl silicone) on 100–120 mesh ChW Ac (3 m × 4 mm, 4.4 g), 2% SF-96 (methyl silicone) on 100–120 mesh ChW Ac DMCS (2 m × 4 mm, 3.2 g), and Durawax-4 (polyethylene glycol stabilized with methyl silicone) fused-silica capillary (30 m × 0.25 mm, film = 0.25 μm) from J&W Scientific (Rancho Cordova, California). Carbon disulfide, used in GC analysis, was redistilled daily.

Complete mass spectra of active components were obtained using a Finnigan 4021 EI/CI capillary gas chromatograph–mass spectrometer (GC-MS) coupled to a INCOS data system. A Grob injector was used in conjunction with

the following fused-silica capillary columns (Chromatographic specialities, Brockville, Ontario): a 30-m DX-4 temperature programmed from 50°C (2 min hold) to 100°C at 30°C/min, then 10°C/min to 200°C; 30-m DB-5 held at 50°C for 1.5 min programmed at 30°C/min to 120°C, then 10°C/min to 250°C. All EI-MS and CI-MS (methane) were generated at 70 eV.

Microchemical reactions were carried out on behaviorally active HPLC fractions for confirmation of the chemical identities of pheromone components. The products of these reactions were analyzed by GC. Evidence for esters was provided by base hydrolysis (Bjostad et al., 1984). After reducing the sample to near dryness with a gentle stream of N_2, 100 μl of ethanol and 20 μl of 5% KOH were added and the solution was allowed to sit in a 1-ml reaction vial with Teflon-lined screw cap at 50°C for 1 hr. Water was then added and the aqueous solution was extracted three times with hexane. The hexane portion was concentrated under N_2 and was slowly replaced by CS_2. The presence of alcohols was established by acetylation, in which a behaviorally active fraction was taken to near dryness and 2–3 drops of acetyl chloride were added. After 1 min, the acetyl chloride was evaporated under N_2 and replaced with CS_2. For determination of double-bond position by ozonolysis (Beroza and Bierl, 1967), ozone was bubbled for 30 sec into 30 μl of CS_2 followed by the addition of 1–5 μl of the sample. Nitrogen was then bubbled through the solution for 30 sec and 1 μg triphenylphosphine in carbon disulfide was added to break up the ozonide product.

Synthetic γ-lactones were obtained from ICN-K&K Laboratories (Plainview, New York), except for γ-decalactone and (*E*)-phytol which were purchased from Aldrich Chemical Co. (Milwaukee, Wisconsin). The (*E*)-configuration of the commercial phytol was determined by 200-MHz proton NMR, GC, and GC-MS analysis. (*Z*)-Phytol was synthesized by a modification of the scheme of Burrell et al. (1966). A solution of commercial (*E*)-phytol (0.10g) in anhydrous methanol (5 ml) at −78°C was treated with ozone for 15 min. After flushing with N_2, the ozonide was discharged with dimethyl sulfide (0.5 ml) and the solvent was evaporated in vacuo. The crude product was purified by flash chromatography (Still et al., 1978) with hexane–ethyl acetate (9:1) to yield 6,10,14-trimethyl-2-pentadecanone (0.095 g). A solution of this ketone in anhydrous tetrahydrofuran (0.5 ml) was added to a mixture of ethoxyacetylene (0.12 g, 50% in hexane), anhydrous THF (0.5 ml), and *n*-butyl lithium (1.6 ml, 1.2 M in hexane) at 0°C. After 1 hr stirring at this temperature, the reaction was quenched with a saturated NH_4Cl solution (5ml) and extracted into ether (5ml).

Evaporation of the organic phase yielded 2-ethoxyethynyl-6,10,14-trimethylpentadecan-2-ol (0.12g). The acid-catalyzed rearrangement of the adduct was carried out with 10% aqueous oxalic acid (1ml) in ethanol (0.5 ml) at 22°C for 18 hr. Purification of the crude product by preparative TLC (silica gel) gave ethyl phytenoate (0.07g) as a mixture of *E*/*Z* isomers in a ratio of 50:50 as determined by GC (relative retention time *E*/*Z* = 1.19) and NMR [(*Z*)-3-methyl,

δ1.86; (*E*)-3-methyl, δ2.11]. A solution of the ester (0.07 g) in dry toluene (1 ml, distilled from sodium) was treated with Vitride (0.04 ml, 70% in toluene) at 0°C for 7 hr and at 22°C for 10 hr with additional Vitride (0.03 ml). Vitride [sodium dihydrobis(2-methoxy-ethoxy)aluminate] was purchased from Hexcel Specialty Chemicals (Zealand, Michigan). The reaction was quenched with methanol (1 ml), concentrated in vacuo, and purified by preparative TLC to give the following: recovered ester (0.028 g), (Z)-phytol (0.011 g), and (*E*)-phytol (0.009 g). These assignments were supported by NMR, GC, and GC-MS analysis.

(E)-*Phytol*. NMR (200MHz, $CDCl_3$): δ0.85 (12H, d, J = 6 Hz), δ1.24–1.54 (20H, m), δ1.65 (3H, s, vinylic CH_3), δ2.00 (2H, t, J = 8 Hz), δ4.14 (2H, m), δ5.40 (1H, broad t, J = 6 Hz); GC (DX-4) retention time ca. 15.4 min; MS (EI 70 eV) *m/e* 296 (M^+), 278, 196, 123, 71 (base peak).

(Z)-*Phytol*. NMR (200MHz, $CDCl_3$): δ0.85 (12H, d, J = 6 Hz), δ1.05–1.34 (20H, m), δ1.72 (3H, d, J = 1 Hz), δ2.03 (2H, t, J = 7 Hz), δ4.14 (2H, m), δ5.40 (1H, broad t, J = 6 Hz); GC (DX-4) retention time ca. 14.4 min; MS (EI 70 eV) *m/e* 296 (M^+, weak), 278, 196, 123, 71 (base peak).

Behavioral Assays. The importance of the wing pheromone in courtship success was investigated by ablation of the gland, using the procedure of Grant and Brady (1975). Within 24 hr of eclosion to the adult, males were cold-anesthetized and either the entire forewing was removed or all of the forewing except the costal wing-gland area. This procedure required that the male be anesthetized <3 min, and the two operations were alternated to control for operator experience. These males were provided sugar water and were tested during their second scotophase, at which time they were introduced into a screen cylinder containing a calling female; the ensuing courtship was video-recorded for more accurate analysis at a later time.

For determination of pheromone components, five male equivalents (ME) of each fraction were tested using a modified version of the Kransnoff and Vick (1984) bioassay, and the responses of the females were compared with those responses elicited by the crude wing-gland extract and clean-air controls. The material to be tested was placed on the inside of a 0.5 cm OD × 10-cm-long glass tube. Air, which was purified by two separated charcoal filters, was passed through this tube at 15 cm/sec. After allowing air to flow through the tube for 10 sec to evaporate the solvent, the end of the tube was presented to a calling virgin female tobacco moth. The use of a gentle airflow ensured that the chemicals were delivered to the female's head. Two- to five-day-old females, which were 3–6 hr into their scotophase, were tested either in small cylindrical cages (2 females/cage) or in a large rearing cage. The cages were backlighted by a 0.2-lux light. Females were considered to show a positive response if they exhibited either a ventral flexion of the abdomen (as described by Krasnoff and Vick, 1984) or turning without forward locomotion. Treatments were presented in a randomized complete-block design, with eight replicates of 10 females per

treatment. Statistical analyses were carried out using Duncan's new multiple-range test or Ryan's (1960) multiple-comparison test for proportions.

RESULTS

Wing Pheromone and Courtship Success. Removal of the wing gland substantially reduced the mating success of male *E. elutella* (Table 1). Males with entire forewings removed recorded a courtship success rate less than half that of either intact males or males with all of the forewing removed except the wing gland. Furthermore, the successful courtships by the glandless males were twice as long as those of males with their wing glands intact; the glandless males met with a much higher frequency of female rejection behaviors, such as turning away from the male or covering the abdomen with their wings, which made copulation more difficult to achieve. Males having all of the forewing removed except for the costal fold were as successful as intact males during courtship. Therefore, courtship success by males appears to depend primarily on the presence of intact costal-fold wing glands and not on mechanical effects such as wind generated by the entire forewings.

Wing Pheromone Identification. Preliminary bioassays (30 females/treatment) of HPLC fractions of male *E. elutella* wing-gland extract indicated that the behaviorally active components were contained in two adjacent 1-ml fractions. Activity elicited by either of these fractions was comparable to that of the complete wing extract (57% and 53% female response for the fractions, respectively, and 63% response for the extract; other fractions evoked $<10\%$ response). These two fractions were characterized by similar complex arrays of peaks on a Silar 10C GC column. Fractional collection of these HPLC fractions from Silar 10C followed by bioassay indicated that full behavioral activity was contained in two adjacent 2.5-min collections. Combining the two GC fractions

TABLE 1. COURTSHIP SUCCESS RATES AND LENGTH OF SUCCESSFUL COURTSHIPS IN MALES WITH FOREWINGS COMPLETELY REMOVED (NO WGs) OR ONLY COSTAL FOLD REMAINING (WGs ONLY) COMPARED TO INTACT MALES

Treatment	*N*	Courtship success (%)	Length of successful courtship (sec ± SD)
No WGs	34	32 b[a]	34.6 ± 10.6 b[b]
WGs only	28	75 a	14.7 ± 4.9 a
Intact males	24	83 a	17.6 ± 4.7 a

[a] Values within the column followed by the same letter not significantly different at $P < 0.05$ by Ryan's multiple-comparison test for proportions.
[b] Values within the column followed by the same letter not significantly different at $P < 0.05$ by Duncan's new multiple-range test.

produced a response of 50% (15/30 females), compared to 53% (16/30) for the combined HPLC fractions. These areas of activity were coincident with two prominent peaks at 8.9 and 11.4 min evident in GC tracings of the original HPLC fractions.

A second HPLC solvent regime (100% methylene chloride to 10% methanol–90% methylene chloride in 10 min) was utilized to fractionally resolve the active components. The component represented by the earlier GC peak was subjected to a number of chemical reagents to aid in its identification. It was unchanged when treated with KOH in EtOH; however, upon treatment with acetyl chloride, the compound (retention time 17.4 min on Durawax-4) was transformed to one with retention time 16.0 min. Base hydrolysis of the acetylated product regenerated the original GC peak. These results strongly suggested the presence of an alcohol. The retention time of this compound on both Durawax-4 and SF-96 was enveloped by those of 1-octadecanol and 1-eicosanol. Ozonolysis of the compound yielded a product with a GC retention time (Durawax-4) and MS fragmentation pattern virtually identical to those of 6,10,14-trimethyl-2-pentadecanone, which was obtained from the ozonolysis of synthetic (*E*)-phytol. Indeed, GC-MS analysis of the putative pheromone component was consistent with that of (*E*)-phytol (3,7,11,15-tetramethyl-2-hexadecenyl alcohol), with identical retention times (*E*/*Z* relative retention time = 1.08 on Durawax-4) and identical fragmentation patterns (Figure 1). (*Z*)-Phytol was apparently absent from the wing-gland extract. Finally, GC-MS analysis of the online hydrogenation (Beroza and Sarmiento, 1966) of (*E*)-phytol and of the natural component yielded products with matching mass spectra and identical GC retention times on SF-96, Silar 10C, Durawax-4, and DB-5 columns.

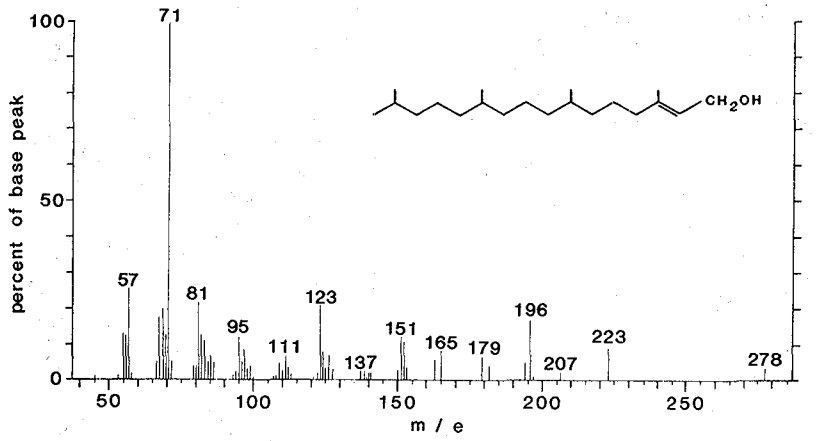


FIG. 1. EI mass spectrum of (*E*)-phytol (3,7,11,15-tetramethyl-2-hexadecenyl alcohol) isolated from *Ephestia elutella* male wing glands.

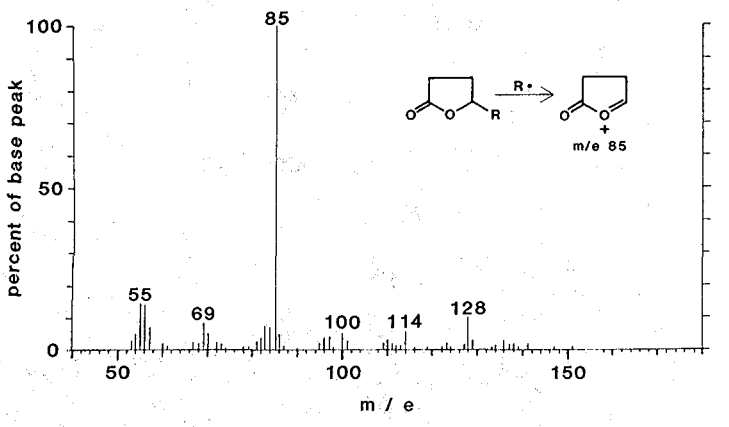
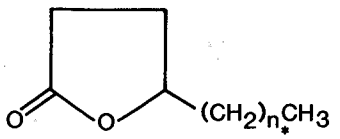


FIG. 2. EI mass spectrum of γ-decalactone isolated from *Ephestia elutella* male wing glands.

The remaining active HPLC fraction, analyzed by GC-MS, contained a series of compounds that exhibited an intense base peak of *m/e* 85 (Figure 2). This fragment is characteristic of the cleavage of the side chain from a γ-lactone (Honkanen et al., 1965). CI-MS (methane) analysis of this series did indeed produce M+1 ions consistent with those of the saturated C_9-, C_{10}-, C_{11}-, C_{12}-, C_{14}-, C_{16}-, and C_{18}-γ-lactones (Figure 3). The identities of two other compounds present with base peaks of *m/e* 85 were not confirmed, although their mass spectra suggested γ-lactones with either unsaturated or substituted side chains. The retention times of the seven wing-extract components matched those of the seven respective synthetic saturated γ-lactones on three GC columns: Silar 10C, SF-96, and Durawax-4. The retention times of C_{14}-, C_{16}-, and C_{18}-γ-lactones were determined by extrapolation of a retention time curve using synthetic C_7-, C_8-, C_9, C_{10}-, C_{11}-, C_{12}-γ-lactones for each GC column.

Behavioral Assays. In the first assay of extracted wing components (Figure 4), a blend of 25 ng each (approx. 5 ME) of synthetic γ-nona-, γ-deca-, and γ-undecalactone was found to elicit a response by females not significantly greater than that produced by clean air; however, when this blend of lactones was combined with 5 ME of the HPLC fraction containing (*E*)-phytol, female response was comparable to that evoked by either the HPLC fraction containing the full complement of natural γ-lactones combined with the (*E*)-phytol-containing HPLC fraction or the unfractionated wing extract. Since the presence of the four longer-chain γ-lactones (C_{12}, C_{14}, C_{16}, and C_{18}) did not appear to increase female response, no further work was attempted on these compounds. When presented alone, the (*E*)-phytol HPLC fraction elicited a response intermediate to that evoked by the clean-air control and the complete wing extract. When individually combined with the (*E*)-phytol fraction (Figure 5), both γ-

Gamma-lactones



*n	
4	nonalactone
5	decalactone
6	undecalactone
7	dodecalactone
9	tetradecalactone
11	hexadecalactone
13	octadecalactone

FIG. 3. γ-Lactones determined to be present in *Ephestia elutella* male wing glands.

decalactone and γ-undecalactone increased female response to a level that was significantly greater than the response to (*E*)-phytol alone and not significantly different from that to the full extract. The addition of γ-nonalactone to (*E*)-phytol, on the other hand, had no effect on female response.

Finally, female response to the synthetic (*E*)-phytol (50 ng, 5 ME) was

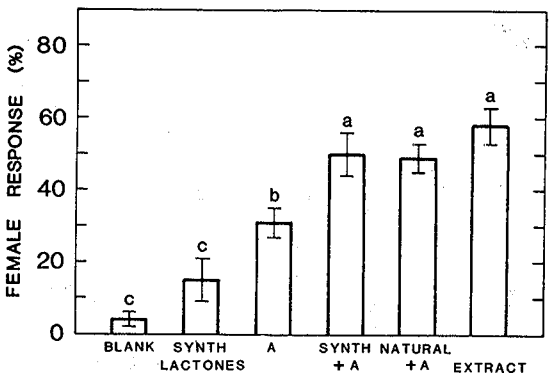


FIG 4. Response of *Ephestia elutella* females to three synthetic lactones presented alone and in combination with an (*E*)-phytol-containing HPLC fraction (A) of *Ephestia elutella* male wing glands. Activity is compared to the complete wing extract and a recombining of A with the entire complement of lactones isolated from the wing gland (Natural). Different letters indicate significant differences at $P < 0.05$ as determined by Duncan's new multiple-range test of arcsin-transformed values. I bars indicate standard errors.

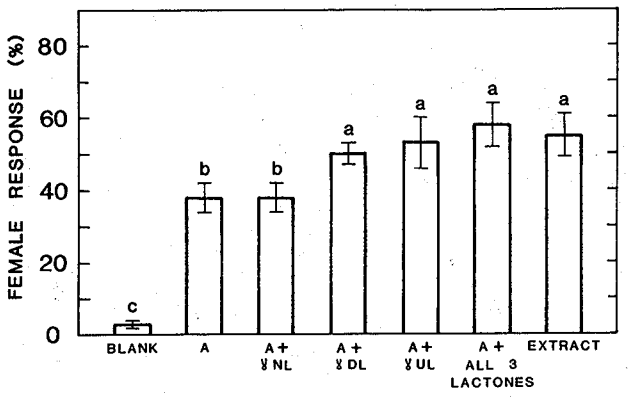


FIG. 5. Response of *Ephestia elutella* females to synthetic lactones when individually added to the (*E*)-phytol-containing HPLC fraction (A) isolated from the male wing gland. Different letters indicate significant differences at $P < 0.05$ as determined by Duncan's new multiple-range test of arcsin-transformed values. I bars indicate standard errors.

assessed (Figure 6). As in earlier assays with the insect-derived (*E*)-phytol, synthetic (*E*)-phytol evoked a response that was intermediate between the clean-air control and the unfractionated wing extract. More significantly, the combination of the synthetic compounds (*E*)-phytol, γ-decalactone, and γ-undecalactone produced a response identical to that elicited by the full wing-gland extract.

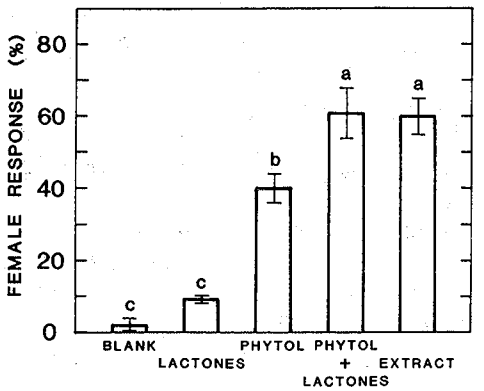


FIG. 6. Response of *Ephestia elutella* females to synthetic (*E*)-phytol alone and in combination with three synthetic lactones. Different letters indicate significant differences at $P < 0.05$ as determined by Duncan's new multiple-range test of arcsin-transformed values. I bars indicate standard errors.

DISCUSSION

We have characterized the importance of the wing pheromone to the mating success of *Ephestia elutella* males. In the past, attempts to identify male pheromones of many species of Lepidoptera have been plagued by the lack of overt behaviors on the part of the female. In *E. elutella*, however, female behaviors important in the courtship sequence are easily observed and can be elicited consistently, using chemicals in the absence of males (Krasnoff and Vick, 1984). Our chemical and behavioral data suggest that the wing pheromone of *E. elutella* consists of a blend of (*E*)-phytol, γ-decalactone, and γ-undecalactone. (*E*)-Phytol appears to be the most important component in that it was the only component that evoked a significicant level of female response when presented alone. The addition of either γ-decalactone or γ-undecalactone to (*E*)-phytol increased the response to a level not significantly different from the complete wing-gland extract. The other lactones identified from the wing glands appeared to be unimportant for female response. Females were not significantly affected by the addition of γ-nonalactone to (*E*)-phytol, and the absence of the longer-chain γ-lactones did not prevent maximum female response from being elicited.

The behavioral activity of (*Z*)-phytol, the stereoisomers of (*Z*)- and (*E*)-phytol, and the enantiomers of the γ-lactones were not studied. Full behavioral activity was evoked by the racemic synthetic compounds; therefore, it would appear that any nonpheromonal enantiomers or stereoisomers present in the synthetic mixture were not behaviorally antagonistic. Complete elucidation of the stereochemistry of this pheromone will require further chemical and behavior testing.

(*E*)-Phytol has long been known as the diterpenoid alcohol moiety of chlorophyll in plants (Willstatter et al., 1919), and both the *Z* and the *E* isomers have been isolated as unbounded molecules from the red algae, *Gracilaria andersonia* (Sims and Pettus, 1976). The present study, however, is the first report of (*E*)-phytol as a volatile component in an animal system, to our knowledge. The report of volatile γ-lactones, on the other hand, is not without precedence. Howard et al. (1983) reported the presence of γ-decalactone in anal droplets formed by the thrips, *Bagnalliella yuccae*. Wheeler et al. (1972) identified γ-dodecalactone from the defensive secretions of several species of *Bledius* rove beetles (Staphylinidae), and Dettner and Schwinger (1982) found γ-decalactone, γ-undecalactone, γ-dodecalactone, and γ-tetradecalactone in the secretions of other staphylinids. In each of these cases, however, the lactones have been found to function in a defensive role, and ours is apparently the first report of γ-decalactone and γ-undecalactone as pheromone components.

Although this bioassay proved to be a convenient method for identifying behaviorally active compounds, it measured only one set of behaviors in the courtship sequence of *E. elutella*. It is possible, therefore, that the roles of other

compounds present in the wing glands have been underestimated. Nevertheless, it seems probable from our behavioral data that these compounds would serve, at most, only a secondary role. This assertion, however, can only be verified by investigating the effect of these synthetic compounds on the complete courtship sequence and on courtship success.

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