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Selection for Altered Pheromone-Component Ratios in the Pink Bollworm Moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae)

R. D. Collins[1,2] and R. T. Cardé[1]

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Female pink bollworm moths, Pectinophora gossypiella *(Saunders), were selected for altered component ratios of the long-distance sex pheromone,* (Z, E)- *and* (Z, Z)-*7,11-hexadecadienyl acetate. Selection for 12 generations increased the mean (±SD) percentage of the* (Z, E) *isomer from 42.9 ± 1.0 in the parental generation to 48.2 ± 1.2. Although statistically significant, a change of this magnitude may be transparent to males because of their relatively broad response spectrum. Selection for a lower percentage of the* (Z, E) *isomer yielded no change in the mean pheromone ratio. The total amount of pheromone produced declined in both selected lines. In the line selected for females producing a high percentage of the* (Z, E) *isomer, the duration of wing fanning by males to high* (Z, E) *blends was elevated.*

KEY WORDS: pink bollworm; *Pectinophora gossypiella*; (Z, *E*)-hexadecadienyl acetate; (Z, Z)-7,11-hexadecadienyl acetate; sex pheromone; genetics; artificial selection.

INTRODUCTION

Evolutionary change in pheromone signaling depends on the genetic variation available and the selective forces acting upon it. The inheritance of pheromone production and response in Lepidoptera have been examined primarily by interspecific (Grant *et al.*, 1975; Sanders *et al.*, 1977; Grula and Taylor, 1979) and interstrain (Klun and Maini, 1979; Lanier *et al.*, 1980) crosses. Genetic control of pheromone communication in two strains of the European corn borer, *Ostri-*

[1] Department of Entomology, University of Massachusetts, Amherst, Massachusetts 01003
[2] Present address: Department of Entomology, Waters Hall, Kansas State University, Manhattan, Kansas 66506.

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nia nubilalis (Hübner), involves an autosomal locus controlling pheromone production by females (Klun and Maini, 1979), an unlinked autosomal locus controlling male pheromone perception, and a sex-linked locus influencing male response behavior (Roelofs *et al.*, 1987). Selection for novel female pheromone ratios in a laboratory population of the redbanded leafroller moth, *Argyrotaenia velutinana* (Walker), yielded small but behaviorally significant ratio shifts, but the changes could not be maintained beyond one generation without brother–sister matings (Du *et al.*, 1984; Roelofs *et al.*, 1986).

The long-distance sex pheromone of the pink bollworm, *Pectinophora gossypiella* (Saunders), consists of a blend of (Z, *E*)- and (Z, Z)-7,11-hexadecadienyl acetate (ZE and ZZ, respectively) (Hummel *et al.*, 1973; Bierl *et al.*, 1974). The mean ($\pm$SD) blend in the pheromone glands of females from our laboratory population is 44.2 $\pm$ 2.3% ZE (Collins and Cardé, 1985). The inheritance of aspects of pheromone communication in this moth is of particular interest because synthetic pheromone is used commercially to disrupt mating in field populations (Doane and Brooks, 1981; Baker *et al.*, 1989).

Significant heritabilities (measuring the fraction of total phenotypic variance attributable to additive genetic effects) have been demonstrated for both female-produced ratio (Collins and Cardé, 1985) and titer (Collins *et al.*, 1989), as well as male response characters (Collins and Cardé, 1989a,b). This paper reports the response to artificial selection for pheromone blends different from the blend produced by unselected females in a laboratory population of the pink bollworm.

Both signal production and response behavior must change in concert to have significant evolutionary consequences for pheromone communication systems. If signal production and response are controlled by the same or closely linked genes, then the rate of evolution in these systems could be greatly enhanced (Alexander, 1962; Kyriacou and Hall, 1986). The relationship between pheromone production and response behavior was examined by measuring the effect of selection for female-produced pheromone blends on male response behavior.

MATERIALS AND METHODS

Rearing Procedures. Moths used to initiate the selected lines and those used as controls were obtained from a laboratory colony maintained at the University of Massachusetts for about 15 generations at the start of this study (Collins and Cardé, 1985). The minimum colony size was about 400 individuals. Our colony was started from about 1200 pupae from the USDA Pink Bollworm Rearing Facility in Phoenix, Ariz. The USDA colony originated in Maricopa Co., Ariz., and has been cultured for approximately 50 generations.

Families used in the selection experiments were started by placing individ-

ual male–female pairs in 7.5 × 7.5 × 2.8-cm clear plastic oviposition cages. Sucrose solution (7.5%) was available to the adults in 1.9-ml vials with cotton wicks on the bottom of each cage. Paper oviposition substrates were changed daily. To segregate the progeny of each male–female pair, oviposition substrates were sealed in 15 × 15 × 2-cm plastic bags until the larvae hatched.

Three larvae were transferred to 21-ml clear plastic cups covered with plastic lids within 2 hr of eclosion. Each cup contained 5 g of wheat germ/soybean flour diet (Collins and Cardé, 1985). Pupae were removed after 17 days, sexed, and placed singly in 85 × 15-mm glass test tubes closed with cork stoppers (males) or cotton (females). Females were fed on the day of adult emergence with 0.5 ml of 7.5% sucrose solution applied to the cotton plug. All life stages were kept at 27°C and under a LD 16:8 photoperiod.

Gland Samples. Pheromone production was measured by gas–liquid chromatographic (GLC) analysis of solvent extracts of pheromone glands excised from 2-day-old virgin females during the first h of the scotophase. Females were immobilized by placing them in a freezer at −15°C for 10 min. The abdominal tip was then excised and immersed for 1 h in 100 μl of *n*-hexane with 20 ng of (*Z*)-9-tetradecenyl acetate added as an internal standard. Samples were stored at −15°C.

In each family, the mean pheromone blend was estimated by a pooled sample of five glands from full-sibling females extracted in the same 100 μl of solvent. Thus, the contribution of each individual to the estimated family mean was weighted by the amount of pheromone produced. The validity of this procedure was assessed by using data previously recorded for individual pink bollworm females (Collins and Cardé, 1985). Means calculated from pooled (weighted) and individual (unweighted) blend estimates were highly correlated ($r = 0.958$, $t = 30.80$, $N = 87$; $P < 0.001$). Based on 5000 randomly generated samples, the average error (±SD) in the blend estimate was 0.65 ± 0.32% when five females were used per sample; 80.1% of the weighted estimates were within 1.0% of the mean estimated from individual measurements.

GLC Analysis. Pooled gland extracts were evaporated to 1.4–1.6 μl under a stream of nitrogen before injection. Samples were analyzed by GLC with a FID detector on a 2 mm × 3-m glass column packed with 10% Silar 10 CP on Chromosorb W, DMCS AWW (100/120 mesh). GLC analyses were run isothermally at 180°C; the N_2 flow rate was 30 ml/min. The product of peak height × retention time was used as an index of peak area for the pheromone components and the internal standard. Amounts of each pheromone component were determined by comparison to the internal standard.

Samples collected for the third generation in the selected lines were evaporated to 0.7–0.8 μl and injected on a 0.32 mm × 30-m SP-2340 fused silica splitless capillary column. Column temperature was increased from 120 to 200°C at a rate of 3°C/min.

Selection Regime. Individual selection based on pheromone production was not possible because the excision of the pheromone gland renders the female incapable of reproduction (cf. Du *et al.*, 1984). Further, examination of pheromone glands after females have completed oviposition is not feasible, as the postmating pheromone titer is negligible. Therefore, sib selection was employed; females used to produce the next generation were siblings of the females that were measured.

Twenty families were started from male–female pairs chosen randomly from the laboratory colony. The pheromone blend (i.e., the percentage of the ZE-isomer) produced by female progeny in each family was measured by GLC analysis of a pooled sample of five full-sib females.

A "high" line (HL) was initiated from moths in the four families with the highest percentage of ZE. Males and unsampled females in these families were paired to produce the families that constituted the first selected generation. To minimize inbreeding, we did not pair siblings. Similarly, males and females were selected from the four families with the lowest percentage of ZE and used to start a "low" line (LL).

In subsequent generations, an average of 21 families was examined in each line (range, 14 to 25), and the highest (and lowest) 4–6 families were selected to begin the next generation. HL selection was continued for 12 generations. The selection differential for a generation is the difference between the mean of the selected individuals (or families) and the population mean. Since selected families differed in their contributions to the next generation, an effective selection differential was calculated by weighting each selected family according to the number of offspring used to produce families that were measured in the next generation. The mean ($\pm$SD) weighted selection differential was $2.02 \pm 1.13\%$; the mean selection intensity (selection differential divided by phenotypic standard deviation) was 1.25 ± 0.28.

Selection in the low line was discontinued after five generations. Thereafter, females chosen randomly from the laboratory colony (LC) were used as controls.

Intergenerational and between-line comparisons were made using the Mann–Whitney U statistic. Where $N > 20$ for either distribution, comparisons were made using a value, t_s, computed from the U statistic (Sokal and Rohlf, 1981, p. 435).

Additional samples were collected for individual females in the twelfth generation from 17 HL families to document further the validity of the pooled-sample procedure. Blends were estimated as before, except that 4.0 ng of (*Z*)-9-tetradecenyl acetate was added as an internal standard. Individual samples were also collected from randomly chosen LC females.

Reciprocal Crosses. Reciprocal crosses between HL and LC moths were

made after 10 generations of selection. Moths from the five HL families with the highest and from the five HL families with the lowest percentage of ZE were not used. Pooled samples from five females in each family were measured as before. Analysis of variance (ANOVA) was used to assess the significance of differences in the amount and blend of pheromone produced among crosses. Differences between specific crosses were evaluated using the Student–Newman–Keuls' multiple-range test (Steel and Torrie, 1980).

Relaxed Selection. Although selection in the high line was discontinued after 12 generations, the line was continued by mass rearing without selection. After six generations of relaxed selection, the blend and amount of pheromone produced by HL females were compared to those of contemporaneous LC females.

Male Response. In each of the female-selected lines, male response was assessed with a still-air, wing-fanning bioassay (detailed by Collins and Cardé, 1989c). Males were kept at 27°C and LD 16:8 and tested during the second or third scotophase post emergence. Bioassays were conducted during the last 4 h of the scotophase when males are most responsive (Graham *et al.*, 1964; Van Steenwyk *et al.*, 1978) at 27°C and a light intensity of 1.8 lux.

Pheromone stimuli consisted of 0.1 ng of pheromone (ZE plus ZZ) (Farchan Chemical Co.). Each male was tested with a 25, 44, or 65% ZE blend. Stimuli were applied in 10 μl of solvent to strips of filter paper.

After solvent evaporation, a pheromone-impregnated filter-paper strip was inserted into a 10-cm-long × 2.5-cm-diameter glass bioassay tube containing a male. Males were observed for 1 min and the total duration of wing fanning was recorded using a stopwatch. Approximately equal numbers of males within families were tested for each blend. Males were tested only once.

Response was recorded for males from the 20 families in the initial unselected generation, the fifth generation for HL and LL males, and the twelfth generation for HL and LC males.

The Mann–Whitney *U* test was used to compare the duration of wing fanning between lines and generations. In each generation, differences within lines were evaluated with the STP method of nonparametric multiple comparisons (Sokal and Rohlf, 1981, p. 438).

RESULTS

Selection for Altered Pheromone Blends. Selection produced a significant increase in the percentage of the ZE isomer. The mean (±SD) pheromone blend increased from 42.9 ± 1.0% ZE in the initial unselected generation to 48.2 ± 1.2% ZE after 12 generations (Fig. 1). By the fourth generation, the mean HL and LL blends were significantly different (Mann–Whitney *U* test; $t_s = 4.20$;

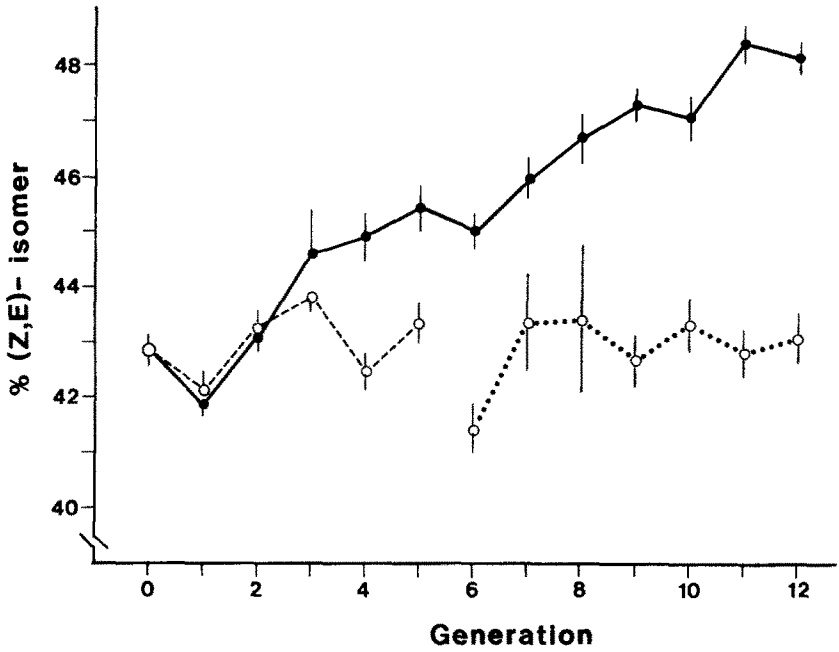

Fig. 1. Mean (±SD) percentage of (*Z*, *E*)-7,11-hexadecadienyl acetate produced by females in lines selected for high (solid line) and low (dashed line) percentages of this isomer and by unselected females in a control line (dotted line).

$P < 0.01$). The proportion of ZE isomer in HL females continued to increase and remained significantly higher than the mean LL and LC blends (Mann–Whitney *U* test; $P < 0.01$).

There was no response to selection in the low line. The mean blend during the five selected generations was 43.0 ± 1.5% ZE and ranged from 42.2 ± 1.4 to 43.8 ± 1.4% ZE (Fig. 1). The distributions of blends in the first and third generations were significantly different from those of females in the initial unselected generation, but blends in generations 2, 4, and 5 were not (Mann–Whitney *U* test; $P = 0.05$). Thus, selection had no consistent effect on the blend produced by LL females.

Realized Heritability. Realized heritability (±SE) for the blend produced by HL females was 0.496 ± 0.041 ($t = 12.01$, df = 11; $P < 0.01$) (Fig. 2). This estimate was based on the slope of the regression line of the weighted cumulated selection differentials on generation means.

Individual Samples. The mean (±SD) blend for individual samples collected from females in 17 HL families in the twelfth generation was 47.9 ± 1.2% ZE, compared to 48.3 ± 1.5% ZE based on pooled samples (not signif-

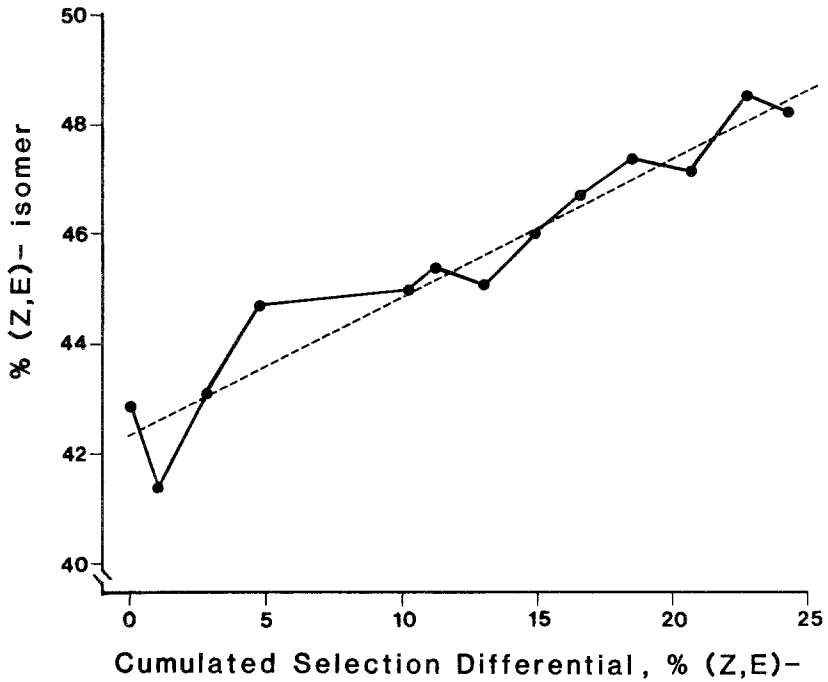

Fig. 2. Response to selection for high ZE:ZZ ratios plotted against the cumulated selection differential. Solid line, selected line; dashed line, regression line ($Y = 42.44 + 0.248\ X$). The realized heritability equals twice the slope of the regression line.

icantly different, $t = 1.08$; $P > 0.05$). The average absolute difference between the two blend estimates for each family was 1.2 ± 0.8% ZE. Although this error is larger than predicted (see Materials and Methods), the two estimates were significantly different for only one family (t test, $P < 0.05$).

A similar concordance was found between blend estimates derived from pooled and individual samples for LC females. The mean estimated from pooled samples was 43.1 ± 1.5% ZE ($N = 10$ samples of 5 females each), whereas the mean for 30 individual samples was 43.4 ± 2.7% ZE (not significantly different, $t = 0.42$; $P > 0.05$). These data, along with the observed response to selection, confirm the validity of pooled samples for measuring pheromone blends for this species.

Pheromone Titer. Although HL families were selected entirely on the basis of blend, the mean (±SD) pheromone titer decreased from 27.4 ± 6.2 to 13.9 ± 4.4 ng after 12 generations (Fig. 3). The mean HL pheromone titer in generation 12 was significantly lower than the mean prior to selection ($t_s = 5.23$; $P < 0.01$) and lower than the mean for contemporaneous LC controls ($t_s =$

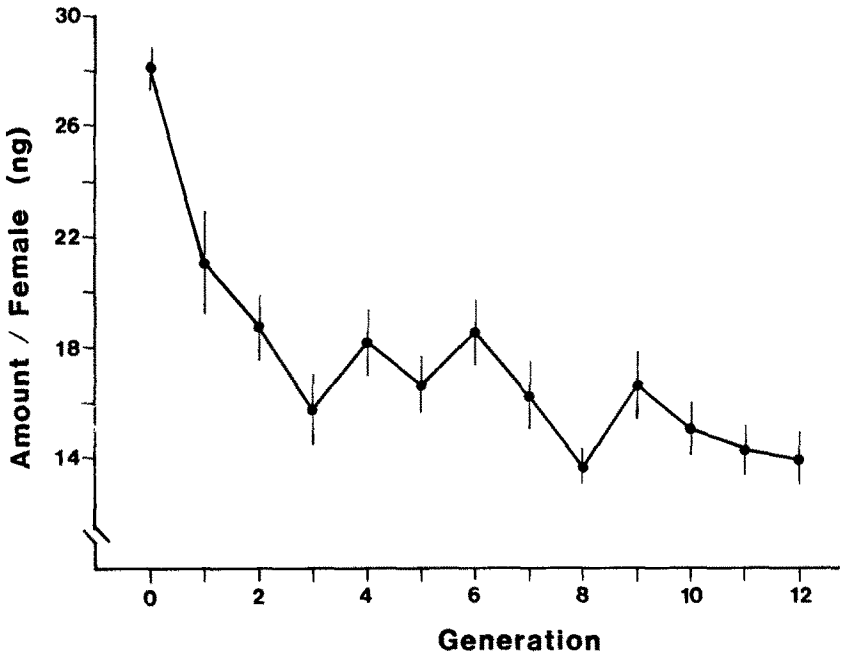

Fig. 3. Mean (±SD) amount of pheromone produced in a line selected for a high proportion of the (*Z*, *E*) isomer.

3.40; $P < 0.01$). The average increment in pheromone blend (percentage ZE) was only 0.44% per generation, whereas titer decreased by 4.66% per generation.

The largest decrement in titer in the high line (23.1%) occurred during the first generation. In contrast, there was no significant change after one generation of selection in the low line ($t_s < 1$). However, the mean titer in the low line fell from 27.48 ± 6.2 to 22.7 ± 4.4 ng after five generations ($t_s = 2.41$; $P < 0.05$), even though the ratio of isomers did not change.

Among HL families, the correlation between mean pheromone titer and mean blend ranged from −0.445 ($t = 2.10$, $N = 20$; $P < 0.05$) in the seventh generation to 0.336 ($t = 1.50$, $N = 20$; $P > 0.05$) in the eleventh generation. No consistent temporal pattern was evident. The correlation for all generations combined was −0.402 ($t = 7.20$, $N = 273$, $P < 0.01$).

Reciprocal Crosses. Mean pheromone blends produced by females from HL × LC crosses were intermediate to blends produced by females in the parental populations (Table I). The mean blend observed in crosses between HL females and LC males was not significantly different from the mean for the reciprocal cross (Student–Newman–Keuls' test, $P > 0.05$; Table I). Phero-

Table I. Mean (±SD) Pheromone Blends and Titers for Females in Crosses Between an Unselected Laboratory Colony (LC) and a Line Selected for a High Percentage of the ZE Isomer (HL)

M × F	Percentage ZE[a,b]	Amount (ng)[a,c]	No. of families
HL × HL	47.26 ± 1.64a	12.40 ± 4.98a	15
HL × LC	44.09 ± 1.60b	18.49 ± 5.18ab	20
LC × HL	44.32 ± 1.91b	21.44 ± 5.76b	20
LC × LC	42.80 ± 1.73c	25.21 ± 6.00c	21

[a]Means within columns not followed by a common letter are significantly different, Student-Newman-Keuls' multiple-range test.
[b]$P = 0.05$.
[c]$P = 0.01$.

mone titer among female progeny of HL × LC crosses was also intermediate to mean titers in the parental populations (Table I). Mean pheromone titers in the reciprocal crosses could not be differentiated statistically.

Relaxed Selection. The mean pheromone blend produced by HL females decreased from 48.2 ± 1.2% ZE in the final (twelfth) selected generation to 45.4 ± 1.0% ZE ($N = 20$ pooled samples of five females each) six generations after selection was discontinued. However, this was still significantly higher than the 43.0 ± 0.9% ZE blend produced by contemporaneous LC females ($U = 1.96$, $n = 10$ pooled samples; $P < 0.01$). Thus, the blend had drifted (or had been selected by unknown forces) in the direction of the unselected population mean but still remained higher after six generations.

Pheromone titer increased from 13.9 ± 4.4 ng per female at the end of 12 generations of selection to 18.6 ± 6.0 ng 6 generations after selection was discontinued. The mean titer after selection was relaxed was not significantly different from the titer for LC females (21.8 ± 7.6 ng; $U = 122$, $P > 0.05$).

Male Response. The mean duration of wing fanning to a 65% ZE blend by HL males increased from 6.3 to 16.8 s after 12 generations (Table II). Response to the 65% ZE blend by HL males in the twelfth generation was significantly greater than the responses to this blend by LC males in the initial unselected generation and after 12 generations ($t_s = 2.73$ and 3.74, respectively; $P < 0.01$).

The durations of wing fanning differed for each of the three blends tested (25, 44, and 65% ZE) for males in the initial unselected generation and for LC males in the twelfth selected generation (STP; $P < 0.01$). In the fifth (and final) generation of the low line, the duration of wing fanning for the 25% ZE blend was significantly greater than for the 65% ZE blend. In contrast, the duration of wing fanning for the 25 and 65% ZE blends were not different among HL males in both the fifth and the twelfth generations.

Table II. Mean (±SD) Duration of Wing Fanning (s) by Males in Lines Selected for High and Low Percentages of ZE Produced by Females (HL and LL, Respectively) and by Males from an Unselected Laboratory Colony (LC), After 0, 5, and 12 Generations

Generation	Line	Pheromone blend (% ZE isomer)[a]			No. of males
		25	44	65	
0	LC	15.9 ± 19.2b	30.4 ± 19.1a	6.2 ± 13.3c	66
5	LL	13.4 ± 17.0a	20.6 ± 21.2a	1.7 ± 7.6b	60
5	HL	10.8 ± 14.6b	23.7 ± 18.1a	7.2 ± 11.8b	78
12	HL	11.4 ± 16.6b	30.8 ± 20.0a	16.8 ± 20.0b	112
12	LC	17.2 ± 21.3b	31.8 ± 22.8a	4.6 ± 12.4c	40

[a] Means within rows not followed by a common letter are significantly different, STP multiple comparison test; $P = 0.05$.

Mean (±SD) wing-fanning durations in the low line to 25 and 44% ZE blends were 13.3 ± 17.0 s ($N = 65$) and 20.6 ± 21.2 s ($N = 60$), respectively, and were not significantly different from corresponding values for HL males ($t_s = 0.80$ and 0.94, respectively; $P > 0.05$). However, the mean response of LL males to the 65% ZE blend was only 1.7 ± 7.6 s ($N = 78$), compared to 7.2 ± 11.8 sec ($N = 63$) for HL males (significantly different, $t_s = 2.98$; $P < 0.01$).

Wing-fanning durations for the 25 and 44% ZE blends were also not significantly different between HL and LC males in the 12th generation ($t_s = 1.29$ and 0.61, respectively; $P > 0.05$). In contrast, the difference between responses to the 65% ZE blend in these lines was significant ($t_s = 3.74$; $P > 0.05$). Thus, in both the high- and the low-selected lines the change in male response involved a change in response to the 65% ZE blend.

DISCUSSION

Selection for blends with a greater proportion of ZE was successful, but selection in the opposite direction was not. Asymmetrical selection responses may be attributable to a variety of genetic and environmental causes (see Falconer, 1981, pp. 190–194). The basis of the asymmetry observed in the present study cannot be identified since the lines were not replicated (Falconer, 1973).

A significant heritability was estimated for the pheromone ratio produced by female pink bollworms in our laboratory population ($h^2 \pm SE = 0.342 \pm 0.084$) (Collins and Cardé, 1985). Based on this estimate, the predicted response to selection in the present study was 4.2% [$= h^2 \times \frac{1}{2}$ (since only females were measured) × the cumulative weighted selection differential]. The observed

response was a 5.3% increase in the percentage of ZE and is in reasonable agreement with the predicted response.

Based on airborne collections of pheromone from field-captured females, Haynes *et al.* (1984) concluded that blend and release rate were independent. Conversely, the findings of the present study suggest an inverse relationship between the pheromone titer and the percentage of ZE. The reduction in pheromone titer in the high line could be a manifestation of a genetic correlation between the pheromone blend and the amount produced. However, a significant positive genetic correlation ($r = 0.236$) between the total amount of pheromone and the percentage of ZE was documented by Collins and Cardé (1985) based on individual gland samples from females in our laboratory colony.

Inbreeding depression may account for part of observed decline in pheromone titer. The estimated inbreeding coefficient in the high line (based on effective population sizes in each generation) was 0.45 after 12 generations. However, the largest decrement in titer (23.1%) occurred after only one generation of selection for a higher percentage of ZE; since sibling matings were not used, no additional inbreeding would have occurred in one generation above the initial (unknown) level in the laboratory colony.

Male response appeared to "track" analogous female blend production that was subjected to artificial selection. Thus, selection for altered blends in females may also result in a concomitant change in male response behavior. The correlated selection response could reinforce assortative mating based on pheromone phenotype and could facilitate the maintenance of communication channel exclusivity.

Evidence of a similar relationship between signal production and response was found in the redbanded leafroller moth (Roelofs *et al.*, 1986); the realized heritability of the pheromone blend was 0.42 when females were selected for production of a higher proportion of (*E*)-11-tetradecenyl acetate but was 0.85 when males that responded to blends with a high proportion of this pheromone component were simultaneously selected.

Although the response to selection for altered blend was statistically significant, the absolute change in the mean blend in the high line was small compared to the relatively broad response spectrum of males (Linn and Roelofs, 1985; Collins and Cardé, 1989c). Thus, heritable variation appears inadequate to bring about a major shift in pheromone blend. However, the size of our laboratory population virtually precludes selection for a rare mutation with major effects. Major changes in field populations are frequently due to initially rare mutations (Roush and Croft, 1986). Further, modest genetically based ratio differences may be transparent to selection because environmental variability in the field may increase phenotypic variation. Response specificity may vary with ambient temperature (Linn *et al.*, 1988). Thus, the impact of the 5.3% blend

shift found in this study cannot be fully evaluated without examining the effects of small blend shifts on male response in the field.

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