Effects of Varying Sex Pheromone Component Ratios on the Zigzagging Flight Movements of the Oriental Fruit Moth, *Grapholita molesta*

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As the ratio of (E)-8-dodecenyl acetate (E8-12:Ac) to (Z)-8-dodecenyl acetate (Z8-12:Ac) increased past optimal low levels in the pheromone blend, fewer males were able to fly 2.5 m upwind to the source. The tracks of males that flew in plumes of such high-(E) off-blends were slower and narrower than those of males flying to lower-(E) blends. The tracks were narrower, first of all, because as the proportion of E8-12:Ac increased, the males steered more into the wind. More of their thrust was directed upwind and therefore their ground-speed to either side of the windline was reduced. In addition, males also reduced their airspeeds to high-(E) blends, which contributed to the decreased ground-speeds and narrower tracks. No significant changes in the frequency of counterturning were found in response to increasing proportions of E8-12:Ac. The inability to continue upwind flight in a plume of an off ratio was indicated by in-flight arrestment in the plume. Arrestment resulted from changes in the course angles steered by the males and the airspeeds flown.

INTRODUCTION

Multicomponent sex pheromone blends are common in the Lepidoptera (Roelofs and Cardé, 1977) and are often composed of specific ratios of geometric

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isomers (Roelofs, 1980). Previous studies with the oriental fruit moth, *Grapholita molesta*, in the laboratory (Baker *et al.*, 1981) and in the field (Baker and Cardé, 1979) have demonstrated that males are able to fly upwind and locate a pheromone source in largest numbers when it emits a blend of components at the precise ratio and release rate of that of conspecific females. In addition, the response specificity of males to their natural blend can be altered by preexposing the males to one of the pheromone components alone (Linn and Roelofs, 1981).

Previous studies, such as the above using altered component ratios, have measured the proportions of males able successfully to make the transition from one step in the sequence of behaviors associated with source location to the next (Baker *et al.*, 1981; Linn and Roelofs, 1981, 1983). These studies consistently showed that inappropriate ratios of (E)-8-dodecenyl acetate to (Z)-8-dodecenyl acetate, the two main pheromone components, resulted in fewer flights to the source. This inability to locate the source was often due to premature in-flight arrestment in the plume once upwind flight in the plume had begun. Although the proximate reasons for the inability of males to locate pheromone sources with too little E isomer were not always clear, too much E consistently seemed to result in arrestment, similar to the behavior observed from males responding to an excessively high dosage of the natural blend (Kuenen and Baker, 1982). However, the maneuvers used by the males, i.e., the behaviors that resulted in either upwind flight or arrestment to different blends, were not described. In the present study, we used the triangle of velocities (Kennedy, 1940) formulas of Marsh *et al.* (1978) and David (1986) to calculate how *G. molesta* males change their flight behaviors in response to different blend ratios as well as the possible visual feedback used to accomplish these changes. We have found that unlike their responses to increased emission rates, males alter both their airspeed and their course angles in response to slight changes in the ratio of components but do not change their frequency of counterturning.

MATERIALS AND METHODS

Insects. Moths were reared on small green thinning apples (Baker *et al.*, 1981); the pupae were separated according to sex, and the adult males were separated daily, according to age. All life stages were maintained at about 25 °C on a 16 : 8 L : D cycle. Adult males were held in an environmental chamber with positive air pressure to eliminate the possibility of exposure to female pheromone prior to the experiments and had an 8 % sucrose solution available to them at all times. All moths were 1–5 days old at the time of the experiments.

Pheromone. The synthetic sex pheromone consisted of the three-component blend emitted by *G. molesta* females: 5.9% (E)-8-dodecenyl acetate (E8-12 : Ac) and 3.8% (Z)-8-dodecenyl alcohol (Z8-12 : OH) (Cardé *et al.*, 1979)

in (Z)-8-dodecenyl acetate (Z8-12:Ac) (Roelofs *et al.*, 1969). The solutions of various E/Z ratios (1.7, 5.9, 10.2, 20.5, and 37.0% E8-12:Ac) were the same as described by Baker *et al.* (1981). A "100%" Z8-12:Ac solution to which no E8-12:Ac was added was also used. However, upon gas–liquid chromatographic (GLC) analysis this solution was found to contain 0.04% E8-12:Ac, possibly the result of a low level of spontaneous isomerization. Final ratios and dosages were verified by GLC using a 3-m × 4-mm glass column packed with 10% Silar-10C on acid-washed 100- to 120-mesh chromosorb W. Under the GLC conditions described, all solutions contained less than 0.5% volatile impurities. Stock solutions were equilibrated to 30 μg of Z8-12:Ac per μl, and 10-μl aliquots of each were applied to the wide end of a rubber septum (A. H. Thomas Co. No. 8753-D22, sleeve type, 5 × 9 mm). We chose the 30-μg dosage in order to elicit moderate levels of arrestment, as well as successful flight to the source (Baker *et al.*, 1981; Linn and Roelofs, 1983). The emission rate from a septum of this dosage is at the upper limit of the optimal range of emission rates of the natural blend. This range is centered around the natural emission rate of a calling female (3.2 ng/h) and approximately that of a septum loaded with 10 μg of the synthetic blend. All septa were impregnated with pheromone on the same day, and were stored separately at 0°C when not in use.

Wind Tunnel and Experimental Procedure. Experiments were performed in a clear polycarbonate plastic wind tunnel, constructed after Miller and Roelofs (1978). Wind (0.7 m/s) was generated by a 1-hp voltage-regulated electric fan which pushed air into a wooden mixing chamber at the front end of the wind tunnel; the airflow was smoothed and laminarized prior to entering the working section of the tunnel by being passed through two fine-meshed fabric screens. Pheromone was eliminated via a 30-cm diameter exhaust duct (air speed in center, 2.9 m/s) positioned (using a $TiCl_4$-generated smoke source) such that it was aligned with the center of the plume. The remainder of the air from the tunnel was recirculated through the room. A floor pattern consisting of randomly arranged 10-cm-diameter red dots on a white background was positioned about 1.5 cm below the 6-mm-thick clear Plexiglas floor of the tunnel. Since red filters were placed over the lenses of the cameras, these dots appeared white in black-and-white video recordings, thus facilitating the later tracing and analysis of moth tracks (David, 1982). The room light intensity was set at 250 lux and was provided by four voltage-regulated incandescent white lights reflected off of an expanded polystyrene ceiling.

Tracks of individual males were recorded using two Sony RSC-1050 rotary-shutter cameras connected to two Sony SLO-340 video recorders. Each camera was positioned about 1 m above, and aimed at, the floor of the tunnel and oriented such that the field of view of each camera was 1 m long and 0.72 m across the tunnel. One camera recorded the movements of males which had

made prolonged upwind flight in the plume. The field of view of this camera began 150 cm downwind of the pheromone source and extended to 50 cm from the source. This camera also recorded the movements made during arrestment of upwind progress. The second camera was positioned above the point where the males were released in the plume, such that the 1-m-long field of view would enable the recording of males as they "locked-on" to the plume. The field of view of the second camera extended from 3 m from the source to 2 m from the source. Thus, the fields of views of the two cameras did not overlap.

Males were released singly from cone-shaped aluminum screen cages (maximum diameter, 10 cm; and maximum height, 7 cm) held in a ring stand 15 cm above the floor of the tunnel and 250 cm downtunnel of the pheromone source. Each cage was used once per treatment and the cages and the ringstand were rinsed with acetone between treatments. Moths were tested in a randomized complete block design, with 10 moths being released per block per treatment. Seventy moths were released to each treatment. The pheromone source was placed on a 15 × 15-cm sheet-metal stand 15 cm above the floor of the tunnel and 40 cm from the upwind end. A fresh sheet-metal platform was used for each treatment. The sheet-metal stand which held these platforms was rinsed with acetone between treatments and the platforms were used once and rinsed in acetone daily.

Data Processing and Analysis. Recordings of both views of each flight track were rerecorded onto a Sony SVM-1010 motion analyzer for better motion resolution and played back frame by frame through a 41-cm (16-in.) Panasonic WV-5470 black-and-white video monitor. The consecutive locations of the males were digitized every 1/30 s.

Tracks were digitized using a T-bar style X/Y digitizer (Radio Shack TRS-80 digitizer), serially interfaced with a microcomputer (Radio Shack TRS-80 Model III), and simultaneously displayed on a flatbed plotter (Radio Shack TRS-80 FP-215) to ensure that the coordinates entered from the digitizer correctly represented the track. The digitized coordinates for each track were stored for later analysis.

All tracks and track sections were analyzed using a program developed (Kuenen and Baker, 1982) to measure pertinent track parameters. These include both linear (net and overall velocity) and angular (turn severity, turn frequency, and angular velocity) track parameters. For the purposes of this experiment a turn was defined as a change of greater than 50° from clockwise to anticlockwise (or vice versa) (Kuenen and Baker, 1982). Track interreversal angles and interreversal distances (the reversal-to-reversal width of each zigzag) were measured according to the criteria of Kuenen and Baker (1982), with an X/Y digitizer pad (Houston Instruments HI-PAD DT-11) which was serially interfaced with a microcomputer. The duration (the number of vectors at 1/30 s per vector) between the apices of successive counterturns was counted manually.

Calculations of the triangles of velocity (Kennedy, 1940) were based on four quantities, two of them measured from tracks, groundspeed (length of the straight-leg/time to fly this leg), and track angle (angle of the straight-leg with respect to the windline) (Marsh *et al.*, 1978). The other two, the windspeed and direction, were known constants throughout these experiments. Angles and lengths of track straight-legs were measured by hand. The importance of using the straight-legs for the track angles is that males appear to fly relatively straight and level along this portion of their flight tracks (Willis *et al.*, unpublished; Baker, 1988), whereas they roll and change pitch through the turns. Their visually mediated steering should be stable as they fly along these straightest portions of their tracks, thus giving the ventral ommatidia full view of the moving ground pattern. These values were then used to calculate airspeed, groundspeed, course angle, and drift angle (Marsh *et al.*, 1978). The values for the longitudinal and transverse components of image flow were calculated from these same triangle of velocities data according to a method outlined by Ludlow (1984) and David (1986).

When arrestment occurred in the field of view of the up-tunnel camera, the tracks were divided into three sections for analysis: (i) upwind flight (pre-arrestment), (ii) arrestment, and (iii) postarrestment. The criteria used for dividing the arrestment tracks were those of Kuenen and Baker (1982). The arrestment portion was the entire track section within a 10-cm-long region at the up-tunnel end of the track. These track sections were then analyzed using the program of Kuenen and Baker (1982). None of the males flying to the 1.7% E blend became arrested in the field of view of the camera, hence the only comparisons were between the 5.9 and the 10.2% E blends.

To examine how the males were changing their actual flight behavior during arrestment (as defined above), we again used the triangles of velocities formulas. For this more detailed analysis arrestment was arbitrarily designated as the first track leg in which upwind displacement stopped (zero point in Figs. 1A–E). The track parameters calculated from the triangle of velocities and interreversal distances were then segregated on a track-leg-by-track-leg basis before and after arrestment. Track data were analyzed using either a one- or a two-way analysis of variance and Duncan's new multiple-range test. The percentages of moths making successful transitions between steps in the behavioral sequence, from takeoff to source location, were compared using a method of adjusted significance levels for proportions (Ryan, 1960).

RESULTS

Behavioral Response to Varying E/Z Ratios. The sequence from takeoff to source location was divided into four categories: (i) taking flight (takeoff); (ii) lock-on and upwind flight in the plume, (iii) upwind flight to within 30 cm of
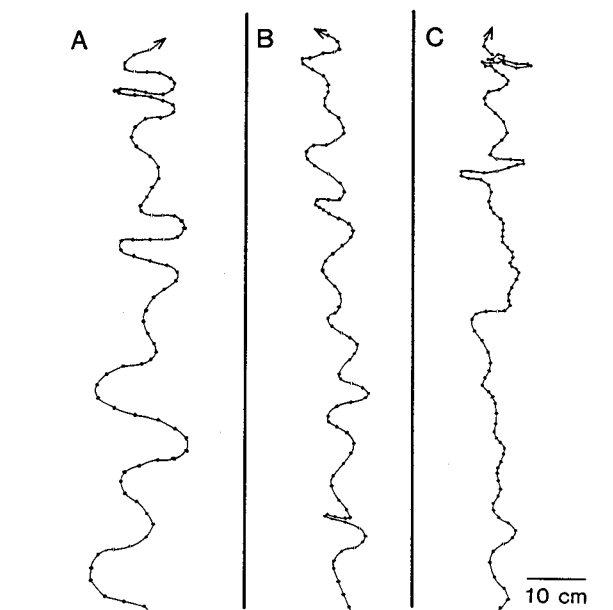
Fig. 1. Typical tracks of *G. molesta* males flying upwind to the three E/Z ratios which elicited upwind flight in the wind tunnel. (A) Track of a *G. molesta* male flying upwind to a pheromone component blend with 1.7% E; (B) track of a *G. molesta* male flying upwind to a pheromone component blend with 5.9% E; (C) track of a *G. molesta* male flying upwind to a pheromone component blend with 10.2% E.

the source, and (iv) touching the source. Across all four categories, significantly fewer males responded to blends containing 0.04, 20.5, and 37% E than to the 1.7, 5.9, and 10.2% E blends (Table I) ($P < 0.05$). Few (<5 total) of the males exposed to the 0.04, 20.5, and 37% E blends locked on and flew upwind, and none of these males reached the source. Of the males responding to the other three blends, those flying in response to 10.2% E exhibited significantly reduced levels of response in all behavioral categories compared to the males responding to 1.7% E and in all but one category (touching the source) compared to the males responding to the 5.9% E blend. Significantly more males were able to locate the 1.7% E source than the 5.9% E (the blend emitted by *G. molesta* females) source. This result was expected because the dosage (30 μg) of pheromone used was higher than optimal in order to ensure a certain number of arrestment tracks. These results are consistent with previous studies describing the effects of optimal blend and dosage (Baker *et al.*, 1981; Linn and Roelofs, 1981, 1983) on the ability of males to locate a pheromone source. Since the numbers of males flying upwind to the 0.04, 20.5, and 37% E were

Table 1. Percentage of Males Responding by Flying Upwind to Different E/Z Blends[a]

Percentages of E in Z	N	% taking flight	% lock-on and upwind flight in the plume	% flight within 30 cm of the source	% touching the source
0.044 (100% Z)	70	44[c]	1.4[c]	0[d]	0[c]
1.7	70	97[a]	86[a]	83[a]	67[a]
5.9	70	97[a]	81[a]	49[b]	13[b]
10.2	70	74[b]	36[b]	10[c]	6[b]
20.5	70	53[c]	0[c]	0[d]	0[c]
37.0	70	50[c]	3[c]	0[d]	0[c]

[a] Percentages in the same column having no superscripts in common are significantly different ($P < 0.05$) according to a method of adjusted significance levels for proportions (Ryan, 1960).

too few and these tracks were too short to allow statistical analysis, only the flight tracks of males responding to the 1.7, 5.9, and 10.2% E blends underwent further analysis.

Upwind Flight in the Plume. Only the flight tracks of those males that locked on and flew upwind the entire length of the field of view of the up-tunnel camera were included in this analysis. The flight tracks of males exhibiting in-flight arrestment in the field of view of the camera were analyzed separately (see the next section).

As the percentage of E8-12:Ac in the blend increased, the overall and net velocities of the males flying upwind in the plume decreased (Table II). The overall velocity is the male's groundspeed along its sinuous flight path, whereas the net velocity is the velocity of the male's net up-tunnel progress (from the release point to the source along a straight line). In both cases the males flying in plumes from the 10.2% E sources flew the slowest, significantly slower ($P < 0.05$) than males flying to the other two E/Z blends. While in both cases there were no statistical differences in the velocities of males flying to 1.7% E

Table II. Mean Track Parameters ($\pm$SD) of Males that Changed Significantly During Upwind Flight to Synthetic Pheromone Sources Emitting Three Different E/Z Blends[a]

Percentage of E in Z	N	Overall velocity (cm/s)	Net velocity (cm/s)	Interreversal distances (cm)
1.7	59	65.6 ± 12.3[a]	31.9 ± 9.8[a]	7.7 ± 2.3[a]
5.9	35	63.8 ± 15.6[a]	29.8 ± 11.7[a]	6.7 ± 2.3[ab]
10.2	10	55.2 ± 10.6[b]	23.3 ± 5.5[b]	6.2 ± 1.9[b]

[a] Means in the same column having no superscripts in common are significantly different ($P < 0.05$) according to a one-way analysis of variance and Duncan's new multiple-range test.

or 5.9% E, there was a consistent trend for the velocity to decrease as the percentage of E in the blend increased. The zigzagging flight paths of the males (interreversal distances) also narrowed significantly ($P < 0.05$) in response to an increasing percentage of E in 'the blend (Fig. 1, Table II). There were no significant differences among any of the angular track parameters ($P > 0.05$) (Table III). Importantly, counterturning frequency was not affected (Table III). There was a significant ($P < 0.05$) increase in the angular-to-linear velocity ratio as the percentage of E in the blend increased (Table III), but this increase was nearly entirely due to the significant decrease in overall velocity alone.

Triangle of velocities analysis of how the males were maneuvering in order to make the above tracks indicated that they steered more into the wind to the 10.2% E blend ($P < 0.05$) than during flight to either the 1.7 or the 5.9% E blends (Table IV). Even if these males had kept a constant airspeed, this would have accounted for the significantly lower groundspeed of the 10.2% E males, but they *also* reduced their airspeed in response to the 10.2% E blend (Table IV; $P < 0.05$). Despite significant changes in other parameters, the drift angle was not significantly affected by changes in the E/Z ratio. These changes in angles and velocities flown resulted in significant changes in both the transverse and the longitudinal components of image flow. As the percentage of E in the blend increased, the males allowed decreasing amounts of both transverse and longitudinal image flow (Table IV).

Thus, for males that continued their upwind flight without becoming arrested, the narrower, slower tracks to higher proportions of E were due to alterations in airspeed and course angle but not to alterations in the self-steered counterturning program; reversal frequency was unaffected. The tracks narrowed because males steered a course more directly into the wind while decreasing their airspeed. Thus their groundspeeds were reduced and they traveled a shorter side-to-side distance per each unvarying interreversal interval.

Arrestment. The switchover from upwind flight to arrestment by males responding to blends with higher than optimum proportions of E was not caused by a decrease in overall velocity or significant changes in turning frequency or turn magnitude. Rather, the key cause of arrestment was that males steered a course more across the wind than during the preceding upwind flight (Fig. 2A). This resulted in the approximately 100° cross-wind track angles typical of arrestment (Fig. 2A). Because the males first reduced, then increased their airspeeds during arrestment, the larger (more cross-wind) course angles steered did not at first allow the males to gain groundspeed (Fig. 2B). As males increased their airspeeds, their groundspeeds also increased, and their tracks became wider, typical of crosswind casting (Fig. 2E) (Kennedy, 1983). No statistical differences were found in any of the parameters measured between males becoming arrested to the 5.9 or the 10.2% E blends (two-way ANOVA; $P > 0.05$).

Table III. Mean Angular Track Parameters ($\pm$SD) of Males During Upwind Flight to Synthetic Pheromone Sources Emitting Three Different E/Z Blends[a]

Percentages of E in Z	N	Turn frequency (turns/s)	Turn magnitude (°/turn)	Angular velocity (°/s)	Interreversal angle (°)	Angular:linear velocity ratio (°/cm)
1.7	59	6.5 $\pm$ 1.0[a]	149 $\pm$ 25[a]	948 $\pm$ 126[a]	65.2 $\pm$ 8.0[a]	11.5 $\pm$ 7.0[b]
5.9	35	6.9 $\pm$ 1.0[a]	150 $\pm$ 22[a]	1018 $\pm$ 151[a]	64.2 $\pm$ 8.3[a]	13.9 $\pm$ 9.0[ab]
10.2	10	6.5 $\pm$ 1.0[a]	152 $\pm$ 24[a]	987 $\pm$ 181[a]	64.2 $\pm$ 9.3[a]	18.2 $\pm$ 8.0[a]

[a] Means in the same column having no superscripts in common are significantly different according to a one-way analysis of variance and Duncan's new multiple-range test ($P < 0.05$).

Table IV. Mean Triangle of Velocity Parameters (±SD) from the Flight Tracks of Males Flying to Three Different E/Z Blends[a]

Percentage of E in Z	N	Airspeed (cm/s)	Groundspeed (cm/s)	Track angle (°)	Course Angle (°)	Drift angle (°)	Transverse image flow	Longitudinal image flow
1.7	59	135.8 ± 15.4[a]	92.0 ± 18.0[a]	63.1 ± 7.1[a]	33.3 ± 5.7[a]	29.8 ± 3.2[a]	44.6 ± 7.3[a]	79.0 ± 17.5[a]
5.9	35	128.6 ± 16.2[ab]	85.9 ± 17.6[ab]	66.0 ± 7.0[a]	33.8 ± 5.3[a]	32.2 ± 4.8[a]	44.1 ± 6.1[a]	72.2 ± 18.0[ab]
10.2	10	122.6 ± 9.2[b]	76.5 ± 14.8[b]	60.8 ± 10.2[b]	29.7 ± 7.1[b]	31.1 ± 3.9[a]	39.4 ± 9.1[b]	63.9 ± 12.5[b]

[a] Means in the same column having no superscripts in common are significantly different according to a one-way analysis of variance and Duncan's new multiple-range test ($P < 0.05$).
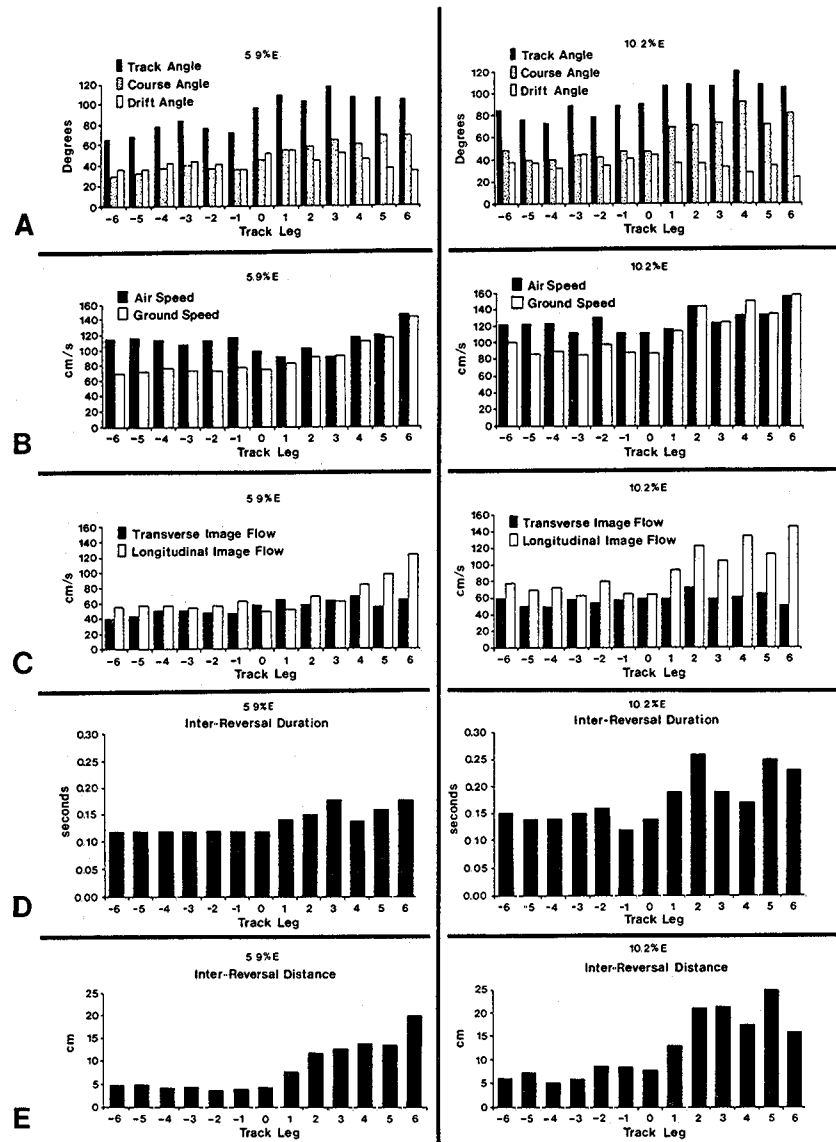
Fig. 2. Means of track parameters taken during the six track legs immediately prior to arrestment (−6 to −1), during arrestment (0) and the six track legs immediately after arrestment (1 to 6) for *G. molesta* males becoming arrested to the 5.9 and 10.2% E blends. (A) Mean track, course, and drift angles; (B) airspeed and groundspeed; (C) transverse and longitudinal image flow; (D) interreversal duration; and (E) interreversal distance. For 5.9 and 10.2% E, *N* is equal to 12 and 6, respectively. There were no statistically significant differences in any of the parameters measured between the 5.9 and 10.2% E blends ($P > 0.05$), according to a two-way ANOVA.

The change in course without the corresponding significant airspeed alterations caused a temporary increase in the drift angle at arrestment, which subsequently returned to its former magnitude (Fig. 2A). Thus, one possible type of feedback males could use to steer a more cross-wind track could be the increased drift angle. However, this increased drift angle was only temporary, lasting only a few reversals, then returning to its former level while the track angle remained at 100°. On the other hand, the transverse component of image flow also increased at arrestment and seems to remain higher when the track angle is greater (Fig. 2C). Changes in the longitudinal component of image flow, both increases and decreases, appear to correspond only to the changes in airspeed and, thus, could serve as feedback for airspeed alterations and groundspeed control (Fig. 2C). This increase coincided with the increase in course angle after arrestment. Transverse and longitudinal image flow in the track legs preceding arrestment appear to be greater during flight in the 10.2% E blend than in the 5.9% E blend (Fig. 2C). However, there were no statistically significant differences when these values were compared using a two-way ANOVA. The trends and changes in image flow before and after arrestment are the same at both blends.

During arrestment, the interreversal duration, or interval between consecutive counterturns, also increased, but only after the first arrestment leg (Fig. 2D). The interreversal duration before arrestment to the 5.9% E blend was remarkably consistent at 0.12 s and then increased beginning with the second arrestment leg, to contribute to the wider track after arrestment. Duration measurements from males responding to the 10.2% E blend were more erratic after arrestment [there was large variation between individuals and small sample size ($N = 6$)], but a similar trend was evident.

Thus, arrestment of upwind progress appears to be due primarily to rapid changes in both steering and airspeed, with the course angle increasing and the airspeed decreasing. Subsequent increases in airspeed plus a reduction in the frequency of counterturns contribute to the increasing width of the track and the transition to casting flight. In the postarrestment phase, casting males typically gained altitude and displaced downwind, up and out of contact with the plume. During this phase, males were no longer flying in the plume area, and the frequency of counterturns decreased still further to make each interreversal leg last 0.24 and 0.22 s on average, for males that had flown to 5.9 and 10.2% E, respectively.

DISCUSSION

The decreased ability of *G. molesta* males to locate the source successfully as the percentage of E in the blend increased was in accordance with other studies in which both blend quality (Baker *et al.*, 1981; Linn and Roelofs, 1981,

1983) and blend quantity were varied (Baker *et al.*, 1981; Kuenen and Baker, 1982; Linn and Roelofs, 1981, 1983). Like *G. molesta* males flying in phero-mone plumes of increasing concentration (Kuenen and Baker, 1982), males in the present study made slower upwind progress and narrowed their tracks in response to increasing percentages of E in the blend. Kuenen and Baker (1982) concluded that the concentration-dependent narrowing of the track was due to *both* an increased frequency of reversals and a reduction of course angle and airspeed. Thus, the pheromone concentration was thought to affect both the self-steered counterturning and the anemotactic maneuvering systems. However, in the present study no significant changes were found in the self-steered coun-terturning program in response to plumes with increasing percentages of E in the blend. The narrowing of the track and some of the decrease in groundspeed could be explained by an increase in the course angle as a result of changes in the visually steered anemotactic maneuvering system.

An additional factor explaining the decrease in groundspeed with increasing E in the blend is the reduction of airspeed exhibited by males. This would reduce the basal rate of movement in any windspeed and at any angle to the wind and, as such, affect the orthokinetic/linear velocity of movement system [orthokinetic (Frankel and Gunn, 1940)]. Kuenen and Baker (1982) observed that, on average, *G. molesta* males reduced their airspeed in response to increased pheromone concentrations.

Two methods of airspeed control are known from insects, variation of wing-beat frequency [P. S. Baker *et al.* (1981), *Locusta migratoria*; Farkas *et al.* (1974), *Pectinophora gossypiella*] and variation in the pitch angle of the body with respect to the wind [Vogel (1967), *Drosophila*]. It is not known which of these two methods is used by *G. molesta* males to change their airspeed or if it is a combination of both.

Kuenen and Baker (1982) suggested that each of the two main pheromone components might modulate a separate aspect of the flight behavior; E8-12:Ac might modulate turning, and Z8-12:Ac might modulate linear velocity. As the amount of E8-12:Ac increased, the males would increase the frequency of counterturning accordingly. Our results do not support this idea because the frequency of turning was not affected by changes in the E/Z blends. Thus our results further substantiate those of previous studies (Baker and Cardé, 1979; Linn and Roelofs, 1981, 1983), indicating that *G. molesta* males do not exhibit separate behavioral responses to the individual components of their pheromone blend.

At the moment of arrestment in the plume, males abruptly steer across the windline and decrease their airspeed, increasing their track angle to greater than 90° without increasing their groundspeed. Thus on this first arrestment leg, upwind displacement ceases without an immediately widening casting track, but on subsequent legs the increased course angle (and eventually the increased

airspeed) causes an increased groundspeed and hence a wider track. On the first leg of arrestment, the counterturning program generates a turn back across the windline only after the same time interval has elapsed as for the preceding six track legs. However, subsequent reversals occur with decreasing frequency and the airspeed gradually increases, resulting in a wider, casting track.

Although similar in appearance, in-flight arrestment and cross-wind casting following the loss of contact with a pheromone plume are the result of different flight maneuvers. Following plume loss the transition to casting flight occurs in a slightly different way (Baker and Haynes, 1987). As in arrestment, beginning with the first leg following loss of pheromone, *G. molesta* males significantly increased their course angle to carry them more crosswind and change their track angles to about 90°. However, they continued to maintain their previous airspeed instead of reducing it as during arrestment, so that the track immediately began to widen due to the increased groundspeed. Moreover, unlike during arrestment, the interreversal duration also increased immediately and contributed to the widening casting track.

To relocate a lost pheromone plume more rapidly it would be advantageous for a male to be able to switch rapidly over to a very wide track and expand the amount of air traversed. Arrestment to an inappropriate emission rate or pheromone blend, on the other hand, has been suggested as a mechanism to avoid interspecific mating mistakes (Baker, 1985), and perhaps males undergoing arrestment need not widen their flight tracks quite as rapidly. Rather, once upwind progress has been arrested due to too high an emission rate or an incorrect ratio of pheromone components, it would be advantageous for the male to leave the immediate area of the plume, as described in this study. By leaving the proximity of the nonconspecific female he would avoid repeatedly responding to a pheromone plume that, at least initially, he perceived as coming from a conspecific female. The continuation of counterturning could enhance his ability to track the wind direction and velocity (Kennedy, 1983; Baker, 1985; Willis and Baker, 1987) and continue his search for a conspecific female.

ACKNOWLEDGMENTS

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