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COMPARISON OF MANOEUVRES USED BY WALKING VERSUS FLYING *GRAPHOLITA MOLESTA* MALES DURING PHEROMONE-MEDIATED UPWIND MOVEMENT

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Abstract—While walking upwind to a pheromone source, male oriental fruit moths, *Grapholita molesta* (Busck) exhibit none of the temporally regular course reversals (counterturns) and resultant zigzag tracks which characterise the tracks of males flying upwind to pheromone. Rather, males walk in a nearly straight line, steering directly upwind, in contrast to flying males, which steer a course alternating back and forth about 15–20° to either side of the windline. These results support the idea that counterturning in males flying to pheromone sources is a mechanism which enhances their visual perception of wind-induced drift. Counterturning would be unnecessary in walking males, which can perceive wind velocity and direction via mechanoreceptors.

Key Word Index: *Grapholita molesta*, pheromone, orientation, flying, walking, behaviour

INTRODUCTION

Recent findings using several species of moths have indicated that in addition to optomotor anemotaxis, flying males employ a self-steered programme of counterturns in the process of locating the pheromone source (Kennedy, 1983; Kuenen and Baker, 1983; Baker *et al.*, 1984). In the oriental fruit moth, *Grapholita molesta*, the programme causes conspicuous, temporally regular zigzags in the flight track. The counterturning programme and anemotaxis are integrated to result in upwind displacement while maintaining contact with the plume. If the concentration suddenly decreases (perhaps due to loss of the plume in shifting wind), the zigzag tempo quickly decreases in conjunction with a change in anemotactic steering to result in "casting" flight across the windline (Marsh *et al.*, 1978; Kuenen and Baker, 1983; Baker and Haynes, 1987). In the oriental fruit moth, the concentration of pheromone affects both the anemotactic and self-steered systems to result in different flight tracks (Kuenen and Baker, 1983), but slight changes in the *quality* of the pheromone blend appear to affect only the anemotactic system (Willis and Baker, unpublished).

Recently, it has been hypothesised that flying moths counterturn rather than fly straight upwind in order to detect shifts in wind direction more accurately (Kennedy, 1983; Cardé, 1984; Baker, 1984). One way of testing this hypothesis would be to compare the maneouvres made by flying vs walking insects, ideally using the same species for the comparisons. The orientation mechanisms of insects that walk to sources of their pheromone have been examined thoroughly for several species (Kramer, 1975; Tobin, 1981; Tobin and Bell, 1982; Bell and Tobin, 1982; Preiss and Kramer, 1986a). Anemotactic chemotactic, and self-steered mechanisms have been implicated in successful source location. However, most of these analyses have been performed on species which exclusively or primarily walk. For the exception, the gypsy moth, recent exhaustive analyses have been performed with males walking to sources of sex pheromone (Preiss and Kramer, 1986a). In addition, a thorough analysis has been performed on the pheromone-mediated flight behaviour of tethered gypsy moth males which were given optical feedback mimicking that during flight (Preiss and Kramer, 1986b). But the validity of using tethered animals has been questioned (David, 1986) and a direct comparison of the movements of male moths walking vs flying under the same conditions of pheromone stimulation, wind etc. was not undertaken. Comparing the manoeuvres during walking vs in-flight used by a species which commonly flies but sometimes walks at least part of the way to a pheromone source could be informative and reveal much about the systems available to insects for chemo-orientation and their function. We made such a comparison, and report here that male *G. molesta* do not use a counterturning programme while walking upwind to pheromone, whereas they do while flying upwind. Consequently, the zigzag tracks characteristic of flying males are absent in walking males, who appear to steer straight upwind rather than back and fourth across the windline. The implication from this finding is that counterturning is important to the optomotor anemotactic system for sampling wind during flight, but is not necessary while walking, since wind direction and velocity can both be detected mechanically.

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MATERIALS AND METHODS

Insects

Grapholita molesta individuals were reared on small green thinning apples according to methods described by Baker *et al.* (1981). Pupae were separated according to sex, adults were allowed to emerge and the males were held separately from the females under conditions described by Willis and Baker (1984).

Pheromone

The synthetic sex pheromone of *G. molesta* females used in these experiments was a three-component blend consisting of varying percentages of (*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 six different blends, 0.04, 1.7, 5.9, 10.2, 20.5 and 37% E8-12:Ac in Z8-12:Ac, were the same solutions formulated by Baker *et al.* (1981). All blends were formulated with the same quantities of Z8-12:Ac and Z8-12:OH, and varied only in the amount of E8-12:Ac, as determined by GLC analysis using a 3 m × 4 mm glass column packed with 10% Silar 10C on acid-washed 100–120 mesh Chromasorb W. All solutions contained less than 5% volatile impurities as measured using the above GLC conditions. Stock solutions were equilibrated to 3.0 μg/μl and 10 μl aliquots were applied to the wide end of a rubber septum (A. H. Thomas Co., No. 8753-D22, sleeve type, 5 × 9 mm). All septa were impregnated the same day and were stored separately at 0°C when not in use.

Experimental procedures

Recordings of males walking upwind in response to the six different E/Z blends were made by inserting an elevated "walking" platform into a previously described 3.4 m-long × 91 cm-wide (Kuenen and Baker, 1982) polycarbonate plastic wind tunnel. The platform was made of a 0.5 mm-thick sheet of aluminum 29 × 91 cm, placed longitudinally in the centre of the tunnel and supported 15 cm above the floor by two sheet metal stands positioned so as not to generate vortices that could interfere with the plume structure. The upwind edge was 90 cm from the upwind end of the tunnel. Each pheromone septum was placed in the centre of the walking platform, 3 cm from its upwind end. Windspeed for both walking and flying males was 0.7 m/s, and the temperature was maintained at between 19–22°C to encourage upwind walking by the males released onto the platform rather than flight (Baker *et al.*, 1981). Males readily took flight at this temperature when released in the plume with no platform present. The recording field of view for flying males extended from 150 to 50 cm downwind from the source and was 0.72 m in width. The recording field of view for walking males was also 1 × 0.72 m extending to the source from 1 m downwind. Only those males which walked from the moment of release were included in the analysis of orientation movements while walking (including those males which began walking and then took off). Males were introduced singly in an aluminium screen cage (8 cm max. dia × 0.5 cm max. height) held at the height of the walking platform in a ringstand. Males walked while wing fanning out of the screen cage and onto the platform. Each release cage was used once per treatment and all release cages were washed in acetone between treatments. The ring stand, walking platform and sheet metal stands were also washed with acetone between treatments. Moths were tested according to a randomized complete block design, with ten males released to each treatment in each block. Seventy moths were released in each treatment.

Data processing and analysis

The tracks of individual males were recorded from above on a Sony SLO 340 video recorder using a Sony RSC 1050 rotary-shutter video camera positioned on top of the tunnel's plexiglas ceiling. All recordings were then re-recorded onto a Sony SVM-1010 motion analyser for better motion resolution, and played back frame-by-frame through a 41 cm (16 inch) Panasonic WV-5470 black-and-white video monitor. The consecutive locations of walking males were digitised from the video monitor every 1/4 s, those of the faster moving flying males every 1/30 s, to minimise angular error. Digitising was done using a T-bar style X/Y digitiser (Radio Shack TRS-80 Digitiser) serially interfaced with a microcomputer (Radio Shack TRS-80 Model III). During digitising the points were simultaneously displayed on a flatbed plotter (Radio Shack FP-215) to ensure that the coordinates entered from the digitiser correctly represented the track. These digitised coordinates were then stored on computer for later analysis. For walking males, track sections where "sitting" (time spent during short stops while walking up the plume), and "looping" (turns of 360° or greater) occurred were analysed separately from sections involving continuous, relatively straight, movement.

The digitised tracks were analysed using a computer programme (Kuenen and Baker, 1982) to measure various linear (overall and net velocity) and angular (angular velocity, turn frequency, and turn severity) parameters. A turn was defined as a change from clockwise to anticlockwise (or vice versa) of greater than 30° for walking males, and 50° for flying males. In order to calculate the course angles steered by flying males (direction of lateral thrust with respect to wind direction), the triangle of velocities method was used (Marsh *et al.*, 1978). The groundspeed and track angle of track segments were measured, and combined with knowledge of wind speed and direction, the males' course angles and airspeeds were solved by geometry.

The temporal regularity of turning in the tracks of males which either flew or walked upwind to the same 5.9% E septum was determined by first having the computer plot the males' lateral movements vs time (Fig. 3 A, B). Distances between apices along the time axis were measured, and the mean and standard deviation of the time intervals between turns were calculated for each track. The temporal regularity, i.e. the standard deviation as a percentage of the mean time interval (tempo) was then calculated. Very small perturbations in these plots due to angular error during digitising were excluded by eliminating any prospective counterturn from each plot in which

the apex-to-apex distance was less than 10% of the maximal distance measured for the widest turn in that plot.

RESULTS

All males walking upwind did so while fanning their wings. The proportion of E to Z in the pheromone blend significantly affected the numbers of *G. molesta* initiating walking and locating the source, but apparently had no significant effect on any one of the categories of movement that we examined while they walked to the source. Males that did not walk all the way to the source either stopped and sat in the (time-averaged) plume area, turned away from the plume and sat outside it, or took off and flew to the ceiling of the wind tunnel and landed. Of the males that were unable to reach the source once wing-fanning-while-walking was initiated, 61.9% ($n = 13$) stopped and sat within the boundaries of the time averaged plume; 28.6% ($n = 6$) stopped in the plume and took off and flew to the ceiling or wall of the wind tunnel and landed; and 9.5% ($n = 2$) walked while wing-fanning out of the boundaries of the time averaged plume and stopped. No cross-wind casting or zigzagging was observed in any of the males that did not reach the source, in contrast to flying males that became arrested in a plume of excessively high concentration (Kuenen and Baker, 1982) or of the wrong E/Z blend (Willis and Baker, unpublished). However, some circular, downwind looping by males did occur in these tracks, which did not occur in tracks of flying males.

Upwind walking vs upwind flying

The tracks of males flying upwind to 5.9% E exhibited a bi-modality of the distribution of inter-reversal track angles that was clearly different from males walking upwind to the same blend (Fig. 1). The mean orientation angle calculated for the inter-reversal track angles (Marsh *et al.*, 1978) of both groups of males was almost due upwind (0°), but walking males achieved this displacement with much less side-to-side variation ($r = 0.9$) than flying males ($r = 0.4$) [Fig. 1A, B]. The use of inter-reversal angles obviously biases against measuring segments that are directly upwind and so instead we plotted the distribution of the track angles of all of the vectors digitised every 1/4 s for walking males and every 1/30 s for flying males (Fig. 1C, D). The mean orientation angles and mean vectors remained similar to those calculated for the inter-reversal angles. Importantly, however, the distribution of track angles for all the vectors of walking males was a single peak centred on 0° and clumped between −30° and 30° (Fig. 1D), whereas the distribution of track angles of all the vectors of flying males was bimodal (Fig. 1C). The symmetry of the left–right track angles in the flying males should be noted, indicating that despite the lower r value, the left-right tracks are accurately steered (Baker *et al.* 1984). Most importantly, the distribution of the *course* angles actually steered by the flying males at each 1/30s interval *also* exhibited a bimodal distribution (Fig. 1E). Thus, while walking males steer a straight line almost due upwind to the pheromone source (Fig. 1D), males flying to the same source steer courses that alternate back and forth across the windline.

One possibility for the differences in the distributions of track angles could be that the self-steered counterturning programme known to be in operation in flying males is dampened or otherwise inoperative in walking males. One characteristic of this programme is its temporal regularity (Von Keyserlingk, 1984; Baker, 1987), in that turns are generated according to an internal oscillator whose frequency is directly proportional to concentration (Kuenen and Baker, 1982, 1983; Baker and Haynes, 1987; Baker, 1985). Gross examination of the actual flight and walking tracks gives some impression of the temporal regularity of counterturning during flight (Fig. 2). However, when the same tracks are plotted against time, and their side-to-side amplitude doubled to increase detection of possible regular movement in the straight walking tracks, differences in the temporal aspects emerged (Fig. 3). The mean interval between reversals was approximately seven times slower in walking compared to flying males (mean interval in walking males was 1.10 ($\pm$ 0.50) [$\pm$ SD]s and in flying males it was 0.15 ($\pm$ 0.03)s; $P < 0.05$, Student's t-test). More importantly, the tracks of walking males were more variable temporally than those of the flying males (Fig. 3A, B). On average the standard deviation was 79.4% of the mean reversal interval while walking ($\pm$ 17.8 SD, $n = 21$), while the standard deviation of the tracks of flying males was only 37.0% of the mean interval ($\pm$ 13.9 SD $n = 35$; $P < 0.05$, Student's t-test). Therefore, it appears that *G. molesta* males walking upwind in a pheromone plume do not zigzag because they do not utilise an internal programme of counterturns. If walking males are utilising such a programme of movements, it is not the same one used by males flying to the same blend, because it has a slower tempo and is not as temporally regular.

Response to different E/Z blends

At 0.04% E in the blend, seven of seventy males intiated upwind walking while wing fanning, and five reached the source (Table 1). Thus for a small percentage of *G. molesta* males even <0.1% of E8-12:Ac in Z8-12:Ac is enough to evoke upwind movement to the source, when perceived within 1 m of the source. This same blend was not able to evoke significant upwind flight to the source from greater than 1.5 m away in other studies (Willis and Baker, unpublished; Baker *et al.*, 1981; Linn and Roelofs, 1983). A significantly greater number of males were able to successfully locate the source of 1.7 and 5.9% E blends than any of the other blends ($P < 0.05$). As the percentage of E in the blend increased further, the percentage of males able to locate the source decreased ($P < 0.05$) [Table 1], similar to the pattern in flying males (Linn and Roeloefs, 1983; Willis and Baker, unpublished).

The major reason for the differences in successful source contact is the incidence of activation to the various blends. However, the further diminution from walking upwind to source contact by males that initiated wing-fanning while walking to 10.2% E compared to other treatments means that some additional differences in males' behaviours must have

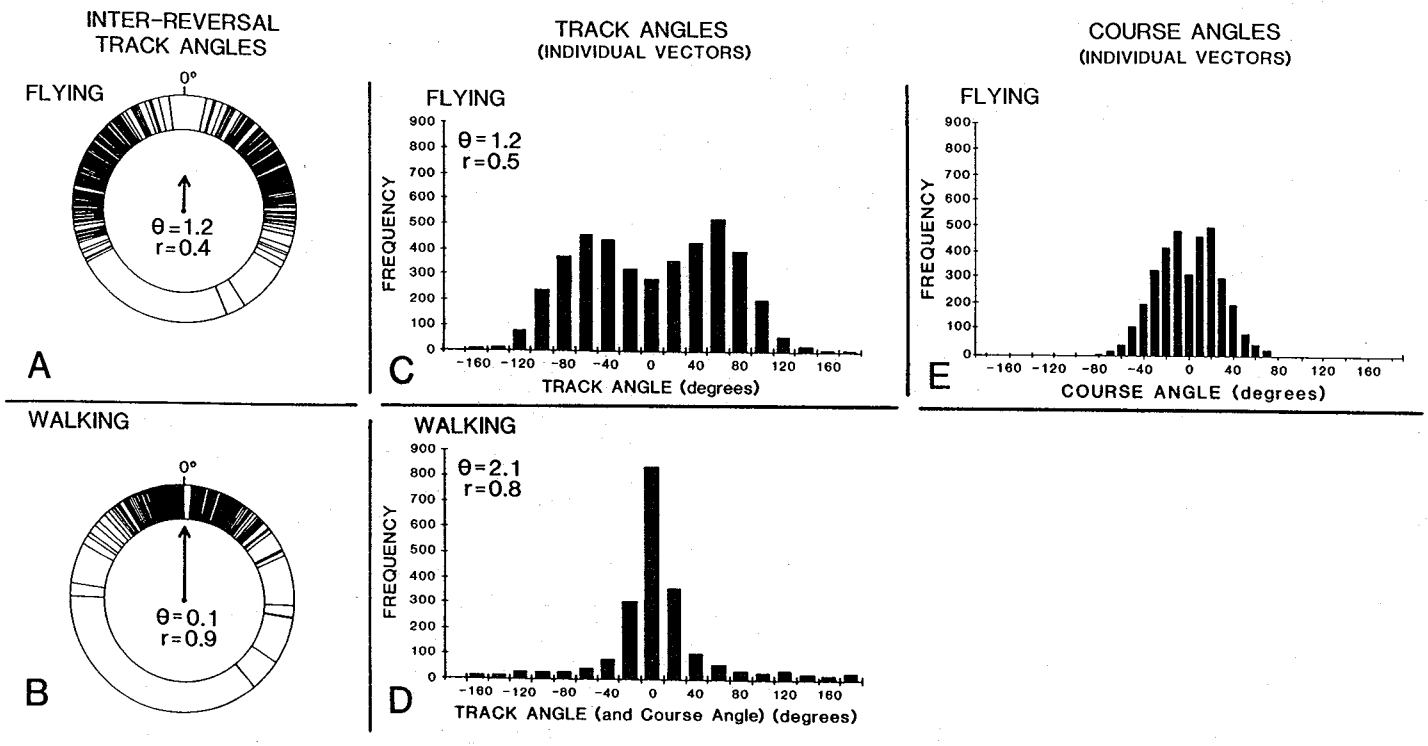

Fig. 1. Circular distributions of inter-reversal track angles and histograms of the distributions of track and course angles of *G. molesta* males walking and flying upwind to the 5.9% E blend. Angles 0 to 180° are for movement from left to right (as viewed facing upwind), and 0 to −180° are for right-to-left movement. (A) Distribution of inter-reversal track angles of males flying upwind to the source ($n = 23$ males). (B) Distribution of inter-reversal track angles of males walking upwind to the source ($n = 25$ males). (C) Distribution of track angles measured continuously each 1/30 s for males flying upwind to the source ($n = 36$ males). (D) Distribution of track angles (which here are identical to course angles) measured continuously each 1/4 s for males walking upwind to the source ($n = 25$ males). (E) Distribution of course angles for flying males calculated from each of the individual track angles in C by using the triangle of velocities technique. The distribution in E was incremented every 10° instead of every 20° unlike C and D, to highlight the depression that occurs at 0°. A still further fine-grained incrementation of the angles would accentuate even more how different this distribution of course angles is from that of tethered gypsy moths in simulated free-flight (Preiss and Kramer, 1986c).

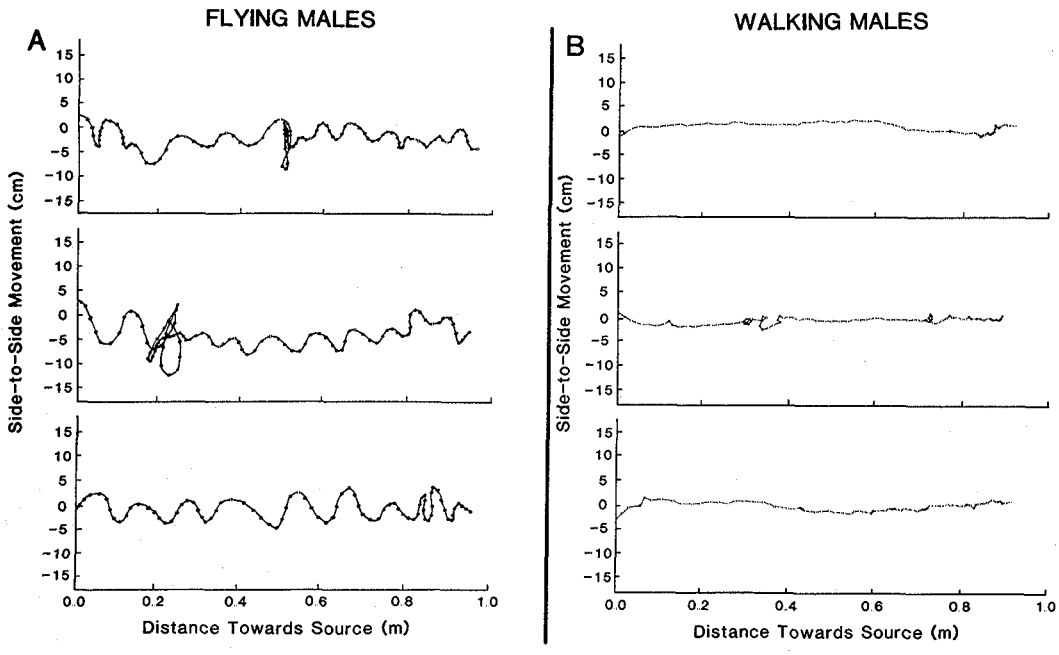

Fig. 2. Plots of the tracks, as viewed from above, of three *G. molesta* males either flying (A) or walking (B) upwind to the 5.9% E blend. Wind was from the right.

occurred while walking upwind (Tables 2 and 3). However, there are no significant differences in the movements of males in any *one* of the categories we chose to analyse (Tables 2 and 3). Even though some turning frequencies were significantly different, there were no consistent trends in any single factor that explains males' reduced source contact after initiation. Rather, it appears that the *compounded* trends toward lowered walking velocity, higher turning frequency, higher incidence of sitting, and greater angular magnitude of looping all contributed to slower progress to the 10.2% E source, and thus

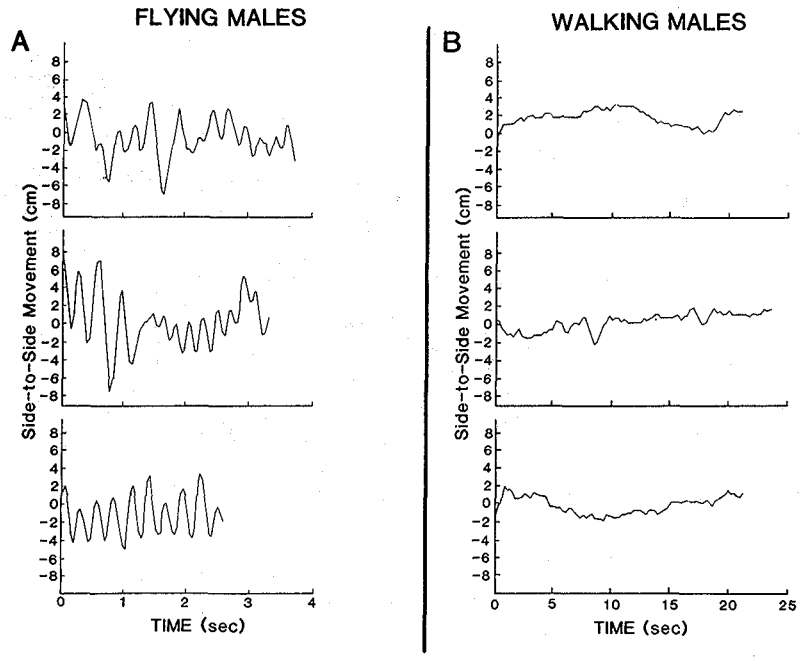

Fig. 3. Plots of the same tracks shown in Fig. 2, but this time plotted against time to examine the regularity of reversal (counterturning) frequency. Note the shorter and more regular intervals between reversals in flying males compared to walking males.

Table 1. Percent of *G. molesta* males responding by walking upwind to different E/Z blends

Percent of E in Z	*n*	% Initiating wing-fanning-while walking†	Of those initiating walking, % reaching the source	% of total (*n*) reaching the source
0.04	70	10.0 b	71.4 ab	7.0 b
1.7	70	38.6 a	96.3 a	37.1 a
5.9	70	47.1 a	78.8 ab	37.1 ab
10.2	70	27.1 a	47.4 b	12.9 b
20.5	70	1.0 bc	0.0 c	0.0 c
37	70	0.0 c	0.0 c	0.0 c

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

†This category incudes only those males which walked while wing fanning all or part of the way to the source. Males which took flight and then landed and walked while wing fanning were excluded from analysis.

Table 2. Mean track parameters* ($\pm$ SD) of *G. molesta* males walking upwind to three different E/Z blends

Percent of E in Z	*n*	Overall velocity (cm/s)	Turn frequency (turns/s)	Turn magnitude (°/turn)	Angular velocity (°/s)	Inter-reversal angle (°)	Inter-reversal distance† (cm) (track width)
0.04	7	4.3 $\pm$ 2.1 a	1.0 $\pm$ 0.5 a	61 $\pm$ 20 a	84 $\pm$ 52 a	25.8 $\pm$ 10.8 a	1.09 $\pm$ 0.2 a
1.7	24	4.8 $\pm$ 1.5 a	0.6 $\pm$ 0.3 b	59 $\pm$ 21 a	73 $\pm$ 54 a	21.5 $\pm$ 7.8 a	1.04 $\pm$ 0.3 a
5.9	30	4.5 $\pm$ 2.0 a	0.8 $\pm$ 0.4 ab	67 $\pm$ 23 a	88 $\pm$ 52 a	22.4 $\pm$ 6.9 a	1.03 $\pm$ 0.3 a
10.2	19	4.0 $\pm$ 1.5 a	0.8 $\pm$ 0.5 ab	65 $\pm$ 22 a	81 $\pm$ 47 a	21.2 $\pm$ 5.0 a	0.99 $\pm$ 0.2 a

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

*All time that the males spent walking in loops or sitting was subtracted from the data, so that only track sections during upwind progress were used to calculate the values in this table.

†For comparison, the mean wingspan of *G. molesta* males reared in our laboratory is 1.2 $\pm$ 0.1 cm ($n = 30$).

Table 3. Analysis of looping and sitting by *G. molesta* males

Percent of E in Z	*n*	% of tracks where sitting occurred	Mean time spent sitting (sec) (per bout)	Mean % of track time spent sitting	% of tracks with loops*	Degrees/loop
0.04	7	43 a	7.3 $\pm$ 4.9 a	38 $\pm$ 41 a	29 a	741 $\pm$ 313 a (5)†
1.7	24	54 a	8.2 $\pm$ 6.3 a	22 $\pm$ 12 a	50 a	575 $\pm$ 335 a (32)
5.9	30	60 a	13.7 $\pm$ 14.8 a	29 $\pm$ 23 a	48 a	579 $\pm$ 294 a (40)
10.2	19	79 a	9.6 $\pm$ 10.8 a	29 $\pm$ 18 a	37 a	696 $\pm$ 432 a (14)

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

*Means in this column having no letters in common are significantly different according to a method of adjusted significance levels for proportions (Ryan, 1960) [$P < 0.05$].

†Numbers in parentheses are the total number (*n*) of track loops at that particular treatment.

reduced source contact by the time observations were terminated.

Additionally, the shapes of the tracks were not significantly different among the treatments. On average, the inter-reversal distances of the tracks of males walking to any of the four E/Z blends that they responded to were less than the average wing span of *G. molesta* males reared in our laboratory (Table 2). At the narrowest point (close to the source) the pheromone plume was about 1 cm wide (as visualised by $TiCl_4$ smoke), increasing to approx 10 cm at the position in the plume where the males were released. Thus, the males that successfully walked to the source appeared to spend most of the time within the boundaries of the time-averaged plume.

DISCUSSION

The results of this study support the idea that one of the advantages of counterturning repeatedly across the windline during flight is to track the wind direction (Kennedy, 1983, 1986; Baker, 1985). In a shifting wind field in nature this ability would result in the male maintaining contact with the pheromone plume or regaining contact with it, should it be lost. Walking males steered a course directly upwind to the pheromone source in a nearly straight path with a side-to-side movement of less than their wing-span. Neither the spatial nor the temporal aspects of the movements during walking could be characterized as having a "regularity" or magnitude at all similar to

the side-to-side zigzags during upwind flight to the same source. Here, flying males steered a course of 15–20° back and forth across the windline (Fig. 1F, E), and not directly upwind, using optomotor anemotaxis. But the temporal regularity of counterturning is indicative of an additional mechanism, an internal programme, integrated into the system. The temporal regularity during flight is even more remarkable given the uneven stimulation from pheromone filaments experienced by the males (Baker and Haynes, unpublished). The counterturning tempo is directly proportional to concentration, and there is evidence that it can change within a single reversal depending on whether pheromone or clean air was experienced on the previous reversal (Baker and Haynes, 1987).

The programme so clearly in operation during flight is apparently absent or suppressed when the males have tarsal contact with the ground. However, walking males were able to steer accurately with respect to the wind to achieve a track oriented almost directly upwind, so the apparent absence of a counterturning programme did not hamper their anemotactic abilities. Walking insects (e.g. locust hoppers and cockroaches) are able to sense wind speed and direction by using mechanoreceptors such as Johnston's organ in the basal segments of the antennae (Gewecke, 1974) or fields of mechanoreceptive hairs on the head (Gewecke and Philippen, 1978). The reason that these mechanoreceptors are effective as wind direction sensors is because a walking insect has constant tarsal contact with the substrate, and hence, a fixed reference point with respect to the wind to create pressure-differentials.

Flying insects have no such fixed reference point and must detect variation in wind direction and velocity visually. In a recent model (David, 1986; Ludlow, 1984) the insect is thought to be able to steer to achieve a particular track angle and set groundspeed by integrating the ratio of transverse and longitudinal image motion. There is neurophysiological evidence that motion detectors on the ventral surfaces of the eyes of some insects are organized along longitudinal and transverse axes (Collett and Blest, 1966). When the relationship between the transverse and longitudinal motion components changes due to changes in the wind velocity or changes in the insect's own movements with respect to the wind, the male may compensate by steering a different course and altering its thrust to achieve the preferred balance of these two components.

Recently, an alternative model for steering by pheromone-stimulated flying moths has been proposed by Preiss and Kramer (1986b, c). Using data from tethered gypsy moths during flight simulated by means of an elegant computerised visual feedback system, they conclude that moths are actually trying to steer a course directly upwind (0°) while in pheromone. In their model, because of the males' inability to fly precisely upwind, i.e. to detect very small amounts of transverse motion, they overshoot this 0° set-point, causing the resultant flight tracks to give the appearance of being steered at an angle to either side of the windline. Additionally, their model does not include a self-steered counterturning mechanism. Their support for this model includes data which shows that there is a unimodal distribution of course angles by their males "flying" upwind, even though the distribution of track angles is bimodal (Preiss and Kramer, 1986b, c).

Our present data, and that from previous studies (Kuenen and Baker, 1983; Baker *et al.*, 1984) for oriental fruit moths do not support the model of Preiss and Kramer. First, from the present study the distribution, sampled continuously, of both the course angles and the track angles of our males flying upwind in pheromone were bimodal, and hence the males were not steering directly upwind, but rather at an angle of 10–20° to either side of the windline (Fig. 1E). We know that these free-flying oriental fruit moths roll and bank near the apices of their turns (Baker, 1987; Willis, Haynes and Baker, unpublished), and thus the lift vector can contribute to a laterally directed course angle force even though the 'thrust" vector, as measured by only the yaw component of the body angle, might be 0°. The technique of Preiss and Kramer (1986b, c) did not include measuring either roll or pitch, only yaw. Thus, in contrast to our measurements of the course angles of free-flying males by means of the triangle of velocities, the lift vector in their studies was not allowed to contribute to lateral flight forces, and hence their results could have missed measuring significant lateral course angles that might occur by even slight rolling by free-flying gypsy moths. Second, with regard to the lack of a counterturning component in their model, Priess and Kramer do not address data from previous studies (Kuenen and Baker, 1983; Baker *et al.*, 1984) which show that *G. molesta* males flying in zero wind counterturn in an angularly and temporally regular fashion, without experiencing any transverse image drift whatsoever. These turns are self-generated and steered, and cannot be a result of anemotaxis plus "pure physics" (Priess and Kramer, 1986c) because there was no wind, or wind simulated by a moving visual pattern. Furthermore, randomly distributed red spots were used as the stationary floor pattern in Baker *et al.* (1984), and so the moths could not even have been giving themselves the illusion of wind (i.e. transverse image motion), which is possible while flying in zero wind over stationary stripes at an angle (David, 1982).

The proposed advantage to counterturning compared to straight-line flight for enhancing detection of shifts in wind direction during flight in pheromone needs to be tested (Kennedy, 1983, 1986; Baker, 1985; Cardé, 1985). In an experimentally shifted wind-field, flying male *G. molesta* had no problem in tracking the wind and plume while zigzagging by integrating counterturning and optomotor anemotaxis (Baker and Haynes, 1987). Whether they could have done as well by using straight-line anemotactic flight is impossible to tell because these males have never been observed to fly straight during pheromone stimulation under similar laboratory conditions. Clearly though, the results of this study indicate that the counterturning programme is not needed during walking to the source in a non-shifting wind field, and importantly, we did not observe it during walking at any time, even when the plume was lost. Even insects that fly in a straight line directly upwind in a plume

of attractive odour to locate the source, such as *Drosophila* (David, 1986), employ counterturning upon odour loss. They cast regularly and symmetrically across the wind (David, 1986). *G. molesta* males did loop while walking in or out of pheromone, but the width of these loops did not approach the same magnitude as the "casting" counterturns observed after plume loss during flight to a pheromone source (Kuenen and Baker, 1983; Baker and Haynes, 1987; Von Keyserlingk, 1984). Also, looping while walking requires a course change of 360° or more, and some period of facing downwind. Therefore looping during walking is quite a different behaviour than movements creating casting flight tracks or looping tracks during flight, which require course changes of only a few degrees while still facing *upwind*, as long as airspeed is made slow enough relative to windspeed.

It has been demonstrated recently that in some walking insects (three species of beetle and an earwig) optomotor control of walking speed is probably not important for the modulation of velocity in these insects (Zanker and Collett, 1985). Zanker and Collett (1985) also demonstrated that ladybird beetles did not modify their velocity in response to proprioceptive feedback. When increasingly heavy weights were attached to the elytra of these beetles their velocities decreased linearly and was significantly correlated with the increase in weight. The beetles did not increase their output to overcome the added weight and thus maintain a constant velocity. Flying moths, on the other hand, will alter their steering and increase their airspeed to maintain constant groundspeed in varying windspeeds (Marsh *et al.*, 1978). In this study, walking *G. molesta* males did not *significantly* reduce their velocity in response to an increasing percentage of E in the blend, as males flying to these same sources did (Willis and Baker, submitted), but there was a trend in this direction. It may be that further studies will reveal a motor link between decreased locomotory rates while walking and decreased airspeed during flight, in response to different pheromone blends. However, in other cases cited above it was shown that walking insects did not respond to stimuli known to alter velocity and orientation in flying insects.

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