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An analysis of anemotactic flight in female moths stimulated by host odour and comparison with the males' response to sex pheromone

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ABSTRACT. The flight pattern of mated female navel orangeworm moths, *Amyelois transitella* (Walker), responding to odour from potential larval hosts is zigzagging upwind flight. However, at times these moths are capable of flying nearly directly upwind towards the odour source (track angles near 0°). This response indicates that these females are capable of very accurate anemotactic control of their heading or course angle, since small angular errors in this measure would translate into larger deviations from direct upwind flight. Males of this species exhibit flight patterns similar to those of females, including track angles clustered about 0° when flying upwind to a source of the female-produced pheromone, but under these experimental conditions they flew with a higher average airspeed than the females. When females lose contact with an odour plume they initiate a well-defined programme of cross-wind counterturning or casting, which may normally increase their chances of retrieving contact with that plume when the wind direction shifts. The resultant track angles of females increase significantly by 0.8 s after plume loss, indicating that the female has initiated changes in both her course angle and airspeed. By 1 s after plume loss the females' track angles are no longer unimodally distributed about 0°, but are bimodally distributed about −90° and +90°. Males responded more rapidly to the loss of a pheromone plume, demonstrating a significant change in track angle 0.4 s after plume loss. Overall, female and male *A. transitella* exhibited remarkably similar anemotactic flight manoeuvres during upwind flight to odour sources as well as after plume loss.

Key words. Optomotor anemotaxis, counterturning, navel orangeworm moth, *Amyelois transitella*, Lepidoptera, Pyralidae, host-odour, pheromone, flight behaviour.

Introduction

The manoeuvres used by flying male moths to locate a distant source of sex pheromone have been studied in some detail (Baker, 1988). The behavioural mechanisms involved may be shared by other insects that locate odour sources while in flight. For example, mated females must locate scattered resources that are suitable sites for oviposition and subsequent larval development. Prior to mating, female navel orange-

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worm, *Amyelois transitella* (Walker), release a volatile sex pheromone that stimulates upwind flight in downwind males (Coffelt *et al.*, 1979a). After mating, almond odours play a key role in host selection by female *A. transitella* (Andrews & Barnes, 1982; Curtis & Clark, 1979; Phelan & Baker, 1987; Rice *et al.*, 1984). Phelan & Baker (1987) documented that crude almond oil, an intermediate product in the processing of almonds for oil, stimulated attraction and oviposition in a wind tunnel bioassay. Thus mating and oviposition depend on in-flight manoeuvres of males and females, respectively.

Insects utilize the mechanism of optomotor anemotaxis in order to progress upwind in an odour plume (Marsh *et al.*, 1978). Sometimes this is integrated with a programme of counterturns to create a more-or-less zigzag track (Kuenen & Baker, 1983; Kennedy, 1983; Baker, 1988). Shortly after loss of contact with an odour plume the programme of counterturns, if already employed while in odour, decreases in frequency, or if not previously employed, is initiated. Coupled with anemotactically controlled changes in steering (course angle) and airspeed, widening cross-wind tracks (casting) result, which increase the probability that the insects will reintercept the odour plume. While the anemotactic mechanisms of flight in male moths have received some attention as of late, no studies have focussed on these manoeuvres in females. The occurrence of chemically mediated flight in both males and females of *A. transitella* has allowed us to examine quantitatively the details of the mechanisms of orientation during upwind flight and after loss of contact with the odour plume, and to make qualitative comparisons between these responses in the two sexes.

Materials and Methods

Navel orangeworm larvae were reared on a diet of honey, bran and glycerol (Strong *et al.*, 1968) at 23±1°C with a photoperiod of LD 16:8 h. Pupae were mixed with moistened vermiculite in a 177 ml waxed cup. For one group of pupae adults eclosed as mixed sexes. A second group contained only males. These groups were contained within screened cages, which were housed in separate environmental chambers. Pupae were removed from these cages every other day leaving behind 0–2-day-old adults. Adults had access to 8% sugar water. Approximately 3 h before lights-off, 3–5-day-old females (> 99% mated) were transferred in groups of ten to screen cylinders (5.5×80 cm) with the one end closed by a petri dish. At 2 h before lights-off females were transferred to the wind-tunnel room, where they were allowed to acclimate to dim lighting conditions (4 lux) for 30 min before light intensity was further reduced to simulated twilight conditions (1 lux at the centre of the wind tunnel, and 21±3°C). After 15 min bioassays began and continued for approximately 1 h. Virgin males were handled in a similar manner except that they were transferred during their night period from an environmental chamber to simulated night-time conditions (0.3 lux) in the wind tunnel room approximately 3 h before lights-on. Bioassays of these males were conducted during the last hour of the scotophase.

For the study involving in-flight response of gravid females to host odour, 100 μl of crude oil (CAO) was placed on a 5.5 cm diameter piece of filter paper. For the male behavioural response, ten female sex-pheromone gland equivalents in 10 μl of hexane were applied to a 2.5 cm×0.5 cm piece of filter paper. This gland extract had been prepared by clipping the females' ovipositors and associated pheromone glands at the peak time of calling. An odour source (either CAO or pheromone) was suspended on fishing line from the top of the wind tunnel and was positioned along the central axis of the tunnel, *c.* 30 cm above the floor, and 0.5 m from the tunnel's upwind end. The wind tunnel was 1 m wide at the floor, 0.9 m high, 3.65 m long, and was modified from the tunnel described by Miller & Roelofs (1978). The wind speed in the tunnel was kept constant at 0.5 m s^{-1}.

Half of the moths that initiated upwind flight in the plume were allowed to contact the odour source. For the other half the odour source was abruptly pulled to the ceiling of the tunnel when a moth entered the field of view of the camera. The actual point at which a moth would lose contact with the odour plume was determined by activating a series of diodes (50 diodes per m) at the time of the source-pull. The diode signal started at a position below the original odour source and would 'travel' downwind through the tunnel at the same rate as the wind (0.5 m s^{-1}). When the position of the advancing diode signal

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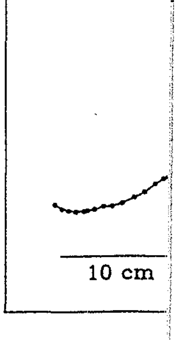

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The flight patterns of moths were video-recorded using a rotary-shutter camera (Willis & Baker, 1984) positioned directly above the wind tunnel. The camera's field of view extended from 45 cm downwind to 5 cm upwind of odour source. Thirty-two flight tracks were digitized at 30 pts/s and the X,Y coordinates were stored on a micro-computer using techniques described previously (Willis & Baker, 1984; Baker *et al.*, 1984, 1985).

From the sequence of X,Y coordinates an insect's *track angle* and *groundspeed* were determined for each 0.033 s vector. From these values *course angles, drift angles* and *airspeeds* were determined using the triangle of velocities (Kennedy, 1940; Marsh *et al.*, 1978). To determine the time course for the behavioural changes that follow plume loss, the values for the above variables were averaged every 0.1 s (average of three consecutive 0.033 s values) starting 0.5 s before plume loss and continuing until 1.8 s after plume loss. For this time-course study the absolute values of the track angles were used because the direction of a reversal (to the right or left of the windline) was not considered to be important. In addition, each track was divided into crosswind track reversals. The *duration* of each of the inter-reversal periods was determined. These variables were analysed by a two-way analysis of variance (time-course analysis, p. 348, Sokal & Rohlf, 1981).

Results

The flight patterns of female *A. transitella* flying upwind towards a source of host odour consisted of zigzagging flight which was sometimes combined with periods during which progress was made directly towards the odour source (Fig. 1). Similar flight patterns were observed as male *A. transitella* progressed upwind towards a source of the female-produced sex pheromone.

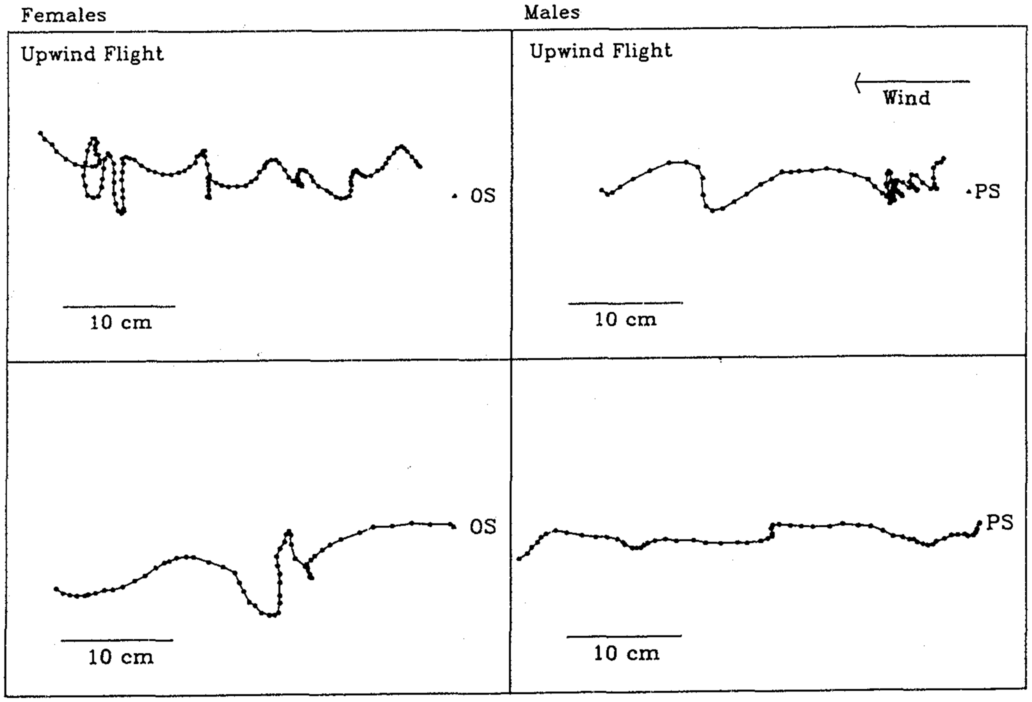


FIG. 1. Top view of flight tracks of female and male *A. transitella* zigzagging upwind to a host odour source (OS) and pheromone source (PS), respectively. Dots indicate the moths' position every 0.033 s. Analyses of upwind flight tracks only included moths that contacted the source. Digitization of tracks was stopped prior to landing, when the moth was at or near the source.

In this study, females flew with lower airspeed than males, which resulted in a significantly lower groundspeed, larger track angles, and slower net upwind progress (Table 1).

TABLE 1. Average velocity and angular components (±SE) of female and male navel orangeworm moths, *A. transitella,* during upwind flight to an attractant source ($n = 8$).

Measurement	Female	Male
Net upwind progress (cm s^{-1})	11.8±1.45	20.7±2.52
Groundspeed (cm s^{-1})	19.8±1.11	29.5±3.53
Airspeed (cm s^{-1})	63.4±1.45	74.3±3.11
Track angle (degrees)	49.1±3.51	36.7±4.70
Course angle (degrees)	10.9±0.36	11.6±1.72
Drift angle (degrees)	38.2±3.52	25.1±3.65

After the odour source was removed and females flew out of the time-averaged odour plume, their flight patterns changed from the narrow pattern of cross-wind counterturning with upwind progress to casting, broader cross-wind counterturning with no upwind progress (Fig. 2). When the upwind movement and crosswind movement of an individual female and male are plotted against time, one can observe that upwind progress ceases within 1 s of plume loss, and counterturning becomes progressively broader and more temporally regular (Fig. 3).

During upwind flight the track angles of both females and males were centred about 0° (Fig. 4). The frequency of track angles between −5° and +5° was greater than any other 10° interval. 1 s and longer after plume loss the distribution of track angles was clearly bimodal with peaks centred at about −90° and +90°. Similarly the distributions of course angles were narrowly distributed about 0° during upwind flight (Fig. 5), and a depression in the distribution was found at 0° by 1 s after plume loss. The behavioural change, from steering straight upwind while in odour to steering alternatively left and right of the wind line following odour loss, accounts for the change from a unimodal distribution of track angles to a bimodal distribution.

The average duration of an inter-reversal leg was significantly greater seven to nine reversals

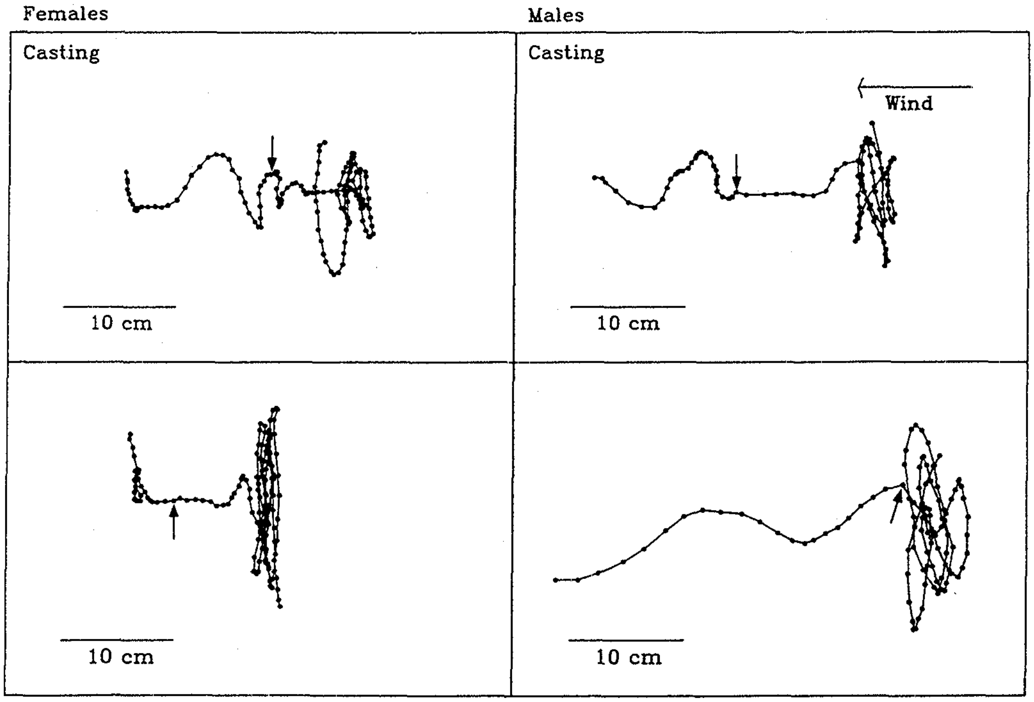
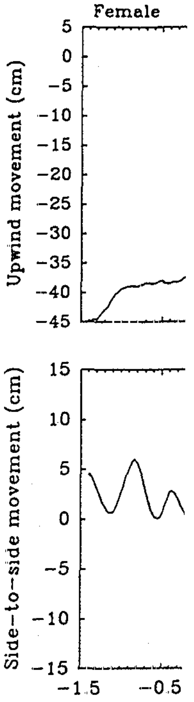


FIG. 2. Top view of flight tracks of female and male *A. transitella* from at least three reversals before plume loss until at least nine reversals after plume loss. Dots indicate the moth's position every 0.033 s. Arrows indicate points of plume loss.



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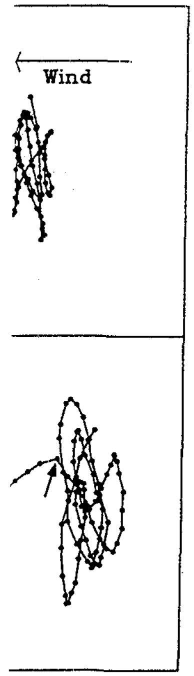

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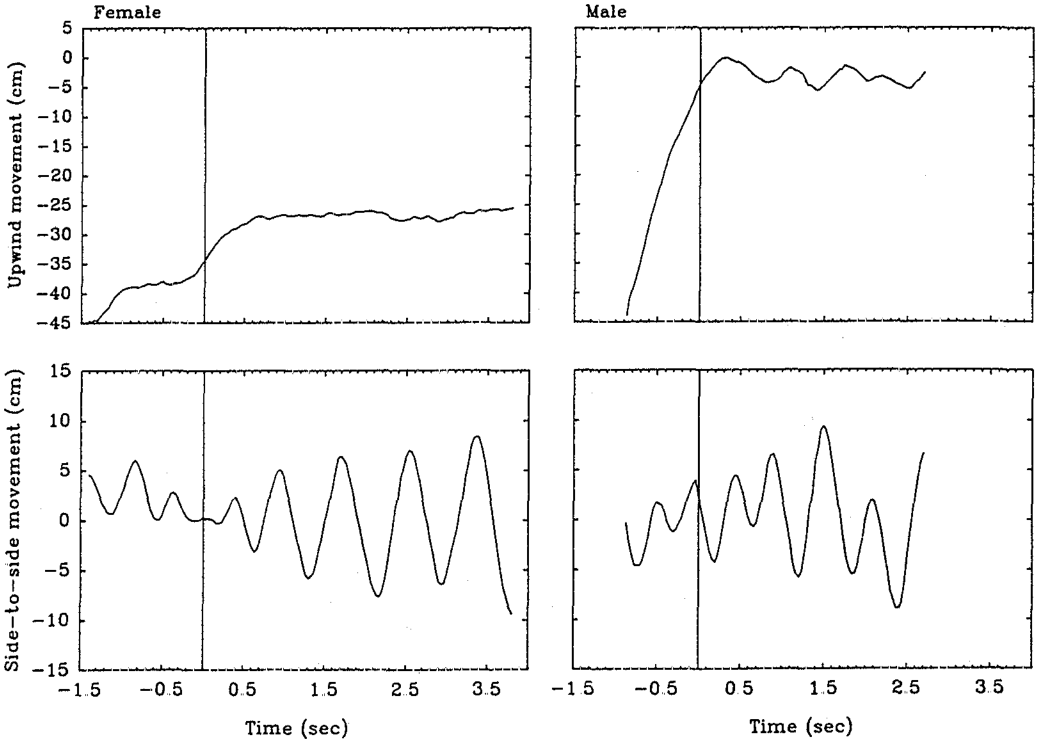


FIG. 3. Compartmentalization of the flight tracks of a female and male *A. transitella* into upwind and cross-wind (side-to-side) components versus time. Plume loss occurs at 0 s.

after plume loss than before plume loss (Fig. 6). There were no significant changes in the moths' groundspeeds before or after plume loss (Fig. 7). However, the airspeed of females was significantly lower by the end of the analysis period following odour loss. The airspeed of males goes through two changes after plume loss. By 0.5 s after plume loss the airspeed drops significantly, but when the last 0.5 s of the experiment are compared to the 0.5 s before plume loss there was no significant difference.

Track angles of both males and females increased after plume loss (Fig. 8). By 0.8 s after plume loss the track angles of females were significantly greater than before plume loss. Likewise by 0.4 s after plume loss the track angles of males were significantly greater than before plume loss. The course angles of females continued to increase gradually after plume loss until they were significantly greater by the last 0.5 s of the experiment.

Discussion

Optomotor anemotaxis and an internal programme of counterturns are two mechanisms that are known to be used by moths flying to a pheromone source. An integration of these two mechanisms can explain both the upwind zigzagging flight within the time-averaged pheromone plume and casting behaviour with little net upwind or downwind displacement that occurs after loss of contact with the pheromone plume. In optomotor anemotaxis, the flying insect can change either its airspeed or its heading (course angle), or both, in order to compensate for wind-induced changes in the apparent motion of images over its ommatidia. An understanding of how an insect controls these two anemotactic variables as well as the counterturning component should help to explain both the way the insect finds a source of odour, and the shape and temporal nature of the resultant flight tracks.

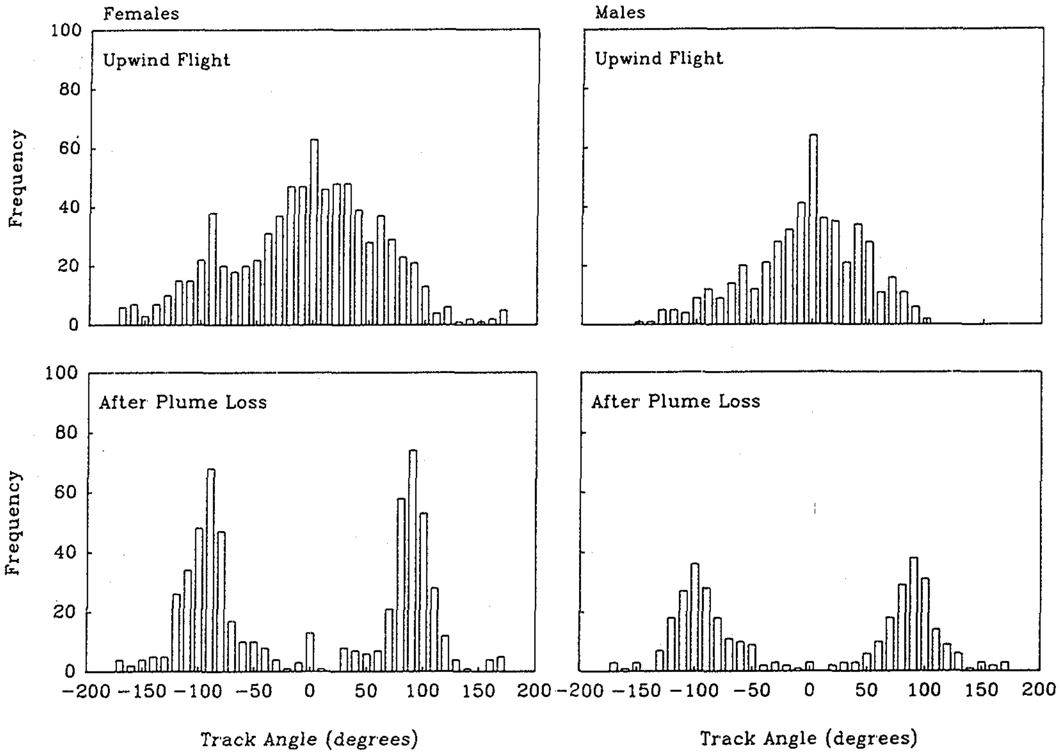
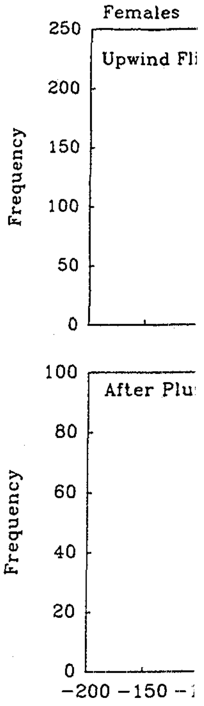


FIG. 4. Track angles of female and male *A. transitella* during upwind flight and 1 s after plume loss ($n = 8$ moths for each graph).

In the present study the most striking difference between the flight patterns of female and male *A. transitella* is the relatively slow upwind progress of the females (Table 1). The difference may be due to the females generating less thrust, resulting in a lower airspeed, or the females may simply be heading on average slightly more across the windline. The course angles of females during upwind flight are very similar to those of males, and thus their lower airspeed (15% lower on average) largely explains the lower average groundspeed (33% lower), their larger track angles (34% greater), and thus their slower progression upwind. In another species, *Grapholita molesta*, the pheromone blend ratio (Willis & Baker, 1988) and the emission rate (Kuenen & Baker, 1982) influence the linear velocities of the male moths' movement. Therefore it is not possible to conclude that there is any inherent difference in the manoeuvres used by male and female navel orangeworm moths, because quantitative and qualitative differences in the emitted attractant blend may influence airspeed.

It was found that during upwind flight in pheromone, male *G. molesta* steered alternatively to the left and right of the windline, and thus neither the course angles nor the resultant track angles were unimodally distributed about 0° (the upwind direction) (Willis & Baker, 1987). Rather, the distributions of these angles were bimodal, with a distinctive depression in the frequency of both about 0°. This species uses a counterturning programme in addition to anemotaxis (Kuenen & Baker, 1983; Baker *et al.*, 1984). Similar evidence has been observed using free-flying gypsy moths, *Lymantria dispar*, demonstrating that these pheromone-stimulated males actively steered an off-wind line course and performed counterturns (David & Kennedy, 1987). In the present study, both male and female free-flying *A. transitella* displayed distinctive unimodal distribution of both course angles and track angles during odour-mediated upwind



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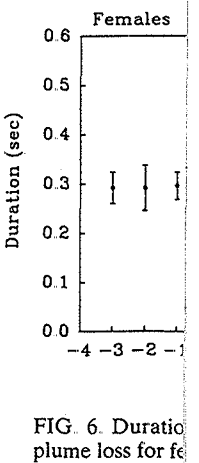

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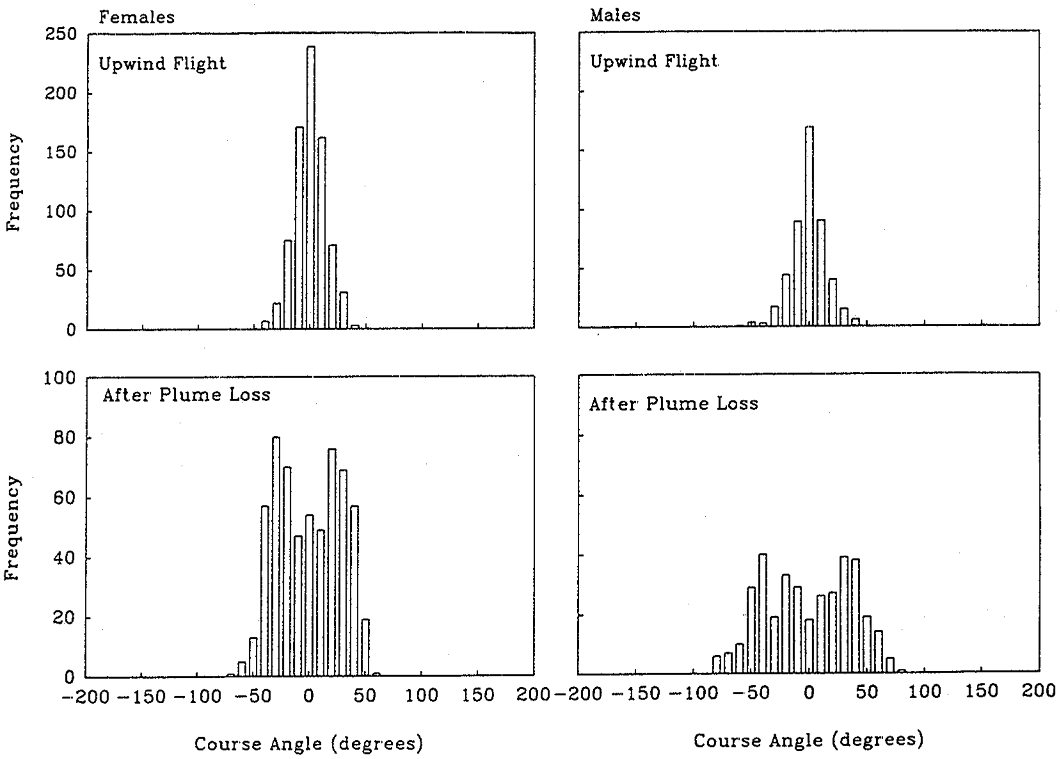


FIG. 5. Course angles of female and male *A. transitella* during upwind flight and 1 s after plume loss ($n = 8$ moths for each graph).

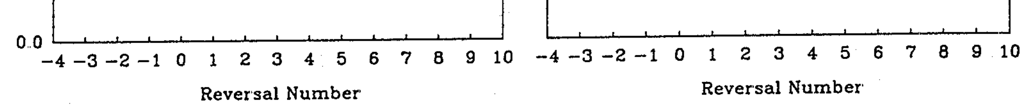


FIG. 6. Duration of inter-reversal periods from three reversals before plume loss to nine reversals after plume loss for female and male *A. transitella*. For both females and males, there were no significant differences between the duration of any single reversal after plume loss and the duration of reversals before plume loss (analysis of variance, $n = 8$, $P > 0.05$). However, the average duration of the last three reversals combined was significantly greater than the average of the three reversals before plume loss (analysis of variance, $n = 8$, $P < 0.05$).

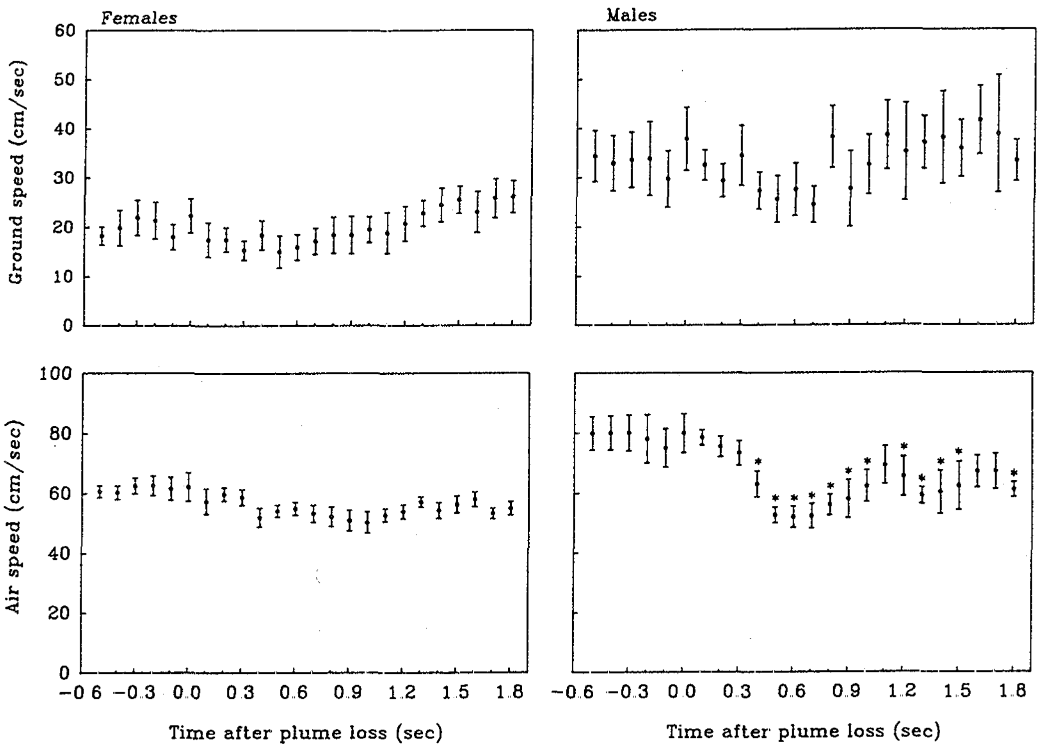
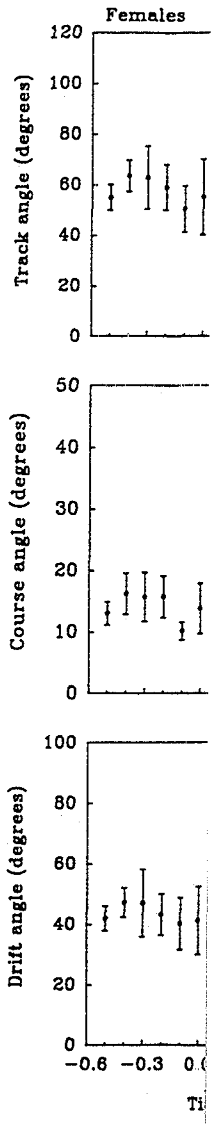


FIG. 7. Groundspeed and airspeed from 0.5 s before plume loss to 1.8 s after plume loss for female and male *A. transitella*. There were no significant differences in the groundspeed for either males or females over the course of the experiment (analysis of variance, $n = 8$, $P > 0.05$). The average airspeed of a female was significantly lower during the last 0.5 s of the experiment than the 0.5 s period that preceded plume loss (analysis of variance, $n = 8$, $P > 0.05$). *Asterisks indicate the 0.1 s intervals that were significantly different* from those before plume loss (two-way analysis of variance, LSD test, $P < 0.05$).

flight (Figs 4 and 5). These distributions were clearly centred about 0°, with the most frequent class being from −5° to +5°. Apparently there are some distinctive differences between species in the presence or expression of a counterturning programme during upwind flight, and there is a similarity between male and female *A. transitella* in this characteristic.

After plume loss both female and male *A. transitella* make a transition to casting behaviour during which the counterturning programme becomes obvious (Figs 4 and 5). Counterturning after plume loss has been observed in every flying insect that has been studied to date, including *Drosophila hydei* which seems to be capable of flying relatively straight upwind when in a plume of banana odour (David, 1982). Counterturning after plume loss would allow a flying insect a greater chance to locate an odour plume if the wind direction were shifting (Baker & Haynes, 1987).

The time it takes to make the transition from the manoeuvres characteristic of upwind flight to casting behaviour is important in determining the potential for that insect to relocate an odour plume once the wind direction has shifted. If the insect has completely lost the odour plume due to a wind shift, flying upwind along the new wind direction will not take the moth to the odour source. A quick response may allow the insect to follow the plume through its shifting course as has been observed in the saw-toothed flight patterns of *G. molesta* (Baker & Haynes, 1987). Our measures of the speed of the reactions of *A. transitella* to plume loss probably slightly overestimate the time it takes for a real behavioural



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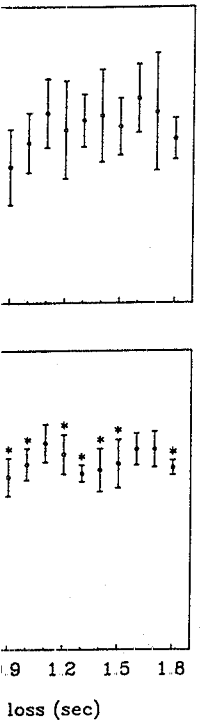

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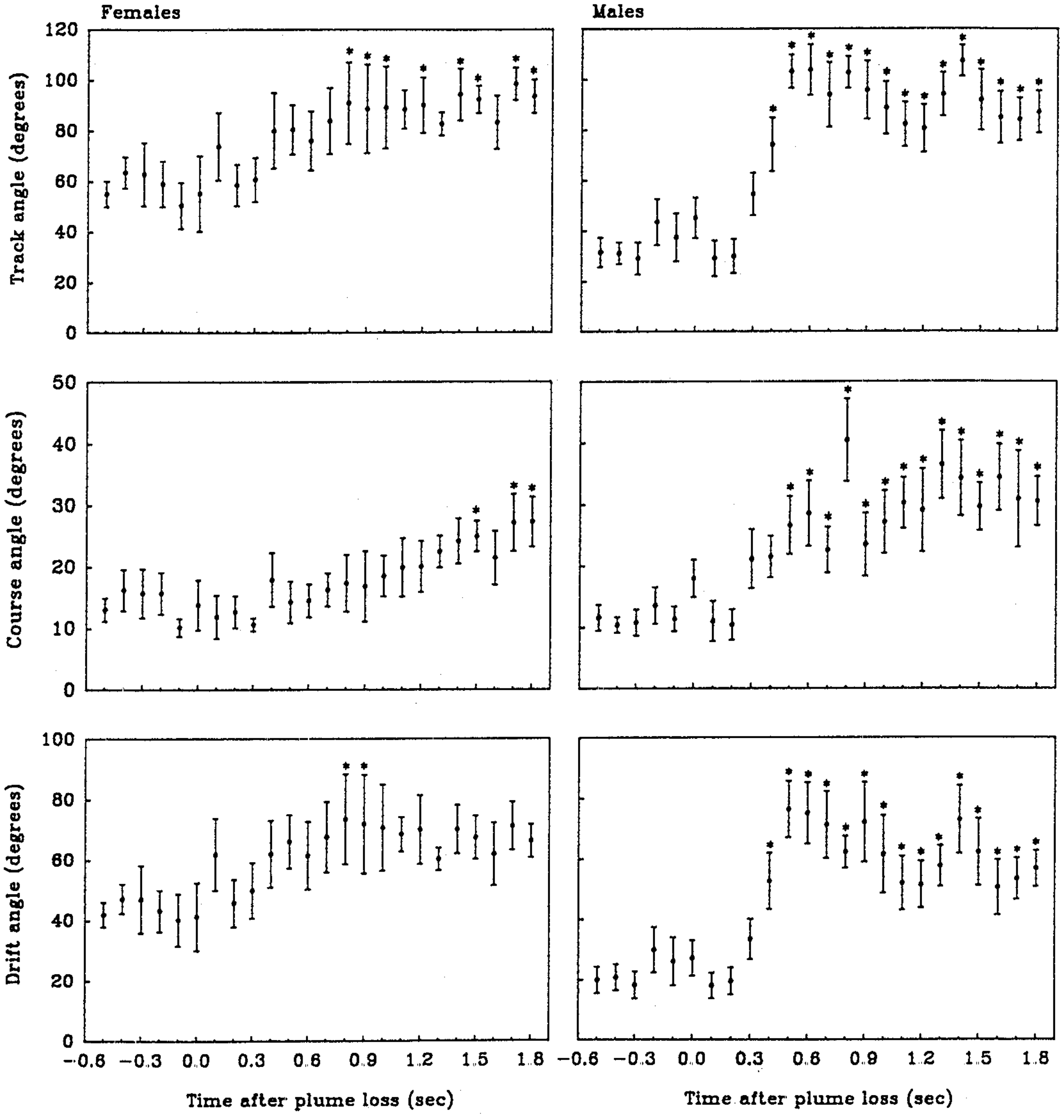

FIG. 8. Track angles, course angles, and drift angles from 0.5 s before plume loss to 1.8 s after plume loss for female and male *A. transitella*. Asterisks indicate the 0.1 s intervals that were significantly different from the period before plume loss (two-way analysis of variance, LSD test, $P<0.05$).

change, because we must wait for a significant change in characteristics which may be changing continuously. For both females and males the first characteristic of the flight track that changes is the track angle. The speed of this reaction is somewhat slower in females (0.8 s after plume loss) than in males (0.4 s after plume loss). These significant changes have been achieved primarily by an increase in course angle (which was not yet significant), but secondarily by a small decrease in airspeed (also not significant). It is interesting that the resultant track angle changes more rapidly than the two variables that the insect can control (course angle and airspeed), because the change in track angle is the characteristic that should have the greatest potential for retrieving a shifting plume through casting.

The time course for the behavioural changes following pheromone plume loss have been estimated for several other species. In *Anthereae polyphemus*, the polyphemus moth, a significant change in the course angle and track angle was detected by 0.5 s after plume loss (Baker & Vogt, 1988). In *Plodia interpunctella* a change in track angle had occurred by 0.5 s after plume loss (Marsh *et al.*, 1981). The fastest response thus far has been documented in male *G. molesta*, which change their course angles within 0.15 s after plume loss. The speed of processing odour onset and loss may depend on selection imposed by the intensity of competition with conspecifics for a valuable resource, either a receptive female or host fruit. There may not be as high an evolutionary premium placed on rapid location of a susceptible almond by a ovipositing female as on the location of a calling female by males. An individual almond can support as many as six *A. transitella* larvae (R. Youngman, personal communication), whereas calling females become refractory to further copulation for at least several days after mating (Coffelt *et al.*, 1979b). Other factors which also may enter into selection on the biochemical and behavioural reaction times are the potential for wind shifts in the natural environment, and the probable distance from the source at the time of plume loss. Infrequent chance of wind shifts would make selection for a fast response less intense and a fast response would not be as critical close to the resource where the linear speed of movement of the plume 'away' from the moth would be lower for a given angle of wind shift (Baker & Haynes, 1987). In the future it may be fruitful to examine the speed of the behavioural and biochemical reactions to odour loss and gain in the context of an animal's habitat.

Acknowledgments

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