

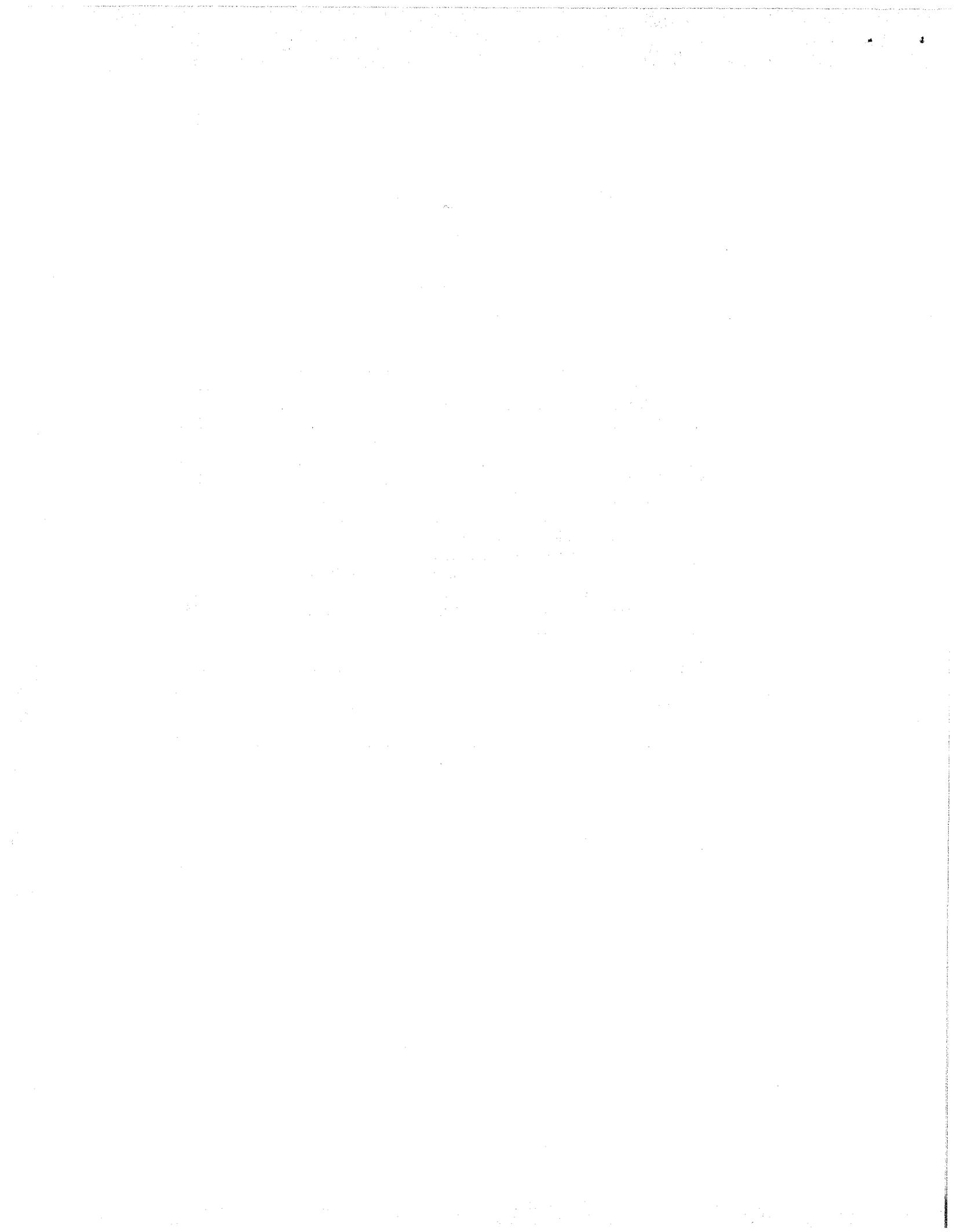
Chapter 10

PHEROMONES AND FLIGHT BEHAVIOR

T. C. Baker

TABLE OF CONTENTS

I.	Introduction	232
II.	Maneuvering Mechanisms	232
	A. Optomotor Anemotaxis	233
	B. Self-Steered Counterturning Program	241
	C. Chemotaxis	242
III.	Factors Influencing the Steering and the Tracks	243
	A. Wind Velocity	243
	B. Pheromone Concentration	243
	1. Time-Averaged Concentration	243
	2. Sudden Decrease in Concentration	245
	3. Sudden Increase in Concentration	249
	4. Short-Term Concentration in Fluctuations Due to Plume Structure	250
	C. Pheromone Component Blend Ratios	251
	D. Temperature	252
IV.	Conclusions	252
	Acknowledgment	252
	References	253



I. INTRODUCTION

Flight is the most common form of locomotion used by insects to locate distant sources of sex pheromone. We are, however, only beginning to understand the flight maneuvers that insects use to locate such sources and to appreciate the complexities of the integration of chemical and visual stimuli they perform in the process. Although sex pheromone-mediated flight occurs in the vast majority of insect orders, by far the group most intensively observed and recorded for the purpose of understanding flight behavior is the Lepidoptera. The emphasis on Lepidoptera, primarily moths, is partly due to the need for entomologists to know how their attractant blends affect moths to optimize control strategies for this economically important insect group and partly because moths' behavioral responses are so reproducible and their olfactory systems are so accessible and simple. As a consequence, zoologists realized early on that by studying this group much could be learned about the neurobiology and behavior related to olfaction.

Thus, this chapter focuses on studies of the flight behavior of male moths. Many of the mechanisms that they use most likely are shared by other insects flying to odor sources. For instance, the tracks of gravid female navel orangeworm moths, *Amyelois transitella*, flying upwind to almond oil volatiles are quite similar to those of males of this species flying to female sex pheromone.¹ Even the switchover from upwind flight to casting flight, following loss of the almond oil odor plume, bears striking resemblance to the same transition made by males losing the sex pheromone plume. Adult *Drosophila hydei* fly upwind to banana odor and switch to casting flight upon odor loss.² These and other species that progress upwind or keep station while flying in odor plumes must, like male moths, necessarily use the mechanism of optomotor (see also Chapter 9) compensation for wind-induced drift.³

The behavioral analysis of lepidopteran pheromone-mediated flight has always been performed with the goal of moving beyond merely counting the number of moths trapped at a source of pheromone and finally understanding what male moths do, how they maneuver in response to their pheromone. However, despite the increase in knowledge gained by video analysis of flight tracks, most studies still unwittingly end up with the results of maneuvers rather than the maneuvers themselves, in the form of average ground speed, track angle, and zigzag width, etc. The research of J. S. Kennedy, A. R. Ludlow, C. T. David, and D. Marsh has been an exception. These researchers consistently communicated the need for understanding the specific maneuvers performed by flying insects and achieved this knowledge in their experiments.

This chapter will attempt to cover what has been learned about pheromone-mediated flight in moths from all levels of studies, but emphasizing what we know about the in-flight maneuvers that affect the moths' immediate complex problem of maintaining contact with the pheromone plume and advancing up it while tracking the wind direction. I will not attempt to cover either visually mediated landing at the source or pheromone-triggered, visually mediated flight toward a target such as a tree or branch at some point near the source. It is clear that these flights to visual cues may be important to males of several moths species^{4,5} in aiding long-distance location of the female in nature. Likewise, the behavior following visitations to the source, often reported to consist of ascending flight coupled with rapid downwind, straight-line displacement,⁶⁻⁸ will not be considered here.

II. MANEUVERING MECHANISMS

Optomotor anemotaxis and a self-steered program of reversals are the two mechanisms known to be used to maneuver during pheromone-mediated flight by all flying insects analyzed thus far. These two mechanisms interact to produce the resultant ground speeds and flight track shapes, as well as the commonly reported resultant displacements *upwind*

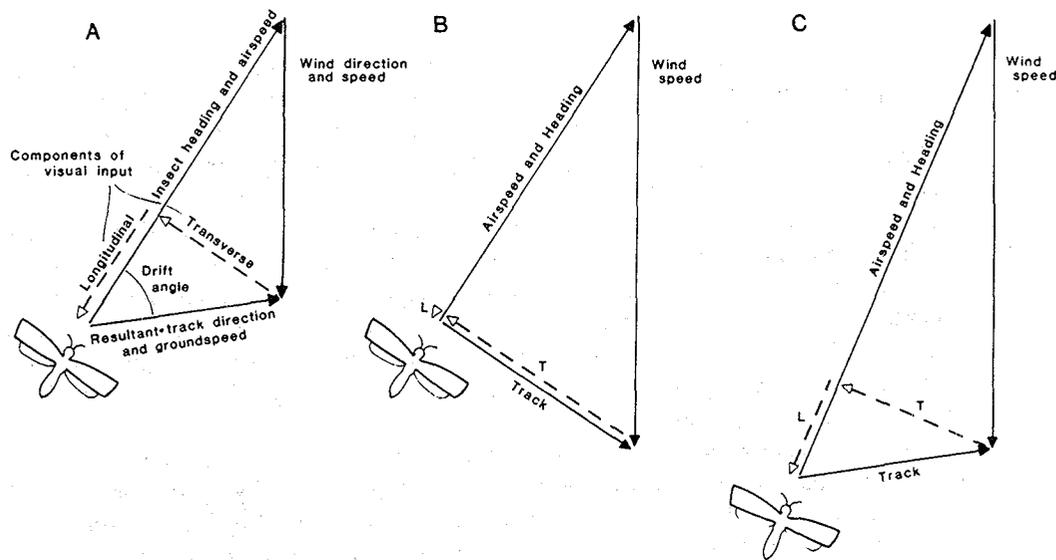


FIGURE 1. (A) The triangle of velocities for a moth flying in wind of a known speed and direction. If the resultant track angle and ground speed are known, then the moth's course (in this case also his heading) and airspeed can be calculated. The transverse and longitudinal components of movement, possibly used as visual feedback for course and airspeed reactions,^{17, 18} are shown. (B) If the wind speed increases suddenly and the moth does not compensate by changing his heading and airspeed, then he will fly along the resultant track at the ground speed indicated. (C) To attain the previous track angle and ground speed, the moth steers more directly into the wind and increases his airspeed, perhaps by attaining the previous sum of the transverse (T) and longitudinal (L) components of movement measured visually. (From David, C. T., *Mechanisms in Insect Olfaction*, Payne, T. L., Birch, M. C., and Kennedy, C., Oxford University Press, Oxford, 1986, 49. With permission.)

flight, in-flight arrestment, and casting flight under different conditions of pheromone stimulation and wind. Pheromone-mediated flight is herein considered to be flight occurring after pheromone contact or shortly after in-flight loss of pheromone. For several species, repeated contact with and loss of pheromone are needed to maintain flight behavior that results in location of the pheromone source.

A. Optomotor Anemotaxis

Optomotor anemotaxis, the use of visual image movement to steer a particular resultant track and ground speed with respect to wind, was first demonstrated for odor-mediated flight in insects by Kennedy⁹ using the yellow fever mosquito. Later Kennedy and Marsh¹⁰ and Marsh et al.¹¹ demonstrated that optomotor anemotaxis was used by *Plodia interpunctella* males during upwind flight to pheromone. Marsh et al.¹¹ pointed out that a male moth has only two reactions available to him to control his horizontal displacement during pheromone-mediated flight in wind: change his *course* (direction of his thrust through the air) or his *airspeed* (his speed through the air). In most recordings of flight tracks, the moth's image is too indistinct to clearly define his anatomical heading (orientation of the body axis) and, furthermore, his heading may not always correspond to his direction of thrust, which is his true course. However, the course of a male and his airspeed may be accurately calculated by the triangle of velocities (Figure 1) if the ground speed, track angle, and wind speed and direction are known.¹¹

These calculations have been performed in behavioral studies involving pheromones. Average airspeeds have sometimes been calculated without knowledge of track angles and have been somewhat useful for inferring that males react anemotactically to pheromone concentration¹²⁻¹⁵ and wind velocity.^{6, 12, 16} A detailed description of the reaction is lost,

however, without further analysis. Optomotor anemotaxis is the only known means that flying males can use to control their flight direction and therefore their displacement in wind.^{3,4} Males on the ground may be able to use mechanoreceptors as pressure sensors and do not need to visually sense wind or monitor their ground speeds. Male moths have no problem maneuvering upwind to pheromone sources in the field at night or in wind tunnels under moonlight levels or below, and so their dark-adapted superposition eyes obviously allow resolution of image motion sufficient for optomotor anemotaxis.

The precise nature of the visual feedback males use to accomplish wind-steering is not known. Ludlow¹⁷ and David¹⁸ point out that for flying insects to maintain a directly up- or downwind track at a particular ground speed, it is a relatively simple matter compared with maintaining some intermediate cross-wind track angle plus a constant ground speed. For the former, all that is needed is for the male to steer a course such that there is no transverse image movement across the eye and to adjust his airspeed so that the back-to-front longitudinal image velocity attains the preferred rate. The more complex problem of a constant nonzero track angle and constant ground speed might be accomplished if the male could integrate both the longitudinal and the transverse components of image movement. Then airspeed and course reactions could both be made by the male to keep the sum of these values (or more precisely, the square root of the sum of the squares) constant and thereby attain a constant track angle and velocity^{17,18} (Figure 1).

Another recent hypothesis concerning feedback for optomotor anemotaxis argues that pheromone-stimulated flying male *Lymantria dispar* are attempting to steer a 0° course, directly upwind, but because of visual error in detecting transverse drift and attaining this desired set point, the male steers through too much of an angle off to one side of the windline. He then attempts to compensate by reversing direction and overshoots to 0° angle in the opposite direction in the same way due to his inability to detect the transverse drift soon enough. The resultant tracks alternate from side-to-side across the windline.¹⁹ Data supporting this hypothesis was obtained using tethered males and an elaborate computer-controlled visual feedback system. Contradictory evidence has recently been obtained, however, using free-flying *L. dispar*, demonstrating that pheromone-stimulated males actively steer cross-wind courses and perform counterturning.⁸² The differences in the results of this study and the previous one were attributed to several shortcomings in the technique of tethering and in the visual feedback system employed. This purely anemotactic model¹⁹ does not explain the regular counterturns in zero wind observed for some species of moths²⁰ nor the temporally regular reversals in wind in a pheromone plume or after pheromone loss during casting flight.²¹ In addition, there is now also evidence that male *Grapholita molesta* actively steer a cross-wind course alternating to one side of the windline or the other⁸¹ and do not steer directly upwind as do tethered gypsy moths. Moreover, tethering which prevents free rotation in all planes¹⁹ will fail to measure non-yaw-related lateral (off-wind-line) flight forces during the rolling and banking that many moths perform^{81,82} (Figure 5). These occurrences are evidence that during upwind flight in the plume for some species and during casting for all species, an independent, self-steered system of programmed reversals (see next section) is integrated with anemotaxis.

Little is known about pheromone-mediated changes in altitude. Priess and Kramer²² demonstrated that with pheromone present, tethered gypsy moth males compensate for the movement of visual stimuli mimicking both altitude and velocity changes by changing their lift and thrust accordingly. When pheromone is absent, no such reactions occur. The visual feedback systems for both reactions appears to involve the ventral ommatidia.

The relationship between vertical and horizontal movement during upwind flight in a plume can be seen for a moth described as zigzagging and one said to loop (Figure 2).²³ Indeed, *Grapholita molesta*, the zigzagging moth, has a greater side-to-side than vertical movement, whereas males of *Heliothis virescens* fly such that the displacement magnitudes

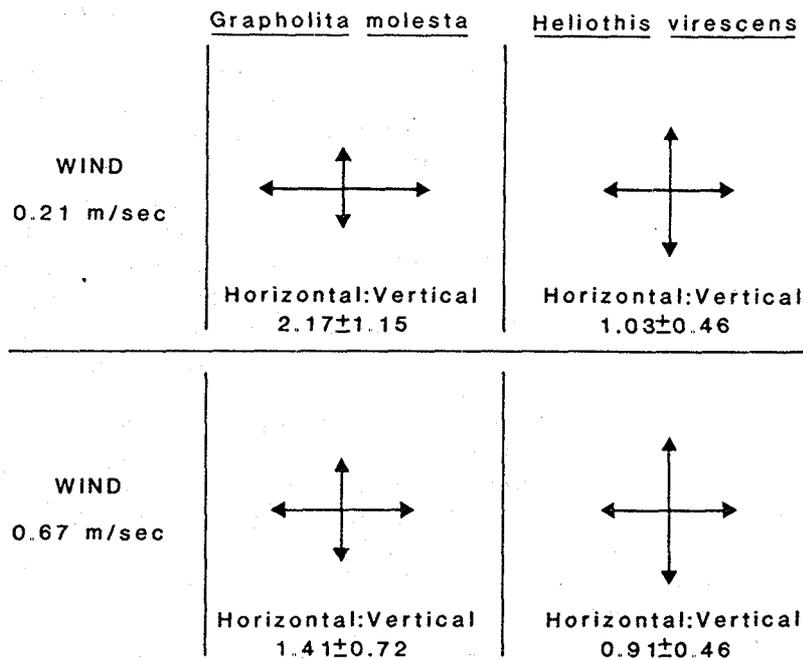


FIGURE 2. The relationship between horizontal and vertical movement in males of two species of moths, one that zigzags (left) and the other that loops during flight in the plume toward the source. The lengths of the bars represent the magnitudes of the mean vertical and horizontal deviations (cm) from the mean position of the moths as they were videorecorded from behind looking up the plume axis toward the source. The length of the horizontal bar in the upper left figure is 3 cm. The mean ratios of horizontal to vertical movement were also calculated; $n = 20$ moths for *G. molesta* and 10 moths for *H. virescens*.

are equal vertically and horizontally. Male *L. dispar* flight tracks have been called zigzagging^{12,24} and exhibit significant horizontal deviations, but they also deviate vertically²⁵ (Figure 3).

The side-to-side movements of some zigzagging species such as *G. molesta* have sometimes been characterized as oscillations because of their spatial and temporal regularity. When such tracks have been analyzed against time in detail, temporal regularity is even more striking (Figure 4B, lower) and seems indicative of a pheromone-mediated motor program^{21,53} rather than a series of individual responses to the less regular arrival of pheromone filaments on the antennae.^{27,28} Less is known about the temporal and spatial regularity of vertical movements and their relationship to lateral movements. For *G. molesta*, there appears to be significantly less temporal regularity in up-and-down movements than side-to-side movements and no strong phase relationship coupling them.²³ The pitch of male *G. molesta* bodies during these comparisons is often near 0° (horizontal) under these wind speeds, and in executing their track reversals, male *G. molesta* roll and bank steeply at the turn apexes (Figure 5). On the fairly straight portions of the reversal legs, they return to a nearly perfectly horizontal attitude with nearly 0° pitch and roll. This is consistent with the idea that the straight legs of the flight track are where the moth is most likely to be reacting to wind direction and velocity through optomotor anemotaxis.¹¹ The flight is relatively level, and motion detectors of the male, positioned on the ventral ommatidia, are all pointing downward.¹⁸

On the other hand, for *H. virescens*, the movements in the two planes seem much more closely coupled in both temporal regularity and phase.²³ At these low wind speeds, the strong-flying male *H. virescens* body angle to the ground (pitch) was usually greater than

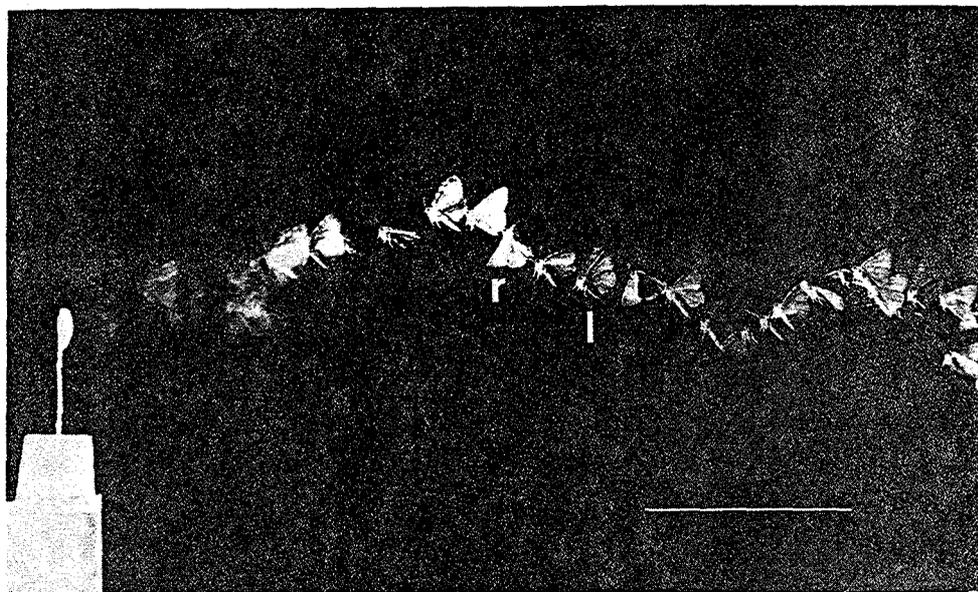


FIGURE 3 View from the side and slightly upwind of the flight of a gypsy moth male flying close to a filter paper source of its sex pheromone at the top of a wire clip in a wind tunnel. Note the body angle with respect to the ground and the vertical displacement during upwind zigzagging flight. Slight left (l) and right (r) rolling and yawing movements by the male are also visible. Length of horizontal white line at lower right is 10 cm. Wind velocity was 70 cm/sec; strobe flashed at ten per second (From Baker, T. C. and Cardé, R. T., *Environ. Entomol.*, 7, 45, 1978. With permission.)

45°. In these same low wind speeds of less than 1m/sec, several species of similarly large and strong moths fly with large pitch within several meters of the source, including black cutworm, *Agrotis ipsilon*,²⁹ *L. dispar*^{12,25} (Figure 3), and *Spodoptera littoralis*.^{6,30}

S. littoralis is capable of upwind progress in the field in winds of 6 m/sec, and so it is obvious that these males plus other noctuids such as *H. virescens* and *A. ipsilon* fly with considerable total wing force and thrust in reserve at lower wind speeds. They may keep their airspeeds low during flight close to the pheromone source by flying with low total wing force and a high degree of pitch, thereby partitioning the wing force mostly into lift with little thrust (see Chapter 1). For these species, the maneuver necessary to generate a programmed track reversal may also generate a change in altitude due to the relatively poorer control of pitch, which perhaps is a reflection of the large pitch angle. Of course, any change in visual feedback indicative of slower ground speed could cause the male to compensate by changing (reducing) the pitch, thus generating more thrust than before and also by increasing the total force generated by the wings. Fruit flies regulate height and ground speed by these two responses, each governed by a different set of motion feedback detectors positioned vertically and horizontally on the equatorial ommatidia.^{2,31}

In moths, height and ground speed detectors appear to be located on the ventral ommatidia,^{18,22} but apart from this it seems possible that the two means of controlling height and ground speed in moths, modulating the total wing force and partitioning this force using body angle, could be similar to *Drosophila hydei*.^{17,18} Feedback for the transverse and longitudinal components of image movement may utilize motion detectors on the ventral ommatidia positioned at right angles to each other.^{17,18} Lift, thrust, wind speed, ground speed, and body angle relationships all must necessarily shape the possible three-dimensional flight tracks of different species during pheromone-mediated flight,¹⁹ but very few studies have been performed with these variables in mind. Much more experimentation is needed

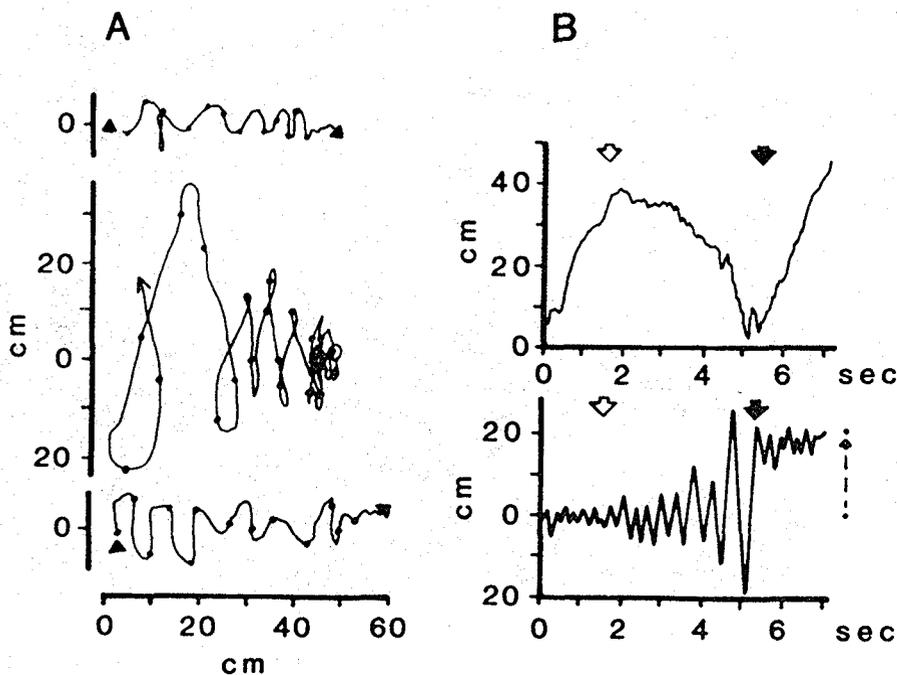


FIGURE 4. (A) Top view of the flight track of a male *G. molesta* in the wind tunnel as it zigzagged upwind toward a source of female sex pheromone (top); after it switched to casting flight following an abrupt reposition of the plume 20 cm to its left (middle); and the switchover to upwind zigzagging following relocation of the plume (bottom). (B) The up-tunnel progress (top) and the horizontal deviation (bottom) of the male in (A) plotted against time. Hollow arrows denote time of plume loss and solid arrows denote time of recontact with the plume as monitored by a simultaneous smoke visualization of the approximate position of the plume. Note the temporal regularity of the reversals (bottom right), during both upwind zigzagging flight when their frequency was approximately eight per second and during casting flight in clean wind when their frequency gradually dropped to approximately three per second just before recontacting the plume. (From Von Keyserlingk, H. C., *Meded. Landbouwwet. Rijksuniv. Gent*, 49, 683, 1984. With permission.)

before any firm conclusions can be made about size- or species-specific three-dimensional shapes of tracks.

It is relatively easy to propose some possible functions of control of track angles by flying moths. Of course, progress directly upwind, 0° , would be the most direct route to the female,⁷⁹ but the reason some insects such as moths fly at other angles may be related to their threshold for detecting transverse image flow (see Section B on counterturning); they fly a resultant 0° and progress upwind by counterturning and flip-flopping across the windline at approximately 60 to 80° track angles. After flight out of the plume in a shifting wind field, further progress up the wind line would take the male in a direction no longer pointing toward the source^{24,47,79} and so males switch to 90 to 100° cross-wind tracks. During casting flight in the "clean" wind, the cross-wind scans eventually help the male reintersect the plume.^{24,47,77} In addition, under some circumstances in shifting wind, the cross-wind tracks enable a male to relocate the plume at a distance significantly closer to the source than where he lost it²⁴ The quick switchover to a more cross-wind track within one reversal of losing pheromone can also help a male follow the shifting plume over to its new location⁴⁷ if the wind is not shifting too quickly (Figure 6).

The functions of controlling ground speed by flying insects are less clear.² Certainly the fact that many species of flying moths keep much thrust in reserve when flying at relatively low ground speeds must have some benefit in improving overall flight control under the

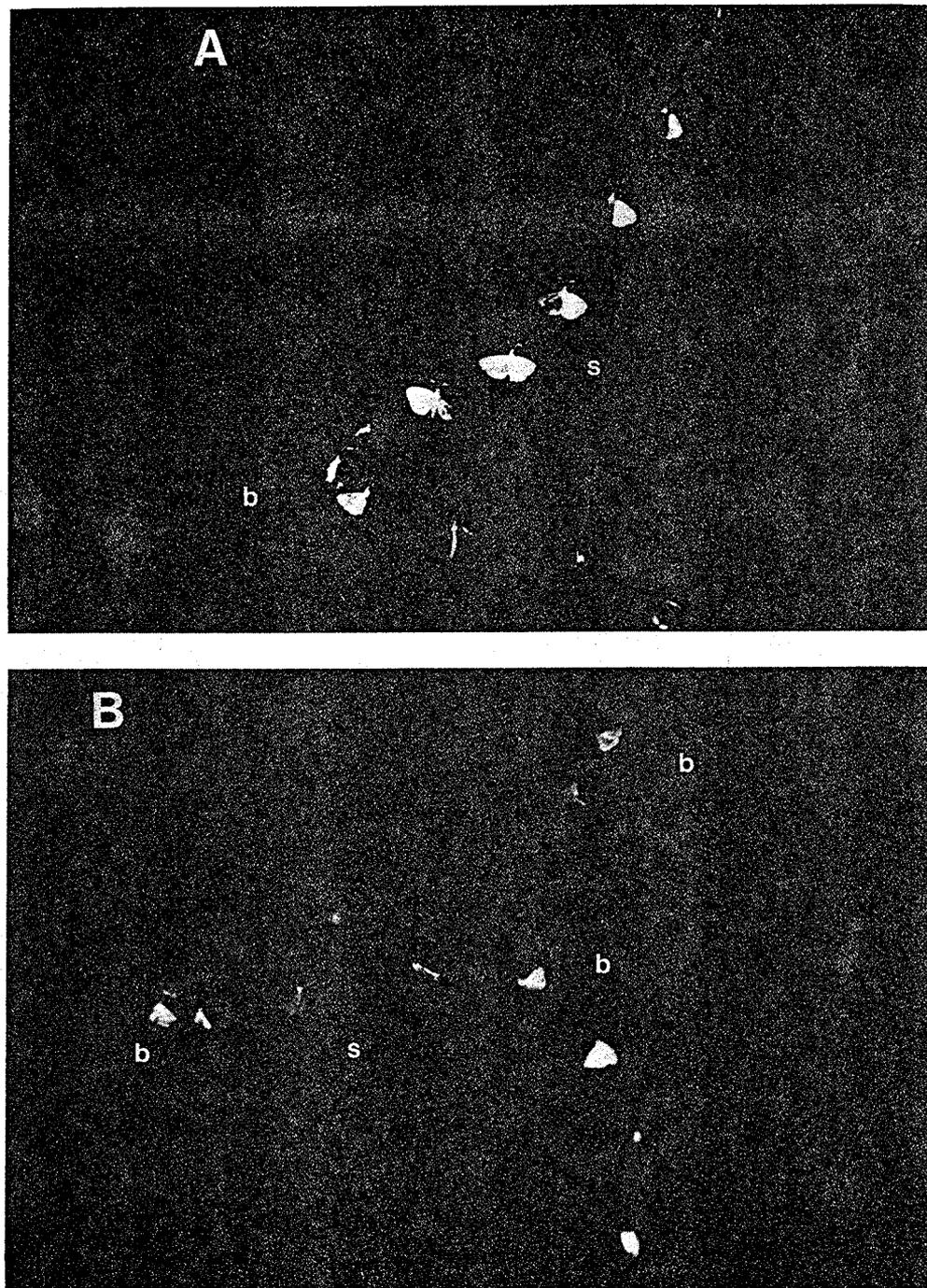


FIGURE 5. Photographs (top view) of *G. molesta* males during upwind flight in pheromone. Both wind (67 cm/sec) and pheromone are from the top in each picture. Note the pronounced banking (b) made by the males at the apices of the reversals, the disparity between heading and track along the relatively straight portions of the interversal legs (s), and the nearly horizontal body angle with respect to the ground along these straight legs. Body length of males is approximately 0.5 cm. Strobe flashed at 30 per second.

A

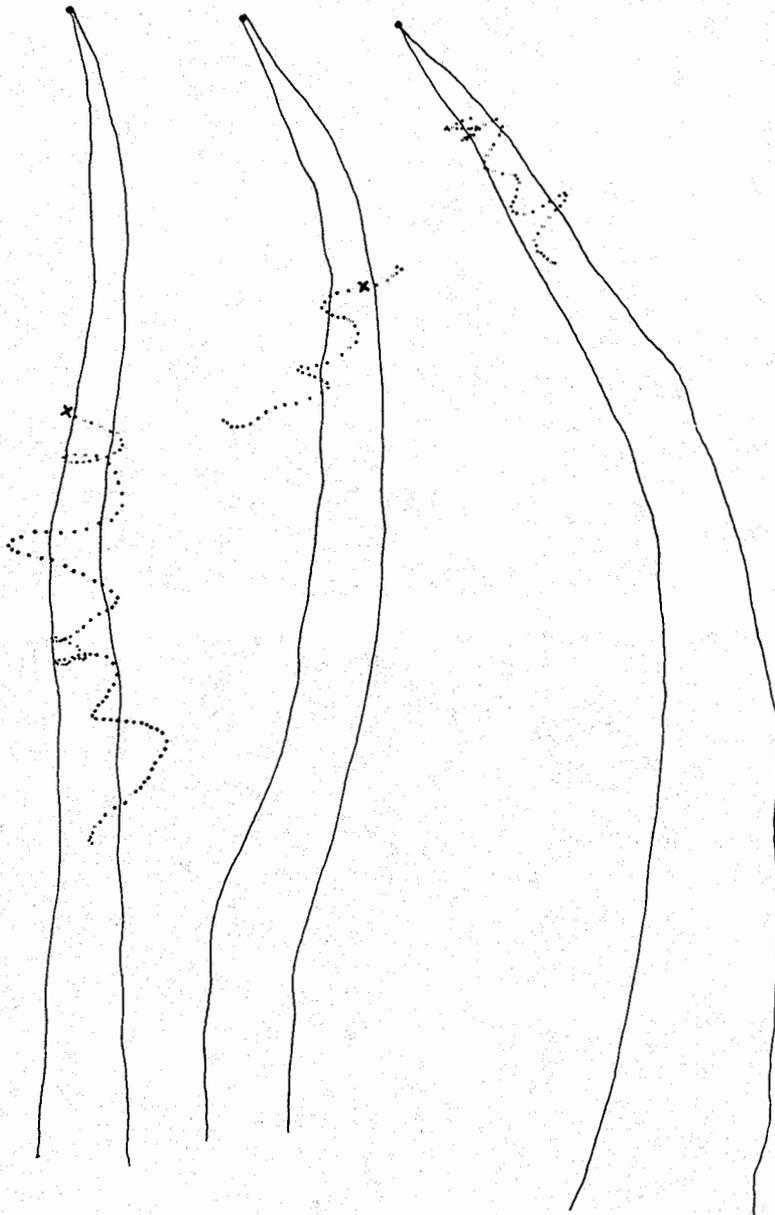


FIGURE 6. (A) The top view of a track of a *G. molesta* male; (left) flying upwind in a pheromone plume; (center) "following" the plume across as an experimentally produced shift in wind direction change the plume's position; (right) flying upwind in the plume in its new, shifted direction. Note the asymmetrical, sawtoothed form of the track in center as the male moved across with the windshift and the plume. The approximate, time-averaged envelope of the plume as visualized by smoke is drawn at time X in the left and center tracks and at the last moth position in the track at right. Dots indicate of the male's position each 1/60 sec. Length of plume at left is 110 cm. (B) The mean course angles, airspeeds, and reversal durations of 16 males that followed the plume across during the windshift. Shaded bars are during left-hand straight legs, white bars are right-hand straight legs, at the indicated interreversal number before, during, and after the wind-shift. Asterisk denotes a significant difference between right and left within a pair of track legs ($p < 0.05$).

B

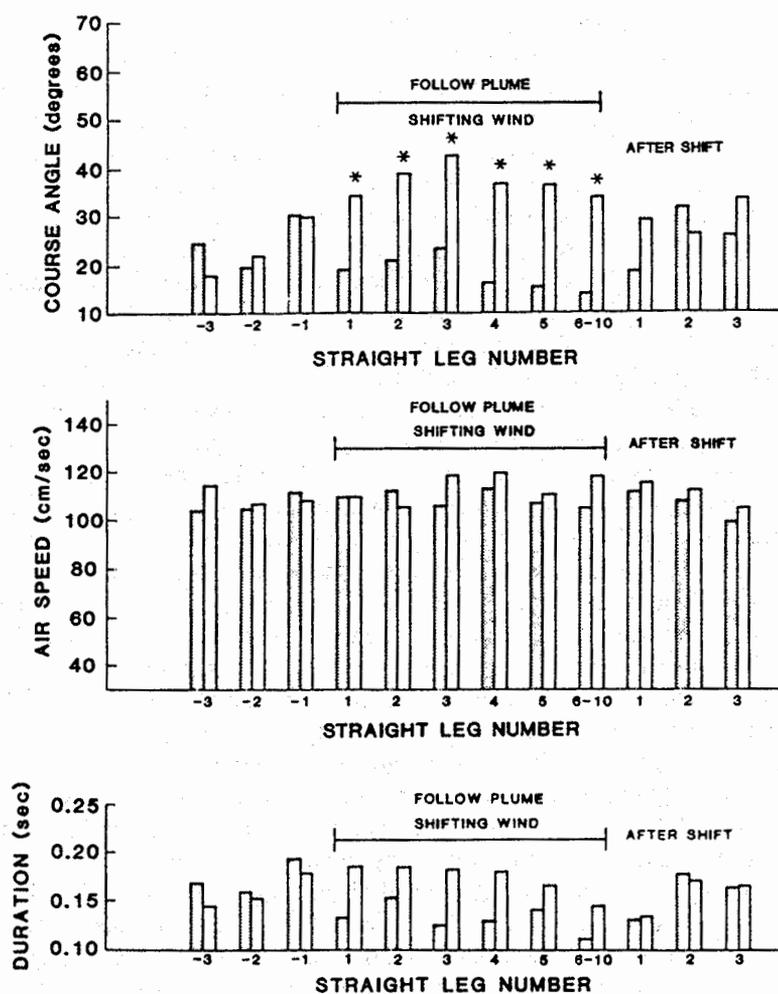


FIGURE 6B

sometimes turbulent and gusty wind conditions in the field.^{2,12} In addition, in pheromone-stimulated males, the fact that higher pheromone concentrations significantly reduce the preferred ground speed of males zigzagging up the windline suggests that indeed ground speed control prevents the males from overshooting the source.² Additionally, the side-to-side narrowing of the track, in part due to lower ground speed along the track, may also help the male maintain contact with the plume and home-in on the location of the female when he is close to her. Angular wind-shift magnitudes close to the source result in much smaller linear distances of plume swing than farther from the source,⁴⁷ and so the narrowing track and slowing of ground speed are less likely to hinder the maintenance of plume contact close to the source. Conversely, high ground speeds farther away at lower pheromone concentrations allow the male to advance rapidly toward the female from great distances and laterally track the more widely swinging plume.⁴ Of course, the highest ground speeds are those during the most severe decrease in concentration, those occurring during casting flight following plume loss. In conjunction with the cross-wind track angle, these ground-

speeds optimize the relocation of the shifted plume, either after one reversal if the shift is not severe or after many when the shift covers a great distance.⁴⁷

B. Self-Steered Counterturning Program

A key mechanism in pheromone-mediated flight, the self-steered system of counterturning, was neglected for a long time^{4,32} and confused with chemotaxis. Implicit in the description of casting flight after a sudden drop in pheromone concentration as reversing anemomenotaxis^{10,11} was the idea that there was an internal mechanism making the moth reverse its course across the windline in a regular fashion. Yet the *program* of reversals during casting, while obviously self-steered and not with regard to chemical cues, was never described as such until a series of experiments brought this concept to the fore. Kennedy and colleagues,³³⁻³⁵ using clouds of pheromone, and Baker and Kuenen³⁶ and Kuenen and Baker,³⁷ using plumes in zero wind, concluded that for two species, a self-steered counterturning program was used not only during casting, but also during flight in the pheromone plume. The only difference would be that during contact with pheromone the self-steered reversals would be more frequent than during casting. This simpler system of a continuum between upwind zigzagging and casting, relying on a programmed response to pheromone,^{32,35} represented a significant change in thinking from the earlier model where flight would either be straight upwind during stimulation or would reverse across-wind according to program following loss of pheromone. The new model would mean that the turns occurring during zigzagging are not solely a response to the repeated loss of pheromone during flight into pockets of clean air in the filamentously structured plume,¹¹ nor are they in response to loss of pheromone during excursions from the time-averaged plume,^{38,39} even though initially they appear to be so due to their proximity to the time-averaged edge. Rather they would occur according to the reversing tempo of the motor program set and reset quickly by the current pheromone concentration or quality.^{32,47}

The transition from high-frequency programmed reversals in a plume to lower frequency reversals upon flight out of a plume (Figure 4) was demonstrated in zero wind for *G. molesta* and *L. dispar*.^{18,36,37} Moreover, for both species the track angles during "up-tunnel" zigzagging in the stationary plume, and during wider reversals in clean still air, were similar to those movements earlier during upwind zigzagging in the plume in wind and to usual cross-wind casting in clean wind. One explanation for these results is that there are two components to the self-steered mechanism, one generating reversals in torque at a particular frequency (a turn generator) and the other measuring the degrees turned to then straighten the track (turn-measuring feedback loop).^{17,18} These two components, modulated by pheromone concentration, would interact to result in a particular balance point that determines the angle between successive track legs, producing either a narrow zigzagging or a wide casting track.^{17,18}

Further experiments with *G. molesta*²⁰ initiating flight in zero wind demonstrated that the counterturns initiated with pheromone present were indeed orderly and accurately executed, but because of a very small error they eventually resulted in meandering tracks that displaced the moths sideways, down, or up the wind tunnel. The addition of wind and therefore wind-induced drift caused the successive track legs to be polarized in the upwind direction by optomotor anemotaxis to result in upwind flight to the source.²⁰

The fact that a self-steered program of counterturns exists in *G. molesta* during flight in a pheromone plume does not mean that other moths employ this same type of program. Self-steered programs may come in various forms⁴⁰ including straight-line movement. *D. hydei* adults fly straight upwind in an odor plume² and thus may use such a straight-line self-steered program. However, for all moth species analyzed in the laboratory and field thus far, except one⁸ (but see Lewis and Macaulay²⁶), upwind flight within several meters of a point source of pheromone is characterized by narrow lateral and vertical movements

coupled with a fairly steady upwind progression toward the source.^{5-7,24,26,29,31,41,42,62} In addition, all male moths examined thus far experiencing in-flight loss of sex pheromone, plus some other insects such as *D. hydei*² and female *Amyelois transitella* experiencing host odor loss,¹ all appear to take up a program of counterturns that, integrated with optomotor anemotaxis, results in casting flight.

The possible functions of a counterturning program as opposed to straight-line movement up a pheromone plume may involve the need to both maintain and regain contact with pheromone under the shifting and turbulent wind conditions of the field.^{4,32} The continuum from narrow, high-frequency counterturning at higher concentrations to wide, low-frequency casting at subthreshold concentrations appears to allow the male to scan for the position of the plume in slow or fast-shifting wind.³² In addition, programmed counterturning may increase the accuracy of the male, compared with straight-line flight, in tracking the wind direction⁴ by optomotor anemotaxis as he attempts to progress up the shifting windline.^{24,79} The self-steered reversals might help the male to remain above the visual threshold for detecting wind by repeatedly sampling for the sign and magnitude of transverse image flow.^{4,37,80}

Recent evidence in support of this function of counterturning comes from *G. molesta* males walking up a pheromone plume compared to those flying upwind to that same blend under the same conditions. Walking males do not exhibit any temporally or spatially regular counterturning, but rather walk nearly perfectly straight upwind with lateral deviations averaging significantly less than their wingspan.⁸¹ The left-right changes in track average around one per second and are quite variable in tempo. Flying males, as usual, zigzag with a regular tempo of approximately seven per second at a magnitude of over six times their wingspan.⁸¹ Thus, it appears that males walking in pheromone have no need to counterturn because they can accurately detect wind direction mechanically by sensing off-axis pressure⁴ to walk straight upwind, and, as stated by Kennedy,⁴ the counterturning program may be performed by flying males to allow them to sense off-axis image flow.^{37,80}

C. Chemotaxis

Despite its repeated evocation in the literature,^{38,39,44,45} the available evidence does not support the hypothesis that male moths use chemotaxis, i.e., use a chemical gradient to steer either longitudinally along the plume toward the source or transversely across the boundaries of the time-averaged plume.^{3,4,10,11,32-35,46} Such chemotactic explanations are difficult to resolve from others because the moths' displacements are necessarily related to these possible gradients. Proving that the movements are steered in response to the gradients in a direct response to the chemicals^{40,46} is another matter.

Cardé and Charlton⁴⁵ recently invoked chemoklinotaxis to explain how a male gypsy moth maintains contact with and follows a snaking, sinuous plume in a nonshifting wind field. There are several problems with this explanation. As pointed out by Kennedy,⁴ the moth supposedly following the edge of the plume chemoklinotactically in this track usually seems to emerge from the plume on its windward side, a hint that anemotaxis is a predominant mechanism. If a male were following or feeling for the edge by means of klinotaxis as proposed by these authors, then he should be equally likely to follow along either edge, not only the upwind one as appears in the single track. Because only one track has been published and there is no quantitative analysis of these experiments, it is difficult to determine what proportion of the time the moths take the windward side. Field evidence²⁴ for gypsy moth males flying upwind in pheromone contradicts the model of Cardé and Charlton: when the plume moves away from the males, they respond predominantly to the wind, not the plume.^{4,24} Another complicating factor is that it is impossible to tell exactly what feedback the males were experiencing in order to maneuver in the experiment of Cardé and Charlton, because the ground pattern was moved in the downwind direction beneath the male at an unrecorded

and varying speed⁴⁵ to keep him in the field of view of the video camera. The direction of transverse image drift from the floor would have been opposite to that produced by the wind, resulting in a conflicting feedback that could have affected the maneuvers at unknown times.

In a recent experiment, there was no evidence that a chemotaxis is used by *G. molesta* males to steer along the edge of a curving plume in a shifting wind field.⁴⁷ The tracks of males that follow the shifting plume over to its new location are distinctly sawtoothed in shape along the shifting portion of the plume (Figure 6A, center). The tracks give the superficial appearance that the moths detect which way the plume has moved from them and chemotactically bias their movements back toward the plume. However, after close examination of the maneuvers of the male it is clear that the sawtoothed asymmetry could easily be explained by rapid changes in both the self-steered and wind-steered systems upon each contact with pheromone to the right and each loss to the left. Thus, no chemotactic component is indicated. Males begin to change both the course angle they steer with respect to the wind and their reversal frequencies on the next track leg (approximately 0.15 sec.) after losing or recontacting pheromone (Figure 6B). Because they do not alter their airspeeds as quickly as their course angles, there are left-right asymmetries in the ground speeds and track angles, resulting in the sawtoothed tracks (Figure 6A). Ground speeds and track angles are greater to the right, and slower and more directly upwind to the left, resulting in longer reversals to the right. This distance asymmetry is enhanced by the reiterative raising of the counterturning frequency after each new contact with pheromone to the right and the lowering of the frequency after contact with clean air to the left.⁴⁷

III. FACTORS INFLUENCING THE STEERING SYSTEMS AND THE TRACKS

A. Wind Velocity

Marsh et al.¹¹ found that at increased wind speeds, male *P. interpunctella* steer more into the wind and increase their airspeeds. As a result, they keep the same resultant track angle and ground speed, on average, on each interreversal leg as they zigzag upwind in the pheromone plume. The reversal frequency does not change significantly under these different wind speeds, and therefore the self-steered system is not affected, only the anemotactic system.

Priess and Kramer¹⁹ varied wind speed using optically simulated wind and tethered *L. dispar* males in their computer-controlled flight simulator. The moths respond to increased wind speed by increasing either thrust alone or both thrust and lift, resulting in males maintaining a constant ground speed under different simulated wind speeds. Thrust and lift are not rigidly coupled under these experimental conditions.

Murlis et al.⁶ recorded that *S. littoralis* males in the field increase their average airspeed to maintain the same average ground speed in winds varying from 0.3 to 6m/sec. This is the only report in field conditions, of compensation for variations in wind speed, although it is not known whether course angle and actual airspeed along each track leg both alter to result in greater net airspeed. Cardé and Hagaman¹² reported that in a wind tunnel the upwind rates of progress of gypsy moths in winds of 0.7 and 2.5 m/sec are not significantly different. Again, it cannot be discerned whether the compensation includes both an increase in actual airspeed along each track leg or a change in course angle or both. Similarly, Kuenen and Baker¹⁶ reported that male *G. molesta* net upwind groundspeeds, and therefore airspeeds, are not significantly different in winds of 24, 38, or 58 cm/sec at any of three heights in a wind tunnel.

B. Pheromone Concentration

1. Time-Averaged Concentration

In both the laboratory and the field, flight tracks of males commonly become narrower^{5,11,14,48}

and either males' net upwind or actual ground speeds along the track become slower^{5,6,11,14,62} as they approach the source. These flight track changes apparently can be explained largely by the overall increase in concentration experienced by males closer to the source and not by the narrowing of the time-averaged plume. The plume does become narrower nearer the source, but there is no evidence that males react at all to the time-averaged edges of a structured plume by turning sooner upon pheromone loss. Moreover, at a given distance from the source where the plume width is constant, higher source concentrations cause the track widths of males of several species to become narrower,^{12,13,15} and either net upwind or actual ground speed along the track to decrease,^{12,13,15} with the reversal frequency either increasing¹⁵ or remaining unchanged.¹³ At the highest concentrations evoking upwind flight in *G. molesta*, reversals of the males generally occur well within the time-average boundaries of the plume.¹⁵

In the field, the reductions in ground speed and increased frequency of zigzagging during approach to within a few meters of the source have been reported to be quite dramatic and sudden. Relatively rapid and level flight (as viewed from the side) by *S. littoralis* changes to relatively slow flight with regular and narrow vertical reversals within 2 to 4 m of the source.^{6,30} In winds of not more than 0.6 m/sec, *Coleophora laricella* males likewise fly a "relatively straight" path upwind toward the source without any pronounced zigzagging when greater than 5 m away, but exhibit "strong lateral and vertical excursions" beginning at 3 to 5 m downwind.⁵ Rothschild and Minks⁴⁹ reported that *G. molesta* males exhibited cross-wind casting movements when within 1 to 2 m of pheromone source in the field, but upwind flight when at a greater distance was much more direct and rapid. My own observations of this species in the field indicate that upwind flight tracks of males approaching within 10 m from the source usually have some degree of zigzagging component to them,⁵⁰ but this becomes more pronounced within approximately 5 m of the source. By their very nature, low-frequency zigzagging some distance from a source are less obvious than the high-frequency oscillations occurring at high concentrations and low ground speeds close to the source. The tracks of *L. dispar* males in the field were reported to be straight upwind and relatively free of zigzags at greater than 10m from the source, whereas zigzags were present in the majority of track legs (51 of 57) closer than 10m.²⁴ The relatively straight upwind flight at greater distances may be due to differences in the overall concentration farther away or perhaps to differences in the plume structure, which at greater distances will cause shallower fluctuations in pheromone concentration due to attenuation of the filaments of the plume.^{3,26,27,46}

The maneuvers performed by males that result in the narrower, slower tracks at higher concentrations involve both the anemotactic^{11,15} and the self-steered systems.¹⁵ Marsh et al.¹¹ found that as male *P. interpunctella* approach a source, they steer more into the wind and reduce their airspeeds, producing the same track angle under the increasing concentration but invariant wind speed.¹⁸ These two reactions result in a reduced ground speed at that same track angle, thus narrowing the track width on average. Male *P. interpunctella* do not increase their reversal frequency as they approach a source, and, therefore, their self-steered system is not affected by this amount of increase in concentration.¹¹ Despite the error in the time-based in Marsh et al.¹¹ that was discovered by the same authors,⁵¹ most of the conclusions they reached are still valid, because the *relative* changes in the moths' behaviors under a step-wise change in conditions reveal how the moths react using anemotaxis and self-steered counterturning.

Male *G. molesta* exhibit a similar anemotactic reaction when flying at a given distance from the source, but at higher plume concentrations.¹⁵ Although in the study of Kuenen and Baker¹⁵ the triangle of velocities was calculated using the average ground speed along the entire track and the average interreversal angles, *G. molesta* males, like those of *P. interpunctella*, also appear to steer more into the wind and reduce their airspeeds at higher

pheromone concentrations, thus partly explaining the narrower track. In addition, the self-steered counterturning program is also affected over the 100-fold increase in pheromone concentration; *G. molesta* males reverse course significantly more frequently at higher concentrations.¹⁵

Farkas et al.¹³ recorded no significant increase in reversal frequency of male *P. gossypiella* with a 100-fold increase in concentration of female extract at a given distance from the source. However, as in other species, ground speed and track width did decrease with concentration although the maneuvers resulting in this effect are unclear. They reported a reduction in the moth's airspeed, which would account for the reduction in ground speed, but their methods for calculating airspeed and track angles precludes further insight into the reactions. They did measure a decrease in average wingbeat frequency as the concentration increased, which supported their conclusion that the moths reduced their airspeeds.

High pheromone concentration can result in arrestment of upwind progress in the plume. During arrestment, several of the reversals of the male are almost as narrow as during upwind flight, before the male switches to casting flight (see below) upward and out of plume contact, followed by displacement downwind.⁵² For *G. molesta*, the maneuvers resulting in arrestment at high pheromone concentrations appear to involve only the anemotactic system.¹⁵ The counterturning frequency upon arrestment remains the same as during the upwind flight that occurred only moments earlier. However, males stop their upwind progress by steering a course more across the wind, and at the same time reducing their airspeed.^{15,53} This results in track angles at arrestment that are approximately 90° across-wind compared with the usual 70° or so during upwind progress. Because the reversal frequency has not changed from that during upwind flight, and the males are traveling at the same ground speed, the reversal width remains the same during arrestment as during narrow upwind zigzagging flight.

Some species, such as *G. molesta*, appear more prone than others to arrestment at excessive pheromone concentrations, and these species may be viewed as having an upper as well as lower threshold to pheromone concentration.⁵² This propensity may be related to the overall lower emission rate of pheromone by females in their natural communication system and to the vapor pressures of the pheromone components of that particular system compared with synthetic sources which may greatly exceed natural emission rates. Other species respond to very high emission rates of their pheromone components without any signs of arrestment of their upwind flight. When males of such species, such as *P. gossypiella* and *Trichoplusia ni*, are made hypersensitive to pheromone by injections of octopamine or chlordimeform however, arrestment occurs in response to pheromone concentrations that previously had resulted in upwind flight all the way to the source.⁵⁴⁻⁵⁶ In *T. ni*, both the lower and upper thresholds for upwind flight are lowered after such treatment, indicating heightened sensitivity.^{55,56}

2. Sudden Decrease in Concentration

Upon losing the pheromone plume, males quickly switch from narrow-reversal upwind flight to casting flight (with significantly wider tracks at approximately 90° or greater across the wind) in which they no longer progress upwind, but now either keep station or displace slightly downwind.³² In males of several species of moths flying to pheromone,^{47,51} and also in female *A. transitella* losing contact with an almond oil odor plume,¹ this switchover occurs on average within ca. 0.5 sec. The casting flight track of *G. molesta* appears to show a concomitant increase in vertical displacement magnitude as well,²¹ but the overall horizontal flattening characteristic of the movements of this zigzagging species is maintained (Figure 7). The casting flight track in three-dimensional space encompasses, but is now higher in altitude than, the previous location of the central axis of the plume. Far from being evidence of a memory of the position of the plume,²¹ this behavior is merely the expected end result of laterally symmetrical programmed reversals at higher airspeeds and lower reversal frequencies than during upwind flight.

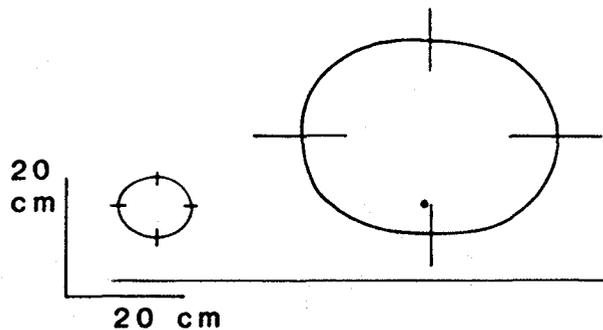


FIGURE 7. View up the plume axis of the average position of 15 *G. molesta* males recorded every 1/60 sec as they (left) zigzagged upwind in a pheromone plume and (right) flew in casting flight in clean wind immediately following plume loss. The curved lines represent the mean values and the bars are the SDs of the vertical and horizontal movements of the males. The dot in the lower portion of the right-hand figure is the former position of the center of the pheromone plume. (From Von Keyserlingk, H. C., *Meded. Fac. Landbouwwet. Rijksuniv. Gent*, 49, 683, 1984. With permission.)

In the field, the casting flight of the gypsy moth is many meters wider than that observed in a laboratory wind tunnel,²⁴ where the walls might have a restrictive effect on casting due to visual cues. Another explanation may involve the closer proximity of the moth to the ground pattern in the wind tunnel, which would create a greater apparent velocity of visual image drift and slower actual ground speed during casting than that needed in the field to produce the same image velocity.

In two species, *P. interpunctella* and *G. molesta*, both the anemotactic and self-steered counterturning system are used by males to change the track angle and ground speed when the pheromone concentration decreases to zero.^{11, 37, 47} In *G. molesta* a switch in course angle appears to occur sooner than the increase in airspeed, while the decrease in counterturning frequency begins about as soon as the course angle adjustment.^{11, 47} Upon flying out of contact with the plume (marked by smoke) in a shifting wind field, *G. molesta* males appear to steer a new course more across-wind on virtually the next reversal following plume loss⁴⁷ (Figure 8). The course angle stabilizes at its new value within a few reversals after that, as does the resultant track angle. Males do not adjust their airspeed as quickly as their course angle, but as a result of the more oblique angle of attack into the wind, the ground speed increases as does the track width per interreversal leg. With time following plume loss, males gradually increase their airspeeds also and thus further boost their ground speeds to result in ever-wider distances per cast (Figure 8).

The programmed counterturning system also appears to diminish in frequency within one reversal following plume loss, and its rate of diminution remains constant thereafter. The longer intervals between reversals accentuate the increase in ground speed, to increase still further the width of the casts across the wind.⁴⁷

In the shifting windfield, male *G. molesta* clearly compensate accurately for the change in wind direction to maintain a constant cross-wind angle slightly greater than 90°. ⁴⁷ Male *L. dispar* in the field likewise shift their 90° cross-wind track along with the shift in wind direction.²⁴

The rapidity of the course angle change following a decrease in concentration was recently measured following a new analysis⁴⁷ of *G. molesta* flight tracks from previous study³⁷ where males zigzagged upwind along the edge of a side corridor of a uniform cloud of pheromone and clean air. The average course angle of males having flown into clean air is significantly

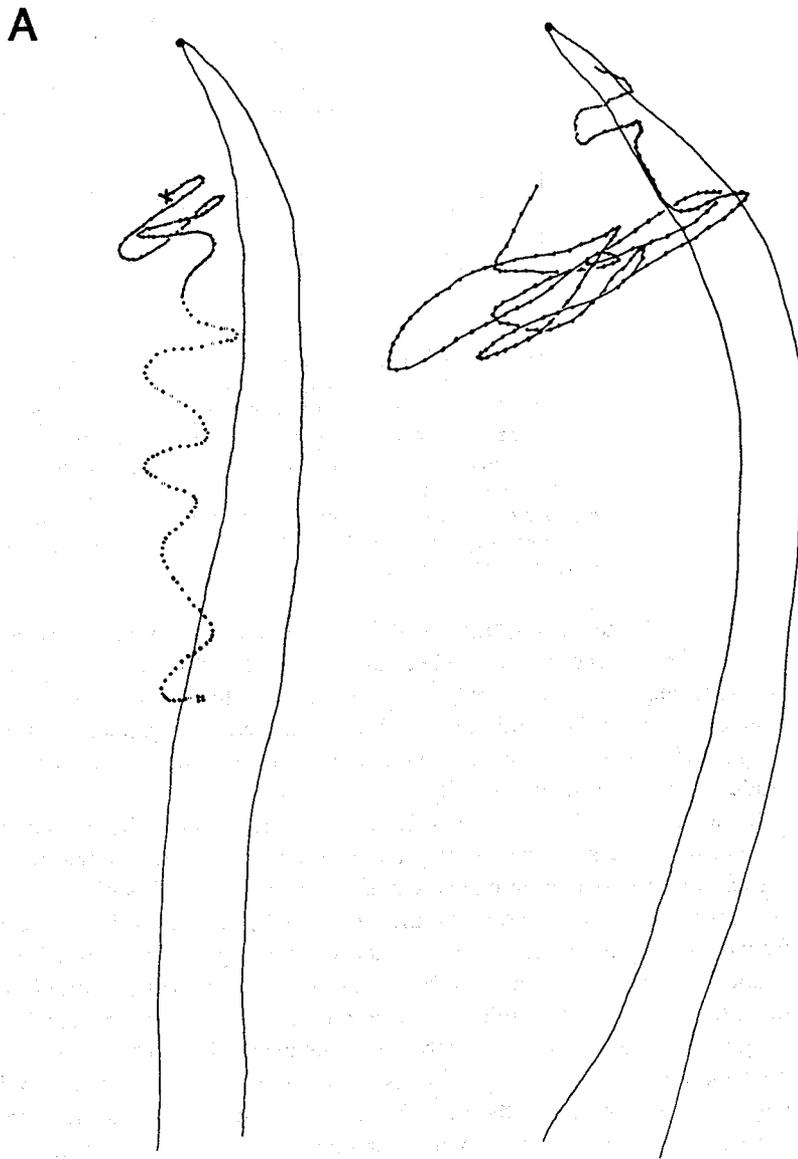


FIGURE 8. (A) (left) Top view of a male *G. molesta* zigzagging upwind in the same shifting wind field as in Figure 6 and losing contact with the plume at the point indicated by the beginning of the solid line of his flight track. The track legs quickly shift to across the new wind line following pheromone loss. (Right) Casting flight across the wind eventually widens and take the male into contact with the plume in its new location, whereupon flight again becomes narrow, upwind zigzagging. (B) The course angles and airspeeds (calculated with knowledge of shifted wind direction) and interversal durations of 20 males losing the plume and then regaining it following casting flight in clean wind in the shifting wind field depicted in A. Shaded bars are left-hand legs and white bars are right-hand legs of males at different interversal numbers relative to losing and regaining the plume. Note the relatively fast course angle and interversal duration reactions to losing and regaining pheromone by the males and the relatively slow airspeed alteration that builds up only after casting has continued for some time. Note also that the upwind surge of narrow zigzagging that follows locking on to the regained plume corresponds to more upwind course angles coupled with a carryover of high airspeed from casting, plus high-frequency (short-duration) reversals. A cross denotes a pair of left-right values that is significantly different from pairs occurring before loss of pheromone; asterisk denotes a significant difference between right and left within a pair of tracks legs ($p < 0.05$).

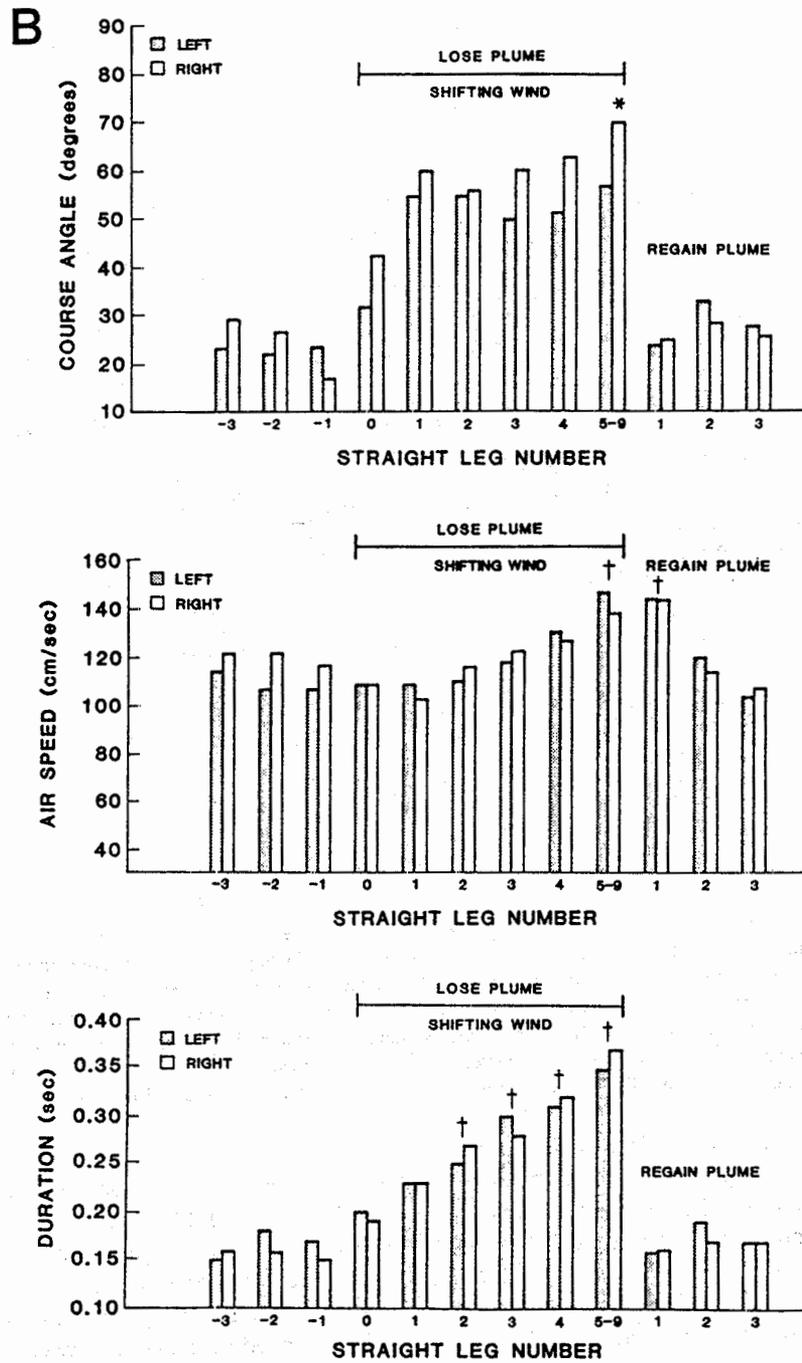


FIGURE 8B

more cross-wind than those following exposure to, and emerging from, the cloud (Figure 9). The course angle following clean air is also significantly more across-wind than those of males zigzagging upwind in a plume immediately preceding flight in the corridor in the same tunnel. The asymmetry in the zigzag tracks up the side corridor is thus due to a course angle increase by males each time they head back into the cloud following clean air.

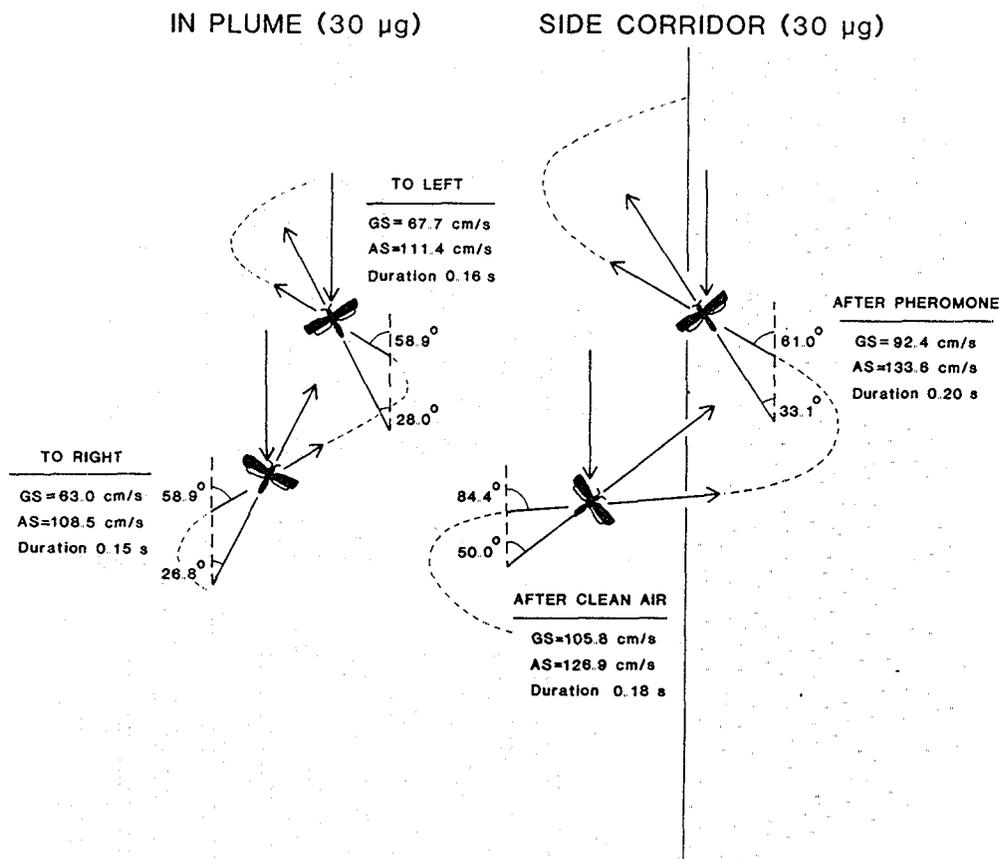


FIGURE 9. The course and track angles of male *G. molesta* flying upwind in a wind tunnel in a pheromone plume from a 30- μg source (left) and, moments later following casting flight after plume removal, zigzagging along the edge of a side corridor cloud of pheromone (right). Males steered a course significantly more directly upwind following contact with the cloud ($p < 0.05$) and more across-wind following excursions into clean air. The result was an asymmetry in the track angles along the corridor, but not in the plume. Airspeed and duration of reversals were not significantly affected, but the more upwind course following contact with the cloud caused ground speed to be slightly reduced; $n = 11$ males along the corridor and 7 males in the plume.

3. Sudden Increase in Concentration

It is apparent that each recontact with the side corridor in the above experiment also causes a course adjustment to more directly upwind⁵⁷ (Figure 9). Males do not change their airspeed significantly, and so the trend is for ground speed to be slightly reduced when steering a course more into the wind. No change in the reversal program is observed here, possibly because the lengthening of interreversal duration following pheromone loss would not be expressed before the cloud was reentered. The speed of the course reaction to the regain of pheromone signal is as fast as to pheromone loss, within one interreversal leg, 0.15 sec.

When *G. molesta*⁵⁷ or *A. orana*³³⁻³⁵ males are engulfed by a cloud of pheromone after a short period of casting flight in clean air, there is a surge in upwind progress in conjunction with a decreased track angle and narrower zigzagging track. These effects are due to a significant increase in counterturning frequency plus obvious adjustments in course angle to more directly upwind.

In a shifting wind field, *G. molesta* males following a plume across with a sawtoothed track steer a course more directly upwind after each contact with pheromone (on each left-hand leg), and have a shorter interreversal duration after pheromone (to the left) as well

(Figure 6).⁴⁷ No adjustments in airspeed occur, but as airspeed appears to be a slower response (Figure 8), this is not surprising. The repeated upwind course without an increase in airspeed makes the ground speed of each left-hand leg slower than to the right, where the course angle more obliquely across the wind allows a greater resultant ground speed for the same effort.⁴⁷ This left-right asymmetry in course angle and reversal duration is not caused by the shifting wind field itself, because no such asymmetries exist during casting flight when males lose the plume completely in the same shifting wind fields. Thus, the course angle and reversal frequency reactions to regaining pheromone in a plume, as in a side-corridor, appear to be very fast, within 0.15 sec.

The process of locking-on to a plume³² after casting flight is more dramatic than the process of continuing to remain locked-on to the plume because it involves a sudden change from wide to narrow zigzagging tracks, plus a significant change in displacement from crosswind to upwind. As pointed out by Kennedy,⁴ part of the locking-on reaction appears to involve a significant change in the counterturning program to a higher-frequency state. This is apparent, as discussed above, for moths in casting flight that are engulfed by a cloud of pheromone.^{33-35,57} Experiments in shifting wind field support this explanation, because males that relocate the lost plume after a period of casting flight react by turning significantly sooner on the first interreversal leg after entry into the plume (Figure 8). The anemotactic system also is affected, however, in that on this same leg males steer a course more directly upwind than before (Figure 8). Because their airspeed reaction is slower than the course reaction, for an extra reversal or two following plume contact their airspeed stays nearly as high as during casting, resulting in rapid upwind displacement or surge upon recontact that is more rapid than during continuous upwind flight in a plume.⁴⁷ When males finally reduce their airspeed after regaining pheromone contact, the ground speed slows to its more moderate level. Thus the upwind surge during the transition to locking-on appears to be due to a carryover of the higher airspeed attained during casting flight, coupled with both the upwind course change and higher counterturning frequency.

4. Short-Term Concentration Fluctuations Due to Plume Structure

An optimal blend and concentration of pheromone will evoke only takeoff or takeoff-type casting flight if males are exposed to relatively uniform concentrations, such as in a cloud or fog of pheromone.^{33-35,57} For *G. molesta*, the tracks following takeoff in clouds are symmetrical across the wind line, indicating compensation for wind-induced drift, but net displacement is either negligible, or slightly downwind, as occurs during casting flight.²⁸ If the same cloud is pulsed, however, by interrupting it once per second with a similar swath of clean air, then narrower upwind zigzagging occurs.²⁸ The track angles are then oriented approximately 70° upwind, indicating a change in course by the males. Airspeed and counterturning adjustments by males have not been measured under such conditions.

Similarly, if a point-source plume of the same blend is placed within the cloud, then narrow upwind zigzagging is readily elicited.^{28,33-35,57} Plumes have a fenestrated, filamentous structure,^{12,21,26,27,43} and the antennae register the fluctuations in concentration.^{28,58,59,60} Single receptor cells appear to adjust their output at higher filament concentrations by reacting with faster action potential offsets so that the onset of the next burst of pheromone is more likely to be detected.⁶⁰

Fluctuations in concentration are necessary for sustained upwind zigzagging flight in three species, *A. orana*, *G. molesta*, and *L. dispar*.^{28,33-35,57,61} More work is needed in which track legs can be segregated precisely according to short-term pheromone experience. It may reveal whether an average track angle, as traditionally depicted during upwind zigzagging flight in a plume, is really due to a male quickly averaging his movements between straight upwind and crosswind resultants¹⁰ or is an artifact stemming from the fact that our measurements of his movements are averaged due to our ignorance of his state of short-term pheromone stimulation.

C. Pheromone Component Blend Ratios

The blend quality, the ratio of pheromone components in the blend, significantly affects the shape of upwind flight tracks and net upwind ground speeds in several species of moths,^{42,53,55,62} although even more commonly the ratio affects whether or not upwind flight is initiated or terminated.^{7,29,42,55,56,62-71} To a suboptimal ratio, males may not make the transition from post-takeoff casting flight to upwind flight, or once upwind flight occurs, arrestment of upwind progress may prematurely terminate upwind flight. Under conditions of optimal responsiveness, a relatively wide range of individual pheromone components and blend ratios can evoke flight in quiescent males of most species, whereas only a narrow range of blends approximating to the optimal blend of components in the natural pheromone can evoke upwind flight and source location.^{62-67,69-71}

The ground speeds and the shapes of the flight tracks are sometimes influenced by different blends of compounds. For instance, Priesner and Witzgall⁴² described the tracks of *C. laricella* as being canalized, or narrower, to a blend of the known attractant containing a small amount of "inhibitor" than to the attractant alone. *L. dispar* flies with lower net upwind ground speed when the amount of (-) disparlure in the plume, an "inhibitor", is increased.^{12,68} However, very little analysis of the maneuvers made by males in plumes of different blends has been reported. To a blend of pheromone components containing slightly excessive amounts of (*E*)-8-dodecenyl acetate, *G. molesta* males zigzag more narrowly and progress more slowly upwind than to the optimal blend. Only the anemotactic system is affected; the males steer a course more into the wind and reduce their airspeed to result in a slower ground speed along a narrower track.⁵³ Counterturning frequency is not significantly altered.

When males become arrested in this situation, they steer a course significantly more across-wind and reduce their airspeed to result in a slow, narrow, cross-wind track, a momentary pause with no progress, before switching to casting flight.⁵³ Arrestment in response to incomplete blends occurs also in *Euxoa ochrogaster*,⁶² *T. ni*,⁴¹ and *Agrotis ipsilon*,²⁹ the latter two of which pause in-flight for 1 to 5 sec or so in the plume before flying rapidly upward or sideways out of the plume and then downwind.

Recently, some authors have debated the possibility that at some distance far downwind of an optimal pheromone blend, such as is emitted by a female, males will detect only a partial blend of components because minor components in the blend will be at concentrations below receptor thresholds.^{45,72-74} Their conclusion is that upwind flight may be initiated by only part of the emitted blend at these distances, whereas upon flight closer to the source, the full blend or even a different set of components will modulate the response. For some species this may happen, but the evidence thus far does not support this concept of nested active spaces.

First, a distinction must be made between the sensory detection of the major components and the behavioral response to them. Further, the types of behavioral responses must be distinguished. For example, for several species the major component alone or even a partial blend can cause quiescent males to fan their wings and takeoff.^{62-67,69-71} It is possible that activation or takeoff may happen, therefore, at some point far downwind of a female where only the most numerous and sensitive receptors respond to the major component. With no upwind flight, however, males will not reach a new zone where upwind flight can occur in response to a blend including minor components. The active space for upwind flight will not have been entered, only that for takeoff. Now, if one considers cases where upwind flight to partial blends has been observed, such as in *G. molesta*, *T. ni*, and *Argyrotaenia velutinana* new evidence demonstrates that the entire blend is the most effective at the lowest concentrations for evoking the upwind flight that is requisite for this whole nested active space scenario to be feasible.^{75,83} Thus upwind flight thresholds of males are lowest to the optimal blend, i.e., to the natural pheromone. Although upwind flight occurs in response

to a partial blend, the concentrations needed to evoke such flight are higher than those to which a male would have already been flying upwind if the complete blend were being emitted. Therefore, in a natural situation involving either calling females or the correct complete blend of synthetic pheromone components, the partial blend would not be encountered at concentrations sufficient to evoke upwind flight without the male first having already encountered and begun flying upwind to the lower concentrations of the complete blend.^{75,83} We know that complete blends continue to modulate upwind flight at higher concentrations closer to the source,^{42,66,69-71,75} and this knowledge obviates any need to explain such flight as being a response to only partial blends.

D. Temperature

In *G. molesta*, temperature influences whether arrestment occurs or upwind flight continues. Higher temperatures cause upwind flight to continue all the way to the source, even to component ratios that otherwise would have evoked premature arrestment.⁷⁶ Low temperatures result in arrestment to all but the optimal ratio at moderate concentrations. Male *L. dispar* progress more slowly and with narrower zigzags at lower temperature.⁷⁷ For these two species, slower flight occurs in response to more concentrated blends or suboptimal ratios at constant temperatures (see above), and so the effects of temperature on flight may be due to temperature-related changes in sensory processing or central integration of olfactory and visual signals.

IV. CONCLUSIONS

By allowing him to track both the wind direction and the position of the plume, the integrated, programmed responses to pheromone, optomotor anemotaxis and self-steered counterturning, appear to meet the needs of a male flying to locate a female. In a pheromone plume, the anemotactic airspeed and course angle reactions allow the male to steer the same track angle and keep the same zigzagging width and rate of upwind progress toward the female under different wind speeds at a given average plume concentration. Upon plume loss, as when the plume changes position in a shifting wind field, the course angle and counterturning reactions occur within one interreversal interval for some moths, resulting in increased track angle, ground speed, and track width on that leg, giving the male a good chance of relocating the plume. If the plume is not relocated immediately, the progressively widening and rapid cross-wind track that occurs with increased airspeed and longer duration of each interreversal leg facilitates an eventual rediscovery of the plume. Plume contact following casting results in an upwind surge of progress toward the female due to a carryover of the high airspeed attained during casting, a quick change in course angle to more directly upwind, and a once-again rapid rate of counterturning. The blend of pheromone components, the emission rate, the plume structure, and temperature all appear to modify various aspects of the anemotactic and self-steered programs.

ACKNOWLEDGMENT

Research of T. C. Baker was supported by National Science Foundation (NSF) Grant BNS8310980. I thank Dr. K. F. Haynes for critically reading and commenting on this manuscript and Richard Vetter for drawing Figures 2, 6, 8, and 9.

REFERENCES

1. Haynes, K. F., and Baker, T. C., unpublished data, 1986.
2. David, C. T., Compensation for height in the control of groundspeed by *Drosophila* in a new, "barber's pole" wind tunnel, *J. Comp. Physiol.*, 147, 485, 1982.
3. Kennedy, J. S., Olfactory responses to distant plants and other odor sources, in *Chemical Control of Insect Behavior: Theory and Application*, Shorey, H. H. and McKelvey, J. J., Eds., John Wiley & Sons, New York, 1977, 67.
4. Kennedy, J. S., Some current issues in orientation to odour sources, in *Mechanisms in Insect Olfaction*, Payne, T. L., Birch, M. C., and Kennedy, C., Eds., Oxford University Press, Oxford, 1986, 11.
5. Witzgal, P. and Priesner, E., Behavioural responses of *Coleophora laricella* male moths to synthetic sex-attractant, (Z)-5-decenol, in the field, *Z. Angew. Entomol.*, 98, 15, 1984.
6. Murlis, J., Bettany, B. W., Kelley, J., and Martin, L., The analysis of flight paths of male Egyptian cotton leafworm moths, *Spodoptera littoralis*, to a sex pheromone source in the field, *Physiol. Entomol.*, 7, 435, 1982.
7. Baker, T. C., Cardé, R. T., and Roelofs, W. L., Behavioral responses of male *Argyrotaenia velutinana* (Lepidoptera: Tortricidae) to components of its sex pheromone, *J. Chem. Ecol.*, 2, 333, 1976.
8. Perry, J. N. and Wall, C., A mathematical model for the flight of pea moth to pheromone traps through a crop, *Philos. Trans. R. Soc. London Ser. B*, 306, 19, 1984.
9. Kennedy, J. S., The visual responses of flying mosquitoes, *Proc. Zool. Soc. London Ser. A*, 109, 221, 1940.
10. Kennedy, J. S. and Marsh, D., Pheromone-regulated anemotaxis in flying moths, *Science*, 184, 999, 1974.
11. Marsh, D., Kennedy, J. S., and Ludlow, A. R., An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone, *Physiol. Entomol.*, 3, 221, 1978.
12. Cardé, R. T. and Hagaman, T. E., Behavioral responses of the gypsy moth in a wind-tunnel to air-borne enantiomers of disparlure, *Environ. Entomol.*, 8, 475, 1979.
13. Farkas, S. R., Shorey, H. H., and Gaston, L. K., Sex pheromones of Lepidoptera. Influence of pheromone concentration and visual cues on aerial odor-trail following by males of *Pectinophora gossypiella*, *Ann. Entomol. Soc. Am.*, 67, 633, 1974.
14. Sanders, C. J., Flight speed of male spruce budworm moths in a wind tunnel at different wind speeds and at different distances from a pheromone source, *Physiol. Entomol.* 10, 83, 1985.
15. Kuenen, L. P. S. and Baker, T. C., The effects of pheromone concentration on the flight behaviour of the oriental fruit moth, *Grapholitha molesta*, *Physiol. Entomol.*, 7, 423, 1982.
16. Kuenen, L. P. S. and Baker, T. C., Optomotor regulation of ground velocity in moths during flight to sex pheromone at different heights, *Physiol. Entomol.*, 7, 193, 1982.
17. Ludlow, A. R., Applications of Computer Modelling to behavioural Co-ordination. Ph.D. thesis, University of London, London, 1984.
18. David, C. T., Mechanisms of directional flight in wind, in *Mechanisms in Insect Olfaction*, Payne, T. L., Birch, M. C., and Kennedy, C., Eds., Oxford University Press, Oxford, 1986, 49.
19. Priess, R. and Kramer, E., The steering of zigzagging flight by male gypsy moths, *Naturwissenschaften*, 73, 555, 1986.
20. Baker, T. C., Willis, M. A., and Phelan, P. L., Optomotor anemotaxis polarizes self-steered zigzagging in flying moths, *Physiol. Entomol.*, 9, 365, 1984.
21. Von Keyserlingk, H. C., Close range orientation of flying Lepidoptera to pheromone sources in a laboratory wind tunnel and the field, *Meded. Fac. Landbouwwet. Rijksuniv. Gent*, 49, 683, 1984.
22. Priess, R. and Kramer, E., Stabilization of altitude and speed in tethered flying gypsy moth males: influence of (+) and (-)-disparlure, *Physiol. Entomol.*, 8, 55, 1983.
23. Willis, M.A., Haynes, K. F., and Baker, T. C., unpublished data, 1986.
24. David, C. T., Kennedy, J. S., and Ludlow, A. R., Finding of a sex pheromone source by gypsy moths released in the field, *Nature (London)*, 303, 804, 1983.
25. Baker, T. C. and Cardé, R. T., Disruption of gypsy moth male sex pheromone behavior by high frequency sound, *Environ. Entomol.*, 7, 45, 1978.
26. Lewis T. and Macaulay, E. D. M., Design and elevation of sex-attractant traps for pea moth, *Cydia nigricana* (Steph.) and the effect of plume shape on catches, *Ecol. Entomol.*, 1, 175, 1976.
27. Murlis, J. and Jones, C. D., Fine-scale structure of odour plumes in relation to distant pheromone and other attractant sources, *Physiol. Entomol.*, 6, 71, 1981.
28. Baker, T. C., Willis, M. A., Haynes, K. F., and Phelan, P. L., A pulsed cloud of pheromone elicits upwind flight in male moths, *Physiol. Entomol.*, 10, 257, 1985.
29. Hill, A. S., Rings, R. W., Swier, S. R., and Roelofs, W. L., Sex pheromone of the black cutworm moth, *Agrotis ipsilon*, *J. Chem. Ecol.*, 5, 439, 1979.

30. Murlis, J. and Bettany, B. W., The night-flight towards a sex pheromone source by male *Spodoptera littoralis* (Boisd.) (Lepidoptera, Noctuidae), *Nature (London)*, 268, 433, 1977.
31. David, C. T., Visual control of the partition of flight force between lift and thrust in free-flying *Drosophila*, *Nature (London)*, 313, 48, 1985.
32. Kennedy, J. S., Zigzagging and casting as a response to windborne odour: a review, *Physiol. Entomol.*, 8, 109, 1983.
33. Kennedy, J. S., Ludlow, A. R., and Sanders, C. J., Guidance system used in moth sex attraction, *Nature (London)*, 295, 475, 1980.
34. Kennedy, J. S., Ludlow, A. R., and Sanders, C. J., Guidance of flying male moths by wind-borne sex pheromone, *Physiol. Entomol.*, 6, 395, 1981.
35. Kennedy, J. S., Mechanism of moth sex attraction: a modified view based on wind-tunnel experiments with flying male *Adoxophyes*, *Colloq. Inst. Natl. Rech. Agron.*, 7, 189, 1982.
36. Baker, T. C. and Kuenen, L. P. S., Pheromone source location by flying moths: a supplementary non-anemotactic mechanism, *Science*, 216, 424, 1982.
37. Kuenen, L. P. S. and Baker, T. C., A non-anemotactic mechanism used in pheromone source location by flying moths, *Physiol. Entomol.*, 8, 277, 1983.
38. Farkas, S. R. and Shorey, H. H., Chemical trail-following by flying insects: a mechanism for orientation to a distant odor source, *Science*, 178, 67, 1972.
39. Shorey, H. H., Behavioral responses to insect pheromones, *Annu. Rev. Entomol.*, 18, 349, 1973.
40. Bell, W. J. and Tobin, T. R., Chemo-orientation, *Biol. Rev.*, 57, 219, 1982.
41. Linn, C. E. and Gaston, L. K., Behavioral responses of male *Trichoplusia ni* in a sustained-flight tunnel to the two sex pheromone components *Environ. Entomol.*, 10, 379, 1981.
42. Priesner, E. and Witzgall, P., Modification of pheromonal behaviour in wild *Coleophora laricella* male moths by (Z)-5-decenyl acetate, and attraction-inhibitor, *Z. Angew. Entomol.*, 98, 118, 1984.
43. Wright, R. H. The olfactory guidance of flying insects, *Can. Entomol.*, 90, 81, 1958.
44. Shorey, H. H. and Farkas, S. R., Sex pheromones of Lepidoptera. XLII. Terrestrial odor-trail following by pheromone-stimulated males of *Trichoplusia ni*, *Ann. Entomol. Soc. Am.*, 66, 1213, 1973.
45. Cardé, R. T. and Charlton, R. E., Olfactory sexual communication in Lepidoptera: strategy, sensitivity, and selectivity, *Symp. R. Entomol. Soc. London*, 12, 241, 1984.
46. Kennedy, J. S., The concepts of olfactory "arrestment" and "attraction", *Physiol. Entomol.*, 3, 91, 1978.
47. Baker, T. C. and Haynes, K. F., Manoeuvres used by flying male oriental fruit moths to relocate a sex pheromone plume in an experimentally shifted wind-field, *Physiol. Entomol.*, 12, 263, 1987.
48. Traynier, R. M. M., Sex attraction in the mediterranean flour moth, *Anagasta kühniella*: location of the
49. Rothschild, G. H. L. and Minks, A. K., Time of activity of male Oriental fruit moths at pheromone sources in the field, *Environ. Entomol.*, 3, 1003, 1974.
50. Baker, T. C., unpublished data, 1979.
51. Marsh, D. Kennedy, J. S., and Ludlow, A. R., Analysis of zigzagging flight in moths: a correction, *Physiol. Entomol.*, 6, 225, 1981.
52. Baker, T. C., Meyer, W., and Roelofs, W. L., Sex pheromone dosage and blend specificity of response by Oriental fruit moth males, *Entomol. Exp. Appl.*, 30, 269, 1981.
53. Willis, M. A. and Baker, T. C., Effects of varying sex pheromone component ratios on the zigzagging flight movements of the oriental fruit moth, *Grapholita molesta*, *J. Insect Behav.*, in press.
54. Haynes, K. F. and Baker, T. C., unpublished data, 1986.
55. Linn, C. E. and Roelofs, W. L., Sublethal effects of neuroactive compounds on pheromone response thresholds in male oriental fruit moths, *Arch. Insect Biochem. Physiol.*, 1, 331, 1984.
56. Linn, C. E. and Roelofs, W. L., Neuropharmacological effects on olfactory perception, in *Mechanisms in Insect Olfaction*, Payne, T. L., Birch M. C., and Kennedy, C., Eds., Oxford University Press, Oxford, 1986, 209.
57. Willis, M. A. and Baker, T. C., Effects of intermittent and continuous pheromone stimulation on the flight behaviour of the oriental fruit moth, *Grapholita molesta*, *Physiol. Entomol.*, 9, 341, 1984.
58. Kennedy, J. S. and Jones, C. D., unpublished data, 1982.
59. Baker, T. C. and Haynes, K. F., Field and laboratory electroantennographic measurements of pheromone plume structure correlated with oriental fruit moth behaviour, *Physiol. Entomol.*, in press.
60. Kaissling, K.-E. Structure and function of olfactory sensilla, in *Mechanisms in Insect Olfaction*, Payne, T. L., Birch, M. C., and Kennedy, C., Eds., Oxford University Press, Oxford, 1986, 193.
61. David, C. T., personal communication, 1984.
62. Palaniswamy, P., Underhill, E. W., Steck, W. F., and Chisholm, M. D., Responses of male redbacked cutworm, *Euxoa ochrogaster* (Lepidoptera: Noctuidae), to sex pheromone components in a flight tunnel, *Environ. Entomol.*, 12, 748, 1983.
63. Teal, P. E. A., Tumlinson, J. H., and Heath, R. R., Chemical and behavioral analyses of volatile sex pheromone components released by calling *Heliothis virescens* (F.) females (Lepidoptera: Noctuidae), *J. Chem. Ecol.*, 12, 107, 1986.

64. Vetter, R. S. and Baker, T. C., Behavioral responses of male *Heliothis virescens* in sustained-flight tunnel to combinations of seven compounds identified from female sex pheromone glands, *J. Chem. Ecol.*, 9, 747, 1983.
65. Vetter, R. S. and Baker, T. C., Behavioral responses of male *Heliothis zea* moths in sustained-flight tunnel to combinations of 4 compounds identified from female sex pheromone glands, *J. Chem. Ecol.*, 10, 193, 1984.
66. Linn, C. E. Jr. and Roelofs, W. L., Effect of varying proportions of the alcohol component on sex pheromone blend discrimination in male Oriental fruit moths, *Physiol. Entomol.*, 8, 291, 1983.
67. Linn, C. E. Jr. and Roelofs, W. L., Response specificity of male pink bollworm moths to different blends and dosages of sex pheromone, *J. Chem. Ecol.*, 11, 1583, 1985.
68. Miller, J. R. and Roelofs, W. L., Gypsy moth responses to pheromone enantiomers as evaluated in a sustained-flight tunnel, *Environ. Entomol.*, 7, 42, 1978.
69. Baker, T. C. and Cardé, R. T., Analysis of pheromone-mediated behaviors in male *Grapholitha molesta*, the Oriental fruit moth (Lepidoptera: Tortricidae), *Environ. Entomol.*, 8, 956, 1979.
70. Linn, C. E., Jr., Bjostad, L. B., Du, J. W., and Roelofs, W. L., Redundancy in a chemical signal: behavioral responses of male *Trichoplusia ni* to a 6-component sex pheromone blend, *J. Chem. Ecol.*, 10, 1635, 1984.
71. Löfstedt, C., Linn, C. E., Jr., and Löfqvist, J., Behavioral responses of male turnip moths, *Agrotis segetum*, to sex pheromone in a flight tunnel and in the field, *J. Chem. Ecol.*, 11, 1209, 1985.
72. Nakamura, K., The effect of wind velocity on the diffusion of *Spodoptera litura* (F.) sex pheromone, *Appl. Entomol. Zool.*, 11, 312, 1976.
73. Nakamura, K., The mate searching behavior of *Spodoptera litura* and components of its sex pheromone, in *Regulation of Insect Development and Behaviour*, Kioza, M., Ed., Wroclaw Technical University Press Wroclaw, Poland, 1981, 941.
74. Bradshaw, J. W. S., Baker, R., and Lisk, J. C., Separate orientation and releaser components in a sex pheromone, *Nature (London)*, 304, 265, 1983.
75. Linn, C. E., Jr., Campbell, M. G., and Roelofs, W. L., Male moth sensitivity to multicomponent pheromones: critical role of female-released blend in determining the functional role of components and active space of the pheromone, *J. Chem. Ecol.*, 12, 659, 1986.
76. Linn, C. E., Jr., Campbell, M. G., and Roelofs, W. L., Temperature modulation of behavioural thresholds controlling male moth pheromone response specificity, *Physiol. Entomol.*, in press.
77. Charlton, R. E., Kanno, H., Collins, R. D., and Cardé, R. T., Influence of pheromone concentration and ambient temperature on flight of the gypsy moth, *Lymantria dispar*, in a sustained-flight wind tunnel, *Physiol. Entomol.*, in press.
78. David, C. T., personal communication, 1984.
79. David, C. T., Kennedy, J. S., Ludlow, A. R., Perry, J. N., and Wall, C., A re-appraisal of insect flight towards a point source of wind-borne odor, *J. Chem. Ecol.*, 8, 1207, 1982.
80. Cardé, R. T., Chemo-orientation in flying insects, in *Chemical Ecology of Insects*, Bell, W. J. and Cardé, R. T., Eds., Chapman and Hall, New York, 1984, 111.
81. Willis, M. A. and Baker, T. C., Comparison of manoeuvres used by walking versus flying *Grapholitha molesta* males during pheromone-mediated upwind movement, *J. Insect Physiol.*, 33, 875, 1987.
82. David, C. T. and Kennedy, J. S., The steering of zigzagging flight by male gypsy moths, *Naturwissenschaften*, 74, 194, 1987.
83. Linn, C. E., Jr., Campbell, M. G., and Roelofs, W. L., Pheromone components and active spaces: what do moths smell and where do they smell it?, *Science*, 237, 650, 1987.