

Navigational Strategies Used by Insects to Find Distant, Wind-Borne Sources of Odor

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Abstract Insects locate many resources important to survival by tracking along wind-borne odor plumes to their source. It is well known that plumes are patchy distributions of high concentration packets of odor interspersed with clean air, not smooth Gaussian distributions of odor intensity. This realization has been crucial to our understanding of plume-tracking behavior, because insect locomotory movements and sensory processing typically take place in the range of tens to hundreds of milliseconds, permitting them to respond to the rapid changes in odor concentration they experience in plumes. Because odor plumes are not comprised of smooth concentration gradients, they cannot provide the directional information necessary to allow plume-tracking insects to steer toward the source. Many experiments have shown that, in the species examined, successful source location requires two sensory inputs: the presence of the attractive odor and the detection of the direction of the wind bearing that odor. All plume-tracking insects use the wind direction as the primary directional cue that enables them to steer their movements toward the odor source. Experimental manipulations of the presence and absence of the odor, and the presence, absence, or direction of the wind during plume tracking, have begun to resolve the relationship between these two sensory inputs and how they shape the maneuvers we observe. Experiments, especially those undertaken in

the natural wind and odor environments of the organisms in question and those directed at understanding the neural processing that underlie plume tracking, promise to enhance our understanding of this remarkable behavior.

Keywords Orientation · Odor dispersion · Optomotor anemotaxis · *Drosophila* · Moth · Tsetse fly · Pheromone · Host odor

Introduction

Many kinds of organisms use odors to locate and identify a wide variety of resources, such as potential mates, conspecifics for aggregation, food, and sites for oviposition. Finding these sources involves a number of potential selective forces—such as economy of movement and the rapidity and likelihood of source location. In some cases, the time to location may be paramount, as in the case of a female moth that is emitting pheromone. She may be mated by the first male that reaches her, and consequently, there should be a considerable selective advantage accorded to males that have an efficient strategy for finding her pheromone plume and then navigating rapidly and accurately along the plume to its source. Greenfield (1981) categorized this competition as “a race to locate females.” In other cases, such as finding a fruit suitable for oviposition, the resource may be available continuously, and, therefore, the importance of rapid navigation to the odor’s source may be lessened.

This review focuses on examples selected to exemplify the diversity of navigational strategies that insects employ to find a distant, wind-borne odor source by navigating along its plume. An odor is typically a mixture of chemicals that evokes a specific behavioral reaction, upwind orientation in

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the context of this review. Odors that are incomplete may not evoke “natural” orientation behavior, as in the case of a partial blend of pheromone components or a complete mixture presented at an unnatural ratio (see Vickers 2006). This review is confined to cases where the odor presented is assumed to be the single natural chemical or the naturally occurring mixture. Among the issues considered are: How the odor is distributed within the plume, strategies for finding an odor plume, mechanisms to detect wind flow, direction of wind flow as a directional guide to the odor’s source, and the kinds of orientation maneuvers used in navigation.

Odor Dispersion

A thorough consideration of the dynamics of odor dispersion in wind is beyond the intent of this review. However, a brief description of this process is necessary to begin to understand how the spatial distribution of odor within the plume and the direction of wind flow modulate orientation maneuvers. In this paper, we define the plume as the volume wherein odor concentration is generally above behavioral threshold; because of turbulence, the odor is unevenly distributed in the plume, with odor-containing eddies interspersed with air that is odor-free or below behavioral threshold. Important reviews on the patterns of odor dispersion in air and water as they affect animal responses to semiochemicals include those of Elkinton and Cardé (1984), Murlis et al. (1992), Weissburg (2000), Conover (2007), Willis (2008), and Riffell et al. (this issue).

Early analyses of the dispersion of a pheromone plume in wind used a time-averaged (Gaussian) model developed by Sutton (1953) to depict concentration distributions downwind of the source (Bossert and Wilson 1963). The work of Fares et al. (1983) incorporated turbulent diffusion and accounted for atmospheric stability, i.e., the scale of turbulence, but these models also generated Gaussian distributions. All such approaches produce time-averaged distributions (e.g., the Sutton equation estimates a 3-min average of concentration), whereas, as first pointed out by Wright (1958), insects typically react to very brief exposures to odors (e.g., ≈ 10 ms in the case of the almond moth, *Cadra cautella*, to a single filament of its pheromone, Mafra-Neto and Cardé 1996). By using the wing-fanning reaction of the male gypsy moth, *Lymantria dispar*, to pheromone, Elkinton et al. (1984) found that time-averaged dispersion models substantially underestimated the instantaneous concentration of pheromone in a forest habitat. Aylor et al. (1976) and Miksad and Kittredge (1979) proposed plume models that calculate instantaneous concentration relative to the plume’s centerline, but these did not account for the lateral movement of the plume (i.e.,

meander), and consequently, these models can not be used to predict concentration at a fixed point downwind (Elkinton and Cardé 1984).

Dispersion of odor in wind is dominated by the forces of turbulent diffusion that stretch and stir odor filaments as they are released from the odor source, simultaneously creating gaps of odor-free air within the plume as it expands and is transported downwind (Murlis et al. 1992). Molecular diffusion, on the other hand, is so slow that it is important only at very small distances. The diffusion coefficient for ethanol is only $1.32 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ and that for hexadecanol (similar in size to many moth pheromones) is $2.5 \times 10^{-6} \text{ m}^2 \text{ s}^{-1}$ (Loudon 2003). The slow rates of molecular diffusion mean that the distribution of odor in the plume is due mainly to turbulence rather than molecular diffusion, and in cases where the odor is a mixture, the ratio of compounds throughout the plume will be close to the ratio emitted at the source. Relatively undiluted packets of odor (“bursts”) can thus persist many meters downwind of the plume’s origin (Murlis and Jones 1981).

Insects navigating along turbulent plumes thus encounter odor in bursts interspersed with patches of clean air (Fig. 1). In analyzing the temporal features of such intermittent signals, it is helpful to use only those portions of the record when the signal is present, the so-called conditional signal. This variable presence of a signal at a fixed sampling point downwind is termed its intermittency (a proportional value that ranges from a value of 1 when the signal is *not* present to zero when it is present continuously—see Fig. 1). Intermittency is caused by turbulent diffusion and plume

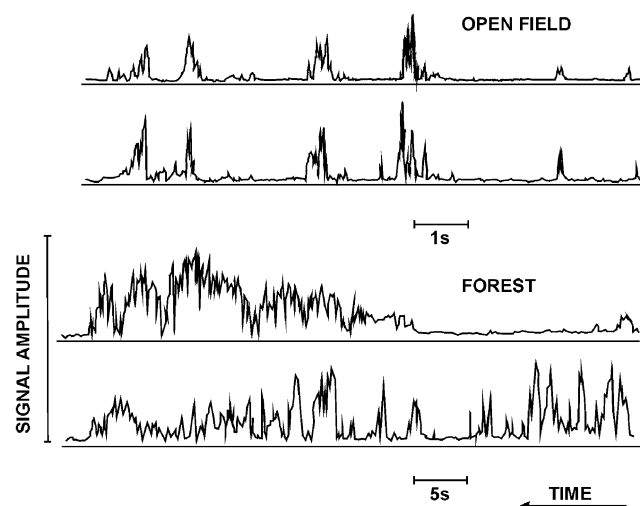


Fig. 1 Ion signals measured in daytime with a Langmuir probe in an open field and in a forest 2.5 m downwind of an ion source. The ions served as a surrogate for odor. Note the difference in the time scales for measurements in the two habitats. In the open field, there are many gaps of several seconds duration when no ions were detected, showing that the signal sampled at a fixed point in space is highly intermittent. When the signal is present (in “bursts”), it varies enormously in concentration. See Murlis et al. (2000) for details.

meander and undulation. As the plume is carried downwind, the conditional mean concentration of odor bursts within the plume and the conditional peak-to-mean ratio of odor intensity both decrease, while signal intermittency increases (Murlis et al. 2000). However, given the patchy distribution and highly variable concentration of odor filaments within the plume, the use of changes in odor concentration as a guide to the direction toward the source is not reliable unless the odor source is decimeters or so away (Murlis et al. 1992).

The effect of wind speed on small and large scale turbulence is complex. As wind velocity increases, generally the directional flow of the plume is more consistent (i.e., the plume is straighter) and thus the plume's outer envelope encompasses a reduced volume and increased concentration (Griffiths et al. 1995). Episodes of increased wind speed and consistency of directional flow seem to account for time periods when gypsy moths navigate successfully over tens of meters along pheromone plumes in a deciduous forest (Elkinton et al. 1987).

The initial size of odor sources that are important to insects varies enormously. Even moderately sized insects such as arctiid moths (e.g., 1–3 cm in length) can generate an initially small plume of pheromone, on the order of several square millimeters in cross-section, emanating from two small pores at the tip of their abdomen. Pheromone-emitting ("calling") arctiid females elevate their wings in a "V" posture, enabling air to flow freely around their body and, thereby, preserving plume size as the odor is carried away from the female (Conner and Best 1988). However, insects may more typically emit odor while perched within foliage or on tree trunks, thereby generating much larger plumes. For example, a gypsy moth (*L. dispar*) female typically calls while perched on a tree trunk. Eddies swirling in the trunk's downwind wake immediately expand her pheromone plume to approximately the tree's diameter (Charlton and Cardé 1990; see also Brady et al. 1989; Willis et al. 1991; Wyatt et al. 1993).

Whether odor emitting individuals choose calling sites specifically to enhance signal propagation is currently not well understood. In the case of the pink bollworm moth, *Pectinophora gossypiella*, Kaae and Shorey (1973) found that females select calling sites near the top of the cotton canopy when night winds are light and farther down in the canopy in windy conditions. Female-baited traps placed in both positions caught more males in the upper position on calm nights and more in the lower position on windy nights, suggesting that the male's orientation success is influenced by wind speed and position of the signal in the canopy. We do not, however, know how the interactions of position in the foliage and wind speed influence the plume's distribution or the male's ability to track it.

Odor plumes from the body of vertebrates generally would have an initial size roughly as large as the size of the

body from which the odor emanates. Sizes range for example from a small bird to a large ungulate or even a herd of ungulates. The odor cues within such plumes, however, may be unevenly distributed, particularly close to the source. A female mosquito blood feeds preferentially, dependent on mosquito species, on different regions of the torso, legs, arms, and head of a seated human (de Jong and Knols 1996). Such partitioning of feeding sites may be mediated in part by odor profiles that differ by body region and may dictate orientation maneuvers. Odor from human breath, particularly CO₂, which itself is highly attractive to host-seeking female mosquitoes, forms a plume that is pulsed with each exhalation; initially, this plume would not overlap with the body odor plume except near the head. A fluctuating intensity of CO₂, due mainly to turbulent diffusion, has been suggested to be the principal odor cue used at a distance by female yellow fever mosquitoes, *Aedes aegypti*, to initiate plume following (Dekker et al. 2005).

Many other odor sources also have an initially large plume size. Mass attack of hundreds of bark (scolytid) beetles boring into a tree releases pheromone and phloem volatiles that generate a plume that initially is as wide as the tree trunk and that has a vertical expanse matching the trunk area that is infested. Volatiles released by leaves often serve as orientation cues, and the odor plume's initial size typically would be as large as the plant. These examples indicate that initial plume size varies enormously with the kind of odor source. Plumes issuing from small sources have reasonably defined borders that are readily crossed and detected by a flying insect within meters to centimeters of the source; such plume boundaries may facilitate orientation by collimating its flight path. Indeed, recent studies of male cockroaches, *Periplaneta americana*, that track plumes of different widths while walking have identified specific turns back into the plume that appear to be triggered by these animals nearing or crossing the lateral boundary of a wind-borne plume (Willis and Avondet 2005). Large plumes may have ragged or ill-defined edges, which, because of the plume's large size, are not routinely traversed or detected during orientation. Far from the source (e.g., tens of meters), plumes may be so wide that the expanded individual filaments of the plume may be treated like "plumes" by animals with the size and movement scales of a flying insect.

Structural features of the habitat also influence a plume's fine-scale distribution and meander. Landscape-level features such as trees and shrubs, when they contact the plume, can stir and dilute it (mechanical turbulence) or cause it to meander around the obstacle. Plume structure also varies with the daily patterns of wind velocity and levels of turbulence. Wind velocities on average peak from late morning to mid afternoon and then generally decline until reaching a daily low near dawn. Levels of turbulence can

be related either to atmospheric stability, which is governed by incoming solar radiation during daytime and the extent of nighttime cloud cover or to vertical temperature gradients (Fares et al. 1983). Directional variability (plume meander) is correlated inversely with wind speed (Brady et al. 1989) and, generally, is less over open ground than in woodlands (Brady et al. 1989; Murlis et al. 2000). Fares et al. (1983) have suggested that observed variation in the daily times that *Dendroctonus* bark beetles are attracted to their pine hosts is correlated with favorable periods for semiochemical dispersal—namely when stable atmospheric conditions tend to “trap” the plume under the canopy. Conover (2007) provides a thorough consideration of how structural features of the habitat such as trees and atmospheric conditions influence plume structure.

Given that weather can differ enormously from day to day and the habitat that a particular species occupies also typically varies in structure, there may be no single, optimal navigational strategy. Rather, the orientation maneuvers must be sufficiently flexible to operate across a range of wind speeds and turbulence conditions (Belanger and Willis 1996).

Wind Direction

Generally, heading upwind while in contact with the odor is the principal mechanism that flying and walking insects employ during orientation along a plume. However, shifting wind direction causes the plume to meander and, surprisingly, the instantaneous wind direction within the plume is not always aligned with the plume’s long (downwind) axis. When the wind holds at a relatively steady speed but changes direction, upwind direction within such a meandering plume generally points toward the odor’s source (David et al. 1982), but heading upwind also may lead the insect out of the plume (Fig. 2b). Surrogate odors (puffs of smoke) released over an open field typically travel in a straight line for at least 25 m. When the wind speed and direction both fluctuate as would be typical in nature, however, the upwind direction may lead out of the plume and be a poor directional guide to the odor’s source. Such meandering can be accentuated by the presence of shrubs and trees around which plumes may flow (Elkinton et al. 1987; Brady et al. 1989). The consequences of variable directionality and wind velocity on plume following are that insects flying upwind along plumes would be expected routinely to exit the plume’s boundaries. As we explain later, insects are well adapted to deal with this challenge.

The last consideration is the possible vertical undulation of the plume. A plume traveling through a forest into a patch of sunlight will be warmed and consequently will rise in thermal chimneys (e.g., Fares et al. 1983). At nighttime in the Costa Rican rain forest, pheromone plumes from

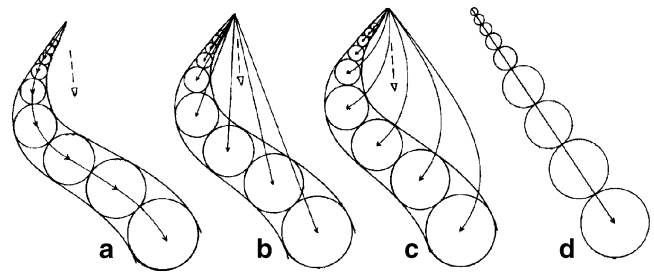


Fig. 2 Schematic of the possible effects of changing wind direction on the trajectory of meandering pheromone plumes as viewed from above. Pheromone is depicted as a series of puffs (circles), which expand with time. The trajectories of the puffs are shown by the lines leading from the source to the center of each puff with the arrow tips depicting the instantaneous wind direction within each puff. The dashed lines and arrow tips represent the mean direction of wind flow measured at the source over the time course of each plume’s meandering. **a** Trajectory assumed by workers before the David et al. (1982) publication. The plume’s centerline and the instantaneous wind direction at any point are assumed to be aligned. Therefore, heading upwind would lead to the odor source. **b** Conforms with the experiments of David et al. (1982) in an open field with a shifting wind direction but a relatively constant wind speed. Heading upwind in the downwind sector of the plume routinely leads the responder out of the plume. **c** Matches observations of Elkinton et al. (1987) beneath a forest canopy and Brady et al. (1989) in an open savannah; this effect is correlated with changes in wind direction and velocity measured at the source. **d** Shows a steady wind direction—during such “favorable” and typically brief alignments of wind direction and the plume’s centerline, insects can make rapid progress toward the source. Reprinted with permission of Wiley–Blackwell from Elkinton et al. (1987), p. 400.

cockroaches calling on tree trunks also flow upward because of a temperature gradient, and accordingly, males of a given species appear to position themselves on trunks higher than conspecific females (Schal 1982). In relatively still air, odor plumes that emanate from a warm source (e.g., odors from human skin) may have a significant vertical component because of convective flow until the plume cools to the ambient temperature. There is not a great deal of information on how much vertical distribution of plumes influences odor plumes at spatial scales relevant to insect orientation, but vertical undulations, when they do occur, must add to the navigational challenge.

Finding an Odor Plume

Although this review emphasizes how the distribution of odors influences the navigation of insects to an odor’s source, also of importance are the strategies employed to contact an odor plume. These have been termed “searching,” “ranging,” “questing,” “wandering,” and “appetitive” behaviors, but their key properties are a straightened-out locomotory path and a lowered threshold of responsiveness to resource-linked stimuli. The optimal strategies to locate a wind-borne odor plume often have been considered as a

separate theoretical issue (e.g., Sabelis and Schipper 1984; Dusenbery 1989, 1990). Generally, implicit in such models is an ability of the organism to estimate and average wind direction and its variability over some time interval, with the resultant optimal course for contacting a wind-borne plume being aimed on average crosswind, upwind, or downwind, depending on the model's assumptions. For example, if the wind is shifting direction more than 60°, it could be more advantageous to head either upwind or downwind than to head crosswind, because the crosswind expanse of the plume will exceed the distance of its downwind projection (Sabelis and Schipper 1984). There are, however, unstated assumptions implicit in this model. The distribution of odor across a plume that shifts more than 60° is patchy because of turbulence, and the probability of meeting odor may differ in traversing such a plume's via its downwind versus its crosswind axis (even if a plume is not continuous along its windline axis, the likelihood of contacting it while heading crosswind ought to be higher than approaching the plume from upwind or downwind directions). Other assumptions are that the searching organism must be able to "calculate" the mean wind direction (Zanen et al. 1994), must be able to determine over the relevant time interval that the wind is shifting by more than 60°, and, most importantly, be able to assign these wind vectors to an absolute cardinal heading, such as fluctuating $\approx 60^\circ$ around due north. This requires the organism to have a directional "map" of the immediate area and a memory of the wind's fluctuations.

Behavioral evidence to support any of these optimality models is scanty. Field observations of gypsy moths (*L. dispar*) have documented that female-seeking males flying within a meter or so of ground level take random courses with respect to the instantaneous wind direction (Elkinton and Cardé 1983). Although many gypsy moth females call from heights within 2 m of ground level, some call throughout the height of the tree canopy. Males observed in dense populations also search for calling females by flying vertically along tree trunks, apparently without reference to wind direction (Cardé and Hagaman 1984). Field observations of initial flight direction upon take-off of female onion flies, *Delia antiqua*, in absence of host plant odor appear random with respect to wind direction (Judd and Borden 1988, 1989). Wind-tunnel observations of the malaria mosquito, *Anopheles gambiae* s.s., in an unscented air flow of steady direction determined that many females in the host-seeking stage generally flew upwind (Takken et al. 1997; Costantini et al. 2001). In field observations of orientation to human "baits" with netting barriers deployed in differing directions of wind flow, mosquitoes were documented to fly downwind before host encounter, in accord with a model of optimal energy expenditure to find a plume (Gillies and Wilkes 1974). However, in subsequent field work Gillies and Wilkes (1978) discounted their

previous interpretation of a downwind host-seeking strategy, because they determined that screened fences had a negligible effect on mosquito movement. However, field observations of tsetse flies in absence of host odor or visual cues indicated that such "ranging" flights have a downwind bias (Gibson et al. 1991). Manipulations of hungry *Drosophila* fruit flies in a small wind tunnel in steady and shifting wind directions, however, suggest that they can shuttle between two strategies (Zanen et al. 1994). In a steady wind direction, they flew generally crosswind, in agreement with the predictions for an optimal path to encounter a plume, whereas in shifting winds they flew upwind in conformity with Dusenbery's (1990) analysis.

Provided the organism could use only currently or very recently sensed wind direction as a guide, a crosswind searching strategy would be optimal if the search organisms detected little variability in wind direction. Conversely, if the organism experienced continual changes in wind direction, then heading upwind or downwind by using the then-sensed wind direction would be optimal. These simple rules would not necessitate knowing the amount of wind variability (is it $>60^\circ$?) nor its cardinal direction, but the general effects on searching success should be similar to using the implicit assumptions of the Sabelis and Schippers model. This suggests that strategies for finding the plume by assuming a particular heading with respect to *current* wind flow would be most effective: upwind or downwind when the wind direction varies, and crosswind when the wind direction holds steady. Additional issues that add to the complexity to calculating an optimal strategy are the relative speed of the wind versus the speed of the flying insect (see Dusenbery 1990).

An interesting "special case" has recently been discovered (Wolf and Wehner 2006). The desert ant *Cataglyphis* sp. uses visual cues from polarized light and inertial cues from the movement of its own body to steer a return course to its nest or good foraging sites (Wehner 1996). However, when returning to distant feeding sites, they apparently approach from downwind and intentionally steer off the wind line to intercept the plume of odor issuing from the food, and thus assure location of its source (Wolf and Wehner 2006). In this case, memory of the location of a good food source is combined with wind information to allow the ant to steer its walking course into a quadrant of the environment where it should encounter a reliable cue to locate important resources.

Finding a "Lost" Odor Plume

An insect flying upwind along the odor plume can lose contact with the plume in three ways: (1) Gaps within the plume caused by turbulence may be of sufficient size to

cause a cessation in upwind displacement; (2) insects may exit the plume's boundaries because the direction upwind may not always lead along the plume's path (Fig. 2b,c); and (3) the moth's own plume-tracking maneuvers may carry it outside the time-averaged plume boundaries. A strategy used by moths to re-contact a lost plume is called "casting," in which upwind displacement ceases and the moth flies to and fro in increasingly wider lateral zigzags across the windline (e.g., David et al. 1983; Kennedy 1983; Kuenen and Cardé 1994). The vertical component of flight also expands upon loss of the pheromone plume (von Keyserlingk 1984; Vickers and Baker 1996). Casting moths have been observed to hold station near the point of plume loss or drift downwind as the width of their tracks increases (Baker and Haynes 1987). This flight pattern may allow the moth to regain contact with the plume by reentering it or, if casting persists for a sufficient time, be in a location where the plume's meander itself causes re-contact. Casting moths continue to orient their flight with respect to the wind direction (David et al. 1983; Baker and Haynes 1987), and in some cases, this may enable them to re-contact the plume closer to the source than where it was lost (David et al. 1983). Another strategy for re-contacting the plume is to loop downwind, as observed in a parasitoid wasp (Kaiser et al. 1994) and the oriental fruit moth (Baker and Haynes 1996). A third option is simply station keeping until the plume swings back to the insect's location. Once the plume is re-contacted, upwind flight can resume. If contact is not re-established within a set time (a "giving-up time"), the insect should return to plume searching (Kuenen and Cardé 1994).

Odor-Induced Orientation to Wind

Important recent reviews of the mechanisms of insect flight to odor sources include those of Gibson and Torr (1999), Vickers (2000, 2006), and Hardie et al. (2001). Kennedy (1983) provided a comprehensive review and analysis of the early literature. Reviews of plume following in water are also of interest, as the issues of turbulent diffusion of an odor in water, information processing, and orientation are parallel to those when the plume is airborne (Atema 1996; Weissburg 2000).

Optomotor Anemotaxis The principal navigational mechanism used by a flying insect in location of an odor source is to head upwind while in contact with the odor. Detection of the direction upwind once an insect is airborne is accomplished by the optomotor response. An insect flying along the windline perceives an image flow viewed below as moving front to rear. When the insect's heading is not due upwind, the image flow has a transverse component because of wind-induced drift. This navigation system was first verified by

Kennedy (1939) by using female *Aedes aegypti* mosquitoes stimulated to fly upwind by human breath introduced into a wind tunnel. Mosquitoes reacted to their apparent visual displacement which was provided by a pattern projected onto the tunnel's floor. Mosquitoes headed in the visually perceived upwind direction when the floor pattern was moved to simulate the effect of downwind displacement. This steering system is termed "optomotor anemotaxis."

Male Moth Orientation to Pheromone Much of what has been learned about odor-induced in-flight orientation has come from studies of male moth navigation along plumes of female-emitted pheromone. Most of these studies have used wind tunnels that permit a moderate degree of manipulation of the pheromone plume's structure, wind speed, and visual environment. The moth's maneuvers generally have been recorded in planar view, and so, the analyses of flight tracks have been two dimensional. A few studies have recorded flight tracks of moths flying freely in the field, often using a visual marker such as soap bubbles to indicate the path the odor plume has taken (Murlis et al. 1982; David et al. 1983; Willis et al. 1994; Vickers and Baker 1997).

Upwind flight of moths along a pheromone plume has typically been described as having a zigzag form, with regular left and right reversals across the windline. These turns in the gypsy moth are remarkably metronomic, occurring ≈ 3.5 to 4 reversals s^{-1} in a variety of conditions of plume concentration, plume structure, ambient temperature, and light level (Charlton et al. 1993; Cardé and Knols 2000), all of which change other flight parameters such as flight speed. A robustness of turning frequency during plume tracking is characteristic of all moth species in which it has been measured (Willis and Arbas 1991—*Manduca sexta*; Vickers and Baker 1992—*Heliothis virescens*; Willis and Baker 1987—*Grapholita molesta*). Often the only way to experimentally alter the turning frequency is to remove the odor plume altogether (Willis and Arbas 1991). Kennedy (1983) viewed zigzag turns in plume following and in casting as modulated by the same motor program and termed them "counterturns." The possibility that counterturns are caused by exiting the plume's boundary and then turning back toward where it was last sensed was once widely assumed (e.g., Farkas and Shorey 1972, 1974; Kennedy and Marsh 1974; Marsh et al. 1978; Cardé and Hagaman 1979) and had been described as "feeling for the edges." However, as turns can be executed well inside a plume (Kuenen and Baker 1982) or successively in clean air (i.e., casting flight; Kennedy and Marsh 1974), loss of odor contact is not the initiating stimulus for counterturning.

The establishment of the direct effects of a plume's internal structure and boundary position on orientation maneuvers has been at times contentious. Wright (1958)

proposed that flight along the plume was governed by encountering successive filaments of odor within the turbulent plume, with the pattern of contact shaping the form of the flight track. His analysis, however, assumed that the directional cues used in orientation were entirely chemical, in the plume's internal fenestration and outer boundaries, a view he later abandoned (Daykin et al. 1965). Simply detecting wind flow and then heading upwind while in contact with the odor was not considered a relevant navigational mechanism.

Farkas and Shorey (1972) proposed that moths sensed the overall shape of the pheromone plume while flying a zigzag path that carried them in and out of the plume's boundaries. The fact that they referred to this behavior as "aerial trail following" suggests that they imagined that plume-tracking male moths used chemo-orientation mechanisms similar to those used by walking ants to follow pheromone trails deposited on the ground (Hangartner 1967). Successive comparisons of the plume's position would enable flight along the plume's long axis toward the pheromone's source. In wind-tunnel experiments with the pink bollworm, *P. gossypiella*, a plume was first drawn out in wind, a male was then released into the plume, and the wind was immediately stopped (Farkas and Shorey 1972). The males' tracks were monitored after wind stop, during which time directional orientation could not be attributed to wind cues. According to Farkas and Shorey (1972), the only possible explanation for the successful plume tracking observed was longitudinal klinotactic chemo-orientation, that is, orientation directed by comparing concentration changes along the plume's length. Farkas and Shorey (1972) attempted to demonstrate an optomotor reaction that could support optomotor anemotaxis by moving a treadmill floor pattern beneath the tunnel, but no consistent response was observed. Therefore, they concluded that pink bollworm moth males did not use optomotor anemotaxis to direct their flight orientation in their wind tunnel, rather that moths steered by orienting directly to the odor concentrations in the plume.

This mechanism was challenged by Kennedy and Marsh (1974) who showed in their wind-tunnel trials that Indian meal moth, *Plodia interpunctella*, males steered their flight toward the source by reacting to changes in feedback from their visual flow field as predicted by optomotor anemotaxis. However, the principal observation of Farkas and Shorey (1972) that moths that have initiated flight along a plume in wind indeed can continue successful orientation along the plume in still air has been substantiated in two additional moths, *G. molesta* (Baker and Kuenen 1982; Kuenen and Baker 1982) and *L. dispar* (Willis and Cardé 1990). Given the variability of wind in nature, the ability to follow plumes in still air or wind velocities too low to resolve wind-induced drift by using optomotor feedback (Cardé and Knols 2000)

should be a great advantage in mate finding. It has been demonstrated (Kennedy and Marsh 1974; Baker et al. 1984; Cardé 1984), and is now widely accepted, that plume-tracking moths use optomotor anemotaxis to direct their flight upwind toward the source. However, the mechanisms used to track plumes during lulls in wind are not well understood and are still open to study.

The first experiments to manipulate plume structure systematically sought to determine if signal intermittency was important to orientation. Kennedy et al. (1981) found with the summerfruit tortrix moth, *Adoxophyes orana*, that initial contact with pheromone initiated regular zigzag turning, but immediately, subsequent emersion in a homogeneous miasma of pheromone inhibited upwind flight; the males initiated casting flight as if they had lost contact with odor. Conversely, flight in a cloud of pheromone with a fluctuating intensity promoted upwind flight similar to that observed during plume tracking (Baker et al. 1985). Cessation of upwind movement in a homogeneous pheromone environment has been observed now in two other moth species, the oriental fruit moth, *G. molesta* (Willis and Baker 1984), and the pink bollworm, *P. gossypiella* (Justus and Cardé 2002). The almond moth, *C. cautella*, however, is capable of flying upwind in a homogeneous cloud of pheromone, at least over short distances, although the heading was aimed at an angle averaging $\approx 15^\circ$ off of due upwind (Justus and Cardé 2002).

A precise role for contact with pheromone filaments in setting an upwind course was proposed by Baker (1990). According to this idea, two parallel control systems are activated upon contact with pheromone. The first generates the regular counterturning thought to underlie the zigzagging flight tracks we observe (either upwind or casting). The second suppresses this turning and steers the moth more directly upwind, resulting in an upwind surge toward the source. Subsequent experiments with *Heliothis virescens* showed that puffs of pheromone generated at the source at a rate of 4 Hz induced sustained upwind flight and source location and in some individuals, almost completely suppressed casting maneuvers, resulting in prolonged bouts of upwind flight with few detectable turns (Vickers and Baker 1992).

Working with the almond moth in a laminar flow wind tunnel, Mafra-Neto and Cardé (1994, 1995) monitored upwind surges after either interception of a filament of pheromone in a ribbon plume or a single puff of pheromone. A single encounter with a filament or puff induced an upwind surge within ≈ 200 ms, followed by initiation of crosswind casting. The duration of pheromone contact positively influenced the distance (and duration) of the surge, and, provided that contacts with filaments occurred at a sufficiently high rate, the surges could be linked into an essentially due-upwind heading. The rate of filament

generation at the pheromone source, ensuring a relatively due upwind course, appeared to be 10 Hz and above (Mafra-Neto and Cardé 1994, 1995; Justus et al. 2002b). Given the moth's airspeed, the in-flight rate of filament encounter would be higher than the rate of production at the source (Baker and Vickers 1994; Mafra-Neto and Cardé 1995).

Vickers and Baker (1994, 1996), working contemporaneously with *H. virescens*, reached the same conclusion: Contact with a sequence of pheromone filaments sets a relatively due-upwind course. The cast—filament contact—upwind surge model seems to explain both the zigzag flight track commonly noted in moth orientation to pheromone (and likely female orientation to host plant and flower volatiles, see Mechaber et al. 2002) and occasional segments of straight upwind flight. Recent studies of freely flying *D. melanogaster* fruit flies show that they behave in a manner similar to the almond moth (Budick and Dickinson 2006). When presented with a ribbon plume of banana odor, *D. melanogaster* individuals generate flight trajectories that are essentially indistinguishable from those of male moths tracking pheromone plumes (Fig. 5 in Budick and Dickinson 2006). Like freely flying moths, *D. melanogaster* responses vary, from tracks almost straight upwind, to moth-like zigzagging. However, unlike most moths studied so far, *D. melanogaster* flies straight upwind when presented with a homogeneous fog of attractive odor. This behavior is consistent with that observed from the almond moth (Justus and Cardé 2002) and with previous anecdotal reports of *D. melanogaster* flight behavior (Kellogg et al. 1962). The common house fly, *Musca domestica*, also generates moth-like flight trajectories when tracking plumes of attractive odors (Cossé and Baker 1996). No experimental manipulation of odor stimuli has been performed with this species, and we can only speculate that the mechanisms underlying its behavior are similar to those that govern the orientation of male moths to pheromone.

Mosquito orientation to host odors Many cues are implicated in the attraction of female mosquitoes to a vertebrate host for a blood meal, including expired CO₂, other body odors, heat, humidity, and visual features (reviewed by Clements 1999). Long-distance orientation (tens of meters downwind of the host and beyond visual range) could be governed by expired CO₂, body odors, or a combination of both. CO₂ is unusual among odors in that it is present as a constant “background” odor ($\approx 0.04\%$ ambient concentration), whereas it is expired by vertebrates at $\approx 4\%$. In the case of CO₂ released from a point source at the same rate as breathe from an ox into a riparian woodland in Africa, bursts of CO₂ above ambient were detected by using a high-resolution analyzer up to 64 m downwind (Zöllner et al. 2004). The importance of CO₂ relative to other host

odors in mosquito attraction to a host is debated, and the value of this cue in inducing upwind flight may be in part contingent on the breadth of the host range of a given mosquito species (Gillies 1980; Takken and Knols 1999; Dekker et al. 2001), with generalist species being more likely to rely on CO₂ alone as a reliable indicator of a possible upwind host and with other body odors (along with humidity, heat, and visual cues) mediating orientation at close range.

Grant and O'Connell (1996) found that receptors on the maxillary palps of female mosquitoes are exquisitely sensitive to changes in concentration of CO₂, with fluctuations of as little as 40 ppm reflected by changes in receptor firing rates. Thus, well downwind of the host, the plume of CO₂ should be detectable by mosquitoes as a fluctuating concentration above ambient. Geier et al. (1998) demonstrated in a small wind tunnel that *A. aegypti* females readily flew upwind in turbulent and filamentous plumes of CO₂, but a homogeneous plume of CO₂ was far less likely to evoke upwind orientation. Conversely, plumes of human skin odor had the opposite effect, with homogeneous plumes being more apt to elicit upwind flights than turbulent and filamentous plumes. Dekker et al. (2001) found with the malaria mosquito, *A. gambiae* s.s., that a turbulent flow of CO₂ improved orientation (measured in a large assay chamber with a choice between two entrance ports) when CO₂ was mixed with skin odor. A homogeneous flow of CO₂ mixed with skin odor, however, depressed the catch over skin odor alone. Although CO₂ alone presented as either a turbulent or homogeneous flow evoked less trap-entering behavior than clean air, CO₂ in either a turbulent or homogeneous flow improved orientation when flight nearby the port entrance was assayed via contact with an electric net. These comparisons establish that a turbulent flow of CO₂ is important to upwind orientation of malaria and yellow fever mosquitoes and suggest that the cast—filament encounter—upwind surge model that dictates moth flight to pheromone is applicable to mosquito response to CO₂ plumes.

Dekker et al. (2001) also assessed the responses of *A. aegypti* to the same combinations of CO₂ plumes and skin odor. In both species, homogeneous CO₂ plumes reduced trap entry compared to a clean air control, whereas homogeneous skin odor plumes increased trap entry over clean air. These studies suggest that processing of CO₂ and complex odor mixtures such as skin odor may have differing time requirements, with the latter requiring longer, continuous exposure.

Further wind tunnel studies with *A. aegypti* have shown that a single, transient encounter with a filament of CO₂ instantly lowers the threshold concentration evoking upwind flight to human skin odor (Dekker et al. 2005). This suggests that CO₂ alone in *A. aegypti* could be the long-

distance orientation cue, with body odors being utilized when the mosquito is close to a potential host. In highly anthropophilic species such as the yellow fever and malaria mosquitoes, females may enter or rest outside human dwellings before feeding. There they would be exposed to residual human odors. The encounter of a fluctuating concentration of CO₂, however, signifies the nearby presence of a potential host whose chemical signature can be verified by sensing the constituents of body odor.

Studies with two highly anthropophilic species point to a fluctuating concentration of CO₂ that induces upwind orientation (Geier et al. 1998; Dekker et al. 2001), with human body odor being most effective when its concentration remains relatively constant, as would be the case close to the host. In the yellow fever mosquito, a transient encounter with a filament of CO₂ induces a salience for skin odor, such that the concentration of skin odor needed to induce orientation is reduced (Dekker et al. 2005). Clearly, we need to know how the structure of odor plumes generally modulates host finding in additional species, especially non-anthropophilic species, with broad host ranges.

Aim-Then-Shoot Orientation of Diptera A second mechanism for orientation relies on mechanoreceptor sensing of wind direction before initiating flight and then heading that direction while in contact with the plume. This navigation system is termed “aim-then-shoot” (Kennedy 1986). Flight is presumably visually guided, as in optomotor anemotaxis, by maintaining a generally front-to-rear image flow of the ground pattern as long as contact with the odor plume is maintained. If the wind direction changes while the organism is in flight, then transverse image flow is generated, which if sensed would indicate an off windline heading. In-flight adjustments to course based on the detection of wind-induced drift are not assumed for the aim and shoot navigation. Orientation to hosts over a distance of many meters presumably consists of a series of short flights interspersed by landings when contact with host odor is lost, “as a series of steps” (Bursell 1987).

Evidence in support for an aim-then-shoot mechanism is, to date, limited to a few Diptera. Some tsetse flies (*Glossina*) upon detection of host odor take off heading directly upwind, quickly achieving an airspeed of $\approx 5 \text{ m s}^{-1}$, considered too fast to permit the flies to detect crosswind drift and, therefore, to use in-flight optomotor anemotaxis (Griffiths et al. 1995). By using released tsetse flies and monitoring their arrival at an upwind source of host odor, Griffiths et al. (1995) found that the “fast cohort” of released flies (about half of the flies) arrived at odor sources 30, 50, and 75 m upwind in less than 40 s! The rest of the flies took from 1 to >20 min, presumably by orienting in a series of short flights and landings. Wind-tunnel trials,

however, also support the ability of tsetse flies to use conventional optomotor anemotaxis (e.g., Colvin et al. 1989), and so, it is possible that tsetse flies toggle between these two navigational mechanisms. The meteorological observations of Brady et al. (1989) in the tsetse’s natural woodland habitat demonstrated that the direction of arrival of wind-borne host-odor would be a reliable guide to the actual direction toward a host 15 m away only about a third of the time; 20% of the time it would direct the fly at least 90° away from the host. How the tsetse fly uses information on wind direction, given its tenuous correlation with direction to the host, remains unclear. Finally, as the tsetse fly closely approaches a prospective host, visual cues presented by the host may become important for orientation. The final stage of orientation may be guided visually and, in fact, may be made from the upwind direction (Gibson and Torr 1999).

Cabbage root flies (Hawkes and Coaker 1979) and onion flies (Dindonis and Miller 1980) also seem to orient toward upwind host plant odors by the aim-then-shoot mechanism, but the use of this orientation strategy by other insect groups remains to be documented. As pointed out by Griffiths et al. (1995), the aim-then-shoot mechanism as used by tsetse seems relatively crude in comparison to the precision track of a male moth locating a female. However, it may serve in locating a large and mobile host by enabling sampling of a large area where the host is many meters away. When the host is in the range of tens of meters, it may be effective in rapid host finding. However, to date, the validity of the aim-then-shoot mechanism by tsetse remains largely an argument by exclusion—tsetse flight speed is too fast to permit in-flight processing of wind drift and, therefore, use optomotor navigation—rather than a mechanism supported by definitive experiments.

Future Work

One of the major impediments to understanding the precise relationship between in-flight orientation maneuvers and the pattern of encountering either odor filaments or more evenly dispersed odor patches is that we cannot readily establish how individual maneuvers correspond to the pattern of encountering patches of odor. We can measure the general, spatial features of odor plumes in wind tunnels (e.g., Justus et al. 2002a, with propylene as an odor) and in the field (Murlis and Jones 1981; Murlis et al. 2000, with negatively charged ions as a surrogate for odor), but it is difficult to establish how the patterns of odor contact in plumes with complex spatial structures modulate orientation, because we can only correlate the average patterns of odor distribution with behavioral output at the most general level of analysis, namely the overall flight track. In wind-

tunnel trials of moth flight along a pheromone plume, moths typically slow their rate of upwind progress and have a more narrow flight track as they approach the source (e.g., Justus et al. 2002b; Willis and Baker 1984; Willis and Arbas 1991). Which of the many features of plume structure (e.g., intermittency, peak concentration, peak-to-mean concentration, etc.) that change with distance to the source (Murlis et al. 1990; Justus et al. 2002a) and dictate these changes in flight track is unknown. By manipulating the rate of odor encounter and concentration, Vickers and Baker (1992) demonstrated that both of these variables affect the structure of *H. virescens* responses. Further studies are needed to determine to what extent other parameters of the odor plume affect the structure of plume-tracking behavior.

To record what a flying insect perceives as odor input while maneuvering along the plume would seem intractable. Vickers and Baker (1994), however, mounted a third antenna on the thorax of an *H. virescens* male and simultaneously recorded, via fine wires, its electroantennogram (EAG) responses to pheromone filaments encountered while it flew along the plume in a wind tunnel. Not surprisingly, bursts of pheromone were most often contacted near the plume's centerline; bursts confirmed the expected intermittency of the signal. The amplitude of flying EAGs, however, was unexpectedly higher than those recorded for a stationary EAG rig mounted at the same positions in the plume or one artificially moved upwind. Recent results from tethered flying *M. sexta* show that air flow, from head to tail, induced by the flapping wings should increase the speed of encounters with odor filaments by the antennae (Sane and Jacobson 2006). This is a possible explanation for the unexpectedly larger EAGs observed previously (Vickers et al. 2001). Unfortunately, no obvious relationship between EAG and moth behavior (other than pheromone present during plume tracking) was observed in this study, and no follow-up study has appeared. One important caveat for studies such as this is that the antenna recorded from was not providing the information that the moth was using to control its flight.

One useful technique for matching odor contact and behavioral reactions is the use of a long, thin ribbon plume in a laminar flow in a wind tunnel and to record the immediate reaction of an insect after it contacts the odor filament (e.g., Mafra-Neto and Cardé 1994; Dekker et al. 2005; Budick and Dickinson 2006). The plume's precise position relative to the insect can be determined by adding a visual tracer to the plume or by three-dimensional video recording. Such stretched-out, narrow plumes do not occur naturally, but an argument can be made that a single encounter with the ribbon plume corresponds to contact with a single odor filament in a turbulent plume. Another approach is to use tethered insects "flying" in a virtual

world with movement simulated by flow of their visual surround (e.g., Gray et al. 2002). This system would enable presentation of precise patterns of odor impingement and measurement of resultant thrust and turning maneuvers. However, tethering may restrict maneuvering, and it has been interpreted to yield misleading conclusions about what inputs control counterturning (cf. Preiss and Kramer 1986; David and Kennedy 1987).

Simulation modeling with virtual insects in a virtual environment is another approach to understanding what kinds of sensory inputs from the plume can be extracted to navigate a course to its source. Models can specify the sensory inputs and navigational rules needed to create a zigzag track along a plume in a wind tunnel (Belanger and Arbas 1998), or the full spectrum of field behavior that include plume finding, plume following, maneuvers to re-contact a lost plume, and declaration that the source has been found (Li et al. 2001) in a simulated plume in a directionally fluctuating wind field (Farrell et al. 2002). These navigational strategies have been implemented and tested on an underwater robotic vehicle that has successfully searched for and located over a range of ≈ 1 km the source of a visual tracer that served as a surrogate for an odor (Li et al. 2006). Simulation models enable us to explore how varying sensory inputs and maneuvering rules modulate the effectiveness of the navigational strategy, but we should recognize that such simulations and robotic implementations can be successful without employing the same inputs and rules as the insects themselves utilize.

Field observations that meld meteorological measurements with flight track records offer insights into the distances over which odors are attractive and the kinds of flight tracks that occur under natural conditions. Such observations, so far, have been limited largely to day-active insects such as tsetse flies, gypsy moths, and oriental fruit moths that can be readily observed (however, see Vickers and Baker 1997), but they provide insights into the real-world capabilities of insects searching for distant odor sources that cannot be gleaned from wind tunnel studies.

Lastly, orientation to odor sources is a common reaction among many kinds of insects, but what we know of the mechanisms that govern this process is based on a handful of model systems. Such orientation is often simply termed "attraction," which as Kennedy (1978) pointed out, is a convenient but teleological term that fails to reveal the complexity of this process and the diversity of underlying mechanisms.

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