Navigation Along Windborne Plumes of Pheromone and Resource-Linked Odors

Ring T. Cardé

Department of Entomology, University of California, Riverside, California 92521, USA;
email: ring.carde@ucr.edu

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Abstract

Many insects locate resources such as a mate, a host, or food by flying upwind along the odor plumes that these resources emit to their source. A windborne plume has a turbulent structure comprised of odor filaments interspersed with clean air. As it propagates downwind, the plume becomes more dispersed and dilute, but filaments with concentrations above the threshold required to elicit a behavioral response from receiving organisms can persist for long distances. Flying insects orient along plumes by steering upwind, triggered by the optomotor reaction. Sequential measurements of differences in odor concentration are unreliable indicators of distance to or direction of the odor source. Plume intermittency and the plume's fine-scale structure can play a role in setting an insect's upwind course. The prowess of insects in navigating to odor sources has spawned bioinspired virtual models and even odor-seeking robots, although some of these approaches use mechanisms that are unnecessarily complex and probably exceed an insect's processing capabilities.

INTRODUCTION

Male moth flight to a pheromone-emitting (calling) female is generally viewed as a paragon of sensitivity to chemical signals and prowess in navigational skills. For example, male silkworm moths, *Bombyx mori*, are calculated to have a response threshold (in this case, for walking upwind; this long-domesticated species is no longer capable of flight) of 3,000 molecules per second in an airflow of 57 cm/sec (58). Other moths are capable of orienting to a female hundreds of meters and perhaps kilometers distant (for reviews, see 19, 112). There should be strong selective pressure for rapid and efficient location of pheromone sources in mate finding, but just how far downwind a male moth can detect a female and successfully navigate a course to her remains debatable because most field trials involve released males, rates of capture are low, and there is uncertainty about how much of the paths are under pheromone guidance. Definitive experiments using activation of caged, quiescent moths as a criterion suggest detection limits of approximately 30 m with the oriental fruit moth, *Grapholita molesta* (75), and 120 m with the gypsy moth, *Lymantria dispar* (39).

More broadly, locating odor-linked resources by steering upwind along odor plumes to their source is common among many insect lineages. Besides mate location, such resources can involve hosts, food, or suitable habitats. The size of such odor sources and the rate of odor emission vary enormously. Some odor sources are quite small, as with pheromone issuing from a calling female moth, or kairomonal attractants from a host insect for a parasitoid. Others are sizable, such as an ungulate for a tsetse fly, a host tree for bark beetles, or a large patch of a host plant. Odors also can be nested in the sense that a discrete plume, for example, from a calling moth, may be embedded within a more diffuse background plume from a host plant (113). The common strategy for plume location by a flying insect is simply to steer upwind when the appropriate odor is sensed. The general topic of insect orientation to odors has been reviewed previously (25, 57, 101, 102).

This review considers the nature of plume structures as they move downwind, search strategies to find a plume, mechanisms for steering upwind along the plume, and specialized maneuvers that rely on sensing odor distribution. The process of plume following has been studied most extensively in moths (19) and various Diptera, but mainly tsetse flies (*Glossina* spp.) (49), *Drosophila* (46), and mosquitoes (22). Manipulation of sensory inputs in wind tunnels during free flight has been a useful method to establish linkages between these inputs and the resultant maneuvers (32, 78, 105), but field observations (7, 29, 116, 117) and tethering (34, 45, 67, 87, 99) have also added to our understanding. Description of the maneuvers and the inputs assumed to govern them have generated a lexicon of many terms (see the sidebar titled Lexicon of Terms and Mechanisms Used in Descriptions of Orientation to Odors), most of which fall under the umbrella of taxes and kineses (both of which use body orientation with respect to a stimulus in classification), a method championed by Fraenkel & Gunn (44) more than 80 years ago. As noted in the lexicon, a taxis can be combined with a stimulus to describe orientation to a chemical gradient (chemotaxis or, more precisely, chemoklinotaxis) or to wind (anemotaxis), or to compare bilateral input (tropotaxis). Such terms can be based on the spatial distribution of a stimulus, the nature of a stimulus, or the spatial distribution of the detectors, rather than being based on a common system of, for example, stimulus combined with body orientation. A further limitation of such categorizations is that they suggest that organisms do not combine orientation mechanisms or combine odor with other stimulus modalities such as vision, sound, and touch; therefore, these terms can fail to consider all possible explanations. Bell's (13) comprehensive review of searching or ranging behavior entirely eschews taxes, kineses, and their derivatives. Nonetheless, these terms are widely used (64), and this terminology is followed in this review.

A related issue is the widespread use of attraction to describe the maneuvers that constitute plume tracking. The odors inducing such navigation are commonly termed attractants, but, as

LEXICON OF TERMS AND MECHANISMS USED IN DESCRIPTIONS OF ORIENTATION TO ODORS

Active space: space in which the odor concentration is above the threshold required to trigger a behavioral response

Aggregation: an accumulation of individuals, possibly mediated by arrestment after attraction

Aim-then-shoot: the process of sensing wind direction while on a substrate, followed by setting a flight course by using a front-to-rear image flow

Allothetic: using information external to the organism (see idiothetic)

Anemotaxis: upwind (or downwind) orientation

Arrestment: cessation of movement

Attraction: orientation toward a stimulus

Chemotaxis: orientation along a plume by sensing the distribution or concentration of an odor

Chemotropism: orientation to the odor via chemotaxis

Idiothetic: spatial information (e.g., proprioceptive, optic, olfactory, sound) stored internally and used to set a course (see allothetic)

Infotaxis: orientation that uses all available information to dictate the most effective plume tracking strategy; it can require information on the position and concentration of previous odor encounters, and it is explicitly not biomimetic

Kinesis (plural kineses): indirect orientation, that is, movement that does not have the body axis aligned toward the stimulus

Klinokinesis: indirect orientation (turning rate) based on differences in stimulus concentration

Klinotaxis: directed orientation based on differences in stimulus concentration

Lévy flights: a form of random walk wherein long legs are less frequent than short ones (a power-law distribution)

Mechano-anemotaxis (positive): orienting to wind flow using mechanosensors such as setae or antennae (this cannot occur while an organism is airborne; it must have contact with a substrate)

Menotaxis: a compass reaction, with the body aligned at a fixed angle to the stimulus

Optomotor anemotaxis (positive): upwind movement in which the wind's direction is gauged by optomotor feedback (front-to-rear image flow indicates upwind or downwind displacement)
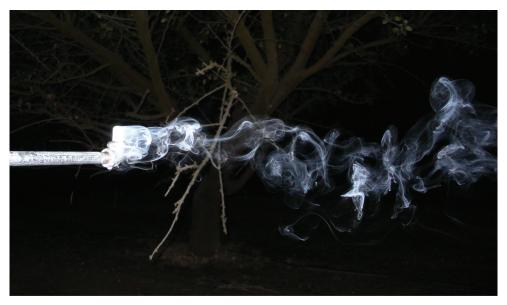
Orthokinesis: rate of movement (including stopping) is modulated by stimulus intensity

Taxis (plural taxes): directed orientation, with the body axis aligned toward the stimulus

Tropotaxis: orientation toward a stimulus by balancing input from bilateral receptors such as the antennae (also termed osmotropotaxis); turning toward the most stimulated side

Kennedy (62) noted, these are teleological or end-point notions that do not specify which inputs are used or how they guide orientation. Kennedy pointed out that, when the odor is windborne, it is not the concentration gradient of the odor that guides orientation. Instead, when the insect detects that an odor is above the threshold required to elicit a response, it simply steers upwind.

Some of these principles can be applied to computer models of orientation in a virtual world and to robotic implementation of these models. Both approaches allow sensitivity testing (i.e., testing which parameters most influence performance), and they allow examination of how non-biomimetic inputs might allow prediction of the optimal path toward the odor source. The latter cues could include a recall of where odor was previously sensed and the then-concurrent wind direction. This useful approach is termed infotaxis, but it is explicitly non-biomimetic (100).
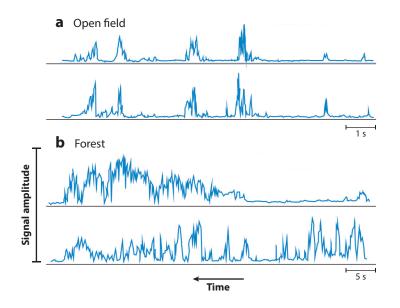
Figure 1

Visualization of an odor plume's fine-scale structure at night in an almond orchard using a 1-cm source of titanium tetrachloride, which combines with atmospheric water vapor to form a visible plume comprised of hydrochloric acid and titanium dioxide (50).

PLUME DISPERSAL IN WIND

Early efforts to describe odor plume dispersal relied on the Sutton equation (e.g., 14, 120), but this Gaussian model calculates a time-averaged concentration over a 3-min interval, depicting the active space as a smooth ellipsoid or semi-ellipsoid when the plume is at ground level. Field evaluations of the Sutton model (38) showed that it underestimates the downwind projection and position of active space for the *L. dispar* pheromone, for the obvious reason that response is governed by time intervals of a fraction of a second, not a 3-min average; during a 3-min interval, the wind direction can shift markedly (15, 39). As an odor plume from a small source is transported downwind, its structure is fragmented and stirred by turbulent diffusion into wisps interspersed with gaps (**Figure 1**), the overall concentration is diluted, and the gaps between wisps with concentrations of odor sufficient to elicit responses increase (85). However, odor filaments can persist relatively undiluted for many meters, and these filaments presumably set the limits for plume detection (83). Reviews of odor dispersion can be found in References 26, 83, 86, and 90.

Molecular diffusion contributes little to plume concentration or, when several compounds are involved, to the ratio between compounds. The rate of diffusion coefficient in air of hexadecanol, a compound similar to many moth pheromones, is 2.5×100^{-6} m^2/sec (76). Because the diffusivity is the inverse of the square root of the compound's molecular weight, even when components differ by two or even four carbons in chain length, as is the case with the 16-, 14-, and 12-carbon pheromone components of the turnip moth, *Agrotis segetum*, their diffusivities will be very similar; thus, the ratio of compounds in the plume as it is carried downwind will not vary sufficiently to alter response (86).

The fine-scale structure of a filamentous pheromone plume can be established using odor surrogates (**Figure 2**). Murlis & Jones (84) found that, within an odor plume, signal intensity fluctuated many times a second and was grouped in bursts interspersed with gaps. Later measurements

a Open field

1 s

b Forest

Signal amplitude

Time

5 s

Figure 2

Structure of plumes from a point source in an open field and a coniferous forest with a relatively open canopy near the height of measurement. The surrogate plume was generated by a point source of negative ions and measured at fixed downwind positions with a Langmuir probe in four separate runs. The signal varied in intensity and persisted for longer periods in the forest, mainly because the wind direction there was less variable. Figure adapted with permission from Reference 85.
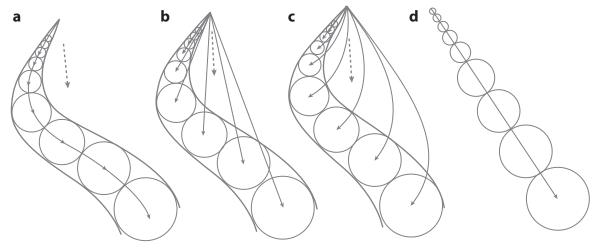
in an open field and in a forest (85) found that, with a fixed downwind sampling point in a forest habitat, the bursts of odor persisted for many seconds, whereas in an open field, bursts were present for far shorter intervals. In both habitats, an insect steering upwind along the plume would encounter frequent, lengthy gaps, complicating orientation.

Habitat and time of day strongly influence plume dispersal. Using an odor surrogate in a forest, Thistle et al. (98) found that plumes meander (move laterally) more widely from late morning to late afternoon, when the boundary layer is unstable. Conversely, during dusk and dawn, when atmospheric conditions were relatively stable, the plume had more directional consistency and higher odor concentrations. In daytime, plumes may rise in forest openings warmed by the sun (40); at night, they may be buoyed by the warmer temperatures at ground level (50, 94).

Changes in wind direction cause the plume to meander (**Figure 3**). What is remarkable is that, when the wind shifts direction (15, 30, 39), the plume's centerline does not, as one might surmise, align with wind direction (**Figure 3b**). Instead, the upwind direction points toward the odor's source (**Figure 3b**). This misalignment can be further exacerbated if the wind speeds up (**Figure 3c**). If the plume encounters foliage, then it either can be fragmented or can meander around relatively impermeable vegetation.

UPWIND ORIENTATION ALONG A PLUME

Steering a course along a windborne plume is not directed by sensing changes in the odor gradient, which is very shallow and, given the chaotic structure of a filamentous plume, would not provide reliable information about direction toward the source of the odor (14, 83, 120). Instead, simply steering upwind when a stimulating odor is sensed is the common strategy. Kennedy (61),
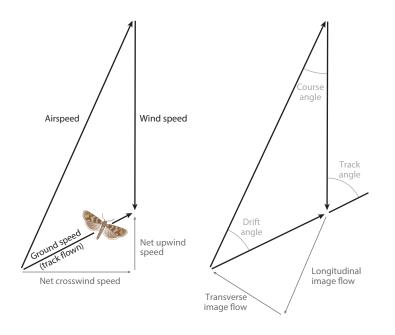
Figure 3

A diagrammatic view from above of how a plume disperses, showing upwind direction. (*a*) How we might imagine wind direction in a meandering plume. (*b*) The actual pattern when wind speed is constant. (*c*) The effect of changing wind speed. (*d*) When the wind does not change direction, a responder can readily fly upwind along the plume. Panel *d* adapted with permission from Reference 39.

working with females of the mosquito *Aedes aegypti* and using his breath (and thereby CO_2) to stimulate flight in a small wind tunnel, was the first to demonstrate how an airborne insect detects wind direction. A mosquito could be drawn downwind by moving the projected floor pattern in the downwind direction or stimulated to speed upwind if the pattern was moved with the direction of the wind flow. The mosquito reacted to its apparent position, appraised visually. This is termed optomotor anemotaxis. An airborne insect cannot gauge ambient wind direction by mechanoreceptors, although mechanosensory input from the antennae can be important in flight control, as shown in the tobacco hornworm moth *Manduca sexta* (93) and *Drosophila* (45).

In 1958, Wright (120), noting that odor plumes are filamentous, speculated that the frequency of encounters with filaments would increase as the source was approached and therefore could serve as an orientation cue. Wright questioned whether there would be sufficient visual feedback for the optomotor response in darkness or well above ground level. However, subsequent wind-tunnel work by Kellogg et al. (60) with *Drosophila* confirmed that visual contact with the ground below was essential to odor-induced upwind navigation.

This phenomenon was not pursued further until 1972, when Farkas & Shorey (41) questioned its validity in studies of moth flight along pheromone plumes. With male pink bollworm moths, *Pectinophora gossypiella*, manipulation of a wind tunnel's floor pattern failed to influence the moths' progress along a pheromone plume in wind. A second test stopped wind flow when moths flying along the plume reached the tunnel's midpoint; most males continued along the suspended plume. It was proposed that males oriented along an aerial trail of pheromone not by orienting upwind, but rather by a form of chemotaxis that used sampling of odor concentration differences along the plume.

This rejection of optomotor anemotaxis spurred Kennedy & Marsh (66) to test the Indian meal moth, *Plodia interpunctella*, and two other pyralid moths in a wind tunnel with a movable floor pattern. Males reacted anemotactically to movement of the floor's visual pattern. A further manipulation was undertaken to explore a possible tropotactic mechanism first suggested by Shorey (95): Could males detect the plume's edge by comparison of right versus left antennal inputs? However, removal of an antenna from *P. interpunctella* males did not impair their ability to orient

Figure 4

The triangle of velocities method is used to calculate, in the horizontal plane, how heading and wind speed influence trajectory, the insect's airspeed, and visual feedback from directly below. In this example, the moth is heading at an angle offset from due upwind, and therefore, it experiences longitudinal and transverse image flow from below. Heading due upwind, only longitudinal (front-to-rear) image flow would be experienced (see 82).

along a pheromone plume; similarly, crossing of the antennae also failed to diminish their plume-following ability (66; see also 103). Given the ragged nature of airborne plumes even a few meters away from their sources, tropotaxis would be an unreliable guide to the plume's boundaries (but see 34). Orientation close to a point source of odor by walking, however, can allow tropotactic orientation, as seen in *B. mori* (96).

With a typical moth flying along a pheromone plume in a wind-tunnel setting, most movement follows a zigzag path in the horizontal plane, centered along the plume's upwind axis (**Figure 4**). A relatively constant height above the floor pattern below keeps the size of the visual pattern (angles subtended) relatively constant. In other insects, such as female *Ae. aegypti*, flight along an odor plume can involve both vertical and horizontal displacement (32), probably as a consequence of the natural odor source, a human, being much larger than a calling moth. Clearly, a three-dimensional analysis is required when tracks have significant vertical displacement, as, for example, in *Drosophila* (99) and the moths *M. sexta* (91) and *Lobesia botrana* (119).

ORIENTATION MANEUVERS

Methods of Study

To establish how flight maneuvers are governed by the interacting variables of odor contact, air-flow, and feedback from the visual field, these inputs can be manipulated in a variety of experimental setups. Flight tracks can be video recorded in wind tunnels or nature in two or three dimensions. Field records of flight paths (7, 29, 116, 117) may be particularly instructive because a plume's overall size and turbulent structure are not readily duplicated in a wind tunnel.

Alternatively, insects can be tethered, and their intended orientation paths can be reconstructed. A visual surround can be offered as a static pattern or manipulated in a dynamic presentation. Tethered and freely flying insects, however, do not experience the same visual and mechanosensory stimuli (28), so caution must be used in interpretation of their optomotor reaction. Tethered apple maggot flies, *Rhagoletis pomonella*, have been interpreted to be able to steer toward a wind-borne odor source without optomotor feedback (59). However, these tethered flies would have experienced mechanosensory input from the odor delivery device and, potentially, additional directional cues from the image of a tree projected ahead; these cues could be used to set a heading upwind. Tethered *L. dispar* moths have been suggested (87) to be unable to gauge upwind direction without continual course reversals; therefore, zigzagging was interpreted by Priess & Kramer (87) as the result of being unable to accurately gauge the direction upwind. However, freely flying gypsy moths actively steer crosswind with course reversals when in contact with pheromone or following its withdrawal (28, 70). In the tethered setup used by Preiss & Kramer (87), moths could not roll or bank, as they would during a counterturn in free flight (28, 121), and therefore the visual feedback experienced would also differ from that experienced during free flight.

In wind tunnels, an odor can be presented as a homogeneous cloud (54) (an unnatural but useful experimental condition), or in simulations of natural turbulent plumes. Using a baffle just upwind of an odor source (24), for example, creates a turbulent structure downwind. Timed odor puffs from a stimulus generator can simulate encounters with odor filaments in a turbulent plume (78, 105). These two methods, however, do not permit correlation of moment-to-moment contacts with odor and the resulting maneuvers. Some insight into such reactions can be established by recording the reaction after contact with a single odor puff (78, 107) or after crossing of a thin ribbon plume issuing from a small point source of odor in a laminar flow (78). It is possible to measure the plume's fine-scale features using surrogate odors in the field (84, 85) and in a wind tunnel (55), but these measurements do not permit matching of reactions with moment-to-moment odor encounters. New approaches (for a review, see 90) to real-time measurement of odors may permit correlation of moment-to-moment maneuvers with a defined odor stimulus.

Interactions of Plume Structure and Flight Tracks

A common form of upwind flight by moths along a pheromone plume assumes a zigzag path, that is, counterturning across the plume several times per second with lateral and upwind displacement but comparatively little change in altitude. There are several possible explanations for this behavior (28, 63, 64, 87). Some hinge on turns being dictated by exiting the plume and turning back in the direction in which the plume was last sensed. The current most-common explanation for zigzagging in moths suggests that it is governed by a turn generator (6, 63, 68, 115) and is self-steered, rather than induced by detection of the plume's edge (see also the above discussion of the effect of tethering on gypsy moth counterturning) (95). In a wind-tunnel trial, males of the summer fruit tortrix moth, *Adoxophes orana*, when confronted with a corridor of homogeneous pheromone bordered by clean air, zigzagged upwind along its border, turning within the odor cloud and in clean air, verifying that loss of contact with pheromone was not required to trigger turns (65). [Zigzagging without upwind displacement also occurs upon loss of the pheromone plume if it is experimentally truncated (see the section titled Recontacting a Lost Plume).]

Plume Structure and Trapping

Many studies have observed that trap design affects the attraction and capture of Coleoptera (see, e.g., 2). Fewer studies have attempted to identify the underlying mechanisms responsible for these

effects, in particular, the effect of trap shape and design on plume structure. As shown with the pea moth, *Cydia nigricana* (71), plume shape affects both the number of moths attracted to a trap's vicinity and the probability of capturing these moths. Conversely, although there were significant differences in how the tracer gas CO_2 accumulated downwind of different trap designs, these differences did not explain differences in the capture rate of *Monochamus* beetles (1). Trap design can have significant effects on plume structure, but our understanding of what these effects mean for trap performance and how this may vary among taxa and habitats is incomplete.

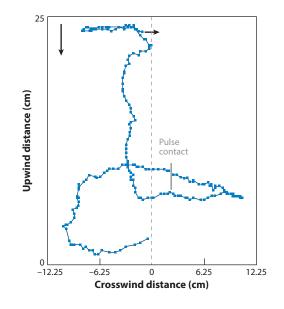## Visual Inputs and the Optomotor Response

In *L. dispar*, altitude appears to be held relatively constant by optomotor feedback (87), whereas ground speed along the track is linked to longitudinal image flow, and sideways movement is linked to transverse image flow. At a given pheromone concentration, ground speed along the track remained relatively constant at wind velocities of 0, 30, 100 and 150 cm/sec (115). Increases in concentration of pheromone (27), however, decreased velocity (an orthokinetic effect) and narrowed the track widths. Light levels also influenced tracks: At 4 lux, moths flew more slowly and had wider tracks than at 450 lux (24). [*L. dispar* is attracted to pheromone both in daytime (when mating typically occurs) and at night (21).] When the effects of wind velocity, pheromone concentration, and light levels were compared, turning rates remained close to 4 turns/sec. Overall, these experiments with *L. dispar* suggest that the counterturn oscillator, track angles, and ground speed are optimized to provide tracks with sufficient wind-induced drift to gauge wind direction and velocity (115). Similar trends were found with *G. molesta* for pheromone concentrations (68) and wind velocities (69). In moths, the image flow and pheromone information are integrated centrally; for a comprehensive review, the reader is referred to Baker & Hansson (5).

Surge-Cast Model of Upwind Orientation

The relevance of the intermittency of an odor plume (83) to upwind flight of male moths to pheromone became evident in wind-tunnel trials with *A. orana* (65) and *G. molesta* (114). Males of these two moths do not fly upwind in a homogeneous cloud of pheromone. Baker and colleagues (9), however, demonstrated that a cloud of pheromone pulsed at once or twice per second evoked upwind flight. These discoveries led to work with stimulus generators (104) to generate plumes comprised of a train of discrete odor puffs. It is now evident that encountering these filament equivalents at rates near 5/sec promotes upwind zigzagging, whereas higher rates of contact, near 10/sec, straighten out the path. Presentation of a single puff to a moth that has lost contact with a plume and is casting from side to side without much upwind displacement causes an upwind surge. The cast-surge-cast model (**Figure 5**), first proposed by Baker (4), was found to apply to the noctuid *Heliothis virescens* (104–109) and the pyralid *Cadra cautella* (56, 78–81). Plume intermittency also appears to modulate track form in *Ae. aegypti*'s response to CO_2 (32) and *Drosophila*'s response to food odor (17), suggesting that the cast-surge-cast model is widely applicable. A homogeneous odor cloud, however, does not universally inhibit upwind flight. For example, *Drosophila* fly upwind in food odor clouds (17), and male *C. cautella* fly upwind in a pheromone cloud (54). Tethered *Drosophila* also are reported to have differing abilities to resolve intermittent odor plumes at the receptor level, dependent on odor identity (67). Such perceptual fusion limits may influence steering and odor perception.

Orientation in Still Air

Farkas & Shorey (41) found that *P. gossypiella*, having set a course along a pheromone plume in moving air, could, if airflow was suddenly stopped, continue navigation along the suspended plume;

Figure 5

The cast-surge-cast reaction proposed by Baker (4), showing top view of the flight path of a *Cadra cautella* moth in a wind tunnel. Each square represents the position of the moth at 0.017-second intervals. The track begins at the bottom with casting that followed withdrawal of the pheromone plume. A single puff of pheromone was then introduced; following contact, the moth surged upwind after a delay of approximately 200 ms. Casting resumed because the moth did not encounter another puff. For details, see Reference 78.

this study was followed by Baker & Kuenen's (8) study with *G. molesta*. Males that had set a course in wind could use visual cues to continue toward the pheromone source while maintaining contact with the plume by longitudinal klinotaxis. *Grapholita molesta* males polarize their counterturns along a plume such that, when wind is stopped, they have a higher probability (46%) of source location than if they are placed in the plume midway in the tunnel in zero wind (21% source location, but over a longer time interval) (10). *Lymantria dispar* is another moth that, having set a course in wind, can continue navigation for a short distance along a pheromone plume if the airflow is stopped (28, 115).

Visual cues play a significant role in trajectory following the cessation of airflow. *Cadra cautella* males presented with a prominent visual pattern below and a 65-cm-wide plume tended to center their path over a 25-cm floor pattern, even if the pattern veered halfway to one side of the wind tunnel (118). This suggests that visual cues can play a collimating role in trajectory. Given the same setup with uninterrupted wind flow, moths also tended to fly over the floor pattern that veered to one side, further suggesting a collimating role for visual cues, even in wind. It is unclear how long a plume would remain coherent under windless conditions in nature, but an ability to track plumes when wind ceases (or when visual cues for optomotor feedback are negligible) obviously would be advantageous.

AIM-THEN-SHOOT ANEMOTAXIS

An alternative to optomotor anemotaxis is a mechanoreceptive anemotaxis in which wind direction is assessed before takeoff; the course is set upwind upon takeoff, but the assumption is that the responder is not sensing wind direction while in flight. Instead, the course is set to use visual cues

to head in the predetermined upwind direction and is presumed to continue as long as odor contact is maintained. Loss of odor contact triggers landing; once odor is again detected, movement directed upwind resumes. This system seems to explain some features of host-finding in tsetse flies (*Glossina*) in studies by Brady, Gibson, and colleagues (15, 16, 47, 48). Following sensing of host odor, flies head upwind with little evident regard for wind direction while in flight. Loss of odor contact, however, triggers a sharp turn, uncorrelated with wind direction. Flies may then backtrack toward where they last sensed odor or head crosswind. One explanation for why orientation may not be governed by the optomotor reaction is the high flight speed of tsetse, between 5 and 10 m/sec. This would provide little ability to gauge transverse image flow. The unsettled nature of tsetse orientation to host odors is reviewed in Reference 49.

Mechanoreceptive anemotaxis also may explain host finding in two anthomyiid flies. Cabbage flies, *Delia brassica*, are proposed to orient to host odor by sequential upwind flights and landings (52). Although visual cues set heading and control flight path, wind direction once airborne is assumed not to be assessed by optomotor anemotaxis. This tactic may also explain the orientation of onion flies, *Hylema antiqua*, within 0.5 m of onion baits (33). Male potato tuberworm moths, *Pthorimaea operculla*, also are suggested to have a short-range aim-then-shoot strategy that follows landing near a pheromone source (97). In a wind tunnel that permitted changes in wind direction, landed moths, sensing pheromone, faced upwind and then took short upwind flights.

FINDING AN ODOR PLUME

Efficient navigation along airborne odor plumes following discovery would seem to be the most relevant metric for resource finding. However, strategies that enhance the likelihood of initial plume contact should be favored and potentially are of great importance. One strategy involves simply perching where interception of a plume is most likely. Schal (94) documented the tree-perching heights of eight cockroach species in a Costa Rican rainforest. Each species had a narrow range of favored height, and within this range, males were generally perched at a higher level than females. This distribution was explained in part by the vertical ascent of plumes due to night-time atmospheric instability, so that males would be situated at an appropriate height for encountering the pheromone plume of a conspecific. How these cockroaches sense their perching heights remains unknown.

In the case of flying insects, scanning the environment for a plume ought to favor strategies that limit energetic expenditure en route and increase the likelihood of rapid plume contact. Dusenbery (35, 36), for example, proposed that heading downwind would increase efficiency in two ways over a random heading with respect to wind flow: More area would be covered per unit time, and at a lower energetic cost.

When wind direction is fairly steady, the plume's downwind projection should not exceed its width; therefore, flying crosswind should enhance the probability of contact (18). However, when wind shifts over 60°, the plume's width matches its downwind projection (92); therefore, heading upwind or downwind could be optimal. To take advantage of such distributions, however, an organism would need to have an explicit memory of where and when it previously experienced the odor and the contemporaneous wind direction. Such processing capabilities generally exceed the idiothetic capacity of most insects.

Because it is difficult to track ranging (non-orienting) insects in the field and to know the instantaneous wind direction that they are experiencing, there are few field studies that bear directly on this issue. Studies with two day-active male moths, *L. dispar* and *Virbia lamae*, which do not feed as adults and therefore can be assumed to be searching for a pheromone plume when exhibiting ranging flight, found no link between wind direction and moth heading (20, 37). As the crosswind

quadrants comprise twice the degree headings of an upwind or downwind quadrant, a random orientation with respect to wind flow is a de facto crosswind strategy, provided that crosswind reversals are infrequent; this strategy has the advantage of not requiring continual processing of wind direction. Male *L. dispar* also exhibit a second ranging strategy. Females of the European strain in North America are flightless, and they call from tree trunks very near where they pupate, which can extend to the top of the forest canopy. In high-density populations, male *L. dispar* search for calling females by vertical flights along the tree boles (23). In contrast, most observations of flight in nature under lower-density population conditions show ranging movement 1–2 m above ground level (37).

Of course, flight direction will deviate from a straight course. Sharp or gradual turns can be punctuated by relatively straight legs. Stopping between turns may include an area-restricted search before resumption of another leg. When short legs (followed by local search) are more frequent than long legs, this distribution is termed a Lévy flight (88). Although Lévy flights are documented, for example, in the foraging activities of honey bees, there are no good field observations to link such patterns to searching for odor plumes.

Another strategy may involve flight to and retention in habitats likely to harbor females (113). These may be identified by background plant odors and/or visual features. It has long been known that host plant volatiles, often common green leaf volatiles, when added to a female's pheromone, increase attraction of males by a small but statistically significant amount (31). In other systems (e.g., Cerambycidae), the response to pheromone can also be synergized by the presence of representative host volatiles (1). It is worth noting that studies that report additive and synergistic effects of host volatiles on pheromone response usually use host volatiles that differ qualitatively (e.g., enantiomeric composition, blend ratios) and quantitatively (synthetic lures usually have higher release rates than the host plant) from odors actually released by host plants.

A study (3) with the moth *H. virescens* found that the host odor bouquet at natural airborne concentrations had no influence on orientation to pheromone. Thus, it may simply be that both pheromone and host volatiles input into the same sensory pathway for orientation, and that combining these in a lure creates a supernormal stimulus.

Another experimental approach to studying odor-mediated flight responses used harmonic radar to track individual *A. segetum* males. A general downwind displacement of moths prior to plume following was detected (89), but at coarser spatial and temporal scales than in the *Lymantria* and *Virbia* studies. Given that the few field observations that are available differ in their temporal precision and the spatial scale of measuring moth and simultaneous wind movement, the question of whether male moths employ optimal strategies (rapidity with minimal energy expenditure) for contacting a pheromone plume remains unresolved. Based on wind-tunnel manipulations, *Drosophila* searching for food seem to have a flexible strategy (122): Head crosswind if the wind direction is fairly stable, and head parallel to the wind if it is not.

RECONTACTING A LOST PLUME

Loss of plume contact can be caused by odor gaps along the plume generated by turbulence and by shifting wind, which can direct an upwind course out of the plume (see **Figure 3**). Maneuvers in moths to recontact the plume include crosswind casting (lateral counterturning mainly in the vertical plane of the plume, usually with progressively wider excursions and with little upwind or downwind displacement). Casting can persist for several seconds. This strategy appears widespread among moths and has been documented in both wind-tunnel (6, 8, 70) and field studies (7, 29). In *G. molesta*, some moths steered downwind following loss of the plume (7). Similar maneuvers to recontact a lost plume were seen in *Drosophila* (17). If food odor was presented as a ribbon plume

(simulating some features of a turbulent plume in the pattern of odor contact), and the odor release was then truncated, then the flies cast like moths. Dropping downwind after losing plume contact seems to serve the same function in tsetse flies (47).

BIOINSPIRED SOURCE LOCATION

Understanding how insects orient to odor sources provides opportunities to model tactics for plume finding and source location (11, 12, 72, 74, 77, 111). These approaches depend on a model of plume dispersal, ideally simulating a plume's turbulent structure (odor present or not), within a shifting wind field (42) with all parameters appropriate to a particular habitat type and daily rhythm appropriate to the organism or the robotic task. Simulation models can then be used to guide real or virtual robots in terrestrial, airborne, or aquatic settings. Modeling can provide an understanding of the probable sensory inputs and navigational instructions used by insects and other organisms in orientation and may provide strategies to guide robots to locate odors from anthropogenic sources, for example, in location of land mines or other hidden explosives. However, it is crucial to recognize that a simulation may faithfully simulate the form and performance of actual insect tracks in a wind tunnel or nature but may not use the same guidance rules. An upwind zigzag path, for example, could be generated by sensing loss of the plume's edge and turning back toward the plume's centerline (51). However, this is not the natural cause of zigzagging in moths. Instead, an internal metronome-like generator sets turns several times per second (63, 115).

In some simulations and robotic implementations, the task is quite simple and uninformative: Head upwind or upstream when the stimulus is detected. In some cases, there is no directed airflow, and only odor gradient information is available. Few examples take robotic vehicles into rigorous test trials. The principles of moth navigation, however, were implemented in an autonomous underwater vehicle (73), substituting GPS-sensed movement for the optomotor response and a plume of rhodamine dye for odor. Plumes were successfully located and tracked to their source over 100 m. Modeling can also explore how changes in strategy improve either the likelihood or the rapidity of source location or, conversely, have minimal or negative effects. To be valuable in understanding innate mechanisms of odor source location, a model needs to use the natural inputs and reactions, and its output needs to mimic orientation observed in the field. Modeling orientation of *L. dispar* was feasible because the rate of pheromone release and male response threshold were known, there was an available plume simulation, upwind orientation and casting behaviors were well characterized, and distance of plume detection and the probability of successful orientation had been measured in the field (11).

Sensitivity analyses can help us understand what selective factors shape natural behaviors and how they interact. In plume finding, for example, do upwind, downwind, or random paths with respect to wind direction improve initial plume detection (11, 20)? In a Lévy flight, what is the optimal distribution of step sizes and time of local search before the next step (11)? Models can also be tested against field data, such as release and recapture of insects in pheromone-trapping grids of varying densities (12).

Some approaches can be explicitly biomimetic, in the sense that they intend to use the rules that efficient navigators such as moths employ (11, 72, 74); others use algorithms that produce flight tracks that mimic natural trajectories (such as a zigzag path along the plume) but do not rely on strictly natural maneuvers, instead relying on a mix of information, for example, about wind direction and plume structure or concentration (77). One approach entirely disregards wind flow and relies on measurements of concentration (110), whereas another model compares anemotaxis with navigation by sensing the plume's edges (51). Another application (111) involved creation of a cyborg, in this case a robotic ground vehicle guided by live antennal sensing of a pheromone.

An explicitly non-biomimetic approach proposed by Vergassola et al. (100) is infotaxis, which can guide a responder using, potentially, all currently or recently sensed cues (reactive or idiothetic) and a recollection of past encounters (allothetic) of plume contact (where, when, odor intensity) and wind field. Together, these values can be used with a Markov model to formulate a most probable route (a source likelihood map) to the odor's source (43), rather than using only idiothetic information. However, as considered above in the section titled Recontacting a Lost Plume, an allothetic strategy needs a recollection of space-time maps of past encounters with odor and wind flow. These strategies well exceed an insect's memory and processing capabilities, and also may limit robotic applications in which miniaturization and low computing power requirements of the vehicle are paramount. Nonetheless, a melding of idiothetic and allothetic strategies may be more useful for guiding robots than using moment-to-moment information (for a review, see 53). Understanding how insects and other organisms perform efficient navigation with simple reactive maneuvers has wide applicability, but a comprehensive appraisal is beyond the scope of this review.

CONCLUSION

Acquisition of resources via orientation to the odors that they emit is common in insects and many other organisms. In some cases, such as mate finding, there is a premium for task efficiency driven by the forces of natural selection. In other examples, such as finding a host plant, the resource is not as ephemeral, but efficient navigation nonetheless remains a selective force. The principal strategy flying insects use in steering upwind along odor plumes is optomotor anemotaxis. Strategies for optimizing initial plume contact, however, are not well understood. Other stimulus modalities such as vision and occasionally sound can also be significant augmentative stimuli for orientation (19), particularly close to the source.

SUMMARY POINTS

1. Airborne navigation to a distant odor source is accomplished by steering upwind when the odor is detected, and not by gradient sampling of the odor plume.

2. Wind direction is gauged by visually appraising how the interaction of wind heading modulates trajectory, an optomotor reaction. A front-to-rear image flow indicates a due upwind course.

3. Gaps in the plume caused by turbulent diffusion and by shifts in wind direction complicate plume tracking, limiting the distance over which plumes can be traced and requiring maneuvers for re-establishing contact with a lost plume.

4. Orientation in still air can utilize detection of plume distribution, at least over short distances.

FUTURE ISSUES

1. Technologies to allow precise tracking of insect movements in the field are needed, but the challenge will be to simultaneously determine the wind flow and odor concentration that an insect experiences moment to moment.

2. Wind-tunnel studies need to create odor distributions and visual fields that mimic field conditions.

3. Much of what we currently understand about in-flight orientation is based on relatively few exemplar species, particularly moths, tsetse flies, *Drosophila melanogaster*, and several mosquitoes. Other species and lineages warrant study.

4. Background odors can attract insects into, and cause them to remain in, a habitat where resources such as a host or mate are most likely to be found. How these orientation reactions integrate with upwind plume tracking is not well understood.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

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