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Modeling Optimal Strategies for Finding a Resource-Linked, Windborne Odor Plume: Theories, Robotics, and Biomimetic Lessons from Flying Insects

Josep Bau* and Ring T. Cardé^{1,†}

*Department of Systems Biology, University of Vic—Central University of Catalonia, 08500 Vic, Spain; [†]Department of Entomology, University of California, Riverside, CA 92521, USA

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¹E-mail: ring.carde@ucr.edu

Synopsis Male moths locate females by navigating along her pheromone plume, often flying hundreds of meters *en route*. As the first male to find a calling female is most apt to be her mate, this can be termed “a race to find the female” and it is assumed to be under strong selective pressure for efficiency and rapidity. Locating a distant, odor-linked resource involves two strategies. The first is to contact the outer envelope of the odor plume. When wind direction is relatively invariant, the plume stretches and then crosswind flights may be favored, although when wind direction shifts over 60°, upwind and downwind paths may be optimal. Alternatively, the path may be random with respect to the direction of wind flow, with periodic changes in direction, as in either Lévy or Random Walks. After first detecting the pheromone, a second strategy follows: moths navigate along the plume by heading upwind when the pheromone is detected, with crosswind casting to re-establish contact if the plume is lost. This orientation path is not straightforward in nature, however, because atmospheric turbulence fragments the plume, thereby creating large odor gaps. Furthermore, a shifting wind direction can lead the responder out of the plume. One way to explore which strategies are optimal for enabling initial contact with the plume and subsequent navigation is through modeling of plumes’ dispersal and of insects’ flight strategies. Our simulations using the flight characteristics of the male gypsy moth (*Lymantria dispar*) suggest that search strategies similar to Lévy Walks are most apt to result in a high probability of contact with plumes. Although a searching trajectory aimed predominately crosswind performed almost as well as those with a random orientation when wind direction was relatively stable, downwind biased trajectories were least successful. A random orientation with respect to immediate wind flow, as used in our simulations of Lévy and Random Walks, seems optimal both for initial discovery of the plume and likelihood of locating an odor source. In the two available direct field observations, moths adopted a random orientation with respect to concurrent wind direction.

Introduction

Many flying insects forage for resources such as a mate, food, or an oviposition site by navigating upwind along a windborne plume of odor that is linked to that resource; this mechanism of in-flight orientation is termed optomotor anemotaxis and the distances traveled can be over hundreds of meters (Cardé and Willis 2008). The necessary prelude to

navigating along a plume is locating it and organisms should select strategies of movement that maximize the probability and rapidity of initial contact with the plume while minimizing the expenditure of energy along the way. The efficiency in finding a plume should be especially important when the source of the odor is ephemeral, as would be the case with a female moth emitting a pheromone;

likely the first male to locate the female will mate with her. Foraging for a plume involves two principal issues: the kind of path used to scan the environment and whether there is a preferred heading with respect to the present and recent directions of wind flow.

There are two general approaches to understanding foraging maneuvers and how they relate to the distribution of the odor plume in space. One method is to document the natural foraging paths taken with respect to measurements of contemporaneous wind flow. This approach has been used with different flying animals such as male moths (Elkinton and Cardé 1983; Cardé et al. 2012), male ants (Buehlmann et al. 2014), tsetse flies (Gibson et al. 1991) and sea birds (Nevitt et al. 2008). In many environments, however, wind direction varies substantially over tens of seconds at a given location (Elkinton et al. 1987; Brady et al. 1989) and its direction at a monitoring station and at the location of an insect several meters away can differ substantially. Therefore, it can be difficult to correlate with precision an insect's heading with the instantaneous wind flow that the insect is experiencing. If the insect and the wind-monitoring system are in close proximity (within several meters of each other), a short segment of the flight track can be compared with nearby contemporaneous wind direction (Cardé et al. 2012), but tracking the movement over long distances and correlating an insect's trajectory with the wind flow it experiences *en route* is a challenging endeavor. In the case of moths, because most species are nocturnal, documenting their flight path is especially problematic. Thus, a direct test in the field whether any of the predictions of paths favoring a particular orientation with respect to wind flow are met is not a simple task.

The other general approach is to model movements and tracks and then establish the likelihood of contact with a plume in a fixed wind flow. Because the odor plume is generally stretched longitudinally as it is transported downwind, in planar view its longitudinal axis will greatly exceed its width, given that the wind's direction is relatively constant, and this alignment suggests that heading crosswind should be the most advantageous strategy (Cardé 1981; Janzen 1984). Several theoretical models (Sabelis and Shippers 1984; Dusenbery 1989, 1990), however, suggest that trajectories should favor an upwind or downwind bias when the wind shifts direction over 60° , thereby creating a plume that has a wider crosswind expanse than its downwind projection (Fig. 1A). When the plume has such a wide swath, however, two other issues arise:

the distribution of odor within the plume is patchy due to turbulent diffusion and changes in wind speed can misalign instantaneous direction of the wind and the plume's centerline (Fig. 2C) (Elkinton et al. 1987). Thus, the assumption that across a 60° swath the odor will always be encountered is questionable and the instantaneous direction of the wind within the plume's boundaries may not always provide a reliable cue to the plume's trajectory or point to its origin. The above approaches are simplistic in the sense that they rely on a set distribution of the plume (e.g., a circular plume created by simple molecular diffusion or a plume elongated by wind), a homogeneous distribution of odor within the plume's boundaries, a fixed wind direction, and a searcher taking a straight-line path that may or may not intersect the plume. Individual-based computer models have been devised with a detailed puff dispersion dynamics in fast and regularly shifting wind conditions (Yamanaka et al. 2003) and anemometer-equipped robotic devices have been programmed to respond to shifts in wind conditions (Harvey and Keller 2008) but in models applied to simulate population dynamics, source attraction is often simplified as effective sampling areas or attraction radius (Byers et al. 1989; Östrand and Anderbrant 2003; Yamanaka 2007; Manouk et al. 2014) which are not affected by changes in wind conditions.

In nature, the behavior employed in finding a plume generally is expected to provide an optimal solution for a given organism and, therefore, the methods used by insects may be applicable to problems of orientation in artificial situations, e.g., robotics. The effectiveness of such maneuvers, however, can be dependent on the characteristics of the environment, the searcher's navigational capabilities and memory, the density and distribution of odor sources, and the rate at which the odor is released from the source. Observations on bacterial chemotaxis (Celani and Vergassola 2010), for example, usually do not apply on a macroscopic scale, but other organisms, like arthropods, that use semiochemicals as a means of finding food or mates and interact with the wind and odor environment at a scale that is similar to that of robotic devices are more likely to provide the basic behavioral patterns that are optimal for finding a source.

Computer models and their application to the location of the source of an odor by robotic devices are often inspired by biological observations and are sometimes devised as a blend of different strategies tried or observed in diverse environments (e.g., Li et al. 2001). Although optimality of a search

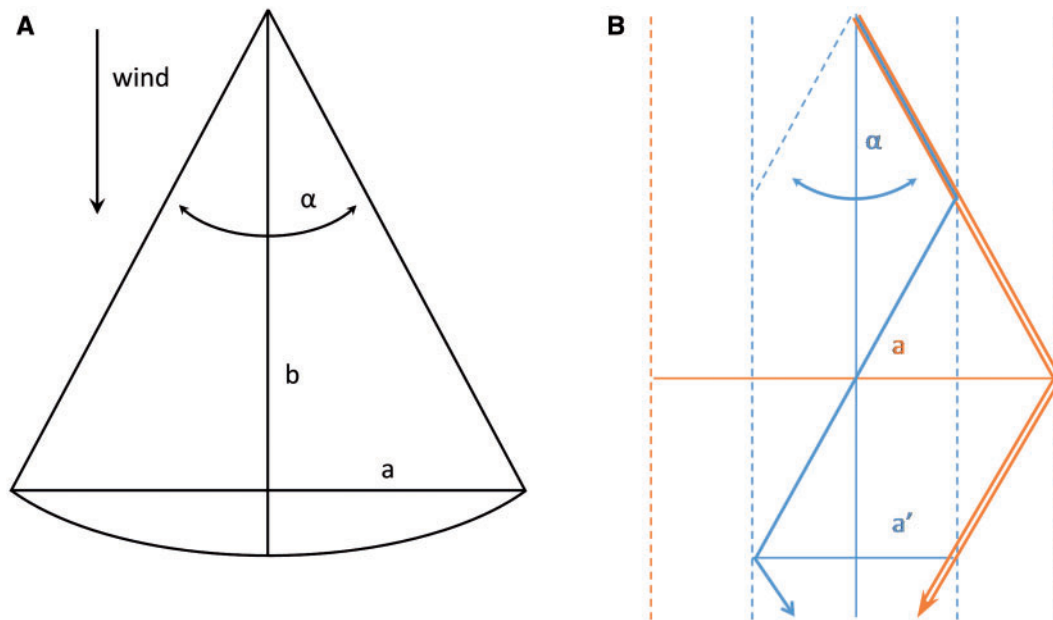


Fig. 1 Possible consequences of shifts in wind direction on optimal strategies for finding an odor-plume. In (A) (see Sabelis and Shippers 1984), when the wind shifts over 60° (α), it would appear more advantageous to head downwind rather than crosswind, because the plume's width (a) will exceed its downwind length (b), and then it is more efficient energetically to head with the mean wind flow (shown by the arrow) and the probability of contacting the plume would be increased (Sabelis and Shippers 1984). In (B) the meandering of the plume is considered, and when the frequency of shifts by the wind is doubled (solid line compared with double line), the resulting crosswind component of the time-averaged plume (a') is halved. The downwind component basically depends on the maximum distance from source at which the threshold for sensing the odor is reached and does not change substantially. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

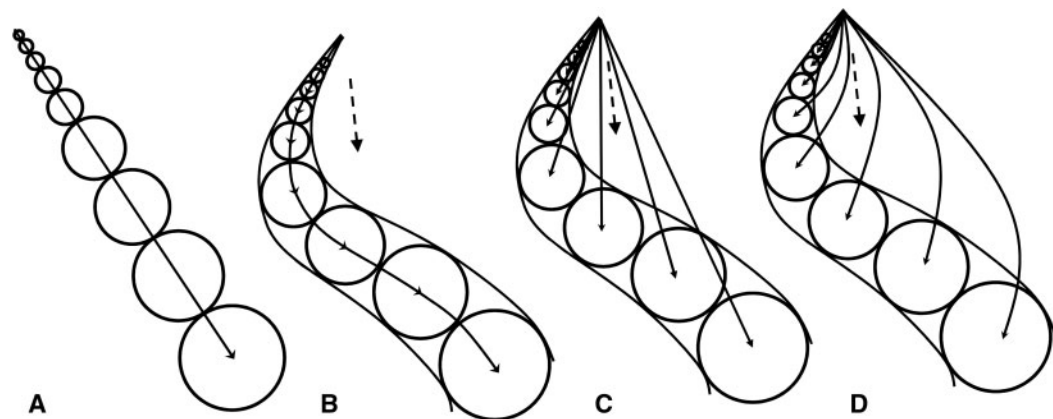


Fig. 2 Schematic of wind directions in meandering odor-plumes when viewed from above. The plume is depicted as a series of puffs that expand by turbulent diffusion. The arrows denote the instantaneous wind direction within each puff. The dashed lines and arrows indicate the mean directions of wind flow. (A) A steady wind direction during which insects can make rapid progress toward the source. (B) Before the paper by David et al. (1982), it was assumed by behavioral biologists that the direction upwind and along the plume's centerline was aligned and so simply heading upwind would lead to the source. (C) Conforms to the observations of David et al. (1982) in an open field with a varying wind direction but a constant wind speed. (D) Matches observations of Elkinton et al. (1987) beneath a forest canopy and Brady et al. (1989) in an open savannah; this effect is caused by an increase in velocity. Heading upwind in both C and D can lead out of the plume (reprinted with permission of Wiley-Blackwell and adapted from Elkinton et al. 1987, 400).

strategy is clearly dependent on context, the observations and simulations of searches in a given environment can provide insights that can be applied to understanding biological problems such as estimating

population size from the incidence of captures in pheromone-baited traps, and suggesting trade-offs in signaling efficiency based on the rate of odor release, threshold of response, and foraging path.

Simulations also provide insights into efficient rules for movement by robotic searchers.

A model that simulates the source-finding behavior of the moth needs to include two strategies: one that allows the searcher to locate the odor plume and a second one to navigate along the plume and reach its source.

Plume-finding strategies

The first step in locating the source of an odor is to engage in locomotory activity that will increase the probability of the searcher detecting traces of odorant carried away from the source by wind. As no previous or recent perception of a chemical has occurred, the cue that could be used as an initial reference to guide the search is the wind's direction, and its detection by an in-flight responder also requires visual feedback to detect the direction of wind flow (Kennedy and Marsh 1974). Changes in concentration of odor within a plume meters or more away from the source are not reliable cues either for distance or for direction to the source (Murlis et al. 1992). There are different theoretical strategies that can be applied to define optimal plume-finding behaviors, but there is no consensus as to which strategy is superior. Mathematical models applied to animals' movements usually are an extension of simple random-walk processes (Codling et al. 2008).

The simplest form of random walks is uncorrelated and unbiased, that is, with complete independence between direction of successive steps, and without a preferred direction (basically like Brownian motion). However, since most animals have a tendency to move forward, a classical approach is the correlated random walk (CRW), in which there is some directional persistence from one step to the next (Patlak 1953; Plank et al. 2013), with variability of lengths of steps having a finite variance, which means that after a sufficient length of time, the location coordinate of an individual on any axis converges to a Gaussian distribution (Codling et al. 2008).

Search paths also can involve sharp changes in direction that would yield a general search pattern similar to the intermittent searching behavior observed in fruit flies (Reynolds and Frye 2007) or in other insects in which active searching phases randomly alternate with relocation stages. Switching between these phases of the search might well occur between interruptions in the flight when the insect temporarily lands on the ground. Such strategies are generally termed Lévy Walks (LW) and have been considered a class of random walk that can be

modeled with a heavy tailed distribution of step-lengths (Shlesinger et al. 1987; James et al. 2011). It has also been proposed that a composite CRW, which occurs when an animal switches between two behavioral modes, can be misidentified as a LW (Plank et al. 2013) and that these can resemble optimal LW (Reynolds 2013). The combination of these two strategies seems to, under certain conditions, perform better than either alone (Pasternak 2009). Both strategies are believed to be optimal for the location of sources that are patchily distributed (Reynolds 2010).

An additional variation on random walks appears when a global directional bias is introduced by increasing the probability of moving in a certain direction. This situation is termed biased-random walks or biased-CRWs (BCRWs) and can be influenced by environmental factors (Codling et al. 2008) such as the direction of fluid flow.

Wind direction by itself does not provide any information about the source's location to an insect that has not recently perceived an odor cue but it produces changes in the overall shape of the plume that can influence the optimality of different search strategies. A plume is stretched along the direction of the wind and, on large spatial and long temporal scales, it meanders from side to side (Murlis et al. 1992; Murlis 1997), widening its crosswind time-averaged section. Therefore, besides energetic considerations (upwind flight would imply a higher cost), search strategies with wind-related directional biases may reduce the average time spent and distance traveled until location of the plume, which can be crucial in the case of ephemeral resources such as pheromone-emitting females. In a situation with a relatively invariant wind direction, the plume projects further downwind than crosswind and, in this case, a crosswind strategy could be optimal. However, in winds shifting over more than 60°, it has been proposed that the shortest distance to a plume would be achieved if the insect flew parallel to the time-averaged direction of the wind (Sabelis and Schippers 1984; Dusenbery 1989, 1990; Zanen et al. 1994).

The ability of an insect to use either a crosswind or an along-the-wind strategy implies an ability to perceive and keep track of such shifts in the wind and the insect's past position in the environment relative to recent wind flow. It has been proposed that insects use the instantaneous wind direction to set a course and that they would not react to changes in average direction of the wind. Assays with *Drosophila* in a wind tunnel comparing constant

and shifting directions of flow seem to favor this view (Zanen et al. 1994).

In anecdotal observations, some insects such as the cabbage root fly (Finch and Skinner 1982) were reported to engage in apparent upwind flight, whereas flying male ants (Kannowski and Johnson 1969) and moths (Lingren et al. 1978) seem to favor a crosswind trajectory. Other insects like the Egyptian cotton leafworm (Murlis et al. 1982), the turnip moth (Reynolds et al. 2007), and tsetse flies (Gibson et al. 1991) have ranging flights with a downwind bias; walking cockroaches also head downwind (Willis and Avondet 2005). The gypsy moth (Elkinton and Cardé 1983) and the moth *Virbia lamae* (Cardé et al. 2012) show no evident preference of orientation with respect to contemporaneous direction of wind flow during mate location.

Navigation along the plume

After initial contact with a plume and during their approach to the source of an odor, moths (Kennedy and Marsh 1974; Willis et al. 2013) and other insects (Wolf and Wehner 2000; Willis and Avondet 2005; Budick and Dickinson 2006; Buehlmann et al. 2012; van Breugel and Dickinson 2014) orient upwind.

Odor plumes in wind that are generated from a point source of pheromone are intermittent owing to the effects of atmospheric turbulence (Murlis et al. 1992, 2000). When inside the active space of the plume, moths respond to an encounter with odor-laden strands of pheromone by brief surges upwind and it is the reiterative perception of filaments of the pheromone that results in sustained upwind progress (Mafra-Neto and Cardé 1994, 1996; Vickers and Baker 1994). An internally controlled counter-turning mechanism results in a zigzagging pattern that turns more toward upwind as the rate of encounter with the filament increases (Vickers 2000). After loss of contact with the pheromone, a so-called “casting flight” (crosswind flight with no net upwind movement), develops quickly (Kuenen and Cardé 1994). It is also established that moths use an optomotor anemotactic mechanism (Kennedy and Marsh 1974) to adjust their airspeed and course angles by visual feedback from the movement of the ground pattern. A widely observed consequence of this is a rather constant ground speed that is maintained (both in presence and absence of odor) across different wind speeds (e.g., Kuenen and Cardé 1994; Cardé et al. 2012).

Is infotaxis a biomimetic strategy?

Insects' navigational strategies along pheromone plumes have often been modeled, compared, and

also applied to robotic search for the sources of odors (Grasso 2001; Li et al. 2001; Grasso and Atema 2002; Farrell et al. 2003; Willis 2008; Ishida et al. 2012). Because natural behaviors are generally assumed to provide optimal solutions for a given organism, these can inspire development of efficient models for artificial searchers. Even artificial strategies like the recently proposed “infotaxis” (Vergassola et al. 2007), which mechanistically are very different from insect models, have been compared with moths' trajectories in terms of the similarity of the tracks (Moraud and Martinez 2010). Infotactic searching is based on using information relative to the spatial distribution of odor, and in some cases of wind flow, collected by the searcher over time. The efficiency of such strategies may be, however, greatly reduced due to inaccurate environmental modeling (Rodríguez et al. 2014) or in situations with unstable winds, as meandering of the plume would probably render unreliable information as to direction to the odor's source to the model. Such approaches assume that the searcher tracks past patterns of the wind and previous encounters with odors, and that it places these within known coordinates of time and space. These capabilities are presumed to be beyond the computational abilities and the capacity for memory of moths and other insects (Cardé and Willis 2008; Cardé et al. 2012), although in principle these requirements could reflect some of the mapping capabilities of honey bees (*Apis mellifera*). Desert ants (*Cataglyphis*) forage for food on featureless salt flats by running crosswind so as to intercept odor plumes from their prey (Buehlmann et al. 2014), evidently using the instantaneous wind-flow as an orientation cue; these ants know the direction to their home nest by celestial cues (Collett and Cardé 2014).

The simulation experiments we present here have been obtained using a model that mimics the observed behaviors of the gypsy moth *Lymantria dispar* (Lepidoptera, Erebidae) in the field and in experiments in wind tunnels. To ensure that the parameters of the model are realistic in terms of a naturally orienting insect, the observed pheromonal communication of this species has been used as an exemplar to parameterize the model's rate of odor release, and the male's threshold of response, flight speed, and reaction to losing contact with the plume.

The detailed wind-and-odor model of Farrell et al. (2002) provides a realistic simulation of the dynamics of pheromone-dispersal, which is essential to reliably emulate the interaction of insects with environment across the range of wind conditions that occur naturally in the field. Changes in the

direction and speed of the wind model produce a patchy distribution of odor within the plume that is used to determine the selective value of searches with either a particular orientation to wind flow or various random-walk processes. By varying the plume's characteristics (variability in the speed and direction of wind) and by using a series of rules for movement of virtual moths, with and without a wind-directed bias, we can determine which strategies for movement are most apt to result in contact with the plume and achieve a high degree of success in reaching the source of the odor.

The dispersal of odor and the movement of the insect both have been simplified to a planar view. Three-dimensional analyses suggest that a moth's trajectory cuts through the plume in all directions with loops of different radii (Rutkowski et al. 2009). However, according to observations in the field and in wind tunnels, the horizontal deviations in moths' flight tracks are greater than the vertical deviations (Baker and Haynes 1996) and, therefore, analysis in a two-dimensional plane should not lead to qualitative differences in the results from our simulations. In the field, however, plumes can move vertically under some atmospheric conditions (Elkinton et al. 1987; Girling et al. 2013); whether such displacements are of sufficient magnitude to impede navigation is not clear.

Simulation models

In the present study we simulated batches of 100 virtual moths that search simultaneously and independently for an odor plume in a boundless area that replicates wind-conditions generated by the Farrell et al. (2002) model in contiguous 100×100 m plots. Sources of odor are simulated in a single location or in square arrays of 5×5 sources. Virtual moths are initialized at random locations within a region that doubles the area of influence of the simulated plume(s), being 100×100 m when one source was used and 500×500 m in the case of the array of 5×5 sources.

In such a stochastic wind model, the conditions that the searcher encounters can be highly variable between different runs of the simulation. To make different behaviors comparable, all tested strategies were run simultaneously against the same wind model, with an equal number of searchers using each strategy. Between 40 and 50 iterations were run for every condition of wind, with a total of 100 searchers simulated in each one.

Every searcher followed the program flow described in Fig. 3 and the initial contact with the

plume and the finding of the source were recorded for each searcher. The locating of the source by the simulated insect was defined by the time the virtual insect entered an area 2 m in radius around the source of the plume, and where they were assumed to use visual cues and engage in a vertical tree-oriented search to locate an actual female. Gypsy moth females typically emit pheromone while perched on tree trunks and male moths begin searching vertically when in close proximity of the visual cue provided by the trunks, thereby giving rise to area-restricted search that can represent the majority of the time spent by foraging males (Elkinton and Cardé 1983; Cardé and Hagaman 1984; Charlton and Cardé 1990). Although not all the males that engage in vertical tree-oriented flight are bound to mate with one of the emitting females perched on a particular tree, we assume they will for simplicity of the model.

Wind model

The filament-based, odor-dispersion model used in these experiments was described in Farrell et al. (2002). It produces intermittent, meandering, simulated plumes with consistency between the fluid-flow field and the shape of the plume, with the resulting plumes mimicking the instantaneous structural features of the plume measured in the field (Jones 1983). The wind and plume models are implemented in a 100×100 m area. Insects, however, can move beyond the boundaries of this 1-ha plot and still interact with the same conditions of wind and odor that are replicated in a boundless grid of $100 \text{ m} \times 100 \text{ m}$. To allow for multiple plumes to be simulated, a source can be declared as "present" in one or more plots of the grid. If the source is not declared in a given plot, the insect located in such a plot will interact with the wind-model but ignore the odor plume. This arrangement allows us to simulate insects in a limitless area while maintaining computational feasibility.

Monitoring of the wing-fanning response in a field assay indicated that the limit of detection of a source releasing the pheromone, at somewhat above the rate that females do, is approximately 100 m (Elkinton et al. 1984, 1987; Elkinton and Cardé 1988). Few male gypsy moths that detect a source of a pheromone (as monitored by wing fanning) at distances greater than 80 m were able to navigate along the plume to its source (8% of males wing fanning when released at 120 m from the source) (Elkinton et al. 1987). Accordingly, our simulated odor plumes do not extend beyond 80 m. The model simulating odor dispersal is described elsewhere (Farrell et al. 2002). The rate of emission of the

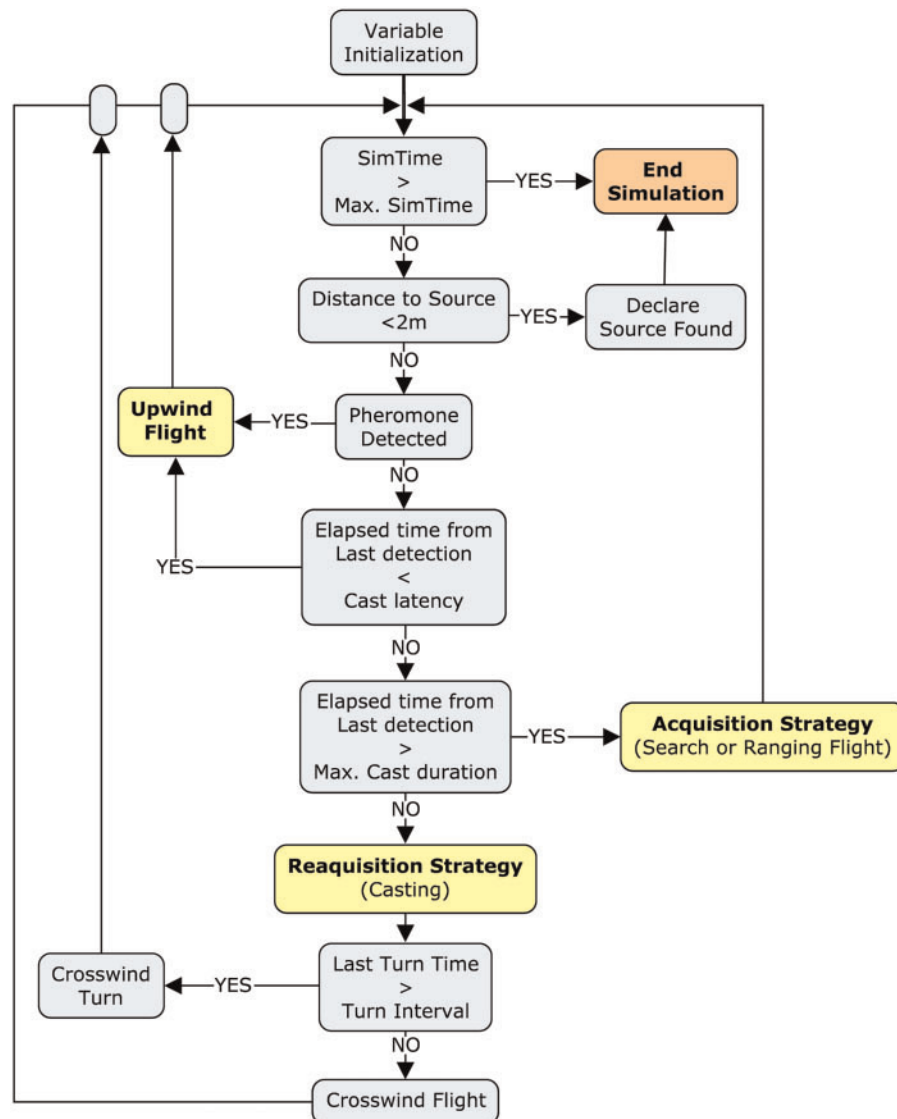


Fig. 3 Program flowchart of the simulated moth behavior. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

pheromone was set to match the rate of production by a female gypsy moth (14 ng hr^{-1}) (Tang et al. 1992); the threshold of detection was set to match the threshold of a male gypsy moth's response to the pheromone ($4 \times 10^4 \text{ molecules cm}^{-3}$) (Elkinton et al. 1984).

Wind conditions recorded during field experiments can range between 0 and 5 m s^{-1} in open fields (David et al. 1983) but lower and less variable speeds (from ca. 0.5 to 1.5 m s^{-1}) usually occur in woodlands where gypsy moths are found (Elkinton and Cardé 1983; Willis et al. 1991, 1994). Changes in wind direction are associated with meandering of the plume, which can have a very high impact on the plume's shape, especially in forested environments where, although wind direction changes less rapidly than in an open field, it does so over a greater range

(Murlis et al. 2000). Measurements in woodlands show that the "odor" can arrive from any direction (including $>90^\circ$ away from the source). The rate of change of direction is negatively correlated with wind speed and directional variability can virtually cease in winds of more than 1 m s^{-1} in such environments (Brady et al. 1989).

In our models we have maintained wind speed that would be consistent with a forested environment (average of 0.75 m s^{-1}). To compare the performance of different strategies in diverse plume-meandering situations, different values for the modeling parameters were defined by adjusting the Wind-Gain and Wind-Damping parameters of the simulation program (Farrell et al. 2002). An increase in Wind Gain produces a wider range of variation in wind

speed, whereas a decrease in the Damping parameter raises its directional variability through time so that, by combining these, increasingly unstable wind conditions can be modeled. Throughout the text, these conditions are referenced in relation to the average directional change over 1-min periods as they were ascertained to produce after 10 simulations of 20 min duration:

- (1) $13^{\circ} \text{ s}^{-1}$ (± 6 SD); wind speeds of 0.71 m s^{-1} (± 0.1 SD); Gain = 10, Damping = 0.4.
- (2) $22^{\circ} \text{ s}^{-1}$ (± 11 SD); wind speeds of 0.78 m s^{-1} (± 0.2 SD); Gain = 20, Damping = 0.4.
- (3) $36^{\circ} \text{ s}^{-1}$ (± 16 SD); wind speeds of 0.78 m s^{-1} (± 0.3 SD); Gain = 20, Damping = 0.2.
- (4) $65^{\circ} \text{ s}^{-1}$ (± 25 SD); wind speeds of 0.99 m s^{-1} (± 0.5 SD); Gain = 20, Damping = 0.05.

The outcome of these different wind settings results in clear differences in meandering and in homogeneity of the distribution of odor along the plume.

Searchers' behavior

The general behavior of the simulated moths in response to encounters with odor has been programmed according to behavioral responses observed both under wind-tunnel conditions and in the field for the gypsy moth. The basic parameters considered in the simulations are: ground speed of the insect, casting latency (time from loss of contact with the plume to casting), frequency of turning, and duration of casting.

Ground speed: flying moths maintain a constant ground speed across a wide range of the velocities of wind by adjusting their airspeed (Cardé and Hagaman 1979). Reported ground speeds of male gypsy moths range between 30 and 65 cm s^{-1} in wind-tunnel experiments (Charlton et al. 1993; Kuenen and Cardé 1993, 1994; Zanen and Cardé 1999; Cardé and Knols 2000), although data from field studies indicate significantly higher ground speeds ($98\text{--}145 \text{ cm s}^{-1}$) (Willis et al. 1994). Random orientation during the search for a plume should require no optomotor processing to maintain a certain orientation with respect to the direction of the wind. However, ranging flight prior to contact with the pheromone, as observed in *V. linae*, showed remarkably constant ground speeds of moths heading in all wind directions, which is consistent with optomotor regulation of the velocity of flight (Cardé et al. 2012). For our simulated moths we used a ground speed of 100 cm s^{-1} during searches for a plume, which is consistent with field data from gypsy moths.

During navigation along the plume, ground speed is reduced from ca. 50 to 25 cm s^{-1} across a 100-fold increase in dosage of the pheromone (Charlton et al. 1993). Although the gypsy moth reduces its speed as it approaches a source of pheromone, we have chosen for our simulated moths a constant ground speed of 60 cm s^{-1} , which is appropriate for this species tracking a plume at a distance from its source. In our simulations, this velocity applies to upwind surges after the moth encounters the odor until the end of the subsequent casting flight.

Casting: typically loss of contact with the pheromone induces casting, a maneuver in which the moth ceases movement upwind and then “casts,” that is moves laterally with reversals of direction (counterturns) across the wind line. Casting latencies measured in wind tunnel mostly range between 0.3 and 0.7 s, depending on the species (Kuenen and Baker 1982; Baker and Haynes 1989; Vickers and Baker 1996); the slightly higher value (ca. 1 s) observed for the gypsy moth (Kuenen and Cardé 1994) is closer to the value we have used in our simulations (1 s). During casting, the value of the track angle (heading with respect to due upwind or 0° , as defined by Marsh et al. 1978) is centered at 90° or due crosswind (Kuenen and Cardé 1994). Consequently, the simulated track angle during casting is headed crosswind, following a normal distribution with mean $\mu = 90^{\circ}$ and deviation $\sigma = 1^{\circ}$ with respect to the instantaneous wind direction at the moment of turning.

Turning frequency: a gypsy moth flying along a pheromone plume generally adopts a zigzag path; the rate of counterturning is remarkably constant, ranging from 2.5 to 4 turns s^{-1} (Kuenen and Cardé 1994; Zanen and Cardé 1999), irrespective of the moth's size (Kuenen and Cardé 1993), concentration of odor in the plume and ambient temperature (Charlton et al. 1993), intensity of light (Cardé and Knols 2000), or wind velocity (Willis and Cardé 1990). Some small differences have been found as the male approaches a source in the forest, with 2.5 turns s^{-1} at 20 m from the source and 3.3 turns s^{-1} at 2.5 m from the source (Willis et al. 1991). Also, a wider plume produced by a cylindrical baffle seems to yield a lower frequency of turning compared with a narrower plume from a point-source emitter (Willis et al. 1994). We have used a turn frequency of 3 turns s^{-1} in our simulations with the exception of the alternative behaviors assayed in the casting strategies experiments, where lower frequencies (wider casts) were used. Considering the insects' ground speed used in our simulations (0.6 m s^{-1}), a turn frequency of 3 s^{-1} results in

average inter-turn legs of 20 cm, which represents the mean cross-sectional width of the casting flight. These narrow casting flights typically end with a return to plume-searching behavior. However, some field recordings of *L. dispar* show large crosswind sweeps after casting, which can be up to 4 m and take the moth back in contact with the plume or closer to the source of the odor (David et al. 1983). There is no clear evidence, however, that such large crosswind excursions are part of the return to plume finding or that they form part of the strategy for re-contacting the plume. In fact, during such a wide crosswind excursion, an insect would probably not maintain an upwind orientation of its body axis, which would be suggestive of a specialized behavior following loss of contact with the odor. Searching for a plume, which assumes no previous or recent contact with odor, does not keep an upwind orientation of body axis. In any case, a strategy employing final wide sweeps might increase the chances of re-contacting a plume and, even if not actually used as such by flying insects, could provide an insight into ways to increase the efficiency of robots' odor-search algorithms. Taking these considerations into account, a narrow casting behavior has been compared in the present work with final-sweep behavior of two different magnitudes, 4 and 6 m. A further behavior considered is an increasing width of the track of the casting flight, a possibility suggested by the reported observation that casting develops gradually with progressively increasing length of inter-turn legs (Kuenen and Cardé 1994). Because this might also increase the chances of re-contacting the plume, we have included a simulation trial with increasing width of the distances of inter-turn legs during casting.

Duration of casting: if 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 returns to searching (Cardé and Willis 2008). There is scant evidence on the approximate duration of casting in the field, but there are reports of male moths still casting 9–34 s after loss of contact with the plume (Marsh et al. 1978). Considering this, we have used a duration of 20 s for casting in our simulations.

Arrangement of the sources

The existence of additional sources of odor in the vicinity of an odor-plume could affect the performance of a given search-strategy. To test for this particular effect on the outcome of the simulation, two different scenarios were tested:

To evaluate the efficiency of the behavioral strategies used under two different conditions:

- (1) Single source.
- (2) Array of 25 sources arranged in a 5×5 grid with inter-source distances of 100 m.

The release area for virtual moths has been defined in order to double the area limited by the 100×100 m plots at the edges of the array. In this case, the array occupied 25 ha and the area of release was consequently 50 ha. In the single-source situation, the release area was 2 ha, with 1 ha considered as the area of influence of the odor's source.

Strategies for searching for plumes

Experiments were conducted to compare five different strategies for locating plumes (Table 1). Success was assessed in terms of percent of insects finding the plume (Plume Found), and the percent of total insects that eventually reached the source of the odor (Source Found). Total simulated time for a given iteration was 45 min (after which the parameters that were measured changed very slowly). A total of 1000 insects were simulated for each strategy.

Casting strategies

To assess the optimal behavior for efficient plume re-acquisition after a recent loss of contact with the odor, a batch of simulations was run with all insects being initialized in the same location 40 m downwind from a single source. The initial heading was set at an interception course with the plume to ensure that all insects would reach the plume almost simultaneously. Success was assessed in terms of the percentage of insects reaching the odor source.

Four maneuvers were modeled in relation to effectiveness of re-contacting the plume:

- (1) Narrow cast: casting behavior similar to the observations in wind-tunnel assays for gypsy moths, with a turning frequency of 3 turns s^{-1} . This produces a mean inter-turn leg of the search of 0.2 m.
- (2) Increasing cast: this behavior progressively reduces the turning frequency from 3 to ca. 0.3 turns s^{-1} producing a mean inter-turn leg of ca. 2 m after the last turn.
- (3) Final sweeps: a narrow cast is followed by two large side-to-side sweeps with an inter-turn distance of ca. 4 m.

Table 1 Characteristics of the different strategies for searching plumes

Strategy	Initial orientation	Exploration phase	Reorientation/relocation phase	
		Directional change	Directional change	Relocation phase duration
Intermittent correlated random Walk (intermittent CRW)	Random	5° $N (\mu = 5, \sigma = 1)$	New random orientation	–
Correlated random walk (CRW)	Random	5° $N (\mu = 5, \sigma = 1)$	–	–
Lévy walk	Random	New random orientation	New random orientation	200 s $N (\mu = 200, \sigma = 20)$
Downwind biased correlated random walk (downwind BCRW)	Downwind (180°)	5° $N (\mu = 5, \sigma = 1)$	–	–
Crosswind biased correlated random walk (crosswind BCRW)	Crosswind (+90° or –90°)	5° $N (\mu = 5, \sigma = 1)$	–	–

Notes: Initial orientation of the searcher at the onset of simulation; exploration phase with frequent directional changes every 20 s $N (\mu = 20, \sigma = 5)$; reorientation/relocation phase with directional changes every 200 s $N (\mu = 200, \sigma = 20)$ that, in the case of relocation behavior, are maintained for the duration of this phase. In all cases, variation has been modeled as a random normal distribution $N (\mu, \sigma)$ around the central value (μ) and with a given variance (σ) set in the simulation parameters.

- (4) Final large sweeps: a narrow cast is followed by two large side-to-side sweeps with an inter-turn distance of ca. 6 m.

All casting behaviors lasted 20 s before orienting downwind. Total simulated time for a given iteration was 15 min. A total of 1000 insects were simulated for each behavior.

Results and discussion

The different strategies for searching for plumes resulted in visibly different flight tracks (Fig. 4). The crosswind-biased (Fig. 4D) and the downwind-biased strategies (not shown) gave long and quite linear paths that quickly take the insect far from the location from which it initiated flight. Under certain conditions, this behavior can drive the insect away from small areas with high densities of females, even after contact and loss of a pheromone plume (as seen in Fig. 4D) and, therefore, might be especially disadvantageous in scenarios of sparsely distributed clusters of calling females. The non-biased strategies (Fig. 4A, B, and C) resulted in similar tracks that differed in the acuteness of the turns, with LW producing the sharpest turns and CRW the most gradual ones.

Our results clearly show that strategies with no directional bias like CRWs and LW yield greater success in finding plumes than biased strategies (either downwind or crosswind) in the three conditions of wind evaluated (Fig. 5). However, there is not a significantly better outcome with any of these non-directionally biased behaviors, at least with the characteristics of paths used here. Because a LW is a scale-free pattern (Reynolds and Frye 2007), differences in the duration of steps between directional

changes would produce equal configurations of paths but probably would affect the overall efficiency, especially in certain distributions of sources. Longer durations would result in wider areas being searched less thoroughly during the exploration phase, while insects would be driven farther away during the relocation phase. For instance, if the patchiness of resources (sources of odor in this case) is great, a LW would probably perform better than any other strategy, especially if the long sections of the path (relocation phases) and the distance between patches or clusters of odor-sources are similar.

Our simulations also show that a crosswind bias improves location of a plume (Fig. 5) and its source (Fig. 6) over a downwind bias. It has been argued that crosswind is actually the result of two possible directional sectors (“left and right” of the wind flow), whereas a purely downwind (or upwind) trajectory encompasses just half of the possible directional orientations of crosswind (Elkinton et al. 1983; Cardé et al. 2012). In our simulations, however, a given insect will randomly start flying either right or left of the wind line and it will not change its crosswind orientation during its BCRW. Considering it has equal chances of being initialized at either side of the pheromone plume, its probability of heading toward a plume are the same in crosswind and downwind strategies. Interestingly, the downwind-biased CRW shows a higher efficiency in plume finding when the wind’s direction shifts widely (Fig. 5), especially away from the odor source (Fig. 6), as suggested by others (Sabelis and Schippers 1984; Dusenbery 1989, 1990; Zanen et al. 1994). A rapidly meandering plume extends the area of influence of a particular source compared with straighter plumes,

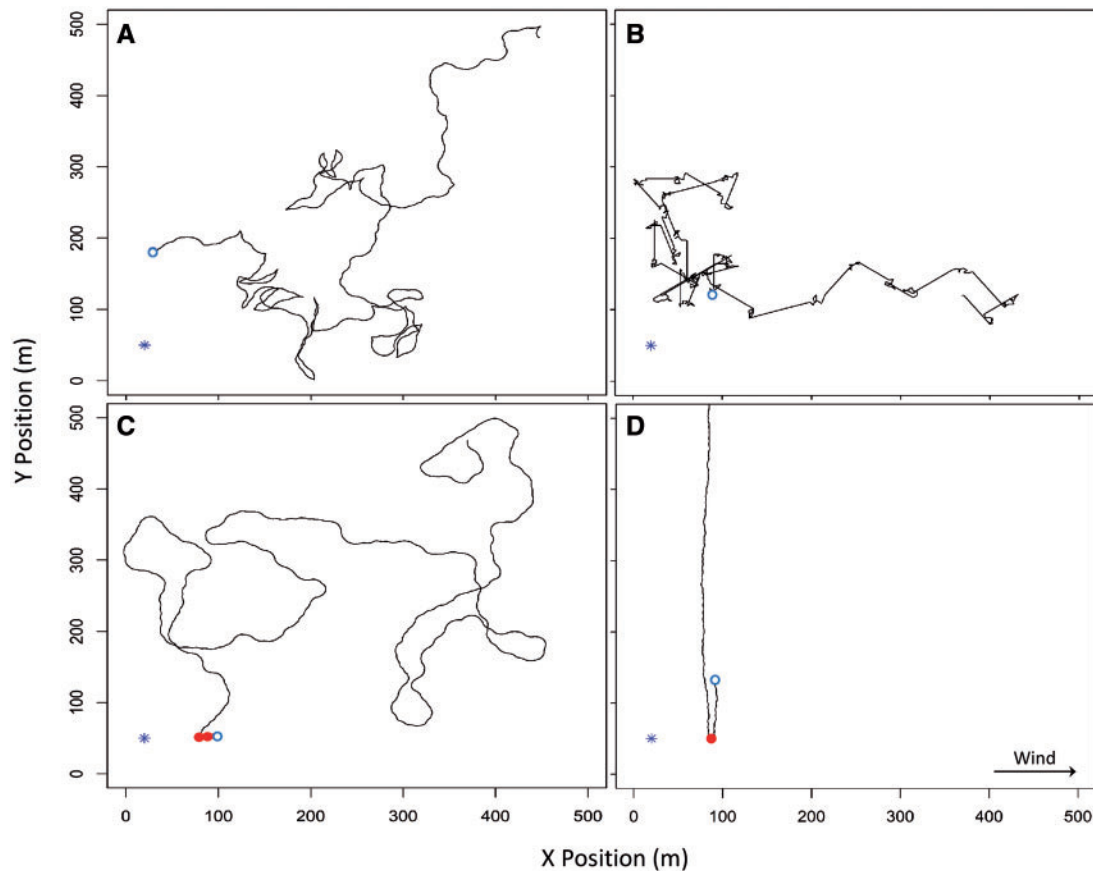


Fig. 4 Examples of simulated flight tracks showing four of the five simulated Search-Strategies. (A) Intermittent correlated random walk; (B) Lévy Walk; (C) correlated random walk; (D) crosswind-biased correlated random walk. Empty circle indicates position at the onset of the simulation and solid circles in C and D indicate transient contact with the odor plume, after which the search behavior is reset. A single odor source (positioned at $x=20$ m, $y=50$ m) is present in these simulated tracks and marked with an asterisk (*). Wind arrow indicates average wind direction for all tracks. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

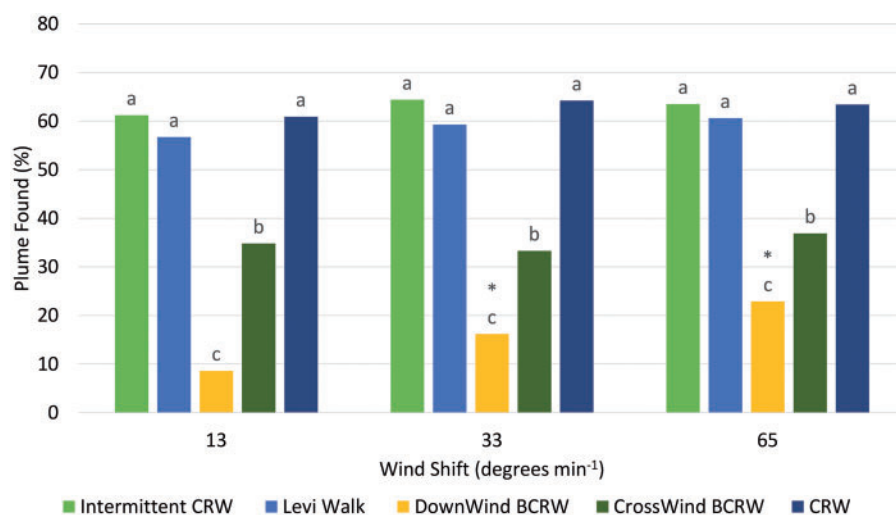


Fig. 5 Comparison of the success of plume finding with three different wind conditions. Arrangement of 5×5 grid of odor sources spaced 100 m apart. Different lowercase letters denote significant differences between strategies for a given wind condition. Asterisks indicate significant differences across wind conditions for a given strategy (Kruskal–Wallis test; $P < 0.05$). A total of 1000 insects were simulated for each behavior in every wind category. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

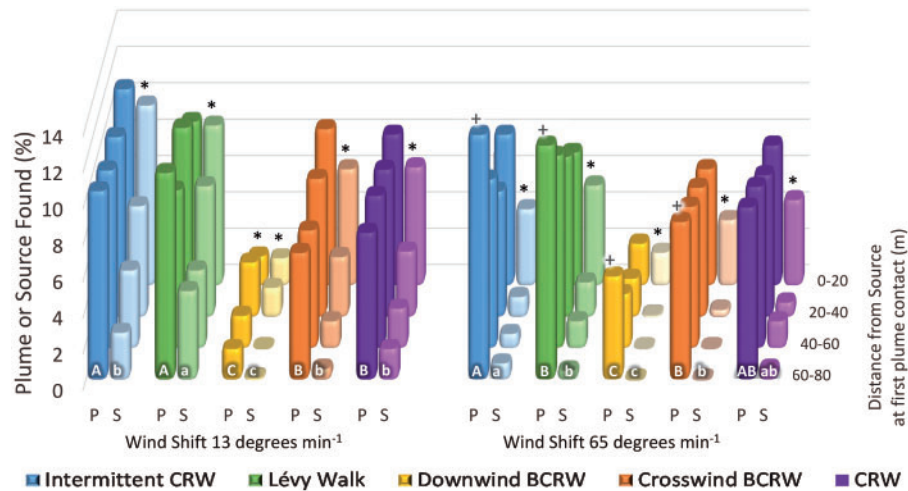


Fig. 6 Percent of insects finding the plume (P) compared with percentage of insects that eventually reach the source (S) versus distance from the point of emission at first contact with the plume (a single source was defined). Narrow (0.2 m wide) casting flights were used in all cases. Asterisks (*) indicate higher occurrence near the source (0–40 m) and crosses (+) higher occurrence away from the source (40–80 m) (Wilcoxon paired test; $P < 0.05$). Different letters at the base of the columns denote significant differences between strategies for Plume Found (uppercase) or Source Found events (lowercase) within a given wind-condition category (considering all insects, regardless of distance at initial contact) (Kruskal–Wallis test; $P < 0.05$). A total of 1000 insects were simulated for each behavior in every wind category.

the effect of which would be especially apparent when the chances of contacting more than one plume in a reduced area are scarce. With a temporal shift of the wind of 65° that allows the plume to fully extend in straight line between directional changes, the along-wind component of the area of influence of an 80-m plume would range between 67.5 and 80 m, while the crosswind component would range between 0 and 86 m. Although the trigonometric calculations point at a potentially wider crosswind section in shifts of the wind of more than 60° , the shape of the area of influence also depends on wind speed and on the rate of change in direction of the wind (Fig. 1B). To reach the maximum area, the wind's dynamics would need to allow the plume to extend to almost its full length in a certain direction before shifting toward a new one. Considering this, whenever the wind blows in a more or less constant direction, the widest section in average would correspond to the downwind component and, therefore, the plume should be more easily encountered by a searcher that moves crosswind, even when the wind shifts as much as 65° . This could explain why our results always show a better performance of crosswind-biased CRW with respect to downwind BCRW even at shifts of $65^\circ \text{ min}^{-1}$ in the wind.

Wind flow-oriented search strategies also proved particularly inefficient in finding the source of a plume when initial contact with the plume was made far away from its source. This was particularly

evident in shifting winds, where no insects found the source when initial contact with the plume was made beyond 40 m (Fig. 6). In such situations, a moth has an increased probability of losing contact with the plume and then returning to search behavior; this would tend to keep it in the vicinity of the surrounding area in the case of CRW-type strategies, especially LW. In fact, mean transit time for insects that eventually find a source in the grid array was higher (ca. 1000 s) for these strategies than for biased strategies like Downwind BCRW (ca. 200 s) or Crosswind BCRW. It is noteworthy that transit time for the latter strategy increased from ca. 300 s in stable wind conditions ($13^\circ \text{ min}^{-1}$ wind shift) to ca. 650 s in variable wind conditions ($65^\circ \text{ min}^{-1}$ wind shift) where lost and found events during plume navigation were more frequent (data not shown). The short transit time for Downwind BCRW would be explained by the fact that only the few flights that rarely lost the plume were eventually able to find the source, since plume finding is less probable for this strategy under any wind condition (Fig. 5).

Once the plume has been contacted, the behavioral response to loss of odor can greatly affect the final efficiency in locating the source. Our simulations show that wide casting-flights result in increased rates of source finding (Fig. 7). As is obvious from the simulated flight tracks (Fig. 8), and considering that plumes can meander for tens of meters when not in close proximity of the source,

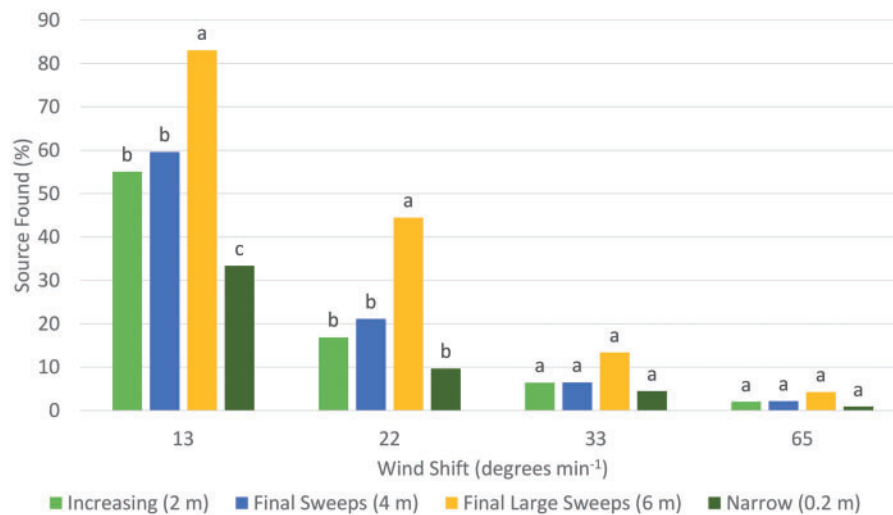


Fig. 7 Comparisons of casting behaviors employed in finding the source after initial contact and loss with the plume under four different conditions of wind. Different lowercase letters denote significant differences between strategies for a given wind conditions (Kruskal–Wallis test; $P < 0.05$). A total of 1000 insects were simulated for each behavior in every wind category. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

the narrow casts observed under wind-tunnel conditions could be viewed as the equivalent of station-keeping when the plume was lost and had not yet been re-located. Large crosswind sweeps before switching back to plume-search strategy (Fig. 8C, D) significantly increased the chances of re-contacting the plume. It is noteworthy that, for this simulation, insects were headed directly downwind immediately after casting behavior. As downwind flight proved to be the least effective in locating the plume, this reduced the effect of source finding after subsequent re-acquisitions of the plume that might introduce more variability in the results.

The difference in source finding using the Final Large Sweep (6 m wide) was the most successful strategy when the wind direction shifted moderately and it is also interesting to point out that Increasing Cast (2 m wide) was as efficient as a wider Final Sweep (4 m wide) (Fig. 7). This finding suggests that progressive increases of the width of casting (as in Fig. 8B) might be a better strategy than abrupt changes in the magnitude of the crosswind component of casting flight (as in Fig. 8C, D). Although there is no evidence that moths increase the width of their casts to that extent (2 m or more), this behavior might be optimal when applied to artificial systems, as it would progressively explore a wider area during an attempt to renew contact with the plume.

Caveats

The simulations described here are explicitly framed around the well-documented behavior of the male

gypsy moth. This species lacks mouthparts and so its foraging behavior for females is not confounded by searching for adult food, nor is there any evidence that the odor of larval host plants influence male behavior. These attributes simplify the model's assumptions. What we have not considered here is the possible presence of multiple pheromone sources in close-enough proximity to create overlapping plumes; clearly in dense populations, calling females can be in such competition (Cardé and Hagaman 1984) and clumping of odor sources could result in an increase in the effective length of the merged plume (Andersson et al. 2013). We also have assumed a simple cycle of less than an hour of response. Male response in the gypsy moth occurs over much of the day and into the night (Cardé et al. 1974, 1996). To simulate a lifetime cycle of a male we would need to extend the model to allow response over a full 24-h cycle and to account for other factors such as predation and other mortality agents (Elkinton and Cardé 1980). These modifications would be useful in trying to understand how a series of pheromone-baited traps deployed at various densities would be useful in surveillance programs aimed at detection of invasions (Cardé 2001; Yamanaka and Liebhold 2009); in this application, capture of a single male would trigger a delimitation survey (deploying traps at an increased density), whereas a false negative (males are present but none are captured) could allow proliferation of an incipient population until another detection event. Other applications of our model are mainly in the realm of exploring other aspects of optimal strategies

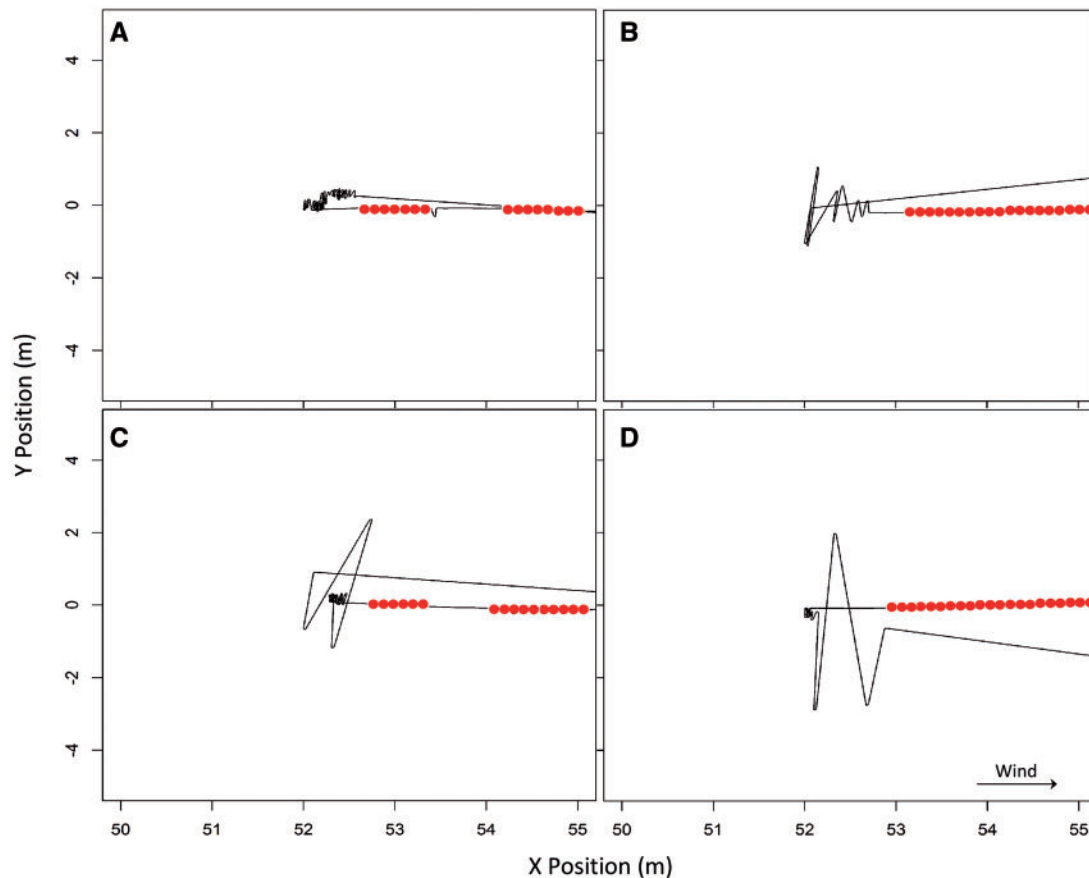


Fig. 8 Simulated flight tracks showing the four assayed casting behaviors. (A) Narrow (0.2 m inter-turn distance); (B) increasing (2 m maximum inter-turn distance); (C) final sweep (4 m maximum inter-turn distance); (D) final large sweep (6 m maximum inter-turn distance). Flight track is initiated when contact is made with the odor (depicted by solid circles), which stimulates the insect to fly upwind (left). After casting for 20 s, the insect flies downwind (right). Wind arrow indicates average wind direction for all tracks. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

of mate location for males and females, such as female competition, including how variation in rate and timing of pheromone release affects the probability of successful mate acquisition in sparse and dense populations.

Conclusion

Our simulations with a variety of strategies with and without wind-correlated biases (Fig. 4) showed that a Downwind CRW strategy was the least effective for establishing initial contact with a plume, followed by a Crosswind CRW. The highest incidences of contacting a plume were provided by the three other modeled strategies, an Intermittent CRW, a LW, and a CRW, all producing similar probabilities of initial contact, with wind fields shifting in direction between 13° and $65^\circ \text{ min}^{-1}$ (Fig. 5). The probability of successfully orientating to within 2 m of the plume's origin was of course partly, but not entirely, contingent upon the probability of initial contact with the plume.

Strategies of ranging flight, like a LW, that explore the surrounding area after losing the plume (at least for some time before initiating attempts at re-location) also seemed to increase the chances of finding the source after re-contacting the plume (Fig. 6).

The optimal casting for re-contacting a pheromone-plume is directly related to the final crosswind section of the casting flight, with better performance with wider sweeps. It is also noteworthy that progressively increasing the width of the casting flight seems to be a better strategy than using narrow casting flights as observed in wind tunnels, even if such flights end with final sweeps of a similar width to the last sections of the increasing casting (Fig. 7). Although there is no evidence that moths use progressively wider castings in the field, this strategy might be a useful application to the tracking of plumes by autonomous robots.

A sustained, preferential orientation to wind flow requires continual processing cues from optomotor feedback, and while this clearly is the case for

tracking of plumes upwind, our simulations suggest that the finding of plumes can be optimized without reference to the instantaneous direction of wind flow. These simulations also suggest that optimal strategies for robotic vehicles (airborne or ground-based) programmed to contact an odor plume need not involve the detection of wind flow in setting a foraging path and this also matches the observed behaviors of two different species moths in the field (Elkinton and Cardé 1983; Cardé et al. 2012) for which flight tracks and contemporaneous measurements of wind flow are available.

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