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Position Around A Tree: Consequences For Pheromone Detection

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Abstract The air flow pattern expected around a cylindrical object such as a tree in slow wind, is predicted from fluid mechanics to have areas of faster flow (upwind) and slower recirculating flow with eddies (downwind). An organism located on the surface of a tree would experience different flow depending on its circumferential position. If that organism was searching for a chemical signal, such as a pheromone plume, it might maximize its probability of chemodetection by placing itself in areas of greatest flow speed (the upwind surface of the cylinder, i.e., in front of the separation points). We tested whether wood cockroaches in the genus *Parcoblatta* exhibit such upwind positioning; they live in forests, and males actively fly from tree to tree, while searching for females releasing sex pheromone. In contrast to an expectation of upwind preference, male cockroaches were evenly distributed around trees relative to upwind (measured with a novel “feather boa” flow visualization technique), even though the wind direction was relatively steady. We investigated whether sex pheromone could be detected at any location around a cylindrical surface in a laboratory flow chamber by using *Bombyx mori* wing fanning as a bioassay. Although upwind moths arrayed on the surface detected pheromone more rapidly, pheromone detection occurred at least a third of the time at any position, which could explain the even distribution of *Parcoblatta* males around trees.

Keywords Air flow · Reynolds number · Forest insect · Velocity boundary layer · Wind variability · Pheromone · Olfaction · Cockroach · Chemoreception · Flow visualization

Introduction

Many forest insects localize potential mates by the use of volatile, airborne pheromones (Elkinton et al., 1987; Brady et al., 1989; Wyatt et al., 1993, 1997). Wind is the primary

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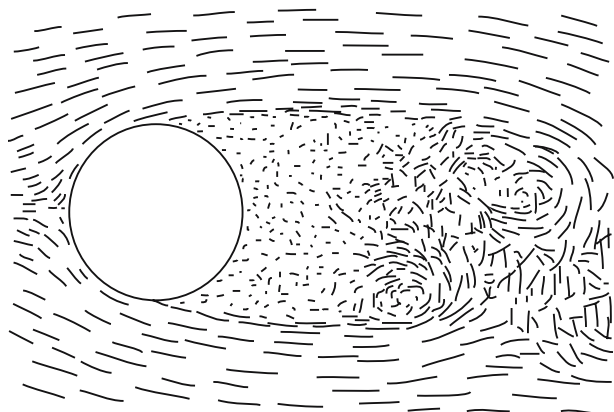
pathway for communication via the olfactory channel; as such, it determines where pheromones will be carried. Although the pheromone molecules and the air currents that bear them are invisible, we can visualize their movements by using smoke, bubbles, and other physical markers. These visualization techniques have been vital in developing our understanding of natural airflow patterns in forests and grasslands (David et al., 1982, 1983; Elkinton et al., 1987; Willis et al., 1994; Murlis et al., 2000). Air flow patterns dictate the shape and behavior of pheromone plumes and the challenges faced by insects tracking such complex and intermittent signals. It is well-established that pheromone released by an insect travels downwind in a meandering sinuous plume as a result of wind shifts (David et al., 1982, 1983; Murlis et al., 1992, 2000). Despite the slow (<1 m/sec) and shifting air movements in a forest (Smith et al., 1972; Oliver, 1975), insects are able to track pheromone or host-odor plumes and locate odor-emitting individuals (Brady et al., 1989, 1990; Willis et al., 1994).

An animal located on a tree or other obstacle, around which pheromone-laden air is swirling, may have opportunities to intercept or miss a pheromone plume, depending on its location around the tree. Downwind of a cylindrical obstacle, the air is moving especially slowly and recirculating in eddies (Fig. 1) (Brady et al., 1989; Vogel, 1994). It follows from this flow pattern that for individuals on a surface: (1) upwind individuals should intercept pheromone first, whereas individuals further downwind on the same tree would receive a delayed and possibly diluted chemical sample; (2) as a result of these velocity differences between upwind and downwind areas, individuals can potentially change the amount of air they sample by changing their position around the cylinder. Therefore, insects on the upwind surface would be sampling a larger volume of air per unit time, which would allow an individual to increase its likelihood of encountering pheromone molecules.

To evaluate whether potential advantages of upwind positioning are utilized by a forest insect that uses volatile sex pheromones to locate a mate, we measured circumferential positions of native wood cockroaches in the genus *Parcoblatta* in a forest. These cockroaches actively court in early summer during the evenings (Hebard, 1931; Helfer, 1953; Lawson, 1967; Horn and Hanula, 2002). The short-winged (nonflying) females are found primarily on the ground and release sex pheromone (Gorton, 1980; Gemeno et al., 2003). Males are long-winged and fly from tree to tree, presumably while searching for a pheromone-releasing female (Gorton, 1981; Miller, personal observation).

In the laboratory, complementary investigations were performed to evaluate how the timing and probability of interception of pheromone plumes varied with location around a

Fig. 1 The pattern of flow around a cylinder. This is visualized by using *pathlines*; a *pathline* shows the path followed by a parcel of air during a set time interval (Vogel, 1994). Flow approaches the cylinder from the left, and *longer pathlines* indicate faster flow. Flow near the downwind surface of the cylinder is much slower and contains swirling eddies. The cylinder and flow are viewed in cross-section. (Pathlines were drawn based on a photograph in Van Dyke, 1982, p. 31, of flow at $Re=2000$)



cylinder. For these measurements, we used a wing fanning assay to visualize pheromone interception by moths arrayed around a cylinder in controlled flows. Adult male *Bombyx mori* show a clear visual response (wing fanning) to detection of the sex pheromone released by the females (Loudon and Koehl, 2000).

If wind direction is shifting substantially, an organism on a tree surface would need to relocate to stay upwind. To measure the rate at which the upwind direction on a tree changed over a biologically relevant time scale (on the order of minutes or hours), we made multiple measurements of upwind direction both in a natural forest and on solitary trees in a field.

Methods and Materials

Distribution of Parcoblatta Relative to Wind Direction Orientation behavior of males from two species of *Parcoblatta* cockroaches (*Parcoblatta pennsylvanica* and *Parcoblatta uhleriana*) was observed during their mating season in June of two successive years. [Note that authorities differ on the spelling for *P. pennsylvanica*; Hebard (1917) uses *P. pennsylvanica*.] The field site was a deciduous forest within the Rockefeller Experimental Tract, Lawrence, KS (Kansas Biological Survey). Male cockroaches became active (were flying around) as darkness fell. After landing on tree trunks, males often touched the tree surface briefly with their antennae before taking off or staying in place, but did not often walk far on the tree surface. Activity of these flying males declined about 4 hr after dark (males were sometimes observed to move under bark). After sighting a male on a tree surface, its circumferential position was measured with a compass, and its height above the ground was measured to the nearest centimeter (cm) with a meter stick. Upwind direction was recorded at each tree at the time the cockroach was sighted by using a novel marabou “feather boa” visualization method (marabou feathers are easily displaced, being fine and light). The boa (marabou feather boa, Hobby Lobby) was wrapped around the tree at the time and height at which the male was located, generating a circumferential wind indicator. The down-like feathers splayed apart in response to the wind, indicating upwind direction at the tree surface, which was recorded with a compass. In addition to upwind direction, the boa visualization method enabled us to determine whether the air speed was below the slow threshold air speed, indicating extremely still air. Thus, this boa method allowed measurement of wind direction, but only a qualitative (or threshold) estimate of wind speed. This method differs from the method of Baker and Cardé (1979) that used the calibrated displacement of a single feather to estimate air speed at a single location.

The response threshold of the marabou boa (minimum air speed required for a detectable response) was determined by placing it around a cylinder (9-cm diameter) placed inside a large slow-flow chamber (cross-sectional area=1,089 cm²). The air moving through the chamber passed through a flowmeter (King Instrument Company) that was used to measure the volume flow rate, from which the average cross-sectional velocity was calculated. The response threshold of the boa, denoted by noticeable parting of feathers showing wind direction, corresponded to an average ambient flow of approximately 2.5 cm/sec (imperceptible by humans).

Variability in Upwind Direction at Tree Surfaces for Solitary Trees Wind direction variability was estimated at tree surfaces during the months of June and early July. Measurements of upwind direction were taken once every minute for solitary trees. Each of the six “solitary” trees was a minimum of 7.5 m from any neighboring tree. The variability

in wind direction over time for individual trees was estimated from multiple measurements; the upwind direction was recorded to the nearest degree at the surface of individual trees by using a compass and boa (as described above) for 10 successive measurements at 1-min intervals for each tree. Three sets of 10 successive measurements were taken at each of three different times: in the morning, midday, and evening for each tree (“morning” times were between 8 and 10:40 A.M., “afternoon” times between 12 and 2:40 P.M., and “evening” times between 8 and 10:40 P.M.). The variability in wind direction was calculated as the circular standard deviation of the 10 successive minute-by-minute measurements at a tree; the circular standard deviations were averaged for the three (or two) sets for each time of day and tree. During one morning, measurements were not taken due to rain. The circumferences of these six trees ranged from 0.17 to 1.45 m.

Variability in Upwind Direction at Tree Surfaces for Forest Trees We also determined whether upwind direction was the same for multiple trees in a group, both in the forest and at its edge, to look at the effect of neighboring trees during the month of June. We selected 10 trees along the edge of the forest and 10 trees within the forest for repeated measurements of wind direction over a 10-d period, recording upwind directions once early in the evening (8–9 P.M.) and once 1/2 to 2 1/2 hr later (weather permitting). We also compared the frequency with which the wind exceeded a slow threshold (proportion of times that wind direction was detectable using the feather boa method) between “edge” and “within forest” trees.

Experimental Animals for Pheromone Detection in Laboratory Measurements *B. mori* were reared on mulberry leaves under a natural light cycle. Once caterpillars had pupated, they were sexed, placed in individual cups, and checked daily for emergence. All males used were at least 1 d old and unmated; some males were used repeatedly by random selection from the available males. Unmated females were used as a sex pheromone source.

Experimental Setup for Controlled Flow in Laboratory Measurements Tethered male moths were arrayed around a vertical cylinder (27 cm tall and 16.6 cm diameter) centered in a flow chamber (60×84×27 cm). The moths were located halfway up the cylinder, spaced 45° apart (eight males total at a time). Moths were secured to wooden supports that passed through slits in the otherwise solid cylinder, allowing them to be positioned at the cylinder surface (“0 cm”) or 5 cm out from the surface. Moths were positioned with their anterior–posterior axes oriented vertically, so that their wing fanning would drive air downwards (Loudon and Koehl, 2000) rather than around the cylinder. The flow chamber was located in a laboratory hood, which generated the air flow and exhausted the pheromone-laden air to the outside. The flow chamber was either centered within the hood opening or positioned against a side to generate different types of flow: symmetrical or asymmetrical (left/right), respectively. These different flows generated pheromone plumes of different shapes (Fig. 2). Cloth mesh covered the front of the flow chamber to slow and smooth the flow. Trials were videotaped by a camera (Sony Digital Handycam DCR-PC101) mounted above the flow chamber.

The cylinder with the array of eight moths was placed in the center of the flow chamber with one male placed directly upwind. Lights were turned on, and the moths were given time to acclimate to the flow (~20 min), because males would wing fan when they were disturbed by movement or changes in lighting. Once most males had ceased fanning, the pheromone was released into the air stream as described below. Any males that were already fanning at the beginning of the trial were not included in the analysis. The response

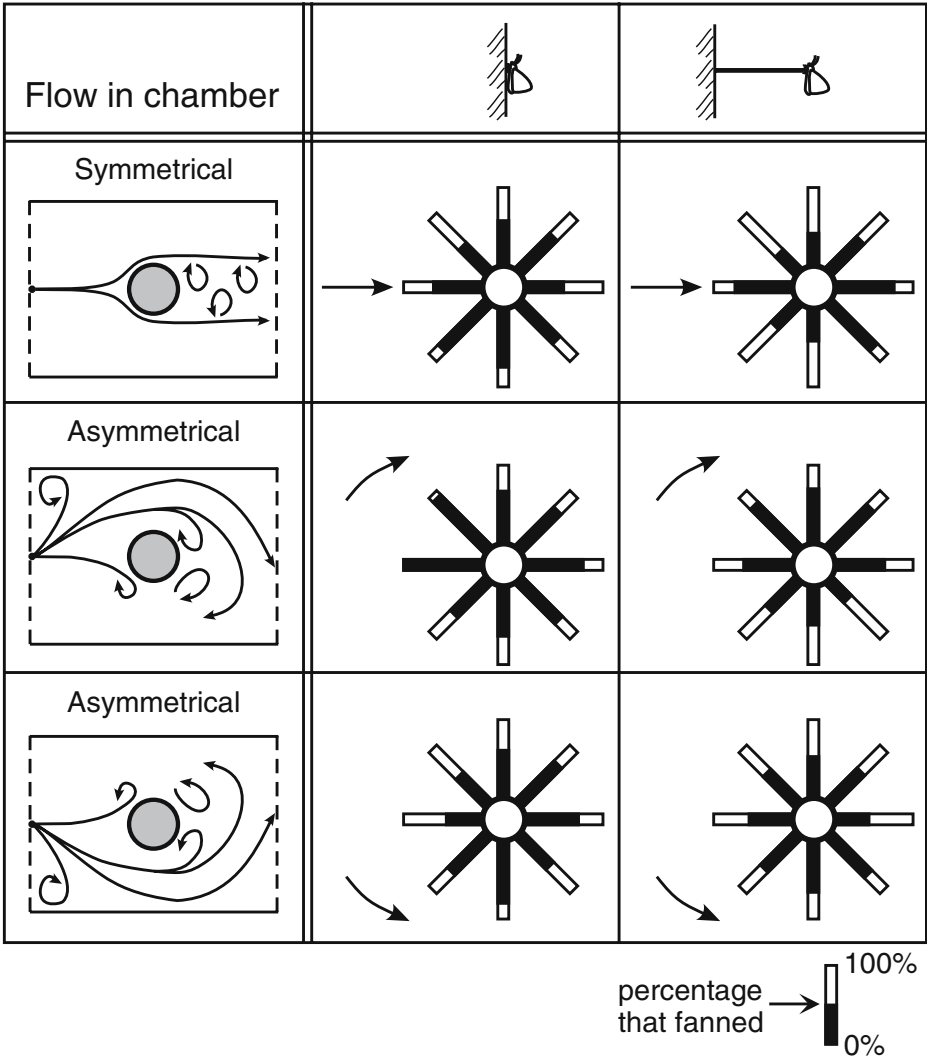


Fig. 2 Male detection of pheromone from all positions around the cylinder. On average, this detection occurred 62% of the time, as indicated by wing fanning, across all flow types and moth positions. The percentage of males that fanned is indicated by the *black fill in the bar*. A *diagrammatic representation* of the flow treatment appears in the left column as viewed from above, with the pheromone plume generated from a point source as shown. The distance of the moth from the surface of the cylinder (0 or 5 cm) is indicated in the *top row*; the moths on supports are shown as viewed from the *side*

times (onset of wing fanning) of the males were recorded for 30 sec starting with the pheromone release. The cylinder was then rotated so that a different male was now in the upwind position (order randomly assigned), the males were given at least 5 min to acclimate to new positions, and the wing fanning response times to the next pheromone plume were recorded. The cylinder was turned repeatedly until each of the eight males had been in each position once (eight rotations). These eight rotations, with eight male responses at each of the eight positions, were considered one “trial.” A pool of 51 male moths was used in the 23 trials.

One to three live females visibly extruding their pheromone glands were placed into a 30-ml syringe centered at the upwind edge of the flow chamber (34 cm upwind). The amount of pheromone released by the females was unknown and presumably variable, which was not a concern because the responses at different positions around the cylinder were compared to each other, thus, providing an internal control. To generate a pheromone plume, air was passed through the syringe slowly and joined the air moving through the flow chamber. The air passed through the syringe at a volume flow rate of 9.9 ml/sec for 8 sec time interval; therefore, approximately twice the volume of the syringe was exchanged during the stimulus. The air flow through the syringe was controlled with an aquarium pump, a solenoid valve, and a custom-built timing circuit (Instrumentation Design Laboratory, University of Kansas) and was calibrated by collecting air in an underwater graduated cylinder with the same setup. A light-emitting diode (LED) light (in view of the video camera but not the moths) was illuminated for the 8 sec that air was passing through the syringe, to record the timing of the pheromone release on the videotape. For the controls ($N=3$ sets of eight males), air was passed through a clean syringe without a female, and the males were observed for 30 sec. The inner surface of the chamber was cleaned daily (wiped with ethanol and air-dried).

Controlled Flow in Chamber We generated slow flows within a flow chamber that contained small, ephemeral eddies to mimic those characteristics of air flow that we would expect in a natural forest (Fig. 2). We generated a symmetrical flow (Fig. 2, top) and asymmetrical flows (Fig. 2, middle and bottom) that contained a large circulating gyre in addition to the flow that separated and moved around both sides of the cylinder. These gyres were either clockwise or counterclockwise when viewed from above, depending on whether the flow chamber was placed against the right or left side of the hood opening, respectively. The large-scale gyration had the effect that the “upwind” area on the cylinder was displaced slightly to one side. Flow visualization by using smoke indicated that small-scale eddies formed and dissipated at a variety of different locations within the chamber at different times leading to a complex and slightly unpredictable flow. The temperature within the chamber ranged between 23 and 24°C.

The flow chamber was illuminated by lamps on both sides; however, lighting was nonuniform due to additional natural lighting from windows. The difference in light levels appeared to change the behavior of the males slightly, with those in brighter lighting fanning more readily. In symmetrical flow, males would be expected to fan at the same time as those opposite them. However, we found that those on the side with brighter lighting fanned earlier than males in dimmer lighting at both 0 and 5 cm from the cylinder (Wilcoxon rank sums; 0 cm, $P_{2\text{-sided}} < 0.001$; 5 cm, $P_{2\text{-sided}} = 0.003$; time difference was 2 sec or less). To compensate for the difference in speed of fanning as a result of differential lighting, we applied a light correction factor. Adjustments of ± 0.5 or 1 sec were applied to each position (except directly upwind or downwind) and distance from the cylinder surface in all flow conditions.

Burning incense sticks were used as a smoke source to visualize air flow patterns and speeds around the cylinder and within the flow chamber. Although incense smoke is not neutrally buoyant, the horizontal component of movement is independent of its upward component. Smoke was illuminated from both sides and filmed from above. Motion analysis software (Motus 8, Vicon/Peak Performance, Englewood, CO, USA) was used to digitize smoke paths across multiple frames of video to determine how long it took smoke to travel from the syringe to the cylinder to the nearest 1/60 of a second. Note that the distance smoke traveled to reach the cylinder is not the same for symmetrical flow as it is

for asymmetrical flow, because in symmetrical flow, smoke traveled directly to the point on the cylinder closest to the syringe. Flow visualization demonstrated that there was no significant difference in the time for smoke to reach analogous points on the left vs. the right sides of the cylinder in symmetrical flow (two-way analysis of variance (ANOVA) with side and position as classes, $N=38$, $P=0.186$ for side comparison).

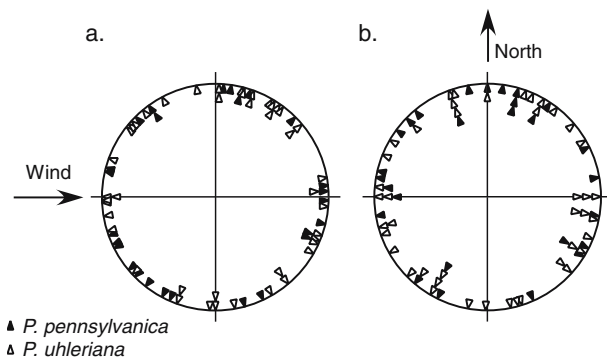
Flow speeds from the syringe to the cylinder estimated by smoke movements (as described above) are as follows: symmetrical 0.5 m/sec (± 0.04 SD, $N=3$), asymmetrical clockwise 0.2 m/sec (± 0.04 SD, $N=18$), and asymmetrical counterclockwise 0.3 m/sec (± 0.6 SD, $N=18$). Therefore, it took approximately 0.5–2 sec for the pheromone to be carried from the syringe to an upwind moth, depending on the flow. For symmetrical flow, it would take approximately 2 sec for the front of a pheromone patch to leave the syringe, diverge, and be carried completely past the two sides of the cylinder. Pheromone that has passed downwind of the cylinder may be caught up in a recirculating eddy and brought back to the surface more slowly (Fig. 2). For asymmetrical flows, it would take approximately 10–20 sec for a pheromone patch to leave the syringe and swirl completely around the cylinder.

Statistical Analysis Circular statistics were performed in Oriana 2.01b (Kovach Computing Systems; Anglesey, Wales). Other statistical analyses were done by using SAS (version 8.2, Cary, NC, USA).

Results

Natural Wind Conditions and *Parcoblatta* Positions Male *Parcoblatta* cockroaches of both species were found in approximately equal numbers on the upwind and downwind halves of trees: *P. pennsylvanica* ($N=14$ upwind, $N=13$ downwind) and *P. uhleriana* ($N=19$ upwind and $N=24$ downwind). The distribution around the circumferences of trees with respect to the upwind direction was not different from a uniform distribution for either species (Fig. 3; Rayleigh's uniformity test for circular statistics $P>0.05$). We also tested whether *Parcoblatta* males were positioning themselves on the tree by compass direction; there was no difference from a uniform distribution for either species (Fig. 3; Rayleigh's uniformity test for circular statistics $P>0.05$). Although males from both species were found at a variety of different heights above the ground (range 0.1 to 2.3 m), the species were found at different heights on average, as has been shown earlier (same species,

Fig. 3 Distribution of cockroaches of both species around tree circumferences. Each triangle corresponds to the position of an individual adult male. Positions are displayed in two different frames of reference (*a* and *b*). *a* Positions relative to the upwind direction. *b* Positions relative to magnetic north



Gorton, 1980; different species and genera, Schal, 1982). *P. pennsylvanica* males were significantly higher up than *P. uhleriana* males (1.1 vs. 0.6 m averages; one-way ANOVA, $P < 0.001$ for species).

Variability of Flow Direction at Tree Surfaces for Solitary Trees Variability in wind direction on a time scale of minutes is significantly affected by time of day, with evening wind direction being the least variable (Fig. 4). Note that our evening measurements were made during the courtship time of *Parcoblatta*. The standard deviation (circular) of wind direction of the minute-by-minute measurements over the 10-min intervals in the mornings averaged 17° ($N=4$ sets), in the afternoon, averaged 24° ($N=6$ sets), and in the evening, averaged 10° ($N=6$ sets) (ANOVA of wind variability with time of day, $P < 0.01$, $N=16$).

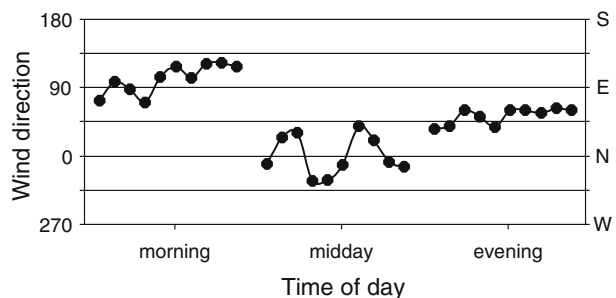
Variability of Flow Direction at Tree Surfaces for Forest Trees Variability in wind direction in the forest was estimated by comparing upwind direction at the surface of trees early in the evening (8–9 P.M.) and later (between 1/2 and 2 1/2 hr later) at the same trees (10 trees at the forest edge and 10 more interior). The upwind direction at these surfaces typically did not change much during an evening: the average difference in upwind direction for individual forest trees was 23° for trees at the edge of the forest ($N=58$; averages of absolute differences) and 31° for the more interior trees ($N=36$; averages of absolute differences).

The variability of upwind direction at the surfaces of trees for a group of 10 trees was not affected by its location (edge vs. within forest) (Wilcoxon sign-rank test, $N=8$ sets of 20 trees, $P > 0.05$). However, there was a small but significant difference in upwind direction at the surface of trees depending on whether the tree was at the edge of the forest or more interior: the average difference was 15° (Wilcoxon sign-rank test, $N=8$ sets of 20 trees, $P < 0.027$), suggesting that the wind direction is shifted by the resistance of the vegetation as the air passes through the forest.

Wind speed was also affected by tree location (edge vs. within forest). The number of times during which flow was too slow to displace the boa feathers was significantly higher within the forest (wind not detectable in 44% of trials) compared to trees at the forest edge (wind not detectable in 17% of trials) (Wilcoxon sign-rank test, $N=17$ sets of 20 trees, $P < 0.005$).

Detection of Pheromone Around a Cylinder in Controlled Flows Within our experimental conditions, sex pheromone was detected by at least some of the male moths, for any flow type, at any position or distance from the cylinder (Fig. 2). Across all trials, an average of 62% of the moths were able to detect pheromone (noted by wing fanning behavior; range

Fig. 4 Variability in upwind direction at a tree surface as a function of time of day. Shown is a representative set of measurements taken every min for 10 successive min at 3 different times during the day (starting at 8 A.M., 12 P.M., and 8 P.M.). Wind striking the tree surface at its northern-most point has a wind direction of “0” (east is 90, south is 180, west is 270)



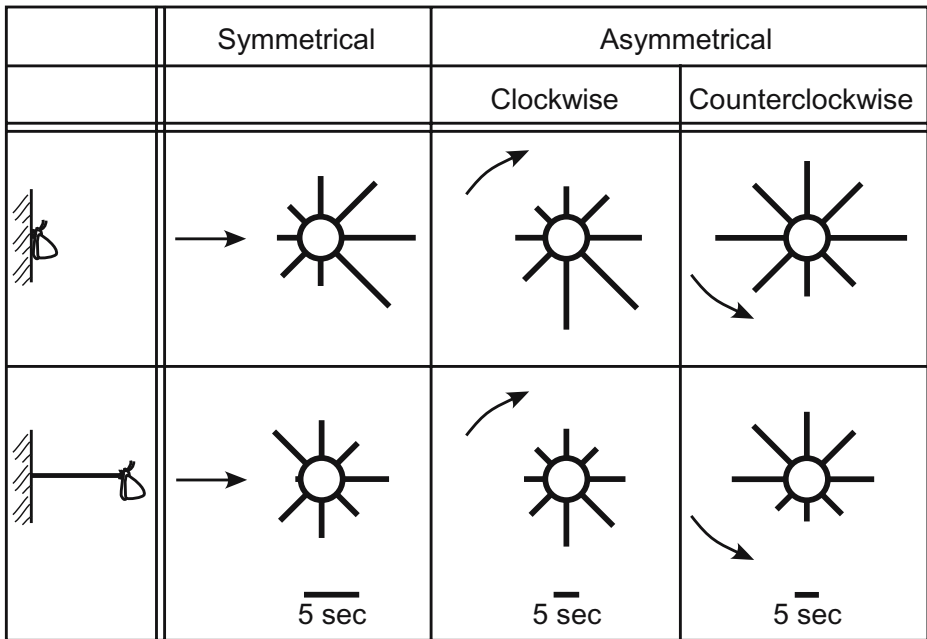


Fig. 5 Male moths at different positions around the cylinder wing at different times. Moths fanned whether the moths were located at the surface (*top row*) or 5 cm from the surface (*bottom row*). The *left column* illustrates the orientation of the moths when viewed from the side. Moths on the upwind areas tended to wing fan before moths on the downwind areas, for all flow types. The *lengths of the lines* represent the median of the wing fan onset times for all moths at that location (during the 30-sec observation period, the light correction factor has been applied as explained in the text; each column is drawn to a different time scale as indicated)

35–100% at any position for any flow/distance from cylinder combination). Male moths at the surface of the cylinder (0 cm) showed a slightly higher tendency to wing fan than males 5 cm from the surface (67 vs. 60%; chi-square $P=0.006$). There was a difference in the probability of pheromone detection at different positions around the cylinder in symmetrical flow for males positioned 5 cm from the cylindrical surface but not for males at the surface (0 cm) (chi-square $P<0.001$ for frequency of wing fanning by position for the symmetrical flow when 5 cm from surface, $P=0.5$ for 0 cm). Position around the cylinder did not affect the probability of pheromone detection in asymmetrical flow (chi-square $P>0.05$ for all four cases).

In almost all cases, males upwind on the cylinder fanned earlier than males downwind. For males in asymmetrical flow at both distances (0 and 5 cm) from the surface and males in symmetrical flow on the surface (0 cm), individuals on the upwind half of the cylinder fanned earlier than those on the downwind half (Mann–Whitney, $P_{Z, 2-tailed}<0.001$; Fig. 5). In symmetrical flow, the narrow pheromone plume closely followed the contour of the cylinder, so for moths 5 cm from the surface, only those directly upwind intercepted the plume as it approached the cylinder, whereas all others experienced a delay as the plume reached them by a combination of eddies and molecular diffusion. These eddies are sufficiently rapid that in this case (symmetrical flow, moths 5 cm from the surface), there was a marginally significant difference in fanning time between the front and back halves of the cylinder with males on the back half fanning slightly earlier on average than males on the front half (Mann–Whitney, $P_{Z, 2-tailed}<0.054$), although males at the single position

most upwind fanned the earliest (Fig. 5). Positions perpendicular to the flow were not included in the analysis for symmetrical flow because they are neither upwind nor downwind.

The median response time for moths in symmetrical flow was the same whether the moths were 0 or 5 cm from the surface (paired *t*-test by position $P=0.554$; Fig. 5). In the more erratic asymmetrical flows, moths positioned 5 cm from the surface responded more rapidly than moths positioned at the surface (paired *t*-test by position $P<0.032$ and $P<0.005$ for clockwise and counterclockwise flows, respectively). Pheromone detection, as denoted by the onset of wing fanning, occurred throughout the 30-sec observation period. No male moths fanned during the three controls. In addition, there was no evidence that a wing fanning male influenced the response of its neighbors by its wing fanning (by changing the probability or timing of their responses), similar to observations on wing fanning in gypsy moths by Elkinton et al. (1984).

Discussion

There are potential advantages of being on the upwind surface of a tree for an organism chemically sampling its environment. An organism there will usually intercept an airborne chemical signal earlier than an organism on the downwind surface, as we have shown here. In addition, an organism on the upwind surface will sample a chemical plume before it has undergone the additional mixing and dilution that usually occurs in the eddies downwind of the object. However, in practice, it may be difficult, if not impossible, for an organism already on the surface to locate the upwind side. Although air strikes the upwind surface, it also strikes the downwind surface as it swirls behind the object (Fig. 2), and therefore, an organism has ambiguous information about the ambient wind direction if it is walking along the surface (Brady et al., 1989, 1990). In contrast, a flying insect approaching a tree could land on either the downwind or the upwind surface, depending on whether it was flying upwind or downwind before landing. The effect of wind direction on landing patterns of flying insects has been investigated by Broce et al. (1991), who found that both stable flies, *Stomoxys calcitrans*, and house flies, *Musca domestica*, were more likely to land on the downwind side of cylinders. Landing in these areas offers increased protection from the wind, and the downwind landing preference was strengthened with increased wind speed (Broce et al., 1991).

We have measured the time delay in pheromone interception experienced by males on the downwind surface of cylinders for a range of slow flow types (Fig. 5). The magnitude of time delay will be a function of the air speed and the size of the tree. For slow air speeds typical of a forest, males on the upwind surface detected pheromone seconds to tens of seconds before the downwind males on the same cylinder. Particularly long delays are a result of the pheromone being returned to the surface after recirculating in an eddy. Whether seconds of difference confer an advantage to an organism on an upwind surface (compared to a downwind surface) may depend on the mating system of that species. For example, for competing organisms tracking a sex pheromone, the first to locate the pheromone-emitting individual could have a mating advantage. In addition, for blood-feeding insects such as tsetse flies, a delay in detection may cause difficulties in locating a host before that host moves away. Note that frequent wind shifting found in some habitats would diminish this prospective small upwind advantage. Willemse and Takken (1994)

have discussed the general difficulty of locating an upwind host by tsetse flies when the wind direction is shifting.

In addition to the velocity differences that exist between the upwind and downwind areas of an object, air moves more slowly next to an object’s surface and diminishes to a velocity of zero at the surface (the “no-slip condition”). This slow flow near a surface can impact the behavior of organisms; for example, minute scale insects need to rear up on their hind legs to reach faster air flow farther from a leaf surface to take off in dispersal (Washburn and Washburn, 1984). Because of slowed air adjacent to a tree surface, an insect on a tree could project its antennae out into faster air flow to sample a larger volume of air per unit time and more rapidly detect pheromone. Using *B. mori* as pheromone detectors, we found that moths positioned 5 cm from the surface responded more rapidly on average than moths positioned at the surface, but pheromone was detectable at both of those distances. *Parcoblatta* cockroaches have long antennae (~2–3 cm), whereas *B. mori* moths’ antennae are a tenth as long (~2–3 mm). By positioning the *Bombyx* moths both 0 and 5 cm from the surface, we encompassed a range potentially sampled by cockroaches and other forest insects. The flow pattern around a cylinder (Fig. 1) is an approximation for a flow pattern around a fairly cylindrical tree; the flow will also be affected by the roughness of the surface of the tree (e.g., bark texture).

The flow behavior depicted in Fig. 1 (eddies moving downwind or shed vortices) will be relevant for a broad range of tree sizes and wind speeds and can be predicted by the magnitude of a dimensionless number, the Reynolds number, $Re = uL/\nu$ (u =velocity of the air, L =tree diameter, ν =kinematic viscosity of the air; Brady et al., 1989; Vogel, 1994). Eddies that move downwind are predicted for the combination of tree sizes and wind speeds that result in $Re > 40$ (Fig. 6), which includes the majority of natural conditions in a forest (Brady et al., 1989). The degree to which this predicted air flow pattern is relevant around trees in a forest depends, in part, on the wind variability. Note that if the wind is shifting direction frequently, the flow pattern will resemble Fig. 1 less closely, and there is less advantage and more difficulty for an organism to position itself upwind.

Our minute-by-minute measurements of wind direction at tree surfaces were significantly less variable in the evening than during the morning and midday (Fig. 4). The circular standard deviation was 10° in the evening, so about 65% of successive minute-by-

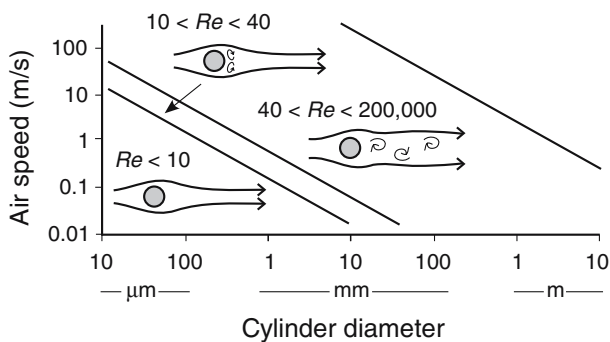


Fig. 6 Air flow patterns around a cylinder as predicted from fluid mechanics. The *air patterns* shown (for air approaching from the left) are expected for a cylinder in cross-flow for a wide range of air speeds and cylinder diameters (Vogel, 1994). The air flow conditions in this study were within the large interval represented by Reynolds numbers (Re) in the range $40 < Re < 200,000$, within which downwind eddies are expected. The kinematic viscosity of air is assumed to be $15 \times 10^{-6} \text{ m}^2/\text{sec}$ in the calculation of Re . See text for the equation to calculate Re . (Figure modified from Fig. 21.4 in Loudon, 2003)

minute measurements of upwind direction are within 10° (normal distribution approximation). Upwind direction measured at tree surfaces in the forest over longer intervals (at least 1/2 hr) during evenings differed only by an average of 26° (between the earlier and later measurements). Under these conditions, a stationary individual on the upwind half of a tree is likely to remain there for at least several minutes. Because of the lower variability in wind direction during evening hours, evening is the most advantageous time for pheromone-detecting individuals to position themselves on the upwind surfaces of trees, but this was not observed in the field for *Parcoblatta* males.

It is difficult to make direct comparisons of wind variability with other studies because the reported variability in wind direction will be strongly influenced by the sampling frequency (Brady et al., 1989) and whether the direction is measured against a tree surface or in the space between trees. However, the wind variability that we documented is similar to that reported by Elkinton et al. (1987) between trees in a coniferous forest, and much less than reported by Brady et al. (1989) adjacent to tree surfaces in a “mopane” woodland. Wind speed also has been reported to be slower and less variable in the evening than in morning or midday (Zöllner et al., 2004).

Our results indicate that pheromone interception occurs from all locations around a cylindrical object such as a tree, which may partially explain the even distribution of *Parcoblatta* males around trees during courtship periods, despite the relatively consistent upwind direction. It is unknown whether a detection advantage of seconds would affect the mating success of a *Parcoblatta* male. It is also possible that not all observed males were actively courting and that individuals on upwind and downwind surfaces were engaged in different activities (e.g., tracking females vs. resting), as is assumed for tsetse flies selecting upwind and downwind resting sites (Brady et al., 1989). The population density is sufficiently low that the observed distribution of cockroaches is unlikely to result from avoidance; usually only one cockroach was seen on a single tree, although two or three were found on occasion, and many trees had none.

The presence of neighboring trees is expected to impact the flow around a tree, in both magnitude and direction (Smith et al., 1972). The physical influence of trees on downwind flow has been considered for the orientation of diurnal forest insects, and in some cases, is more important than the visual stimulus provided by the tree (Wyatt et al., 1993, 1997; Foster and Ayers, 1995). We found that the magnitude of the wind speed was lower within the forest than at its edge. As a result of the slow wind speed in a forest, the flow pattern will be controlled largely by the spatial pattern of tree trunks, branches, and leaves, instead of by large-scale atmospheric processes (Smith et al., 1972). For example, air may move more rapidly through a natural channel offering less resistance to the wind than within adjacent denser areas of the forest. A difference in air flow speeds between channels and denser areas may induce slow areas of circulation and weak ephemeral eddies that we attempted to mimic in our experimental flow chamber (“asymmetrical” flows; Fig. 2 middle and bottom). Even in these complex asymmetrical flows, we found earlier wing fanning response times for individuals positioned on the upwind halves of the cylinders.

The use of wing fanning to infer pheromone detection has been an influential and useful technique for understanding the behavior of pheromone plumes traveling through the environment (Elkinton et al., 1984; Sanders, 1986; Charlton and Cardé 1990). The use of wing fanning as a proxy for pheromone interception requires appropriate experimental design to control for other factors that influence fanning. We observed that wing fanning may be initiated by environmental stimuli in addition to the presence of sex pheromone, such as a sudden increase in light intensity or air movement, so we avoided supplying such stimuli as much as possible. No males wing fanned during the controls. In addition, the

small light gradient in our experimental flow chamber resulted in a small but consistent difference in fanning response; we corrected for this difference as described above, and used both clockwise and counterclockwise gyres for our asymmetrical flow patterns (Fig. 2). Wing fanning may be affected by other factors, such as temperature (Elkinton et al., 1984).

The microhabitat selected by an organism will influence both the type and amount of information available to that organism because the characteristics of the environment will affect stimulus transmission (Dusenbery, 1992). Transmission of a chemical stimulus will be particularly dependent on air flow (or water flow for aquatic organisms) in the microhabitat (Atema, 1988; Murlis et al., 1992; Koehl, 2006). Organisms at different locations around the surface of an object will experience differences in flow, with upwind organisms usually intercepting a chemical signal earlier. Although the potential advantages of earlier interception from an upwind surface do not appear to be utilized by male *Parcoblatta* wood cockroaches in a forest, we have demonstrated that pheromone detection can occur at any position around a cylindrical object in a flow chamber, which could explain the even distribution of *Parcoblatta* males around trees.

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