

ODOR PLUMES AND HOW INSECTS USE THEM

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INTRODUCTION

Odor plumes form as the wind disperses odor molecules from their source. Their structure is complex and is much like that seen in smoke plumes. The plume as a whole wanders, apparently randomly, over a wide area. Many species of insects, however, have behavior that enables them to follow odor plumes to their source and in this way to find mates or distant resources.

Research on odor communication has important practical implications. The pheromones of many important pest species have been identified, synthesized, and formulated for use in pest-management schemes, and they are widely used in traps for population monitoring. Several pheromone formulations are marketed, and many more are under development. They are widely used in crop fields to disrupt insect mating (70, 103).

Despite considerable research, however, pheromones have not been universally successful in these applications (32). Pheromone traps have been used to detect insects at remarkably low population densities, but numbers caught often do not correlate well with density of these insects. Catch is affected by features of population ecology (86), and various factors modify

trap efficiency, including trap shape, placement, and weather (79). Even more variables influence the success of mating disruption (9, 22).

Entomologists recognize the need for more fundamental understanding of the factors affecting pheromone communication. They seek answers to several practical questions concerning, for instance, the effective range of pheromone traps or the strength and positioning of sources for mating disruption. To provide answers, both the odor plume and the insects' response to it need study. In this review, we summarize the current knowledge on plumes and how insects orient to them.

PLUMES IN THE ATMOSPHERE: OBSERVATIONS AND THE MECHANICS OF DIFFUSION

Everyday observation of smoke plumes from chimneys, stacks, and bonfires provides insight into their structure. Seen from a distance, smoke from an elevated source appears as a discrete undulating cloud. In a brisk wind, the cloud seems to widen rapidly close to the source, after which it expands steadily at a lesser rate. It rises and falls as it leaves the chimney, but, soon after, the shape becomes frozen into a sinuous pattern that changes little as it moves with the wind. From a closer vantage, the cloud contains considerable fine-scale structure, wispy in its center and ragged at the edges. Filaments of dense smoke intertwine with regions of clean air. The range covered by a discrete source is indicated, for example, by the deposits of ash on the ground downwind of a bonfire. These observations suggest three levels of odor plume structure:

1. Large-scale structure—the shape and average odor strength of the body of the plume affect the orientation strategy of insects.
2. Small-scale structure—the fluctuating odor concentrations within the plume body affects the input to insects' central nervous systems and hence their instantaneous response to the plume.
3. Time-averaged structure—determines the probability that an insect will contact the odor plume at different locations downwind of the source.

Odor-plume structure is determined by the physics of atmospheric dispersion. Odor plumes are created when odor molecules are released from their source and are taken away in the wind. As the cloud of molecules moves away from the source, it expands and the mean concentration of molecules within it falls. Two processes are at work: (a) molecular diffusion in which random motion of the molecules causes them to move gradually apart and (b) turbulent diffusion in which the cloud of molecules is physically torn apart by air turbulence. The temporal and spatial scales of the two processes are very

different. Molecular diffusion is a slow and small-scale phenomenon. Turbulent diffusion, by contrast, is vigorous and covers a wide range of temporal and spatial scales. It dominates plume development.

Several authors have summarized the mechanics of turbulent diffusion in the atmosphere (57, 99, 109). Turbulence arises from the asymmetry of forces in the earth's boundary layer, which causes large air masses many hundreds of meters across to tumble as the wind drives them along. Its production and maintenance depend on a balance of inertial and buoyancy forces known as atmospheric stability. When the atmosphere is stable (typically at night under clear skies), buoyancy forces dampen down turbulence and inhibit its production, but in an unstable atmosphere, buoyancy forces encourage the generation of turbulence. Unstable conditions occur on sunny days when the ground absorbs heat from the sun's rays. This heat is transmitted to the air at ground level and convective updrafts ensue. Under neutral conditions (heavy overcast), turbulence generated by nonbuoyancy forces is sustained. The energy contained in the giant vortices or eddies is transferred to smaller vortices that in turn transfer it to yet smaller vortices. As the vortices become smaller, they become more randomly oriented until they show no preferred direction. The result is that the wind speed measured in a given direction fluctuates continually. The energy injected into the turbulence by the largest eddies is finally removed by viscous dissipation in the smallest eddies. The size of the dissipation range of eddies is determined by viscosity of the air and characterized by a parameter known as the Kolmogoroff length. The Kolmogoroff length is a measure of the size of the smallest turbulent motions. In the atmosphere, it is roughly a function of wind speed and height (88) and is typically a centimeter or so. Therefore, turbulent eddies have a minimum size. Instruments used to measure turbulence are stationary and record wind speed as a function of time. They register the frequency of wind speed fluctuations or their period rather than the length scales of the eddies that create them. Conversion from frequency or period to a length scale can be made using the approximations: $L = U/n = Up$, where L is the length scale, n is the frequency, p is the period (time scale), and U is the mean wind speed.

The instantaneous recorded wind speed, U , can be resolved into two components, a mean component, \bar{u} (the overbar denotes a time mean quantity), and a fluctuating component, u' , so that $U = \bar{u} + u'$. The strength of a fluctuating quantity is often expressed as the root mean square (rms) of deviations from the mean; for example, the strength of an alternating current (AC) power supply is given as the rms voltage. The rms of a fluctuating signal is the equivalent of the standard deviation of samples of a distributed quantity. The rms of the fluctuating wind speed is a good measure of the intensity of the turbulence. By convention, the intensity is given as a nondimensional quantity by dividing the rms by the mean wind speed.

The energy contained in a unit volume of a flow is given by a product of density and half the square of the speed. In the case of turbulence, the variance of the fluctuating component, \bar{u}^2 , gives a measure of the turbulent energy. The fluctuations that contribute to the turbulent energy come from a wide range of different frequencies. The convention is to present measurements of turbulent energy as a spectrum showing how much of the turbulence energy is contained in each frequency band (84) (Figure 1, top). Currently, energy spectra are usually derived from anemometer records through digital processing (12), but the idea is more simply explained by considering the

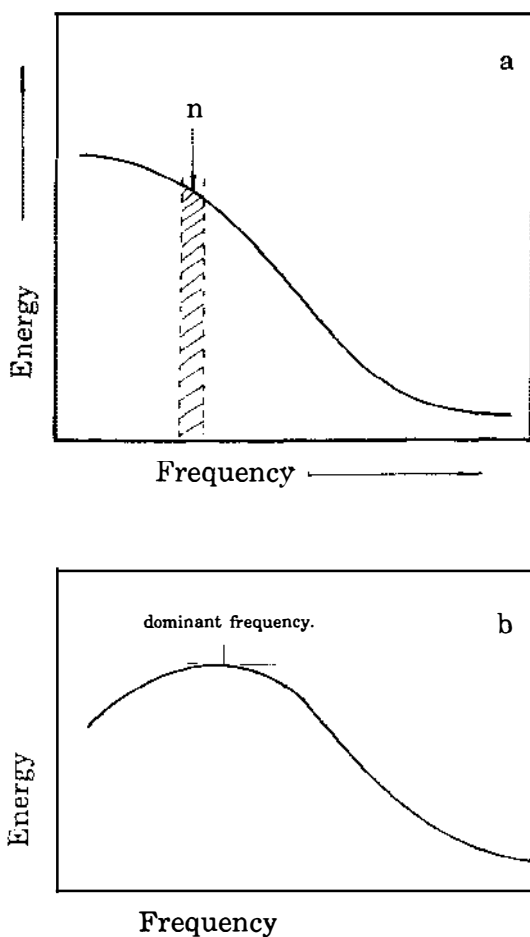


Figure 1 (Top) Energy spectrum showing the energy contained in the frequency band centered on n . (Bottom) Normalized energy spectrum, showing the dominant frequency.

analog methods used originally (69). The fluctuating part of the signal is played into a series of band pass filters, each of which allows only frequencies in a narrow range to pass through. The energy content of each band, derived from the square of the amplitude of the signal passed (with suitable scaling factors), is plotted against the center frequency of the band (Figure 1, top). To make spectra measured in different atmospheric conditions comparable, they can be normalized by dividing by the total variance (Figure 1, bottom).

Spectra contain information about the relative importance of different turbulence scales. They relate directly to the form taken by dispersion and hence to the structure of plumes (60). Normalized spectra of turbulence measured in the open atmosphere have a characteristic shape. The energy peak, corresponding to the dominant frequency, occurs at time scales of some hundreds of seconds. Allen (1) measured turbulence spectra in a forest and reported a progressive change in the spectra from above the forest through the canopy to ground level. Trees removed energy from the largest and smallest eddies, leaving a more peaky spectrum dominated heavily by eddies of a size comparable to the tree spacing. Measurements by Wang (121) show a similar form with a strongly dominant turbulent scale of a few meters. Turbulence in the forest is organized into a narrower range of eddy sizes than in the open atmosphere.

In the following sections we summarize what is now known about the different levels of structure in an odor plume, the influences of habitat and atmospheric conditions, and how insects respond to them.

THE STRUCTURE OF ODOR PLUMES

If an odor source is smaller than the Kolmogoroff scale, odor molecules released into the wind form a filament that expands slowly by molecular diffusion until it reaches the size of the smallest eddies, when the rapid and vigorous process of turbulence diffusion takes over. During the period of molecular diffusion, the development of the plume depends on the characteristics of the odor molecules. Plumes of different materials may behave differently.

The length of this molecular-diffusion stage of plume growth depends on source size and wind speed. Miksad & Kittredge (88) calculated its length in the case of a small source and concluded that the length could be some meters. Aylor et al (4), however, argued that for most odor plumes to which insects respond, for example, pheromone emitted by a female insect perched on a leaf, the source aerodynamically includes both leaf and insect and compares in size to the smallest eddies. If so, this first stage would probably not exceed a centimeter or so.

Beyond this point, the plume structure becomes practically independent of

the properties of the material within it and resembles the familiar form seen in a smoke plume. Thus a variety of tracers, chosen for visibility or ease of measurement, may be used to study plume structure. Observations with tracers show the progressive influence of larger turbulence scales on a developing odor plume (58). Eddies in the size range from the Kolmogoroff length up to some hundreds of millimeters determine the small-scale structure: they stretch and stir the filaments in the plume (66). Those of some meters in size influence the large-scale structure; they cause the fluctuations in the initial direction of the plume that create the undulating and meandering patterns. Eddies on the scale of hundreds to thousands of meters give rise to long-term changes in plume direction.

Pasquill & Smith (99) describe the effect of atmospheric stability on the large-scale structure of a smoke plume. In unstable conditions, one sees vigorous vertical and horizontal undulation, which is reduced in neutral and almost absent in stable conditions. In stable conditions, the continual changing of wind direction causes the smoke to fan out widely horizontally. A plume generated in typical daytime conditions will therefore be of a very different form from one generated at night. Understanding of plume structure has been advanced by making direct measurements and by the development of mathematical models based on the physics of diffusion. Recent progress is summarized below.

Time-Averaged Plume Structure

The first models to be developed provided estimates of mean concentration of odor downwind of a point source based on studies of the dispersion of battlefield gases following World War I (104). Sutton (112) developed a semiempirical equation for a plume generated from a point source at ground level. Sutton's model assumed a Gaussian (normal) distribution of mean concentration in all directions perpendicular to the plume center line and a simple power law to describe the fall in the mean concentration along the plume center line at increasing distances from the source (Figure 2, top). The equation included constants known as dispersion coefficients that were determined by the level of turbulence or atmospheric stability.

Wright (126) and Bossert & Wilson (15) applied the Sutton model to estimate concentrations of insect pheromones downwind of a source. They used typical values for the dispersion coefficients suggested by Sutton for neutral atmospheric conditions. Numerous subsequent applications of the Sutton and related models to estimate pheromone concentrations are reviewed elsewhere (41).

The Sutton model lacks flexibility, however, as the dispersion coefficients do not adequately reflect the physical processes they describe. The Gaussian plume models currently used to predict mean concentrations for air pollutants

(29, 117) or radioactive materials (63) are more general and empirically based (Figure 2, top). The basic equation for a Gaussian plume is:

$$C_{(x,y,z)} = \frac{Q}{2\pi u_r \sigma_y \sigma_z} \exp\left[-\frac{y^2}{2\sigma_y^2}\right] \left[\exp\left(-\frac{(z-h)^2}{2\sigma_z^2}\right) + \alpha \exp\left(-\frac{(z+h)^2}{2\sigma_z^2}\right) \right],$$

where $C_{(x,y,z)}$ is the mean concentration at any position (x,y,z) with the x axis aligned with the mean horizontal wind direction, the y axis aligned horizontally cross-wind, and the z axis representing height above ground (Figure 2, top). Q is the release rate of the material in the plume, and u_r is the mean wind speed at a standard reference height (10 m is usual). The coefficients σ_y , σ_z are standard deviations of the concentration distributions in the respective horizontal and vertical directions, and h is the height of the source of emission above ground. The equation also contains a constant, α , the proportion of material reflected back into the plume when it reaches ground level.

The coefficients, σ_y , σ_z , are analogous to the dispersion coefficients of the Sutton model. They are not constants, however; instead they vary with distance from the source in addition to atmospheric stability and wind speed. They are derived from trials such as the US Prairie Grass project (31, 59). In practice, estimating the atmospheric stability is difficult. The Richardson number, a function of the rates of change of temperature and wind speed with height, is commonly used (99), but it is not convenient to measure. Pasquill (98) proposed a classification system for stability based on observations of wind speed and cloud cover. The resulting dispersion coefficients can be obtained from charts (29, 117). A more quantitative method based on surface measurements of heat flux and wind speed was recently proposed by Hunt et al (62).

Elkinton et al (42) tested a range of Gaussian plume models in analysis of gypsy moth response to pheromone. The moths, in field cages, were exposed to pheromone from a distant point source roughly upwind and the onset and duration of wing fanning was recorded. The time-averaged plume models tested did not predict where wing fanning took place in relation to the mean wind direction. The work revealed two main kinds of difficulty with time-average plume models:

1. Insects do not respond to mean concentration as calculated by these models (over an averaging time of 3 min in the case of the Sutton model). Instead, insects respond to instantaneous concentrations that are frequently many-fold higher than mean concentrations (91).
2. The averaging times implied by the model are themselves physically unrealistic in the atmosphere where, because of the influence of continual shifting in the mean wind direction, stable means do not form.

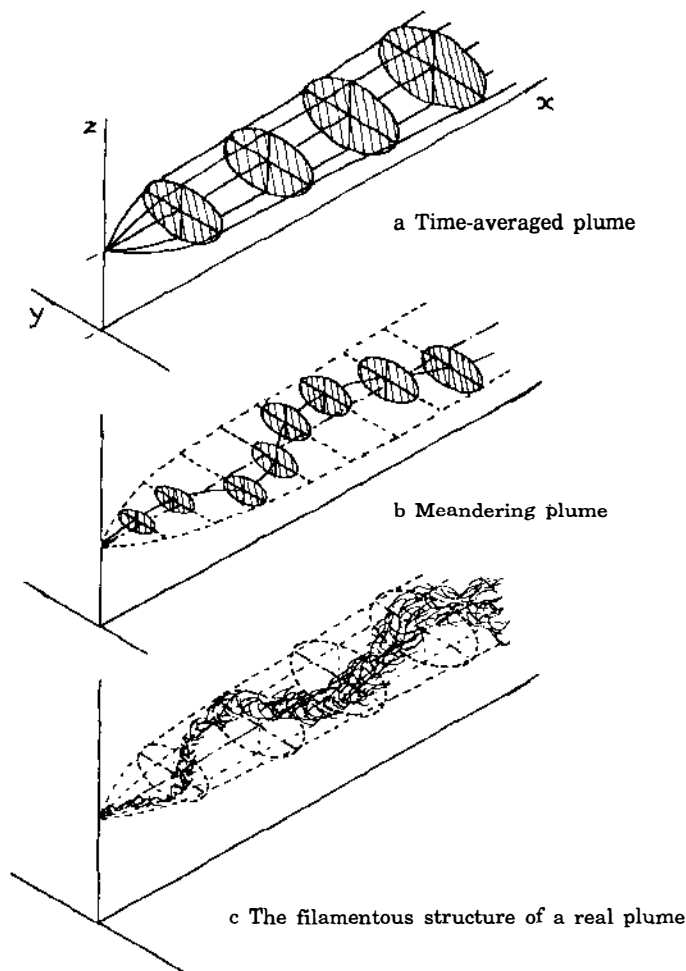


Figure 2 (Top) Time-average Gaussian plume model, showing the principle axes and the source positioned at height h . (Middle) A meandering plume model with concentration in each disc distributed normally about the meandering center line. (Bottom) The structure of a real plume.

Models of this type cannot provide a general framework for the analysis of insect odor communication (41), but they may be useful in specific cases, for example, where there is significant contamination of vegetation by an odor source (120). Gaussian plume models could be used to map the contaminated area downwind.

Large-Scale Structure: Meandering Plumes

The most obvious feature of a plume is that it meanders (Figure 2, bottom) and insects will encounter much higher levels of odor than the time mean. Predicting concentration in the meandering plume is therefore of great practical importance, but concentration is difficult to assess. In the absence of helpful experimental data, the problem was first tackled theoretically.

Gifford (51) suggested a meandering plume model in which Gaussian functions described the distribution of material across the plume, but the position of the plume center was free to move. He assumed that the plume was made up of a series of disks in a plane perpendicular to the mean wind direction, the centers of which were displaced around the mean wind axis according to the displacement of the meandering plume (Figure 2, middle). The overall variance of the concentration fluctuations is a combination of the variance of the concentration fluctuations with respect to the center of each disk and the variance of the position of each disk relative to the mean wind axis:

$$\{\overline{c'^2}\}_1 = \{\overline{c'^2}\}_2 + \{\overline{c'^2}\}_3,$$

where

- 1 is the overall variance,
- 2 is the variance of concentration across the disk, and
- 3 is the variance of the position of disk centers.

If the odor is normally distributed along any axis perpendicular to the plume centerline, the ratio of peak to mean concentration on the mean wind axis is:

$$\frac{\text{peak}}{\text{mean}} = \frac{\overline{c'^2}_I + \overline{c'^2}_M}{\overline{c'^2}_I}.$$

More general equations for the ratio of the instantaneous concentration to the local mean concentration can be obtained. Venkatacham (118) proposed a simple model based on the assumption that small parcels of material from an elevated source are carried downwind at the mean wind speed along straight lines that deviate vertically and horizontally from the mean wind direction. The deviations give the parcels a vertical and horizontal speed component, and by making assumptions about the distributions of these, one can calculate the distribution of concentration across the plume downwind. Models of this kind are known as PDF (probability density function) models.

A plume meandering in roughly sinusoidal form spends most of its time

around the edges of its range. Ride (102) predicted that the cross-wind distribution of mean concentration from a narrow plume subject to wide meandering should be bimodal with peaks towards the edges of the plume's cross-wind range. Studies with smoke plumes by Hanna (55) illustrate this bimodal cross-wind distribution. Calculations predict that the degree of bimodality would depend on the ratio of plume body width to the width of meandering, r . Bimodality in Ride's model starts to appear at $r = 0.50$ and becomes well developed at $r = 0.75$. Hanna's data correspond to $r = 0.65$. For pheromone plumes in unstable or neutral conditions, the source is usually small compared to the size of the eddies responsible for meandering, and r will be well above 0.5. Ride's model suggests that the edges of the envelope in which an odor plume meanders contain higher mean concentrations. These findings contradict the earlier assumptions of normal distributions of odor embodied in Gaussian plume models.

Models of these types are simple but powerful. They fit the experimental data well (46) and have considerable potential for further development (54). Höglström (61) used Gifford's model for predicting fluctuating odor concentrations, and this model seems an ideal basis for the analysis of trap interaction (17). These models are still designed to give averaged concentrations, however, and do not address the question of the small-scale structure of a plume. For this, experimental data remain the most reliable source of information.

Small-Scale Structure

Odors insects use, for example pheromones, cannot at present be measured with sufficient time resolution to allow the fine-scale structure of odor plumes to be assessed directly. We rely on data from trials with tracers for this information.

Concentrations in a smoke plume can be measured over short averaging periods with photometers [6 s (108), 1 s (55), < 1 s (37)]. Other studies (10, 53) obtained resolutions better than 30 ms using sulphur dioxide and phosphorus pentafluoride tracers with fast flame photometric detectors. Studies with propylene (93, 94) obtained resolution to better than one second at distances up to 1000 m from source: digital processing improved this figure to approximately 0.1 s. Fackrell (44, 45) obtained response times of a few milliseconds in a wind tunnel with methane and propane.

Jones (64) and Jones & Griffiths (67) described a simple and robust system for generating and detecting unipolar ions in the atmosphere. Ion plumes can be used to model plumes of odor provided that repulsion between ions and deflection of the plume (resulting from image forces in the ground) are minimized or allowances are made for them in analysis (27). Both unipolar (68) and bipolar (13) ion tracers have also been used in wind-tunnel work on diffusion.

Analysis of Small-Scale Plume Structure

High-resolution tracer detectors produce a signal consisting of a series of short bursts of activity, separated by periods of zero signal (Figure 3). At the leading and trailing edges, the signal amplitude rises sharply. Bursts sometimes consist of one clearly defined spike but more often they have considerable structure within them. Murlis & Jones (91) defined the burst length as the time between leading and trailing edges and the burst return period as the time between the leading edge of one burst and the next.

As with instantaneous recorded wind speed (U), one can resolve the instantaneous concentration, C , into two components, a mean concentration \bar{c} and a fluctuating component, c' , such that: $C = \bar{c} + c'$. The intensity of concentration fluctuations is given by the rms of the fluctuating component divided by the mean concentration. The variance in the fluctuating component can be broken down into contributions from the range of frequencies and formed into a spectrum. Hanna & Insley (58) showed that smoke-plume data from large-scale field trials produce well-defined spectra but the dominant scales of concentration fluctuations are considerably shorter than the dominant turbulence scales.

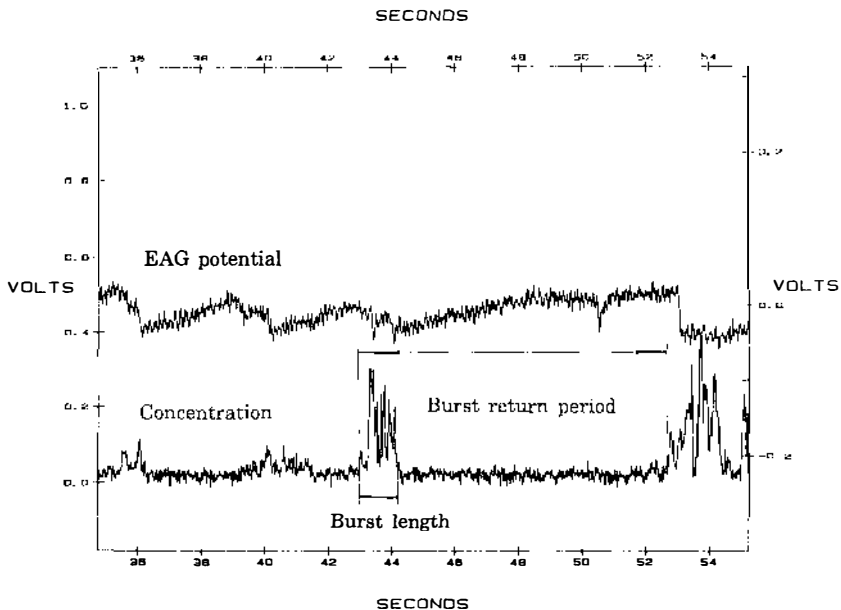


Figure 3 Fluctuating signal from an ion concentration sensor showing burst length and burst return period. Electroantennogram (EAG) signal recorded from a gypsy moth antenna responding to pheromone at the same time and in the same position as the ion sensor. Taken from Murlis et al (92).

Time Dependency of Concentration Fluctuations

The few published measurements of the temporal structure of plumes show that the burst lengths and burst return periods at a fixed position range widely with an approximately log-normal distribution. Bursts last from less than 10 ms to over a second and burst return periods from 500 ms to several minutes (66, 90–92). If the turbulence scales responsible for the large-scale structure of the plume as a whole were distinct from those responsible for the small-scale structure within the plume (56), then the distributions of burst return period would be bimodal. Evidence of bimodality, however, can only be found in distributions of return period measured at great distances from the source (66) and where the criterion for positioning leading and trailing edges of bursts was set at higher concentration values (90). The large- and small-scale structure is not therefore easily separable. A continuum of scales corresponds to the continuum of eddy sizes. Typical values for burst length and burst return period (the value of the mode of their distributions) are, respectively, a few hundreds of milliseconds and a second or so.

As conventionally measured, distributions of neither burst lengths nor burst return period show significant trends related to source-to-receptor distance (66). Murlis et al (92), however, took an ensemble mean of both return period and length measured over short sections of active signal 90 s and 180 s long. Mean burst length and mean burst return period measured in this way increased as source-to-receptor distance increased from 2.5 m to 20 m; mean burst length increased by a factor of 2, and burst return period increased by a factor of >7 .

Intermittency of Fluctuating Concentration

Intermittency is defined as the proportion of time when the signal is absent. Because it is also sometimes defined as the proportion of time when the signal is present (the one being 1.0 minus the other), we have converted where necessary.

Intermittency, arising from zero concentrations inside the plume and the meandering of the plume as a whole, considerably affects concentration measurements. Zero values can, however, be rejected through a procedure known as conditional sampling (108). Conditionally sampled means are formed from ensembles containing only values that meet some set condition—for example, that they are nonzero.

Jones (65) measured intermittency over successive 1-h samples of an ion detector signal. He found it varied widely and concluded that intermittency is a highly unreliable signal characteristic because long period events have a disproportionate effect on samples. The wind may shift away from the measurement point, for example, for minutes at a time. Murlis et al (92)

estimated intermittency from short samples of active signal (90-s and 180-s durations) to remove the influence of long periods of zero concentration. Intermittency estimated in this way increased systematically with increasing distance from the source, from over 60% at 2.5 m to 90% or more at 20 m.

Much intermittency comes from movements of the plume as a whole, but a significant part is derived from patches of clean air inside the plume (Figure 1, bottom). Fackrell & Robins (47) show that intermittency depends on the turbulence structure of the air flow and the source size. Intermittency inside their wind-tunnel plume decreased as the distance from the source increased, until at large distances downwind it became close to 0% (no patches of uncontaminated air left). In the atmosphere, however, where source size is comparable to that of the smallest eddies, Mylne & Mason (93, 94) found that the minimum intermittency in the center of a plume reaches an asymptotic value significantly greater than zero. In the atmosphere, some patches of odor-free air are apparently always inside a plume from a small source—the smaller the source relative to the smallest turbulence, the more significant the patches are.

Concentration Fluctuations in a Plume

Probability distributions of concentration fluctuations are highly skewed towards high values, low concentration values being disproportionately numerous. Functions proposed for the distributions include exponential, log normal, and clipped normal (52, 55, 65, 66, 114). The intensity of concentration fluctuations decreases with increasing distance from source more rapidly than mean concentration. The intensity seems eventually to reach some approximately constant (nonzero) value dependent on source size and the turbulence scale (46, 47, 93, 94).

Mylne & Mason (93, 94) found that the distribution of mean concentration across the plume, obtained by conditional sampling, corresponded to a roughly Gaussian form. However, intermittency showed a complementary trend, and these authors concluded that the lower conditional mean concentrations found at the edges of the plume were produced by the higher intermittency, the concentration in odor bearing filaments remaining unchanged.

Aylor (3) recognized the probable behavioral importance of extreme values in pheromone plumes. Hence, an alternative way of assessing odor concentration is to focus on peak values in bursts. Storebø et al (111) found patches of undilute material 100 m and more from its source. Murlis & Jones (91) measured probability distributions of peaks of concentration. They were skewed to higher values, but less so than mean concentrations in bursts. Distributions of burst-peak concentrations from signals recorded at different positions overlapped significantly, even when they were as much as 5 m apart.

One can estimate the strength of odor in a plume in other ways. In experiments with smell in the atmosphere (10, 61), observers found that smell arrived in short bursts, both because the plume switched back and forth and because the human nose is itself a sampling organ, with an averaging period of a few seconds. Similarly, an insect flying in an odor plume samples (though over shorter times). Because of its movement through the plume and because the plume is being driven past it by the wind, the concentration in the plume has less direct impact on the insect than the flux of material past it (41). Murlis et al (92) measured the mean flux, the dose (the quantity of ions contained in each burst), the peak value of flux in each burst, and the maximum peak recorded in each 90-s or 180-s sample of active signal using Langmuir ion probes (13, 14) (Figure 3). Strength as assessed in all these ways decreased systematically as source-to-receptor distance increased according to simple power laws, but the mean flux and dose decreased more rapidly than the peak values.

Effects of Habitat and the Size and Position of an Odor Source

In an open habitat, dominant turbulent scales are some hundreds of meters and energy is progressively transferred from large to small scales. There is considerable energy at small scales, and mixing is vigorous. David et al showed that, for smoke puffs released from a low source over open ground (36), each followed (different) linear trajectories for at least 20 m, showing that individual segments of a plume travel long distances in straight lines despite differences in original orientation as they leave the source. Meandering is produced as successive plume segments set out in a slightly different direction from their immediate neighbors.

In a forest, however, where small-scale turbulence is relatively less energetic and the dominant scale is only a few meters, mixing is far more leisurely and the directional sense of plume segments is less well sustained. The structure in a forest smoke plume seems almost frozen as it is carried downwind on a path winding on the scale of the dominant eddy size. Elkinton et al (43) showed that individual puffs of pheromone beneath a forest canopy would follow highly nonlinear trajectories even within a few meters of the source. Under light wind conditions in a forest, tracers (smoke puffs or bubbles) are frequently observed to change direction by more than 180° over a distance of 20 m or so. Consecutive puffs follow similar paths to about 20 m where they frequently become very different, sometimes one in a sequence doubling back on its trajectory. Brady et al (18) also recorded trajectories of this kind in studies of tsetse response to host odors in African bush (low shrub).

Recordings of tracer signals made in a forest (92) had longer bursts than in an equivalent trial in an open field. Flux decreased as source-to-receptor

distance increased less rapidly than in the field. Peak-to-mean ratios were lower close to the source and increased less rapidly in a forest.

The size of the source has a considerable effect on plume structure (47, 88); in general, the smaller the source, the higher are the intermittency and the intensity of concentration fluctuations. An odor source's size depends on the size of the insect's perch rather than the size of the insect or its odor-emitting gland (4). The size of the perch clearly depends on the habitat. Even in a forest, where the typical source is about the size of the diameter of the tree trunks, the effective source size is small compared with the energetic turbulent scales and corresponds to the smallest source sizes considered in the wind tunnel trials of Fackrell & Robins (47).

Fine-scale structure in plumes is also affected by height of the source. From sources at ground level, it is dominated by intense mixing at the surface (101) and is independent of source size (47). Hanna & Insley (58) found no systematic data on elevated sources. It is generally assumed (91, 111) that at greater heights than about 1.5 m above ground, the structure of plumes from sources whose effective size is a few centimeters is affected little by the surface for distances of tens of meters from the source.

Models for Predicting Concentration Fluctuations

Experimental data of the kind detailed above has enabled modelers to test a range of different approaches to the prediction of fluctuating concentration. Hanna (54) reviewed such models and tested them against field data. He concluded that simple analytical formulae derived from such models fit the data well, but that considerable potential for further development remained.

The most common output from these models is a distribution of concentration fluctuation intensity, which can be considered as a property to be created, removed, and transported. For an idealized plume with its center line on the x axis, the conservation equation for the fluctuating concentration (c') is given by Pasquill & Smith (99) as:

$$\left\{ u \frac{\partial c'^2}{\partial t} \right\}_1 = \left\{ -2 \left[\overline{w'c'} \frac{\partial C}{\partial z} + \overline{v'c'} \frac{\partial C}{\partial y} \right] \right\}_2 - \left\{ \left[\frac{\partial \overline{w'c'^2}}{\partial z} + \frac{\partial \overline{v'c'^2}}{\partial y} \right] \right\}_3 - \{S\}_4,$$

where

- 1 is an advection term (transport of c' along the x axis),
 - 2 is a production term,
 - 3 is a diffusion term (transport of c'^2 by the cross-wind gradients of c'), and
 - 4 is a dissipation term (loss of c'^2 by molecular diffusion).
- The terms v' and w' are the fluctuations of wind speed in the y and z directions, respectively.

The equation can be solved only by making several assumptions and simplifications. Csanady (33, 34) made the major simplifying assumption that the cross product terms involving w' , v' , and c' could be represented by the product of the mean gradient and a coefficient of diffusivity, K . The conservation equation then becomes:

$$\left\{ u \frac{\partial c'^2}{\partial x} \right\}_1 = \left\{ K_y \frac{\partial^2 \overline{c'^2}}{\partial y^2} + \frac{\partial}{\partial z} K_z \frac{\partial \overline{c'^2}}{\partial z} \right\}_3 + \left\{ 2K_y \left(\frac{\partial C}{\partial y} \right)^2 + 2K_z \left(\frac{\partial C}{\partial z} \right)^2 \right\}_2 - \left\{ \frac{\sigma^2 c}{T_d} \right\}_4,$$

where T_d is a time constant for the decay of concentration fluctuations and is a function of x . K_y and K_z are the coefficients of diffusivity in the y and z directions, respectively, and are also functions of x .

Although this equation still appears somewhat intractable, all the terms can be estimated or derived from experiments, and a solution can be found for c' as a function of downwind position for a specified mean concentration distribution, $C = f(x, y, z)$. Further simplifications are possible. For example, far downwind, the production term is small. If it is neglected and $K_y = K_z = K$, a constant, the distribution of variance is Gaussian and the equation for cross-wind distribution of intensity becomes:

$$\frac{\sqrt{c'^2}}{C} = \left(\frac{\sqrt{c'^2}_{y,z=0}}{C_{y,z=0}} \right) \exp \left(\frac{y^2}{4\sigma_y^2} \right) \exp \left(\frac{z^2}{4\sigma_z^2} \right)$$

where $y, z=0$ refers to values on the plume centerline. As a consequence of this relationship, intensity of concentration fluctuation is greatest at the edges of the plume body.

Wilson et al (124) proposed an empirical Gaussian model for c'^2 , assuming it is produced from point sources positioned independently of the source of the plume. The cross-wind profiles were similar at each position down wind and were scaled on plume-body widths. The parameters describing position and strength of the variance sources, the form of cross-wind profiles, and other input needed were chosen to fit the wind tunnel data of Fackrell & Robins (46, 47). The parameters themselves have a sound physical basis, and the model therefore has potential for general application. Wilson et al (125) modified it to predict conditionally sampled concentrations and intermittency.

Models of both these kinds predict fluctuations in the plume, but they can be combined with meandering plume models to predict the overall fluctuation (54).

Two kinds of advanced models have been developed: (a) mathematical models that solve equations for fluctuation variance directly, such as the

second-order closure models of Sykes and coworkers (113, 114), and (b) statistical models, such as random walk models (107, 115, 116) or large eddy simulations (85, 97). Second-order closure methods use more physically defensible means of calculating the difficult cross-product terms in the continuity equation for c'^2 . Numerical simulations of dispersion calculate large numbers of trajectories of particles or particle pairs. Single particle models yield mean concentrations, but by considering particle separation in particle-pair models, one can also obtain a statistical description of concentration fluctuations. Once fully developed, numerical simulations should offer significant new possibilities. By tracing paths of populations of particles, they could provide a unique realization of the fluctuating concentrations in a plume. A model of this kind could be used in combination with a model of insects' instantaneous response to odor to evaluate theories about orientation.

Mason (85) noted that the influence of large-scale motions responsible for movements of the plume as a whole are often neglected in dispersion modeling. He proposed a model in which the movements of large eddies are simulated by a numerical scheme and the small-scale motions are parameterized. The model produced results that agreed well with experimental data but was costly in computer resources.

Therefore, one has several options for modeling the distribution of fluctuating concentration in a plume. The concept of active space could be revived with the mean concentration replaced with one or other measure of fluctuating concentration.

BEHAVIORAL IMPLICATIONS

With an understanding of the generation and structure of odor plumes, we may now ask what features of the plume are detected and used by insects in walking and flying toward the odor's source. This line of inquiry requires knowledge of the mechanisms of insect orientation to odors (73) and the sensory inputs that mediate them.

Insects produce and respond to odor plumes that differ markedly. Bark beetles (Scolytidae) can generate a large plume with an effective source the size of an entire tree trunk with hundreds of odor-emitting beetles. Arctiid moths may release pheromone as both a vapor and an aerosol (76), and because the pheromone gland is rhythmically protruded, the plume is released as a series of pulses (30). Parasitoid wasps following a plume to a prospective host may need to navigate a narrow plume of host-released kairomone within a larger diffuse plume of odor from the plant harboring the host. Such different plume structures certainly exert different selective pressures. Insects

with differing phylogenies and therefore independently evolved orientation mechanisms assure multiple solutions to the location of odor sources (21).

Most of our examples are of orientation to odors by flying insects, which entails the difficult navigational task of detecting wind direction while air-borne. Most of the evidence on this phenomenon has been accumulated on the attraction of male moths to a female.

Search Strategies

Which attributes of the plume's structure and an insect's pattern of movement with respect to the wind's direction are important to the initial contact with an odor source? Most insects actively move about before entering the plume, and several modeling studies have asked: are there optimal strategies for contacting the plume?

This approach requires assumptions about plume structure. Some have suggested that the optimal strategy for the animal is to fly cross-wind if the plume length exceeds its width and up or downwind otherwise (20, 83). Sabelis & Schippers (106) provided mathematical expressions of this idea. Dusenbery (38, 39) developed similar predictive models that incorporated the cost of moving with or against the air stream. These treatments assumed simplistic time-average plumes. For instance, plume width has been defined by the range of the wind direction (106); when the range exceeds 60°, the plume is wider than long. However, the range of the wind direction depends on the time interval over which it is measured (41). These studies further assumed that the insect can estimate the mean (as opposed to instantaneous) wind direction and can fly at some fixed angle with respect to it. They also assumed that the insect would inevitably contact the plume and locate the source once within the time-average boundaries. However, much evidence is to the contrary (e.g. 43).

Few good field data are available on the actual search strategies employed by flying insects before they contact odor plumes. Some studies suggest a cross-wind tactic, whereas others do not (e.g. 40). A deficiency in many field observations is the anecdotal estimation of the instantaneous orientations of wind and the organism's path. Realistic models of optimal foraging for a plume await construction. Such models would incorporate improved representations of plume size and shape based on isopleths that indicate the probability of contacting the instantaneous plume at each point downwind of the source (54, 102).

Orientation Toward the Source

HEADING UPWIND USING OPTOMOTOR ANEMOTAXIS Walking toward an odor in wind is a simple task because gauging the wind's instantaneous direction only requires mechanoreceptive input (11). Upwind flight, however,

requires that the airborne organism determine the wind's direction by judging visually how wind has deflected the flyer from its heading. Although an organism can estimate its airspeed by mechanoreceptive input, the optomotor reaction (comparing the discrepancy between heading and track over ground as visually detected drift or side slip) is the only verified mechanism by which an airborne organism can reckon wind direction (72). When side slip is zero, the organism is heading due up (or down) wind. The optomotor reaction to wind appears to explain nearly all cases of flying orientation to odor, except an aim and shoot strategy in which insects determine upwind heading while perched on a substrate and then fly in that direction (19).

HEADING TOWARD THE PLUME'S SOURCE The instantaneous wind direction and the plume's axis are only infrequently coincident, so that simply heading upwind while in the plume will not routinely lead toward the odor's source. In open fields, moving upwind while in a plume should aim the insect toward the odor's source, particularly within tens of meters (36), but because the plume meanders, often an insect heading upwind will exit the plume. In forests (43) and the African bush (18), the meandering plume can be overtaken by large-scale eddies traveling in different directions, often producing highly contorted plume paths. Flight upwind in such plumes often carries an insect out of the plume. In addition, the upwind direction is only infrequently aimed toward the odor's source.

Both of these constraints imply that successful location of an odor over distances of tens of meters requires a tactic to enable relocation of the plume when upwind flight carries the insect beyond the plume's boundary. Casting, a reiterative zigzag that may progressively widen but does not progress upwind, enhances the likelihood of directly recontacting the plume as the cast widens or provides a station-keeping maneuver until the plume shifts back to the insect's position (35).

Successful flight toward the source may depend upon sustained (tens of seconds) intervals when the wind vectors are parallel, such that the directions along the plume's axis and upwind are coincident. Such parallel wind fields within which an insect may successfully follow a plume are more diagnostic of active spaces than the mere concentration of odor (43). The effective distance over which insects follow odor sources may be related to the dominant frequency of the large-scale eddies responsible for the major wind shifts. Models of such large-scale structure might be applicable to insect orientation strategy.

NONANEMOTACTIC MECHANISMS OF ORIENTATION Although odor-induced anemotaxis is the primary mechanism for locating a distant odor source (74), various forms of chemotaxis have been hypothesized to play a

role in orientation. Such a navigational system might rely upon directional cues extracted from the plume's structure (such as the position of the boundary) or temporally monitored changes in intensity of the plume's signal. To verify that factors other than the optomotor reaction to wind do contribute to orientation, one experimental scheme is to impose windless conditions. In their wind tunnel trials, Farkas & Shorey (48) observed that some moths continued flight along the plume's axis following a sudden cessation of the wind. A similar response to a plume in zero wind was verified with *Grapholita molesta* (78) and *Lymantria dispar* (123). Longitudinal klinotaxis (sequential sampling of concentration) appeared to contribute to flight along the plume in concert with an initial setting of course polarity by optomotor anemotaxis (78). In nature, this maneuver is potentially useful for distances on the order of meters when wind speed falls below the level needed for the optomotor reaction.

Wright (126) was the first to point out that the filamentous nature of odor plumes might provide directional cues. He proposed that flying insects could measure frequency of bursts to determine source's direction, but he later abandoned this idea in favor of anemotaxis (127). Moore & Atema (89) have proposed that lobsters (at relatively close range and in water) extract directional information from the changes in the rate of increase in concentration at the leading edges of odor bursts. However, Murlis & Jones (91) concluded from ion plume trials in the atmosphere that the rates of change in concentration or other plume characteristics with distance from the source are unreliable indicators of direction to the source, unless, perhaps, the source was very close.

Detection of Fine-Scale Structure

Scrutiny of the flight tracks of *G. molesta* suggests that either contact or loss of the plume can induce a change in course angle within 0.15 s (5). This is expressed as a surge upwind in pheromone and a tendency toward cross-wind casting upon loss of the scent. In the silkworm *Antheraea polyphemus*, casting latency following odor loss was not as rapid—0.3–0.5 s (7). Not only does the fine-scale structure of plumes alter behavior, it appears to be required for sustained upwind flight. In wind-tunnel trials with two tortricid moths, continued upwind progress did not occur in a homogeneous cloud of pheromone (75, 122). Rather, a plume or a naturally fenestrated (or experimentally pulsed) cloud of odor was needed.

Baker et al (8) proposed that cessation of upwind progress, as occurs near the pheromone source, might be triggered by fusing of the receptor output when the receptor system could no longer resolve the individual odor pulses.

Field and wind-tunnel electroantennogram (EAG) recordings of *G. molesta* suggested that peak-to-mean ratio rather than either the peak or mean concentrations induced in-flight arrestment (6).

The ability of an organism to resolve individual bursts of odor and possibly features of individual bursts rests on the characteristics of the odor-detection system. In the case of attractant pheromones, odor molecules are thought (110) to enter pores on the sensilla and bind to receptor proteins on the surface of the sensory dendrites. The receptor cells themselves, at least in the case of moth pheromones, appear to have a narrowly tuned specificity. Populations of such receptors on the antenna respond to a single or perhaps two closely related compounds in the blend. Other odor receptors many have broad tuning (2). Graded potentials arising from the dendrite are transduced into trains of action potentials that propagate along the sensory axon to the central nervous system. The frequency of such action potentials is proportional to the odor intensity. The odor molecules are rapidly degraded by enzymes (119) so that receptors are available to respond to a new odor pulse. The latency of axon response is on the order of 100 ms.

Most receptors exhibit a phasic/tonic response to odor signals of a second or more duration (71). A strong odor causes an initial high-frequency burst of action potentials (the phasic response), followed by a period of reduced frequency (the tonic response) that persists for the duration of the odor pulse. At low odor concentrations, only the tonic phase occurs.

In the receptor cells of *A. polyphemus*, the two receptor cell types (each sensitive to a different pheromone component) have different response patterns (105). One cell type can resolve 20-ms pulses at 5 or more stimuli/s, while another can only distinguish 2 stimuli/s. Thus in *A. polyphemus*, the structure of the odor plume might be registered in a different pattern by each receptor type. At the level of the antenna as a whole, much of the small-scale plume structure in a plume is reflected in EAG signals (92) (Figure 3).

Central olfactory neurons can detect the pheromone plume's discontinuous structure. Christensen & Hildebrand (28) recorded from higher-order interneurons in the deutocerebrum of *Manduca sexta* and found that pulses were resolved up to 10/s.

Changes in Behavior as Insects Approach the Source

As flying insects approach an odor source, their flight patterns typically change, and ultimately landing may ensue. The site of landing may be close to the odor source, or if the effective source size is large, as occurs for example when a female gypsy moth calls from a tree trunk, landing may be many centimeters away from the source. The insect locates the source following walking orientation (26). Of particular interest are the alterations in the

plume's signal that influence these behavioral changes. In moths, a typical change seen in wind-tunnel trials employing lures of varying strength is a reduction in ground speed and a decrease in the width of the zigzag path, both of which can be attributed to increases in pheromone concentration because the plume's dimensions are essentially unaltered (25, 49, 50, 77, 84a). Farkas et al (50) found that landing was induced by a high concentration of pheromone accompanied by an appropriate visual stimulus.

Pheromone Blends and the Role of Individual Components

Most attractant pheromones (indeed most behaviorally relevant odors) consist of blends. Much debate has focused on the possibility that in moths a portion of the blend mediates the earliest behaviors in source location (such as locking on to a plume), whereas the entire mixture (or the natural component ratio) evokes later behaviors (such as landing or courtship) (24, cf. 82). The alternative system envisages the complete blend evoking all behaviors at a lower threshold than partial blends (82). Although several behavioral studies suggest such a nested active-space system (16, 23, 95, 96), the blends tested have not always been complete (23), and alternative behavioral interpretations exist. The complete blend has the lowest concentration threshold for eliciting all behaviors observed in *Argyrotaenia velutinana*, *Tricoplusia ni*, and *G. molesta* (80, 81) and thus the entire blend governed the active space.

Support for the potential differences in active spaces of partial and complete blends comes from a study of receptors for *Antheraea polyphemus* and *Antheraea pernyi*. The relative number of cells sensitive to each component of the pheromone, their relative sensitivity, and the release rates of components from the female suggest that the active space of the major component could project farther downwind than that of the blend (87). The dynamics of the receptor's response to different components in the blend also play a part. The rapid cells in *A. polyphemus* antennae (105) are highly responsive at low concentrations but would soon be overwhelmed by high stimulus levels. The slower cells are less sensitive to low concentrations but continue to function at high stimulus levels. There may be no generic solution to how moths organize a system of thresholds for blends.

CONCLUSIONS

Considerable progress has been made in understanding the fine-scale structure of odor plumes and consequently in unraveling the information available to insects. Odor signals consist of short bursts of odor of greatly varying intensity. Farther from the source, bursts are on average weaker (but not reliably so). They are also slightly longer and there is a lengthened gap between them. Overall, the intermittency of the signal is higher at greater

distances from the odor source. Nearer the source, the peak-to-mean ratio is considerably reduced, but the rate at which the odor concentration rises at the leading edge of the bursts increases. How much of this rich array of information is used in orientation remains to be established.

Insects can resolve odor bursts at least as fast as 10/s in the peripheral receptors and in interneurons farther up the afferent pathway. The kind of information derived from these patterns is not yet clear.

Progress in modeling plumes has also been substantial and a variety of approaches have emerged to deal with fluctuating concentration and its time dependency. These models have application in the studies of active spaces. Deterministic plume models based on numerical simulation of diffusion could improve our understanding of orientation strategies.

There is promise in applying advanced plume models and field measurements of simulated plumes in different habitats to define the temporal and spatial cues available in odor plumes. In turn, such information will engender the behavioral and neurophysiological experiments requisite to explain the navigational mechanisms used by insects to locate odor sources.

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Literature Cited

1. Allen, L. H. 1968. Turbulence and wind-speed spectra within a Japanese larch plantation. *J. Appl. Meteorol.* 7:73-78
2. Atema, J. 1988. Distribution of chemical stimuli. In *Sensory Biology of Aquatic Animals*, ed. J. Atema, R. R. Fay, A. N. Popper, W. N. Tavolga, pp. 29-56. NY: Springer-Verlag
3. Aylor, D. E. 1976. Estimating peak concentrations of pheromones in the forest. In *Perspectives in Forest Entomology*, ed. J. F. Anderson, M. K. Kaya, pp. 177-88. New York: Academic
4. Aylor, D. E., Parlange, J.-Y., Grannett, J. 1976. Turbulent dispersion of disparlure in the forest and male gypsy moth response. *Environ. Entomol.* 5:1026-32
5. Baker, T. C., Haynes, K. F. 1987. Maneuvers used by flying male oriental fruit moths to relocate a sex-pheromone plume in an experimentally shifted wind-field. *Physiol. Entomol.* 12:263-79
6. Baker, T. C., Haynes, K. F. 1989. Field and laboratory electroantennographic measurements of pheromone plume structure correlated with oriental fruit moth behavior. *Physiol. Entomol.* 14:1-12
7. Baker, T. C., Vogt, R. G. 1988. Measured behavioral latency in response to sex-pheromone loss in the large silk moth *Antheraea polyphemus*. *J. Exp. Biol.* 137:29-38
8. Baker, T. C., Willis, M. A., Haynes, K. F., Phelan, P. L. 1985. A pulsed cloud of pheromone elicits upwind flight in male moths. *Physiol. Entomol.* 10:257-65
9. Bartell, R. J. 1982. Mechanism of communication disruption by pheromone in the control of Lepidoptera: a review. *Physiol. Entomol.* 7:353-64
10. Barynin, J. A. M., Wilson, M. J. G. 1972. Outdoor experiments on smell. *Atmos. Environ.* 6:197-207
11. Bell, W. J. 1984. Chemo-orientation in walking insects. See Ref. 11a, pp. 93-109
- 11a. Bell, W. J., Cardé, R. T., eds. 1984.

- Chemical Ecology of Insects*, London/New York: Chapman and Hall. 524 pp.
12. Bendat, J. S., Piersol, A. G. 1980. *Engineering Applications of Correlation and Spectral Analysis*. New York: Wiley.
 13. Boreham, B. W., Harvey, J. K. 1984. Dipolar charged particles as markers for dispersion simulation in wind tunnels. *J. Phys. E*: 17:994-98.
 14. Boreham, B. W., Jones, C. D., Griffiths, R. F. 1985. Field evaluation of a new Langmuir-type probe for atmospheric dispersion studies using ions as a tracer. *J. Phys. E*: 18:218-23.
 15. Bossert, W. H., Wilson, E. O. 1963. The analysis of olfactory communication among animals. *J. Theor. Biol.* 5:443-69.
 16. Bradshaw, J. W. S., Baker, R., Lisk, J. C. 1983. Separate orientation and releaser components in a sex pheromone. *Nature* 304:265-67.
 17. Bradshaw, J. W. S., Ellis, N. W., Hand, S. C., Stoakley, J. T. 1989. Interaction between pheromone traps with different strength lures for the pine beauty moth. *J. Chem. Ecol.* 15:2485-94.
 18. Brady, J., Gibson, G., Packer, M. J. 1989. Odour movement, wind direction, and the problem of host-finding by tsetse flies. *Physiol. Entomol.* 14:369-80.
 19. Bursell, E. 1984. Observations on the orientation of tsetse flies (*Glossina pallidipes*) to wind-borne odours. *Physiol. Entomol.* 9:133-37.
 20. Cardé, R. T. 1981. Precopulatory sexual behavior of the adult gypsy moth. In *The Gypsy Moth: Research Toward Integrated Pest Management. Technical Bulletin 1584*, ed. C. C. Doane, M. L. McManus, pp. 572-87. Washington, DC: US Dept. of Agriculture.
 21. Cardé, R. T. 1986. Epilogue: behavioural mechanisms. See Ref. 100, pp. 175-86.
 22. Cardé, R. T. 1990. Principles of mating disruption. See Ref. 103, pp. 42-71.
 23. Cardé, R. T., Baker, T., Roelofs, W. 1975. Ethological function of components of a sex attractant system for Oriental fruit moth males, *Grapholitha molesta*. *J. Chem. Ecol.* 1:475-91.
 24. Cardé, R. T., Charlton, R. E. 1984. Olfactory sexual communication in Lepidoptera: strategy, sensitivity, and selectivity. In *Insect Communication*, ed. T. Lewis, pp. 241-64. New York: Academic.
 25. Cardé, R. T., Hagaman, T. E. 1979. Behavioral responses of the gypsy moth in a wind-tunnel to air-borne enantiomers of disparlure. *Environ. Entomol.* 8:475-84.
 26. Charlton, R. E., Cardé, R. T. 1990. Orientation of male gypsy moths, *Lymantria dispar* (L.), to pheromone sources: the role of olfactory and visual cues. *J. Insect Behav.* 3:443-69.
 27. Chatwin, P. C. 1985. *Interaction Between Turbulent and Electrostatic Effects in the Atmospheric Dispersion of Electrically Charged Tracers. Report PTA/AZ/209*. Porton Down: Chemical Defense Establishment.
 28. Christensen, T. A., Hildebrand, J. G. 1987. Male-specific, sex pheromone-selective projection neurons in the antennal lobes of the moth *Manduca sexta*. *J. Comp. Physiol. A* 160:553-69.
 29. Clarke, R. H. 1979. *A model for short and medium range dispersion of radionuclides released to the atmosphere*. Harwell, UK: National Radiological Protection Board Report NRPB-R91.
 30. Conner, W. E., Eisner, T., Vander Meer, R. K., Guerrero, A., Ghiringelli, D., Meinwald, J. 1980. Sex attractant of an arctiid moth (*Utethesia ornatrix*): a pulsed signal. *Behav. Ecol. Sociobiol.* 7:55-63.
 31. Cramer, H. E., Record, F. A., Vaughan, H. C. 1958. *The study of the diffusion of gasses in the lower atmosphere*. Cambridge, MA: MIT Department of Meteorology, Final Report under Contract AF 19(604)-1058.
 32. Critchley, B., Campion, D. G., McVeigh, L. J. 1989. Pheromone Control in the Integrated Pest Management of Cotton. In *Pest Management of Cotton*, ed. M. V. Green, D. J. deB. Lyon, pp. 83-92. Chichester: Horwood.
 33. Csanady, G. T. 1967. Concentration fluctuations in turbulent diffusion. *J. Atmos. Sci.* 24:21-28.
 34. Csanady, G. T. 1973. *Turbulent Diffusion in the Environment*. Dordrecht, Holland: Reidel.
 35. David, C. T., Kennedy, J. S., Ludlow, A. R. 1983. Finding of a sex pheromone source by gypsy moths released in the field. *Nature* 303:804-6.
 36. David, C. T., Kennedy, J. S., Ludlow, A. R., Perry, J. N., Wall, C. 1982. A reappraisal of insect flight towards a distant, point source of wind-borne odor. *J. Chem. Ecol.* 8:1207-15.
 37. Dinar, N., Kaplan, H., Kleiman, M. 1988. Characterization of concentration fluctuations of a surface plume in a neutral boundary layer. *Boundary-Layer Meteorol.* 45:157-75.
 38. Dusenbery, D. B. 1989. Optimal search direction for an animal flying or swimming in a wind or current. *J. Chem. Ecol.* 15:2511-19.

39. Dusenbery, D. B. 1990. Upwind searching for an odor plume is sometimes optimal. *J. Chem. Ecol.* 16:1971-76
40. Elkinton, J. S., Cardé, R. T. 1983. Appetitive flight behavior of male gypsy moths (Lepidoptera: Lymantriidae). *Environ. Entomol.* 12:1702-7
41. Elkinton, J. S., Cardé, R. T. 1984. Odor dispersion. See Ref. 11a, pp. 73-91
42. Elkinton, J. S., Cardé, R. T., Mason, C. J. 1984. Evaluation of time-average dispersion models for estimating pheromone concentration in a deciduous forest. *J. Chem. Ecol.* 10:1081-1108
43. Elkinton, J. S., Schal, C. S., Cardé, R. T. 1987. Pheromone puff trajectory and the upwind flight of male gypsy moths in a forest. *Physiol. Entomol.* 12:399-406
44. Fackrell, J. E. 1978. A system for turbulent concentration measurement. *J. Phys. E* 11:1015-22
45. Fackrell, J. E. 1989. A flame ionization detector for measuring fluctuating concentration. *J. Phys. E* 13:888-93
46. Fackrell, J. E., Robins, A. G. 1982. Concentration fluctuations and fluxes in plumes from point sources in a turbulent boundary layer. *J. Fluid Mech.* 117:1-26
47. Fackrell, J. E., Robins, A. G. 1982. The effect of source size on concentration fluctuations in plumes. *Boundary-Layer Meteorol.* 22:335-50
48. Farkas, S. R., Shorey, H. H. 1972. Chemical trail following by flying insects: a mechanism for orientation to a distant odor source. *Science* 178:67-68
49. Farkas, S. R., Shorey, H. H. 1974. Mechanisms of orientation to a distant pheromone source. In *Pheromones*, Part 5, ed. M. C. Birch, pp. 81-95. Amsterdam: North-Holland Research Monographs
50. Farkas, S. R., Shorey, H. H., Gaston, L. K. 1974. Sex pheromones of Lepidoptera. Influence of pheromone concentration and visual clues on aerial odour trail following by male of *Pectinophora gossypiella*. *Ann. Entomol. Soc. Am.* 67:633-38
51. Gifford, F. A. 1959. Statistical properties of a fluctuating plume dispersion model. In *Advances in Geophysics*, Vol. 6, *Atmospheric Diffusion and Air Pollution*, ed. F. N. Frankel, R. A. Shepard, p. 117. New York: Academic
52. Gifford, F. A. 1974. The form of the frequency distribution of air pollution concentrations. *Proc. Symp. on Statistical Aspects of Air Quality Data. Report 650/4-74-038*. Washington DC: USA Environmental Protection Agency
53. Hadjitoffi, A., Wilson, M. J. G. 1979. Fast response measurement of air pollution. *Atmos. Environ.* 13:755-60
54. Hanna, S. R. 1984. Concentration fluctuations in a smoke plume. *Atmos. Environ.* 18:1091-1106
55. Hanna, S. R. 1984. The exponential PDF and concentration fluctuations in smoke plumes. *Boundary-Layer Meteorol.* 29:361-75
56. Hanna, S. R. 1986. Spectra of concentration fluctuations: the two time scales of a meandering plume. *Atmos. Environ.* 20:1131-37
57. Hanna, S. R., Briggs, G. A., Hosker, R. P. 1982. *Handbook on Atmospheric Diffusion*. Washington DC: Technical Information Center. US Dept. of Energy
58. Hanna, S. R., Insley, E. M. 1989. Time series analyses of concentration and wind fluctuations. *Boundary-Layer Meteorol.* 47:131-47
59. Haugen, D. A. 1959. *Project Prairie Grass, a Field Programme in Diffusion*. Vol. 3, Geographical Research Paper No. 59. Bedford, MA: G.R.D.A.F.C.
60. Hay, J. S., Pasquill, F. 1959. Diffusion from a continuous source in relation to the spectrum and scale of turbulence. *Adv. Geophys.* 6:345
61. Högestrom, U. 1972. A method for predicting odour frequencies from a point source. *Atmos. Environ.* 6:103-21
62. Hunt, J. C. R., Holroyd, R. J., Carruthers, D. J., Robbins, A. G., Apsley, D. D., et al. 1990. Developments in modelling air pollution for regulatory uses. *Proc. 18th NATO-CCMS Int. Conf. Air Pollution Modelling and Its Application, Vancouver, Canada*
63. International Atomic Energy Agency. 1980. *Atmospheric dispersion in nuclear power plant siting, a safety guide*. IAEA Safety Guides No. 50-SG-S3. Vienna: IAEA
64. Jones, C. D. 1977. Ion concentration variations at short distances downwind of continuous and quasi-continuous point sources. *Pestic. Sci.* 8:84-95
65. Jones, C. D. 1978. Statistics of the concentration fluctuations in short range atmospheric dispersion. In *Proc. Conf. Mathematical Modelling of Turbulent Diffusion in the Environment*, Liverpool, ed. C. J. Harris, pp. 277-98. London: Academic
66. Jones, C. D. 1983. On the structure of instantaneous plumes in the atmosphere. *J. Hazard. Mater.* 7:87-112
67. Jones, C. D., Griffiths, R. F. 1984. Full scale experiments on dispersion round an isolated building using an ionized air tracer technique with very short averaging time. *Atmos. Environ.* 18:903-16

68. Jones, C. D., Gulliford, N. T. 1979. Developments in the use of ionized air as a wind tunnel tracer. *J. Phys. E*: 12:321–25
69. Jones, J. I. P. 1963. A band-pass filter technique for recording atmospheric turbulence. *Br. J. Appl. Phys.* 14:95–101
70. Justum, A. R., Gordon, R. F. S., eds. 1989. *Insect Pheromones in Plant Protection*. New York: Wiley
71. Kaissling, K. E. 1986. Chemo-electrical transduction in insect olfactory receptors. *Annu. Rev. Neurosci.* 9:121–45
72. Kennedy, J. S. 1940. The visual response of flying mosquitoes. *Proc. Zool. Soc. London Ser. A* 109:221–42
73. Kennedy, J. S. 1986. Some current issues in orientation to odour sources. See Ref. 100, pp. 11–25
74. Kennedy, J. S. 1977. Olfactory responses to distant plants and other odor sources. In *Chemical Control of Insect Behavior: Theory and Application*, ed. H. H. Shorey, J. J. McKelvey, Jr., pp. 76–91. New York: Wiley Interscience. 414 pp.
75. Kennedy, J. S., Ludlow, A. R., Sanders, C. J. 1981. Guidance of flying male moths by wind-borne sex pheromone. *Physiol. Entomol.* 6:395–412
76. Krasnoff, S. B., Roelofs, W. L. 1988. Sex pheromone released as an aerosol by the moth *Pyrharcia isabella*. *Nature* 33:263–65
77. Kuenen, L. P. S., Baker, T. C. 1982. Optomotor regulation of ground velocity in moths during flight to sex pheromone at different heights. *Physiol. Entomol.* 7:193–202
78. Kuenen, L. P. S., Baker, T. C. 1983. A non-anemotactic mechanism used in pheromone source location by flying moths. *Physiol. Entomol.* 8:277–89
79. Lewis, T., Macauley, E. D. M. 1976. Design and elevation of sex attractant traps for pea moth *Cydia nigricana* (Steph.) and the effect of plume shape on catches. *Ecol. Entomol.* 1:175–87
80. Linn, C. E., Campbell, M. G., Roelofs, W. L. 1986. Male moth sensitivity to multicomponent pheromones: critical role of female-released blend in determining the functional role of components and active space of the pheromone. *J. Chem. Ecol.* 12:659–68
81. Linn, C. E., Campbell, M. G., Roelofs, W. L. 1987. Pheromone components and active spaces: what do moths smell and where do they smell it? *Science* 237:650–52
82. Linn, C. E., Roelofs, W. L. 1989. Response specificity of male moths to multicomponent pheromones. *Chem. Senses* 14:421–37
83. Linsenmair, K. E. 1969. Anemotactische orientierung bei Tenebrioniden und Mistkäfern (Insecta, Coleoptera). *Z. Vgl. Physiol.* 64:154–211
84. Lumley, J. L., Panofsky, H. A. 1964. *The Structure of Atmospheric Turbulence*. New York: Wiley
- 84a. Marsh, D., Kennedy, J. S., Ludlow, A. R. 1978. An analysis of anemotactic zigzagging flight in male moths stimulated by pheromone. *Physiol. Entomol.* 3:221–40
85. Mason, P. J. 1989. Large eddy simulation of the convective boundary layer. *J. Atmos. Sci.* 46:1492–1516
86. McNeil, J. N. 1991. Behavioral ecology of pheromone-mediated communication in moths and its importance in the use of pheromone traps. *Annu. Rev. Entomol.* 36:407–30
87. Meng, L. Z., Wu, C. H., Wicklein, M., Kaissling, K.-E., Bestmann, H. J. 1989. Number and sensitivity of three types of pheromone receptor cells in *Antheraea pernyi* and *A. polyphemus*. *J. Comp. Physiol. A* 165:139–46
88. Miksad, R. W., Kittredge, J. 1979. Pheromone aerial dispersion: a filament model. In *14th Conf. Agriculture and Forest Meteorology*, pp. 238–43. Boston, MA: Am. Meteorol. Soc.
89. Moore, P., Atema, J. 1988. A model of a temporal filter in chemoreception to extract directional information from a turbulent odour plume. *Biol. Bull.* 174:355–63
90. Murlis, J. 1986. The structure of odour plumes. See Ref. 100, pp. 27–38
91. Murlis, J., Jones, C. D. 1981. Fine-scale structure of odour plumes in relation to insect orientation to distant pheromone and other attractant sources. *Physiol. Entomol.* 6:71–86
92. Murlis, J., Willis, M. A., Cardé, R. T. 1990. Odour signals: patterns in time and space. *Proc. 10th Int. Symp. Olfaction and Taste, Oslo*, ed. K. B. Døving, pp. 6–17. Oslo: Univ. Oslo
93. Mylne, K. R. 1988. Experimental measurements of concentration fluctuations. See Ref. 117a, 7:555–65
94. Mylne, K. R., Mason, P. J. 1991. Concentration fluctuation measurements in a dispersing plume at a range of up to 100 m. *Q. J. R. Meteorol. Soc.* 117:177–206
95. Nakamura, K. 1979. Effect of the minor component of the sex pheromone on the male orientation to pheromone source in

- Spodoptera litura* (F.). *Chem. Rev. Insect Russia* 4:153-56
96. Nakamura, K., Kawasaki, F. 1977. The active space of *Spodoptera litura* (F.) sex pheromone and the pheromone component determining this space. *Appl. Entomol. Zool.* 12:162-77
 97. Nieuwstadt, T. F. M., van Harem, L. 1988. A large eddy simulation of buoyant and non-buoyant plume dispersion in the convective atmospheric boundary layer. See Ref. 117a, 6:525-38
 98. Pasquill, F. 1961. The estimation of the dispersion of windborne material. *Meteorol. Mag.* 90:33-49
 99. Pasquill, F., Smith, F. B. 1983. *Atmospheric Diffusion*. Chichester: Horwood. 3rd ed.
 100. Payne, T. L., Birch, M. C., Kennedy, C. E. J., eds. 1986. *Mechanisms in Insect Olfaction*. Oxford: Clarendon. 364 pp.
 101. Ramsdell, J. V., Hinds, W. T. 1979. Concentration fluctuations and peak-to-mean concentration ratios in plumes from a ground level source. *Atmos. Environ.* 5:483-95
 102. Ride, D. J. 1988. A model for the observed intermittency of a meandering plume. *J. Hazard. Mater.* 19:131-37
 103. Ridgway, R. L., Silverstein, R. M., Inscocoe, M. N., eds. 1990. *Behavior-Modifying Chemicals for Insect Management*. New York: Dekker. 761 pp.
 104. Roberts, O. F. T. 1923. The theoretical scattering of smoke in turbulent atmosphere. *Proc. R. Soc. London Ser. A* 104:640-54
 105. Rumbo, R., Kaissling, K. E. 1989. Temporal resolution of odour pulses by three types of pheromone receptor cells in *Antheraea polyphemus*. *J. Comp. Physiol. A* 165:281-91
 106. Sabelis, M. W., Schippers, P. 1984. Variable wind directions and anemotactic strategies of searching for an odour plume. *Oecologia* 63:225-28
 107. Sawford, B. L. 1983. The effect of Gaussian particle-pair distribution functions in the statistical theory of concentration fluctuations in homogeneous turbulence. *Q. J. R. Meteorol. Soc.* 109:339-54
 108. Sawford, B. L. 1987. Conditional concentration statistics for surface plumes in the atmospheric boundary layer. *Boundary-Layer Meteorol.* 38:209-23
 109. Smith, F. B. 1990. *Proceeding of Course on Atmospheric Dispersion*. Trieste, Italy: Int. Centre for Theoretical Physics
 110. Steinbrecht, R. A. 1987. Functional morphology of pheromone-sensitive sensilla. In *Pheromone Biochemistry*, ed. G. D. Prestwich, G. L. Blomquist, pp. 353-84. New York: Academic
 111. Storebø, P. B., Bjørvatten, T., Hønnashagen, K., Lillegraven, A., Jones, C. D., van Buijtenen, C. J. P. 1983. Tracer experiments with turbulently dispersed air ions. *Boundary-Layer Meteorol.* 26:127-39
 112. Sutton, O. G. 1953. *Micrometeorology*. New York: McGraw-Hill
 113. Sykes, R. I. 1988. Concentration fluctuations in dispersing plumes. In *Lectures on Air Pollution Modelling*, ed. A. Venkatram, J. C. Wyngaard, pp. 325-56. Boston: Am. Meteorol. Soc.
 114. Sykes, R. I., Lewellen, W. S., Parker, S. F. 1984. A turbulent transport model for concentration fluctuations and fluxes. *J. Fluid Mech.* 139:193-218
 115. Thompson, D. J. 1986. A random walk model of dispersion in turbulent flows and its application to dispersion in a valley. *Q. J. R. Meteorol. Soc.* 112:511-30
 116. Thompson, D. J. 1990. A stochastic model for the motion of particle pairs in isotropic high Reynolds number turbulence and its application to the problem of concentration variance. *J. Fluid Mech.* 210:113-53
 117. Turner, D. B. 1970. *Workbook of Atmospheric Dispersion Estimates*. Washington DC: Office of Air Programs, Pub. No. AP-26, US Environ. Prot. Agency
 - 117a. van Dop, H., ed. 1988. *Air Pollution Modelling and Its Applications*. New York: Plenum
 118. Venkatacham, A. 1983. On dispersion in the convective boundary layer. *Atmos. Environ.* 17:5529-33
 119. Vogt, R. G., Riddiford, L. M. 1986. Pheromone reception: a kinetic equilibrium. See Ref. 100, pp. 201-8
 120. Wall, C., Sturgeon, D. M., Greenway, A. R., Perry, J. N. 1981. Contamination of vegetation with synthetic sex-attractant released from traps for the pea moth *Cydia nigricana* (F.). *Entomol. Exp. Appl.* 30:111-15
 121. Wang, Y. 1989. Turbulence structure, momentum and heat transport in the edge of broad leaf tree stands. *Technical Report US Forest Service*
 122. Willis, M. A., Baker, T. C. 1984. Effects of intermittent and continuous pheromone stimulation on the flight behavior of the oriental fruit moth, *Grapholitha molesta*. *Physiol. Entomol.* 9:341-58

123. Willis, M. A., Cardé, R. T. 1990. Pheromone-modulated optomotor response in male gypsy moths, *Lymantria dispar* L.: upwind flight in a pheromone plume in different wind velocities. *J. Comp. Physiol. A*. 167:699–706
124. Wilson, D. J., Robins, A. G., Fackrell, J. E. 1982. Predicting the spatial distribution of concentration fluctuation from a ground level source. *Atmos. Environ.* 16:497–504
125. Wilson, D. J., Robins, A. G., Fackrell, J. E. 1985. Intermittency and conditionally averaged concentration fluctuation statistics in plumes. *Atmos. Environ.* 19:1053–64
126. Wright, R.H. 1958. The olfactory guidance of flying insects. *Can. Entomol.* 90:81–89
127. Wright, R.H. 1964. *The Science of Smell*. London: Allen and Unwin



CONTENTS

THE ANALYSIS OF PARASITE TRANSMISSION BY BLOODSUCKING INSECTS, <i>Christopher Dye</i>	1
HOST-SEEKING BEHAVIOR AND MANAGEMENT OF TSETSE, <i>John Colvin and Gabriella Gibson</i>	21
SMALL ERMINE MOTHS (<i>YPONOMEUTA</i>): Their Host Relations and Evolution, <i>Steph B. J. Menken, W. M. Herrebout, and J. T. Wiebes</i>	41
THE CHEMICAL ECOLOGY OF APHIDS, <i>J. A. Pickett, L. J. Wadhams, C. M. Woodcock, and J. Hardie</i>	67
TACTICS FOR MANAGING PESTICIDE RESISTANCE IN ARTHROPODS: Theory and Practice, <i>I. Denholm and M. W. Rowland</i>	91
FUNCTIONAL MORPHOLOGY OF INSECT WINGS, <i>Robin J. Wootton</i>	113
ECOLOGY OF INFOCHEMICAL USE BY NATURAL ENEMIES IN A TRITROPHIC CONTEXT, <i>Louise E. M. Vet and Marcel Dicke</i>	141
THE BIOLOGY AND MANAGEMENT OF AFRICANIZED HONEY BEES, <i>Mark L. Winston</i>	173
IRON ECONOMY IN INSECTS: Transport, Metabolism, and Storage, <i>Michael Locke and H. Nichol</i>	195
ACCUMULATION OF YOLK PROTEINS IN INSECT OOCYTES, <i>Alexander S. Raikhel and Tarlochan S. Dhadialla</i>	217
FORENSIC ENTOMOLOGY IN CRIMINAL INVESTIGATIONS, <i>E. P. Catts and M. L. Goff</i>	253
INSECT CUTICLE SCLEROTIZATION, <i>Theodore L. Hopkins and Karl J. Kramer</i>	273
MATURATION OF THE MALE REPRODUCTIVE SYSTEM AND ITS ENDOCRINE REGULATION, <i>George M. Happ</i>	303
THE EVOLUTION OF APHID LIFE CYCLES, <i>Nancy A. Moran</i>	321
FEEDING BEHAVIOR, NATURAL FOOD, AND NUTRITIONAL RELATIONSHIPS OF LARVAL MOSQUITOES, <i>R. W. Merritt, R. H. Dadd, and E. D. Walker</i>	349

FRUGIVORY, SEED PREDATION, AND INSECT-VERTEBRATE INTERACTIONS, <i>R. Sallabanks and S. P. Courtney</i>	377
POLYDNAVIRUSES: Mutualists and Pathogens, <i>Jo-Ann G. W. Fleming</i>	401
SAMPLING INSECT POPULATIONS FOR THE PURPOSE OF IPM DECISION MAKING, <i>M. R. Binns and J. P. Nyrop</i>	427
NONLINEAR DYNAMICS AND CHAOS IN INSECT POPULATIONS, <i>J. A. Logan and J. C. Allen</i>	455
ROLE OF ANTS IN PEST MANAGEMENT, <i>M. J. Way and K. C. Khoo</i>	479
ODOR PLUMES AND HOW INSECTS USE THEM, <i>John Murlis, Joseph S. Elkinton, and Ring T. Cardé</i>	505
THE COST OF MIGRATION IN INSECTS, <i>M. A. Rankin and J. C. A. Burchsted</i>	533
ADVANCES IN IMPLEMENTING INTEGRATED PEST MANAGEMENT FOR WOODY LANDSCAPE PLANTS, <i>M. J. Raupp, C. S. Koehler, and J. A. Davidson</i>	561
LIFE-TABLE CONSTRUCTION AND ANALYSIS IN THE EVALUATION OF NATURAL ENEMIES, <i>T. S. Bellows, Jr., R. G. Van Driesche, and J. S. Elkinton</i>	587
THE MODE OF ACTION OF <i>BACILLUS THURINGIENSIS</i> ENDOTOXINS, <i>Sarjeet S. Gill, Elizabeth A. Cowles, and Patricia V. Pietrantonio</i>	615
REGULATION OF DIVISION OF LABOR IN INSECTS SOCIETIES, <i>Gene E. Robinson</i>	637
INDEXES	
Subject Index	667
Cumulative Index of Contributing Authors, Volumes 28–37	676
Cumulative Index of Chapter Titles, Volumes 28–37	679