

MODELS FOR DISPERSAL OF VAPORS IN OPEN AND CONFINED SPACES: Applications to Sex Pheromone Trapping in a Warehouse

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Abstract—Methods are presented for mathematically determining dispersal of a vapor in still air, in turbulent air of zero average velocity, and in turbulent or laminar air currents of constant, nonzero average velocity. The methods are combined with several assumptions about insect behavior to derive an insect attraction model that predicts: (1) In a warehouse a searching insect is likely to be attracted to a calling insect if it comes within an attraction sphere, 0.4–2.5 m in radius. (2) The attraction spaces of typical sex pheromone-baited traps that emit pheromone at rates greater than 0.01 ng/sec extend beyond the boundaries of a $10 \times 10 \times 10$ -m warehouse. (3) The searching behavior of an attracted insect is likely to be altered from an extensive to an intensive pattern if it comes within an altered-behavior sphere, 6–60 cm from a calling insect or within 10 m of a trap emitting 0.76 ng/sec. (4) Pheromone does not sink unless it is emitted along with a large amount of a high-vapor pressure solvent. The model is used in support of several hypotheses, including: (1) The effect of an adsorptive surface on the vapor concentration after an extended period of emission is negligible except at positions near the surface. (2) Sex pheromone-baited traps with sources of small dimensions have greater trapping efficiency than otherwise identical traps with sources of large dimensions.

Key Words—Sex pheromone, attractance, behavioral threshold, *Plodia interpunctella*, Indian meal moth, Lepidoptera, Pyralidae, orientation, chemical communication.

INTRODUCTION

The probability of an insect finding a source of an attractant vapor is determined by the pattern and intensity of its searching behavior. Both the

searching pattern and the intensity are strongly affected by the attractant concentration and the dynamics of the airflow (Roelofs, 1975; Shorey and McKelvey, 1977). Several different mathematical expressions of the relationships between behavior and airflow dynamics have been presented in insect attractance models by Wright (1958), Bossert and Wilson (1963), Bossert (1968), Hartstack et al. (1976), Hirooka and Suwanai (1976), Aylor (1976), Aylor et al. (1976), Nakamura (1976), Nakamura and Kawasaki (1977), and Roelofs (1978). None of these models considers jointly three problems frequently encountered in a warehouse environment: the deposition of attractant onto exposed surfaces, the restricted dispersal of attractant near obstructions, and the complicated, rapidly changing pattern of the airflow. The need for methods of resolving such problems is increasing because of the growing number of sex pheromone trapping experiments involving post-harvest pests (Sower et al., 1975; Barak and Burkholder, 1976; Read and Haines, 1976; Reichmuth et al., 1976, 1978; Shapas and Burkholder, 1978; Vick et al., 1979).

Although the model we present applies primarily to attraction in a warehouse, it also applies to field and forest environments because it incorporates many elements of previous models. The part of the model dealing with dispersal patterns applies to any vapor, whether or not it is odorous to a given animal. The part dealing with attraction applies primarily to animals that orient to a particular vapor by a taxis, e.g., upwind anemotaxis or chemotaxis. The model incorporates the concept of active space (Bossert and Wilson, 1963), which is a zone where the average vapor concentration is above a perceptual or behavioral threshold, i.e., above a level that generally induces attraction behavior. Like the Bossert and Wilson (1963) model, the new model calculates the dimensions of an attraction space with either still air or steady airflow conditions; and like the Aylor (1976) model, it treats the effects of turbulence in some detail. It also includes the effects of an altered-behavior threshold (Roelofs, 1978), which is a level of concentration about three orders of magnitude above the perceptual threshold. The searching behavior of an insect stimulated at this level changes from an extensive to an intensive searching pattern, thus increasing the likelihood of finding close-range sources. Moreover, it considers adsorption processes, the positions of boundaries or obstructions, gravitation, and the instantaneous structure of the vapor plume.

METHODS AND MATERIALS

The derivation of the model proceeds in stages of increasing complexity. First, a simplified mathematical description of dispersal and attraction processes is presented. Then the description is elaborated by examining the

qualitative effects of several unquantified factors. The simplified description is based on the following assumptions: (1) For any attractant vapor there is a threshold concentration below which the probability of the vapor inducing attraction behavior in a representative insect is negligible. Above this threshold the probability is high that the insect will find the source of the vapor. (2) For any attractant vapor there is a corresponding altered-behavior threshold concentration above which the vapor evokes a qualitative change in the initially induced attraction behavior which decreases the probability of the insect finding a distant source and increases the probability of finding a local source. (3) These attraction and altered-behavior thresholds depend upon the physiological state of the insect, the temperature, and the chemical nature of the attractant, all of which are fixed in a given application of the model. (4) The emission rate of the attractant source is constant. None of these assumptions is strictly valid under the usual modeling applications in which the physiological state of the insect, the ambient temperature, and the source emission rate vary, but they are nevertheless useful heuristically.

Assumptions 1-4 result in a simplified model of insect attraction that is essentially a mathematical description of the attractant dispersal pattern. But this description is quite complicated in itself. The plume emitted from an attractant source disperses in a manner that depends on the characteristics of the airflow (Skelland, 1974). Three different cases will be considered in the derivation: dispersal in still air by molecular diffusion, dispersal in turbulent air currents of zero average speed and direction, and dispersal in turbulent or laminar air current of constant average speed and direction.

Case I: Molecular Diffusion. In still air a vapor disperses by molecular diffusion, a process described by the mass-balance equation (Veigle and Head, 1978):

$$q = \left(\frac{\partial}{\partial t} - D \nabla^2 \right) C \quad (1)$$

where q is the rate of emission per unit volume, with units of $\text{g}/\text{sec}/\text{cm}^3$; D is the diffusion coefficient, cm^2/sec ; C is the vapor concentration, g/cm^3 ; $\partial/\partial t$ represents differentiation with respect to time; ∇^2 represents the Laplacian differential operator (Protter and Morrey, 1966; p. 567).

Theoretically equation 1 has many solutions, depending on the initial concentration distribution and the first partial derivative, $\partial C/\partial r$, at all boundary surfaces. For heuristic purposes it is convenient to assume that the source is surrounded by a single boundary surface and that the initial ($t = 0$) concentration is zero everywhere inside the boundary. The value of $\partial C/\partial r$ at this boundary is (Chamberlain, 1953; Judéikis and Stewart, 1976; Draxler and Elliot, 1977):

$$\partial C/\partial r = (V_d/D) C \quad (2)$$

where: V_d is an empirical parameter, the deposition velocity, cm/sec.

The solution to equations 1 and 2 for dispersal inside a spherical boundary is (Carslaw and Jaeger, 1967, p. 367, and Appendix):

$$C = \frac{Q}{2\pi arD} \left\{ \sum_{n=1}^{\infty} \left[\frac{(ah - 1)^2 + a^2\theta_n^2}{a^2\theta_n^2 + ah(ah - 1)} \right] \right\} [\sin(r\theta_n)/\theta_n][1 - \exp(-D\theta_n^2 t)] \quad (3)$$

where: Q is the emission rate of the source, g/sec; a is the distance of the boundary sphere from the source, cm; r is the distance of the measurement position from the source, cm; t is the duration of emission, sec; h is the ratio V_d/D , cm^{-1} ; θ_n is the n th positive root of the equation

$$a\theta \cot(a\theta) + ah = 1 \quad (4)$$

Equations 3 and 4 are not restricted particularly to attraction problems with spherical boundaries because most attractants have values of D and V_d that fall within fairly narrow ranges and thus limit the extent of boundary effects. The molecular diffusion coefficient of a typical sex pheromone is about $0.05 \text{ cm}^2/\text{sec}$ (Wilson et al., 1969; Hirooka and Suwanai, 1976), and most other attractants have molecular diffusion coefficients near $0.03\text{--}0.07 \text{ cm}^2/\text{sec}$ (Monchiek and Mason, 1961; Lugg, 1968). Unless conditions are strictly controlled, air currents usually occur that effectively increase D to $0.1\text{--}0.5 \text{ cm}^2/\text{sec}$ (Bossert and Wilson, 1963). The magnitude of the deposition velocity depends primarily upon the forces causing adsorption of the attractant vapor to the substrate. Interfaces composed of different vapors and different substrates have similar deposition velocities inasmuch as the vapor-substrate interactive forces are similar (Judeikis and Stewart, 1976). Measurements of deposition velocity typically vary over the range $0.1\text{--}10 \text{ cm}/\text{sec}$ for iodine-plastic, SO_2 -concrete, and pheromone-vegetation interfaces (Chamberlain, 1953, 1966; Judeikis and Stewart, 1976; Nakamura and Kawasaki, 1977). The following analysis of equations 3 and 4 shows that when D and V_d fall within the indicated ranges the effect of a boundary on the vapor distribution is usually small.

The spatial variation of the vapor concentration is depicted in Figures 1-4 at several values of boundary position, a ; diffusion coefficient, D ; deposition velocity, V_d ; and time, t . The ordinate is the ratio of the concentration to the emission rate, $C_r = C/Q$, hereafter called the relative concentration. For determination of the actual concentration from the figures, the relative concentration is multiplied by the emission rate of the source. The curves were calculated from the first 700 terms of the series in equation 3, which converged after about 200 terms except at small r and t . The curve for $a = \infty$ corresponds to the boundless case previously discussed by Bossert and Wilson (1963), in which the solution reduces to:

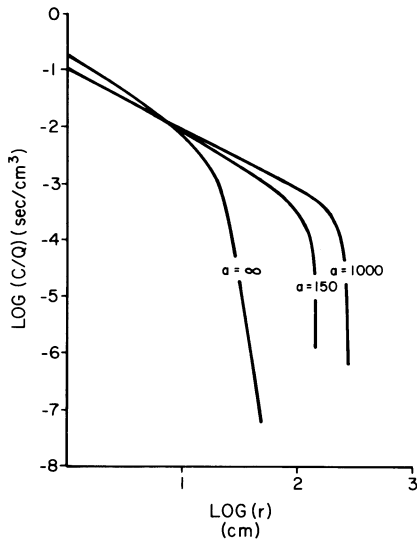


FIG. 1. Spatial variation of the relative concentration, $C_r = C/Q$, at $t = 60$ sec. The regression lines are calculated from equations 3 and 4 with $D = 1 \text{ cm}^2/\text{sec}$, and $V_d = 1 \text{ cm}/\text{sec}$. The radius of the boundary sphere, a , is in units of cm.

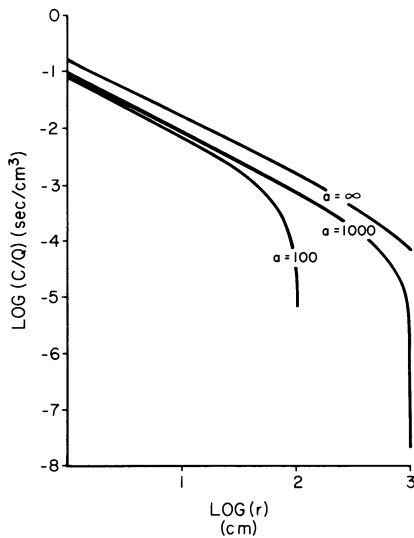


FIG. 2. Spatial variation of the relative concentration, $C_r = C/Q$, at $t = 8.6 \times 10^9$ sec. The regression lines are calculated from equations 3 and 4 with $D = 1 \text{ cm}^2/\text{sec}$, and $V_d = 1 \text{ cm}/\text{sec}$. The radius of the boundary sphere, a , is in units of cm.

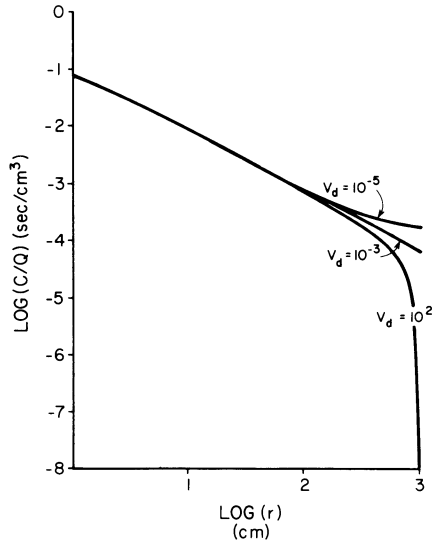


FIG. 3. Variation of the relative concentration, $C_r = C/Q$, with respect to the deposition velocity, V_d . The regression lines are calculated from equations 3 and 4 with $t = 8.6 \times 10^5$ sec, $D = 1$ cm²/sec, and $a = 1000$ cm. V_d is in units of cm/sec.

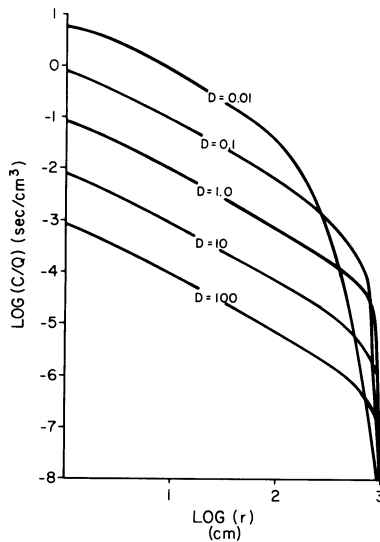


FIG. 4. Variation of the relative concentration, $C_r = C/Q$, with respect to the diffusion coefficient D . The regression lines are calculated from equations 3 and 4 with $t = 8.6 \times 10^5$ sec, $V_d = 1$ cm/sec, and $a = 1000$ cm. D is in units of cm²/sec.

$$C = \frac{Q}{2\pi Dr} \operatorname{erfc} [r/(4Dt)^{1/2}] \quad (5)$$

where: erfc is the complementary error function (Carslaw and Jaeger, 1967).

Inspection of Figures 1 and 2 shows that the smaller the boundary radius, the smaller the variation of C , with time; as t increases, the difference between C , in a bounded and a boundless environment decreases. The two curves for $a = \infty$ differ considerably, but the curve for $a = 150$ at $t = 60$ sec is quite similar to the curve for $a = 100$ at $t = 8.6 \times 10^5$ sec. After 10^3 sec there is little difference between the curves $a = \infty$, $a = 1000$, and $a = 100$, within short distances of the respective boundaries. The curves for 10^3 sec are not plotted because they are similar to the curves shown in Figure 2. Indeed, the effect of the boundary can be disregarded so long as $r/a < 0.9$ unless D is considerably smaller than $1 \text{ cm}^2/\text{sec}$. This is shown in Figures 3 and 4, where D ranges from 10^{-2} to $10^2 \text{ cm}^2/\text{sec}$ and V_a from 10^{-5} to $10^2 \text{ cm}/\text{sec}$, at $t = 8.6 \times 10^5$ sec and $a = 1000$ cm. Even at the hypothetical lower limit of the molecular diffusion coefficient, $0.1 \text{ cm}^2/\text{sec}$, the influence of the boundary is negligible until $r/a > 0.75$. Under these conditions, the exact geometry of a boundary is unimportant, and the solution to equations 1 and 2 for any boundary geometry is similar to the solution to equations 3 and 4. This justifies the general use of equations 3 and 4 in a model for attraction in still air, provided that the results are interpreted with caution when $r/a > 0.9$ inside boundaries where the geometry is highly nonspherical or when the emission duration is less than about an hour.

Case II: Dispersal in Airflow of Zero Average Velocity. The next step is to consider the effect of random whirls or eddies of air on the diffusion process. Even in relatively still air, small velocity fluctuations often occur, caused by superimposed whirls or eddies of various sizes. Eddies with a diameter greater than about 100 cm or smaller than about 5 cm have little effect on a vapor plume, but eddies of intermediate diameter cause the plume to disperse rapidly (Aylor, 1976). This kind of dispersal is called turbulent or eddy diffusion because the resultant dispersal pattern is analogous to that of molecular diffusion. If the airflow has a near-zero average velocity, eddy diffusion can be described via equation 1, by replacing the molecular diffusion coefficient with the sum of the molecular and eddy diffusion coefficients. The eddy diffusion coefficient of a vapor or an aerosol is $0.1\text{--}10 \text{ cm}^2/\text{sec}$ in a calm environment (Sutton, 1953; Pasquill, 1961; Bossert and Wilson, 1963; Allen, 1975). Just as in molecular diffusion, equations 3 and 4 can be used as a general solution to the turbulent diffusion problem, provided the results are interpreted with caution when $t < 3600$ sec and/or $r/a > 0.9$ inside boundaries where the geometry is highly nonspherical. In the case of a spherical boundary, equations 3 and 4 could be unreliable over time periods of less than ca. 3 min because the eddy diffusion coefficient is a time-averaged quantity.

An equation for case II dispersal that is valid after long periods of emission ($> 10^3$ – 10^4 sec) and is somewhat simpler than equations 3 and 4 can be derived by setting $\frac{\partial C}{\partial t} = 0$ in equation 1. The solution to this steady-state

diffusion equation is discussed in detail elsewhere (e.g., Skelland, 1974; pp. 18–20) so it will not be considered further here. Even further simplification results from setting $a = \infty$, which yields the steady-state solution for the boundless case: $C = Q/2\pi rD$. It should be noted that either of these steady-state alternatives overestimates the actual vapor concentration.

Case III: Dispersal in Airflow of Constant Average Velocity. The derivation of an attraction model is now completed by considering the effect of relatively stable convection on molecular and turbulent diffusion processes. An exact mathematical description of convective–diffusive dispersal does not exist, but many time-averaged statistical descriptions have been published (e.g., Sutton, 1953; Pasquill, 1961; Lamb et al., 1975). The Sutton equation is:

$$C = \frac{2Q}{\pi K_y K_z v X^{1.75}} \exp \left[-X^{1.75} \left(\frac{Y^2}{K_y^2} + \frac{Z^2}{K_z^2} \right) \right] \quad (6)$$

where: v is the mean air velocity, cm/sec; X is the distance from the source along the airflow axis, cm; Y is the distance from the source along the crosswind horizontal axis, cm; Z is the distance from the source along the vertical axis, cm; K_y , K_z are empirical constants whose values have been tabulated for different turbulence levels, $\text{cm}^{0.125}$ (Gifford, 1960). Equation 6 has been incorporated into several of the models cited in the introduction.

There are several caveats to the use of equation 6. When barriers or thermal stratification interfere with free air movement or the airflow becomes highly unstable, tabulated values of K_y and K_z are not reliable (Sutton, 1953). In that case, the dispersal pattern can be observed directly by using smoke plumes, and the tabulated values of K_y and K_z can be replaced with values determined by the extent of the plumes (Pasquill, 1961). Also, equation 6 provides no information about the instantaneous concentration distribution, which may be a more important determinant of the searching behavior of the insect than the average distribution (Aylor, 1976). Qualitative effects of differences in the instantaneous distribution can nevertheless be incorporated into the model as follows:

A vapor plume typically consists of three distinct regions that differ in shape (Aylor, 1976; Kittredge, Marine Biomedical Institute, Galveston, Texas, personal communication). Region I extends 0.5–10 m downwind of the source. The plume in this region is a single filament with a width smaller than the widths of the smallest eddies; thus, it disperses solely by the slow process of molecular diffusion. In region II which extends from the edge of region I to

about 50–70 m downwind, depending on the turbulence and the air velocity, the plume splits into several filaments and begins to expand rapidly because its width, which is now comparable to the widths of the smaller eddies, allows dispersal by turbulent diffusion (Hinze, 1976). This expansion continues until the limits of the plume become indistinct in the final region, which extends downwind indefinitely from the edge of region II. The plume has greater definition in region I than in region II, and the least definition in region III.

The regional differences in plume shape can be used to improve predictions about insect behavior inside the attraction space. According to current theories of flight orientation behavior (Farkas and Shorey, 1974; Kennedy, 1974; and references therein), an insect finds it easier to steer toward a source when the attractant plume structure is well defined. Incorporating this hypothesis into the model leads to a prediction that an insect is more likely to reach the source if it enters region I than if it enters the other two regions. A corollary is that the smaller the dimensions of the source, the greater the extent of region I, and the greater the probability of an insect finding the source.

The choice between equation 6 or equations 3 and 4 for a particular application of the model depends on the level of turbulence, the obstructing boundaries, and the shape of the plume. If the shape of the attractant plume is unknown, it can be determined by smoke plume observations (Mankin et al., 1980). Generally case I dispersal, which is characterized by the absence of turbulence, occurs only in a highly controlled environment. If a plume in turbulent air is nearly spherical, case II applies; if the plume is ellipsoidal, case III applies. The movement of a plume in sheltered areas, cul-de-sacs, or a closed, empty warehouse with an isothermal temperature distribution usually fits a case II dispersal pattern. Case III dispersal is more likely to occur in open ventilated corridors or highly stratified air. Neither equation 6 nor equations 3 and 4 are accurate within short emission durations.

Before proceeding with applications of the model it is appropriate to consider briefly the validity of assumptions 1–4 and the precision of the dispersal equations. The simplified description obtained by adopting the assumptions neglects such behavioral factors as visual attraction (Shorey and Gaston, 1965; Hienton, 1974), the complexity of anemotaxis (Kennedy, 1974), habituation (Thompson and Spencer, 1966; Traynier, 1968; Sower et al., 1973; Marks, 1978), and changes in the intensity of a response at different attractant concentrations (Cain and Engen, 1969; Mayer, 1973; Bartell and Lawrence, 1977). However, these factors remain to be quantified precisely so their inclusion in the model cannot yet improve its precision. The model also neglects such physical factors as the effect of the trap on the pheromone distribution, pheromonal lability (Lundberg, 1961; Sower et al., 1975), differences in the ratios of attractant components (Roelofs, 1978), and changes in the emission rate of the source at different temperatures and

airflows. These factors, as well as the statistical nature of atmospheric mass-transfer processes, limit the precision of the dispersal equations used in the model. Because of such limitations, the model must be used in conjunction with, rather than instead of, experimental studies. These caveats notwithstanding, the model provides considerable insight into the attraction process, as shown by the following applications.

RESULTS

In this section, the first application (with case I dispersal) treats the hypothesis (Traynier, 1968; Perez and Hensley, 1973) that pheromone-laden air tends to sink. The next application (with case II dispersal) considers attraction spaces and altered-behavior spaces for calling insects and sex pheromone traps. Attraction to competing sources is also considered. The last application (with case III dispersal) entertains the possibility that insects can be attracted from outside a warehouse.

Case I Dispersal: Effect of Gravity on Pheromone in Still Air. According to equations 3 and 4 sex pheromone disperses spherically from a source in still air. At any given time the concentration away from a source tends to decrease logarithmically with increased distance, i.e., a 10-fold increase in distance results in a 10-fold decrease in concentration up to a certain "point" of inflection. Thereafter the relative concentration decreases much more rapidly with distance. As time passes this point of inflection moves farther and farther away from the source. The presence of a boundary tends to flatten the distribution except at points close to the boundary. The effects of gravity are neglected in equations 3 and 4, so these equations predict, by default, that the dispersal of pheromone in still air is unaffected by the high molecular weight of pheromone molecules relative to the weight of air molecules. However, even if gravitation is incorporated into the model, the argument presented below indicates that this prediction still holds.

The effect of gravity is determined by Archimedes' principle (Sears, 1958, p. 365) in that an air-pheromone mixture is subject to a gravitational force proportional to the difference between the density of the mixture and the density of the air surrounding it. The standard density of air is $\rho_a = 1.3 \times 10^{-3}$ g/cm³ (Sears, 1958). The density of the air-pheromone mixture is, by definition:

$$\rho_{ap} = \frac{m_a}{V} + \frac{m_p}{V} \quad (7)$$

where: ρ_{ap} is the density of the air-pheromone mixture, g/cm³; m_a is the mass of air inside V , g; m_p is the mass of pheromone inside V , g; V is the volume, cm³.

The pheromone vapor density, m_p/V , reaches a maximum at partial pressures approaching the vapor pressure, the pressure exerted by the pheromone vapor when the air is saturated. The vapor pressure and the corresponding saturated vapor density of a 12 to 16-carbon sex pheromone are about 1×10^{-4} cm Hg and 10 ng/cm^3 , respectively (Hirooka and Suwanai, 1976). The magnitude of m_a/V in equation 7 can be calculated by combining Dalton's Law of Partial Pressures, the Ideal Gas Law, and the relationship between mass and molecular weight, which are, respectively,

$$P_{at} = P_p + P_a \quad (8)$$

$$PV = NRT \quad (9)$$

$$m = NM \quad (10)$$

where: P is the pressure in units of cm Hg or dyne/cm²; N is the number of moles; R is the gas constant, 8.31×10^7 ergs/mol Kelvin; T is the temperature, degrees Kelvin; m is the mass, g; M is the molecular weight, g/mol. The subscripts a , p , and at , refer to unadulterated air, pheromone, and atmosphere, respectively. The result of combining equations 8-10 is

$$m_a/V = \rho_a - m_p M_a / V M_p \quad (11)$$

which yields, upon substitution into equation 7:

$$\rho_{ap} = \rho_a + m_p(1 - M_a/M_p)/V \quad (12)$$

M_a , the molecular weight of air, is about 29 g/mol and M_p , the molecular weight of the pheromone, is about 225 g/mol. On the basis of a maximum value of 10 ng/cm^3 for m_p/V , the maximum density of the air-pheromone mixture is

$$\rho_{ap} = 1.3 \times 10^{-3} + 8.7 \times 10^{-9} \text{ g/cm}^3 \quad (13)$$

There is thus essentially no difference between the density of the air-pheromone mixture and the unadulterated air; so by Archimedes' principle, gravity has little effect on the mixture.

By contrast, a solvent such as diethyl ether may sink in still air because it has a high vapor pressure, about 442 mm Hg. The combination of equation 9 and the conversion factor, 1 cm Hg = 1.33×10^4 dynes/cm, yields

$$\frac{m_e}{V} = \frac{M_e P}{RT} = 1.75 \times 10^{-3} \text{ g/cm}^3 \quad (14)$$

where: M_e is the molecular weight of diethyl ether, 74 g/mol; m_e is the mass of ether inside V , g.

Accordingly, the density of the air - diethyl ether mixture is $\rho_{ae} = 2.36 \times 10^{-3} \text{ g/cm}^3$.

To estimate the rate of fall of the mixture we calculate the net force on 1 ml of ether-saturated air by Archimedes' principle:

$$F = (\rho_{ae} - \rho_a) 980 \text{ cm}^4/\text{sec}^2 = 1.04 \text{ dynes} \quad (15)$$

After 1 sec a milliliter of ether-saturated air falls at the velocity

$$V = \frac{F}{\rho_{ae} \times 1 \text{ ml}} (1 \text{ sec}) = 440.7 \text{ cm/sec} \quad (16)$$

which is about half the rate of fall of a solid object. However, immediately after the mixture is emitted it begins to disperse into the air. Within a short period, the density inside V equilibrates with that of the surrounding air, and the rate of fall decreases to zero.

Case II Dispersal: Attraction and Altered Behavior Spaces of IMM. The generalized picture of pheromone dispersal in a case II environment is similar to that described for a case I environment. One difference is that, because the eddy diffusion coefficient is a time-averaged quantity, the instantaneous vapor distribution may or may not be spherical. Another difference is due to the eddy diffusion coefficient being much larger than the molecular diffusion coefficient. Increasing the magnitude of the diffusion coefficient tends to push the position of the inflection point away from the source (see Figure 4). Figures 1 and 2 provide estimates of the attraction and altered-behavior spaces of an attractant source when the corresponding thresholds are known.

To demonstrate the calculation of attraction and altered-behavior spaces, we consider as an example the Indian meal moth (IMM), *Plodia interpunctella* (Hübner). A male IMM has an upwind anemotactic threshold of $6.8 \times 10^{-9} \text{ ng/cm}^3$ (10^{-17} molar) at 34°C , $5.6 \times 10^{-7} \text{ ng/cm}^3$ at 23°C , a hypothetical altered-behavior threshold of about 10^{-5} ng/cm^3 (Mankin et al., 1980), and a calling virgin female IMM emits pheromone at a rate of $8 \times 10^{-4} \text{ ng/sec}$ (Sower and Fish, 1975). The corresponding relative thresholds calculated from these estimates are listed in Table 1. Inserting the relative thresholds into Figure 1, we find that the attraction space of a female after 1 min of calling is rather insensitive to temperature but somewhat dependent on boundary position. For example, the entire volume inside a boundary of 150-cm radius would be an attraction space, but the attraction space inside a boundary of 1000-cm radius would be a sphere of about 250-cm radius. With a boundless environment, the attraction sphere would have a radius of about 40 cm. Actually, there is little practical difference among these radii. The spaces calculated by the model for the IMM are compared in Table 2 with the attraction spaces derived for other insects. The difference between the first two estimates, derived from equations 3 and 4, and the last four estimates, derived from equation 6, indicates primarily the effect of convection on the pheromone dispersal pattern.

TABLE 1. RELATIVE ATTRACTION THRESHOLDS, $C_r = C/Q$, AND RELATIVE ALTERED-BEHAVIOR THRESHOLDS, C_{rd} , FOR FEMALE IMM AND 2 SEX PHEROMONE TRAPS^a

Parameter	Female IMM	Pheromone trap 1	Pheromone trap 2
Q (ng/sec)	8×10^{-4}	0.01	0.76
C_r at 23°C	7×10^{-4}	5.6×10^{-5}	7.4×10^{-7}
34°C	8.5×10^{-6}	6.8×10^{-7}	8.9×10^{-9}
C_{rd}	1.25×10^{-2}	10^{-3}	1.3×10^{-5}

^aThe emission rates listed for the traps are typical of rates for traps commonly used to monitor IMM populations, e.g., Vick et al. (1979). Units of C_r and C_{rd} are sec/cm³.

The calculation of the altered-behavior space of a female IMM follows a similar procedure. According to Table 1 and Figure 2 calling females are surrounded by altered-behavior spaces of about 6-cm radius. It is interesting to compare these dimensions with the dimensions of the space surrounding a female *Trichoplusia ni* (Hübner). The *T. ni* altered space can be estimated from previous studies by Sower et al. (1971), and Bjostad (1978), who found that the female emits pheromone at the rate of 0.1–0.4 ng/sec, and a male has an activation threshold of about 3×10^{-7} ng/cm³. If it is assumed that the altered-behavior threshold of a male *T. ni* is 10^{-4} ng/cm³, three orders of magnitude above the activation threshold (Roelofs, 1978), the relative threshold is $C_{rd} = 10^{-3}$, and from Figure 1, the altered-behavior space is a sphere of about 15 to 60-cm radius. The size of the *T. ni* altered-behavior space is thus quite similar to that for the IMM.

The attraction and altered-behavior spaces of IMM sex pheromone traps can also be determined from Table 1 and Figure 2. If either trap in Table 1 is

TABLE 2. CALCULATED VALUES FOR MAXIMUM COMMUNICATION DISTANCE (ATTRACTIVE RANGE) OF 6 SPECIES OF INSECTS^a

Insect	Range (m)	Reference
<i>Plodia interpunctella</i> (Hübner)	0.4–2.5	This paper
<i>Pogonomyrmex badius</i> (Latreille)	1.04	Bossert and Wilson (1963)
<i>Trogoderma glabrum</i> (Herbst)	0.8–10	Shapas and Burkholder (1978)
<i>Hyphantria cunea</i> (Drury)	3–10	Hirooka and Suwanai (1976)
<i>Spodoptera litura</i> (F.)	80	Nakamura and Kawasaki (1976)
<i>Trichoplusia ni</i> (Hübner)	1–100	Sower et al. (1971)

^aValues for *Plodia* and *Pogonomyrmex* are calculated from equations 3 and 4. Values for the other species are calculated from equation 6.

the source, essentially the entire volume inside a boundary of 100- or 1000-cm radius is above the attraction threshold. With the trap 2 source, the entire volume is also above the altered-behavior threshold, but the trap 1 source has an altered-behavior sphere of 71-cm radius inside a 1000-cm boundary and 45-cm radius inside a 100-cm boundary. Thus a trap emitting 1 ng/sec might capture fewer IMM than an otherwise identical trap emitting 10^{-3} ng/sec.

It is surprising that there is little effect of temperature on the predicted attraction space of a calling female or a pheromone trap, since the male IMM anemotactic threshold to sex pheromone is about two orders of magnitude higher at 23°C than at 34°C. However, due to the rapid decrease in C_r , once it falls below the inflection point of about 10^{-4} sec/cm³, the radius of the attraction space decreases very little. The temperature could have a large effect if the threshold C_r were higher than the inflection point. This circumstance would be most likely to occur when the attractant was not a sex pheromone.

In general, the model cannot be used to calculate attraction to competing sources. If the insect searches by such mechanisms as klinokinesis, chemokinesis, or vision (Wright, 1958; Farkas and Shorey, 1974; Wall and Perry, 1978; Baker and Carde, 1979), the problem of attraction to competing sources is complicated, particularly if trap-female competition is considered. For example, a female IMM generally calls from walls, ceilings, or other exposed surfaces. Typically, a male IMM stimulated by sex pheromone orients visually to such surfaces and investigates objects resembling female IMM (Sower et al., 1975). This behavior increases the probability of locating a female but decreases the probability of capture by a trap unless the trap is highly attractive visually. Thus, as the density of female IMM increases, a trap could lose efficiency much more rapidly than the model would predict from comparisons of the attraction spaces.

However, if the attraction spaces do not overlap or if the principal searching mechanism is chemotaxis, attraction to competing sources can be calculated by superimposition of individual solutions of the model equations. The procedure for nonoverlapping sources has been treated in detail elsewhere (Knippling and McGuire, 1966; Nakamura and Oyama, 1978), so only attraction under chemotaxis will be considered here. Suppose two sources, E1 and E2, are located 500 cm apart in a warehouse with length-width-height dimensions of 20 m each. If the emission rates of E1 and E2 are equal and the attraction spaces overlap, an insect inside the overlapping region will fly to the closest source. If the emission rates are unequal, the probability of attraction to either source can be predicted from Figure 2, which indicates that a 10-fold decrease in pheromone concentration is roughly equivalent to a 10-fold increase in the distance from the source. Accordingly, when the emission rate of E1 is 10-fold greater than that of E2, an insect inside the overlapping space flies to E1 unless it is within about 45 cm of E2.

Case III Dispersal: Attraction of Insects from Outside a Warehouse. If one allows for the caveats listed in the methods section (case III), equations 3 and 4 can be combined with equation 6 to determine whether emission from a trap inside a warehouse produces an above-threshold concentration of pheromone outside. Suppose that a trap emitting IMM sex pheromone at the rate of 0.1 ng/sec is placed near the middle of a warehouse with length-width-height dimensions of about 20 m each. Several days later when the ambient temperature is 27° C and the outside airflow is a constant 50 cm/sec, a 2 × 2-m door is opened. K_y and K_z in equation 6 are assumed to have the values tabulated by Sutton (1953) for dispersal under stable conditions, i.e., 0.4 and 0.2 cm^{0.125}, respectively. The maximum rate of flow of pheromone through the door is (Judeikis and Stewart, 1976):

$$Q = (RT/2\pi M_p)^{1/2} C(4 \times 10^4 \text{ cm}^2) \quad (17)$$

In this equation, C is the only undetermined parameter. We estimate its magnitude using Figure 2, which indicates that the pheromone concentration near the door is about 10⁻⁶ ng/cm³ ($C_r = 10^{-5}$ sec/cm³). When these values are inserted into equation 17, $Q = 168$ ng/sec. This rate decreases immediately after the door is opened and continues to decrease to 0.1 ng/sec. A representative value would be $Q = 10$ ng/sec. If we consider only points directly downwind, so that $Y = Z = 0$ in equation 6, the equation for the pheromone concentration reduces to

$$C = 1.59 \times 10^{-9} X^{-1.75} \text{ g/cm}^{1.25} \quad (18)$$

Finally, to determine X we use the behavioral threshold of a male IMM measured by Mankin et al. (1980) as 10⁻¹⁷ g/cm³. The maximum downwind distance from which a male IMM can be attracted is

$$\begin{aligned} X &= (10^{-17} \text{ cm}^{1.75} / 1.59 \times 10^{-9} \text{ cm}^{1.75})^{-0.571} \\ &= 4.82 \times 10^4 \text{ cm} \end{aligned} \quad (19)$$

By contrast, if the pheromone is emitted from a 1-cm² hole instead of a 2 × 2-m door, the emission rate is $Q = 4.2 \times 10^{-12}$ g/sec, and equation 6 reduces to

$$\begin{aligned} X &= (10^{-17} \text{ cm}^{1.75} / 6.68 \times 10^{-13} \text{ cm}^{1.75})^{-0.571} \\ &= 569 \text{ cm} \end{aligned} \quad (20)$$

Thus, the attraction of insects from outside the warehouse cannot be neglected unless the external openings are less than about 1-cm² area.

DISCUSSION

Some of the predictions resulting from the incorporation of boundary effects, plume-shape effects, altered-behavior thresholds, and gravitation into

the attraction model warrant further discussion in the context of previously published work. Consider, for example the two predictions resulting from the inclusion of boundary effects in the model. First, according to Figures 1 and 2, the position of the boundary is important when emissions are of short duration as is characteristic of a calling insect; it is not important when they are of long duration as is characteristic of a trap. Second, near a typical boundary surface the attractant concentration is much lower than it would be without the boundary, although the concentration may remain high if the deposition velocity is extremely low, e.g., 10^{-5} cm/sec in Figure 3. In the latter case, the boundary would be considered a reflector rather than an adsorber. On the basis of these predictions, we propose that a flying insect is more likely to be stimulated by sex pheromone or other attractants than an insect sitting or walking on an adsorptive surface. Visser (1976) presented a similar hypothesis based on other evidence. A yet unconsidered corollary is that a calling insect can expand its attraction space by extending its pheromone gland away from nearby surfaces. This calling behavior is seen frequently in female IMM, *Bombyx mori*, and several other insects (e.g., Hammack et al., 1976).

After considering the effects of plume shape on insect searching behavior, we proposed that well-defined plumes from attractant sources of small dimensions are more efficient in attracting insects than indistinct plumes from attractant sources of large dimensions. At least two experimental studies bear in part on this hypothesis. Lewis and Macaulay (1976) found that traps emitting well-defined smoke plumes tended to capture more insects than those emitting indistinct smoke plumes. In a related study Macaulay and Lewis (1977) obtained inconclusive results when they examined the effect of source dimensions on trap catches. However, in the 2nd study, the large-sized sources had 10 to 100-fold higher rates of emission than the small-sized sources. As a result, the attraction spaces of the large-sized sources were much larger and the attraction efficiencies cannot be compared directly.

The concept of an altered-behavior space was originally introduced to explain decreases in trap catches with increases in emission rate (Roelofs, 1978). Because the entire volume inside a 100- or 1000-cm radius around an IMM sex pheromone trap emitting 0.1 ng/sec is an altered-behavior space, we suggested that a trap emitting 10^{-3} ng/sec might collect insects at a greater rate in a warehouse than a trap emitting 1 ng/sec. Although such an effect has not been observed with IMM, Vick et al. (1979) reported that traps emitting the sex pheromone of *Sitotroga cerealella* (Olivier) at a rate of 0.02 ng/sec in a $6.1 \times 6.1 \times 2$ -m room captured more males than traps emitting 0.2 ng/sec.

The dimensions of the altered-behavior spaces of calling insects indicate a possible evolutionary function for the altered-behavior threshold. In case II, the threshold occurs about 6 cm away from an IMM female and 60 cm away from a *T. ni* female. The corresponding distances can also be calculated for

case III by using equation 6. With a relatively calm airflow of 50 cm/sec, the estimated altered-behavior threshold occurs about 4 cm downwind from an IMM female and 18 cm downwind from a *T. ni* female ($K_y K_z = 0.08 \text{ cm}^{0.25}$, $C_{rd} = 1.25 \times 10^{-2} \text{ sec/cm}^3$ for IMM, and $C_{rd} = 10^{-3} \text{ sec/cm}^3$ for *T. ni*). Thus, in either a case II or case III environment the altered-behavior threshold occurs within a short distance of the calling insect. As such close range it is reproductively advantageous for the searching insect to begin an intensive localized search pattern. If the function of the altered-behavior threshold is to increase the probability of finding a mate, this threshold will likely be found in many insects besides those in which it has already been observed (e.g., Roelofs, 1978; Mankin et al., 1980).

It remains to discuss hypotheses explaining why searching insects often approach calling insects or sex pheromone traps from below in still or nearly still air (Killinen and Ost, 1971; Murlis and Bettany, 1977; Traynier, 1968). The usual explanation is that pheromone falls in still air, but this proved theoretically invalid. One alternative is the suggestion that the presence of a reflective boundary below the source could produce a greater concentration of pheromone just above the boundary surface than at positions some distance above the plume axis, although Figures 1, 2, and 4 indicate that this could happen only if both V_d and t were small. Another possibility is that the turbulence level tends to be proportional to height above ground so the plume may be better defined and easier to follow near the ground than at greater heights. Further study is necessary to resolve these questions.

Consideration of predictions based on the model leads to the following hypotheses for optimizing sex pheromone trap design and placement: (1) Sources of small dimensions produce plumes of better definition for longer distances than sources of large dimensions. Thus, trap catches could be improved by reducing the dimensions of the source and by designing the traps so they do not interfere significantly with plume formation. (2) If the insect has an altered-behavior threshold, a trap emitting at a high rate may capture fewer insects than a trap with a low emission rate. A large number of traps that produce small active spaces may be more effective as monitors of the pest population than a small number of traps that produce large active spaces. A side benefit of the former design is that it mitigates the effects of temperature inversions and barriers on pheromonal distribution. (3) If there are openings greater than about 1 cm^2 in a warehouse, pheromone sources inside can attract pests from outside the warehouse. Warehouse pest monitoring experiments should be designed to account for this effect.

APPENDIX

Derivation of Equation 3. Because the mathematics of thermal and mass diffusion are equivalent, equation 3 can be derived from the heat-transfer

equation for a unit instantaneous heat source (Carslaw and Jaeger, 1967, p. 367):

$$T = \frac{1}{2\pi arr'} \sum_{n=1}^{\infty} \frac{(ah' - 1)^2 + a^2\theta_n^2}{a^2\theta_n^2 + ah'(ah' - 1)} \tag{A1}$$

$$\sin(r\theta_n) \sin(r'\theta_n) \exp(-\kappa\theta_n^2 t)$$

where: T is the temperature, °C; a is the boundary radius, cm; r is the radius at which the temperature is calculated, cm; r' is the radius of the source, cm; h' is the ratio H/K , cm^{-1} ; H is the coefficient of surface heat transfer, $\text{cal}/\text{cm}^2 \text{ sec}^\circ\text{C}$; K is the thermal conductivity, $\text{cal}/\text{sec cm}^\circ\text{C}$; κ is the thermometric conductivity, cm^2/sec ; θ_n is the n th positive root of the equation

$$a\theta \cot(a\theta) + (ah' - 1) = 0. \tag{A2}$$

The boundary conditions specify that $0 \leq r < a$. There is a unit instantaneous source at $r = r'$. Heat transfer at a is governed by the equation

$$\phi = HT \tag{A3}$$

where: Φ is the flux, the number of calories transferred across a 1-cm^2 surface in 1 sec (Carslaw and Jaeger, 1967, p. 19).

The heat diffusion equation can be transformed to a mass diffusion equation by replacing T with C , κ with D , and H with V_d (Carslaw and Jaeger, 1967, p. 28):

$$C = \frac{1}{2\pi arr'} \sum_{n=1}^{\infty} \frac{(ah - 1)^2 + a^2\theta_n^2}{a^2\theta_n^2 + ah(ah - 1)} \tag{A4}$$

$$[\sin(r\theta_n)\sin(r'\theta_n)\exp(-D\theta_n^2 t)]$$

where: h is the ratio, V_d/D , cm^{-1} .

To convert from a diffusion equation for a unit instantaneous source to the equation for a source emitting at the constant rate, Q , equation A4 must be integrated over the measurement period. It is also convenient to use the approximation:

$$\frac{\sin(r'\theta_n)}{r'\theta_n} \approx 1 \tag{A5}$$

which is valid for $r' \ll a$. Accordingly,

$$C = \frac{Q}{2\pi ar} \sum_{n=1}^{\infty} \frac{(ah - 1)^2 + a^2\theta_n^2}{a^2\theta_n^2 + ah(ah - 1)} (\theta_n) \sin(r\theta_n) \tag{A6}$$

$$\int_0^t \exp[-D\theta_n^2(t-t')] dt'$$

which gives equation 3 in the text:

$$C = \frac{Q}{2\pi arD} \sum_{n=1}^{\infty} \frac{(ah-1)^2 + a^2\theta_n^2}{a^2\theta_n^2 + ah(ah-1)} \quad (A7)$$

$$[\sin(r\theta_n)/\theta_n][1 - \exp(-D\theta_n^2 t)]$$

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