The Analysis of Olfactory Communication Among Animals

WILLIAM H. BOSSERT

AND

EDWARD O. WILSON

Biological Laboratories, Harvard University
Cambridge, Massachusetts, U.S.A.

Methods are presented for determining those parameters of olfactory communication systems most closely related to the diffusion process. Four general cases of diffusion are considered: instantaneous release of the communicating substance in still air, continuous release in still air, continuous release from a moving source as in an odor trail, and continuous release in a wind. The techniques have been applied in the analysis of three real communication systems, involving an alarm substance, a recruitment trail, and a sex attractant respectively. It has been possible to demonstrate the effect of differing values of the parameters in fulfilling the design requirements of a particular system with respect to range of the signal, its rate of spread, and its persistence.

Introduction

This report is concerned with communication by smell, that is, the perception of molecules borne from one animal to another through air or water which results in a more or less quick alteration of behavior in the receiver animal. Our attempts at analysis will be directed at examples of chemical transmission in the air, in which cases the expression "odorant" and "smell" are used with some degree of precision (cf. Behnke *et al.*, 1954). We are dealing specifically with communication among members of the same species; hence the substances studied are "olfactorily acting" pheromones (Karlson & Butenandt, 1959) in the strict sense. The mathematical models and techniques of analysis can be applied equally well to interspecific communication and, with suitable adjustments, to chemical communication in water.

Although still a relatively limited enterprise, the study of chemical communication has been accelerating in the past several years. A great deal of new information has been produced on the existence and function of the exocrine systems and the behavior of animals during the communication. Some of the chemical releasers themselves have been identified. (Recent

general papers on the subject include Lederer, 1950; Davenport, 1955; Kullenberg, 1956; Karlson & Butenandt, 1959; Green, Beroza & Hall, 1960.) A conspicuous remaining gap is the analysis of the transmission itself. Given the identification of a chemical releaser used by a species in a certain way, some key questions remain. How much of the releaser is emitted? How fast does it travel? As a signal, how quickly does it fade out? Looked at from the evolutionist's point of view, what are the optimal molecules for a given function? And what are the most efficient ways of transmitting them? The attack on these questions has scarcely begun in any rigorous manner. This is due to some formidable inherent difficulties in the subject. The secretions involved are often produced in invisible quantities and are hard to detect even by chemical analysis, and the response thresholds are difficult to measure (Dethier, 1953; de Vries & Sturver, 1961). Further, transmission is by the process of diffusion, which is greatly complicated by naturally occurring turbulance and requires mathematical methods of treatment not familiar to most biologists.

Nevertheless, the empirical information is adequate to allow a start on a theory of olfactory transmission. Many results on the diffusion process are available. In this report we will use them to relate the parameters of the diffusion process, rate of emission of the pheromone, the threshold concentration, and rates of diffusion (ignoring for the present such problems as variable threshold, instability of the diffusing molecules, etc.), to the persistence, range, and rate of spread of effect of the pheromone. Then we will apply the models in an analysis of several actual cases in an attempt to demonstrate the design features of particular communication systems. In some cases the estimates will be reliable only to the order of magnitude, but this will be close enough to make various comparisons of functional categories of communication systems.

Four general cases of the diffusion of pheromones will be covered:

(1) the substance is released as a puff in still air;

(2) the substance is released continuously in still air;

(3) the substance is released continuously from a moving source, as in the laying of an odor trail;

(4) the substance is released continuously in a wind.

The results of cases (1) and (2) will be applied to the analysis of the alarm communication of the harvester ant *Pogonomyrmex badius*, case (3) in the analysis of the recruitment trail of the fire ant *Solenopsis saevissima*, and case (4) in the analysis of the sex attractant of the gypsy moth *Porthetria dispar*.

Case 1: Instantaneous Emission in Still Air

The instantaneous release of a substance, in a puff, would be the ideal design for communications requiring rapid fade-out. In nature, emission somewhat like this ideal form is approached in the release of alarm substances (Schutz, 1956; Wilson, 1963). The expanding sphere of diffusing pheromone will remain centered on the animal, if it is in still air, or else be carried along with moving air (or water) currents. The measurement techniques would be similar in both cases, but in order to analyze one particular case (in the ants) the former case will be specifically considered.

Suppose Q molecules of the odor chemical are released at the origin of a cartesian coordinate system at time $t = 0$. The density U in mol/cm^3, in space through time is given by Roberts (1923) as

$$U(x, y, z, t) = \frac{Q}{(4\pi Dt)^{3/2}} e^{-r^2/4Dt} \tag{1.1}$$

where $r^2 = x^2 + y^2 + z^2$ and D is the diffusion constant in cm^2/sec. This result assumes that the molecules are free to diffuse infinitely in all directions. If the additional condition that $U = 0$ for all $z < 0$ is imposed, corresponding to the source being on the ground, a reflecting plane at $z = 0$, the density function becomes

$$U(x, y, z, t) = \frac{2Q}{(4\pi Dt)^{3/2}} e^{-r^2/4Dt} \tag{1.2}$$

The rest of the formulae for this case will be derived from the latter equation since it seems to apply to the majority of biological situations. For sources not near the ground, however, the results may be applied by merely first dividing the actual value of Q in half.

Assume there is some threshold density K in mol/cm^3 such that the animals receiving the communication of the odor respond to concentrations of the odor substance of K and greater. The surface of concentration K in space at time t is a sphere with center at the origin and radius

$$R(t) = \sqrt{4Dt \log\left(\frac{2Q}{K(4\pi Dt)^{3/2}}\right)} \tag{1.3}$$

$$\text{for } 0 \leq t \leq \frac{1}{4\pi D}\left(\frac{2Q}{K}\right)^{2/3}$$

$$= 0 \text{ otherwise}$$

Because the density function is monotonic, the concentration is above threshold within this sphere and nowhere else. The radius of the threshold sphere increases through time to a maximum

$$R_{max} = \sqrt{\left(\frac{2Q}{K}\right)^{2/3} \times \frac{3}{2\pi e}} = 0.527 \left(\frac{Q}{K}\right)^{1/3} \tag{1.4}$$

at time

$$t_{R_{max}} = \frac{1}{4\pi De}\left(\frac{2Q}{K}\right)^{2/3} = \frac{0.0464}{D}\left(\frac{Q}{K}\right)^{2/3} \tag{1.5}$$

then decreases to zero at which time the concentration is everywhere below threshold. The time of ultimate fade out is

$$t_{\text{fade out}} = \frac{1}{4\pi D}\left(\frac{2Q}{K}\right)^{2/3} = e \cdot t_{R_{max}} = \frac{0.126}{D}\left(\frac{Q}{K}\right)^{2/3} \tag{1.6}$$

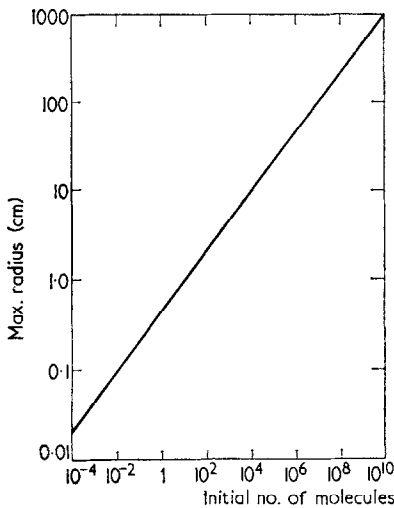Initial no. of molecules/threshold concn (mol/cm³)

FIG. 1. Maximum radius of threshold sphere from an instantaneous point source *versus* Q/K, the ratio of number of molecules released to the threshold density. For a source on the ground, Q should be doubled in applying the graph.
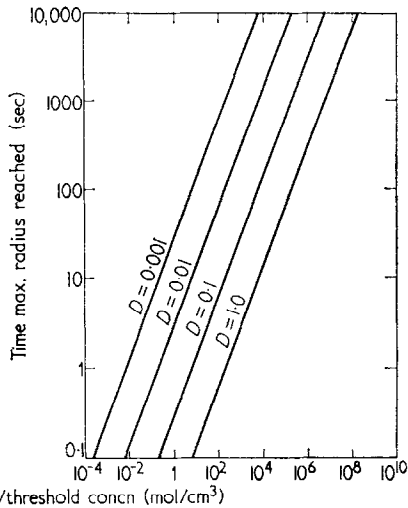
FIG. 2. Time at which maximum radius of threshold sphere is reached after instantaneous release of molecules from a point source *versus* Q/K, the ratio of number of molecules released to the threshold density, for various coefficients of diffusion, D. For a source on the ground, Q should be doubled in applying the graph.

These three functions are graphed in Figs. 1, 2, and 3 with respect to the ratio Q/K, for a source away from the ground.

If R and t in equation (1.3) are replaced by R/R_{max} and $t/t_{\text{fade out}}$ respectively, the resulting equation is free of the parameters D, Q, and K. The quantity R/R_{max} as a function of $t/t_{\text{fade out}}$ is graphed in Fig. 4.
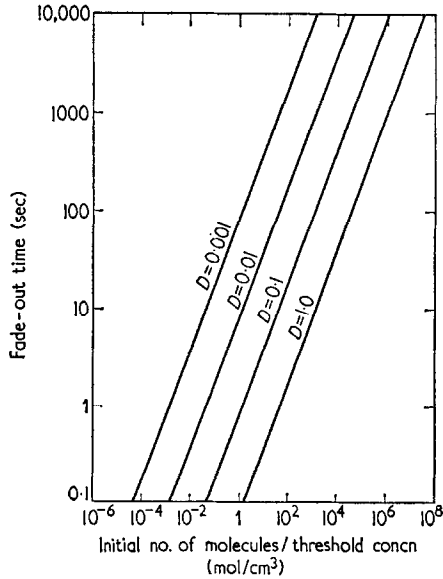
FIG. 3. Time at which radius of threshold sphere around an instantaneous point source diminishes to zero, the ultimate fade out of the signal *versus* Q/K, the ratio of number of molecules released to the threshold density, for various coefficients of diffusion, D. For a source on the ground, Q should be doubled in applying the graph.
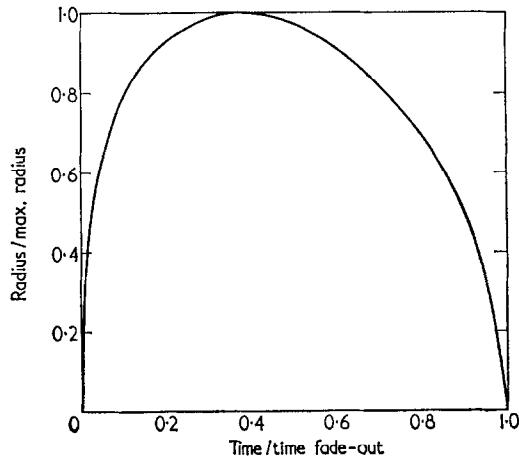

FIG. 4. The radius of the threshold sphere around an instantaneous point source through time. Both radius and time are given as proportions of their maximum values.

The gradient of concentration along a radius from the source is

$$\frac{dU}{dr} = \frac{-Qr}{(4\pi)^{3/2}(Dt)^{5/2}}\,e^{-r^2/4Dt} \tag{1.7}$$

At the surface of the threshold sphere when it reaches maximum radius this becomes

$$\frac{dU}{dr}\bigg|_{R_{max}} = \frac{-K^{4/3}}{Q^{1/3}} 2^{1/6} (3\pi e)^{1/2}$$

$$= \frac{-5\cdot681K^{4/3}}{Q^{1/3}} \tag{1.8}$$

And the relative gradient, the gradient as a proportion of the concentration at the surface is

$$\frac{\dfrac{dU}{dr}}{U}\bigg|_{R_{max}} = -5\cdot681\left(\frac{Q}{K}\right)^{-1/3} \tag{1.9}$$

In the analysis of particular systems of this type, D, Q, and K might be unknown. Note that all of the equations describing the diffusion of the odor involve Q and K in their ratio, hence only Q/K is of interest with respect to the diffusion process, and not the absolute values of Q and K which, of course, are important to the study of the sensory physiology of the communications system. There are two straightforward methods of empirically determining the parameters D and Q/K. First, the maximum radius over which the odor has effect can be measured, along with the time it takes for this maximum to be reached after emission of the substance. Then Q/K can be computed from (1.4) as

$$Q/K = 6\cdot834\,(R_{max})^3 \tag{1.10}$$

and substituting in (1.5)

$$D = 0\cdot167\frac{(R_{max})^2}{t_{R_{max}}} \tag{1.11}$$

Alternatively, the times to the onset of effect of the odor at two distances from the origin might be measured. Let (t_1, r_1) and (t_2, r_2) be two such pairs of measurements, then

$$D = \frac{\dfrac{(r_1)^2}{t_1} - \dfrac{(r_2)^2}{t^2}}{6\log\dfrac{t_2}{t_1}} \tag{1.12}$$

and after D is computed Q/K can be found by

$$Q/K = (4\pi Dt)^{3/2}\,e^{r^2/4Dt} \tag{1.13}$$

The value of Q/K can be taken as the average of the values obtained from (1.13) for both pairs of measurements.

Often, as for the study of the *Pogonomyrmex badius* alarm communication system to be discussed below, it is simpler to perform a controlled experiment

in one dimension than in the natural three dimensional situation. We therefore list here the one dimensional result corresponding to equations (1.2 to 1.6) for three dimensions. Suppose the source is at one end of a very long tube whose cross-sectional area is A, and the inside walls of the tube are impervious to the diffusing substance. Suppose also that there is a reflecting barrier at the source end of the tube. If x is taken as the distance down the tube from the source, and X the limit of the threshold volume, then

$$U(x, t) = \frac{Q}{A\sqrt{\pi Dt}} e^{-x^2/4Dt} \tag{1.14}$$

$$X(t) = 4Dt \log \frac{Q}{AK\sqrt{\pi Dt}} \tag{1.15}$$

$$= 0 \text{ otherwise}$$

$$X_{max} = \frac{Q}{AK} \sqrt{\frac{2}{\pi e}} = 0\cdot484 \frac{Q}{AK} \tag{1.16}$$

$$t_{x\,max} = \left(\frac{Q}{AK}\right)^2 \frac{1}{\pi De} = \frac{0\cdot117}{D}\left(\frac{Q}{AK}\right)^2 \tag{1.17}$$

$$t_{fade\,out} = \left(\frac{Q}{AK}\right)^2 \frac{1}{\pi D} = e\,.\,t_{X\,max} = \frac{0\cdot318}{D}\left(\frac{Q}{AK}\right)^2 \tag{1.18}$$

As before, D and Q/K can be obtained experimentally from measurements of the maximum distance of the effect and the time to the maximum, or from pairs of measurements, (X_1, t_1) and (X_2, t_2) of distance and time to onset of the effect. In the first method,

$$Q/K = \sqrt{\frac{\pi e}{2}} A X_{max}$$

$$= 2\cdot066\, A X_{max} \tag{1.19}$$

$$D = 1/2 \frac{(X_{max})^2}{t_{X\,max}} \tag{1.20}$$

for the second method,

$$D = \frac{\dfrac{(X_1)^2}{t_1} - \dfrac{(X_2)^2}{t_2}}{2\log\dfrac{t_2}{t_1}} \tag{1.21}$$

the value of D can then be substituted in

$$Q/K = A(\pi Dt)\, e^{x^2/4Dt} \tag{1.22}$$

for each of the pairs of measurements to get an average value of Q/K.

Wilson (1958) has described the alarm substance originating in the mandibular glands of the harvester ant *Pogonomyrmex badius*. Under certain circumstances the substance, which has not yet been chemically identified, might be expected to be released in a puff and hence subject to analysis by the methods of this case. The substance is certainly very volatile, as will be shown, so that quantities emitted as a liquid evaporate rapidly, approximating the theoretical instantaneous puff. The alarm substance elicts two distinct responses in sister workers. When a head of a minor worker is thoroughly crushed near a group of workers, they soon show mild excitation and are attracted toward the source. As they approach the source, or after a longer period of time at the original distance (when we might assume the substance is in higher concentration) they abruptly begin to run in circles in a manner similar to a worker tactilely disturbed by a foreign object. When the workers reach the second state of agitation they sometimes appear to emit the alarm substance themselves. The extreme-alarm communication therefore passes in relays through space, in a manner which cannot be described by the methods of this paper. In the initial state of attraction, however, it seems unlikely that the receivers emit the substance themselves, as when a worker is attracted there is never a sign of extreme behavior in other workers no matter how close they stand. Except for estimating the extreme-alarm threshold we will therefore concern ourselves entirely with this lower concentration effect of the alarm substance.

The experiments to determine Q/K and D were performed in a glass tube, 122 cm long and with 2·6 cm inner diameter. Both ends of the tube were capped securely with aluminum foil. A circle of copper screen was placed 14 cm from one end of the tube, the end containing the source in all the experiments. This barrier kept the ants in the tube away from the source and the regions of highest concentration of the alarm substance so that they were not stimulated to highest excitement with subsequent secondary release of the alarm substance. For the experiments about seventy-five workers were placed in the tube with a small amount of sand. The tube was warmed with flood lamps to 31°C. The ants, after about an hour in the tube, showed behavior similar to that seen normally around nests during the peak of foraging activity in the field. At the time of the experiments, a few were exploring but most were resting quietly. On several occasions the same ants were used for two trials, the tube being opened, blown out, and left to ventilate at least an hour and a half between trials.

The release of a puff of the alarm substance was simulated by crushing the head of a minor worker thoroughly in the source end of the tube and removing it three seconds later. The head was taken from an ant quietly anesthetized with CO_2 so that little or no alarm substance was lost before

the experiment. The head was held in forceps and inserted into the tube through a small incision in the foil cap. Three seconds after crushing the timing began and the head, still held in the forceps, was removed carefully so as not to set up air currents inside the tube. In most cases the flaps of the incision closed fairly tightly on removal of the head, and never did the opening remain large enough to permit significant leakage or air flow into the tube. As the attraction behavior was noticed among ants in the tube, the location was marked and the time of onset noted. The onset of the behavior was

TABLE 1

Diffusion of attractive alarm substance from crushed head of minor worker, exposed for three seconds (Trials 1 to 5), exposed indefinitely (6 and 7), and allowed to evaporate separately before experiment (8 and 9)

| Trial | Onset of attraction | | D (cm²/sec) | Q/K (cm³) |
	Distance (cm)	Time (sec)		
1	18 20·5	60 90	0·80	693
2	15 18 20·5	58 91 180	0·57	918
3	14 18	60 100	0·03	1013
4	†			
5	16 20·5	81 160	0·47	635
6	16 20	59 100	0·32	1500
7	18 22	91 150	0·33	1800
8	11·5 27	38 160	‡	‡
9	16 32·5	60 360	0·52	939

† Measurements ignored since a receiving ant passed the barrier and became extremely alarmed between 5 and 10 cm from the source.

‡ These data do not fit the model. They give a negative value of D in equation (1.21).

recognized by the arousal and mild excitation of several nearby ants, followed by their movement directly toward the source culminating in attempts to get past the screen barrier. At least two readings were taken in each trial so that equations (1.21) and (1.22) could be applied. The results of five trials are given in Table 1 (trials 1 to 5). The measurements of the fourth trial were discarded since one ant managed to get past the barrier and went into the extreme alarm behavior, probably emitting the alarm substance herself. The extremely deviant values of D and Q/K from the data for the third trial cannot be explained. Because of the conformity of the other trials, and subsequent ones to be discussed, it seems that the measurements are in error. In themselves they do not appear to differ greatly from the other measurements, but as this instance points out, the variation in the result from errors in the measurements is very large. In particular, this is due to the steep slope of the function for computing D (equation (1.21)) for the small values of D which naturally occur. The results given in the table are averages of values obtained by (1.21) and (1.22) for all pairs of measurements. It should be mentioned that the D determined in this manner is not necessarily the coefficient of diffusion of the alarm substance in perfectly still air, but includes a factor due to turbulent diffusion caused by movement of the ants which was considerable after the onset of attraction along the tube. This movement would be found in natural situations also, however, and may be considered a characteristic of the diffusion system.

In an attempt to estimate how much of the available substance was evolved in the three second exposure, two different types of experiments were performed. In two trials, 6 and 7 of Table 1, the crushed head was not removed from the tube but held in the forceps in the incision throughout the trial. The closure of the foil around the forceps was particularly good. Care was taken not to introduce air currents in the tube through movements of the forceps. In trials 8 and 9 the heads were crushed in small glass vials, quickly stoppered with foil-covered stoppers, and allowed to set for an hour so that most of the substance could evaporate. Separate experiments showed that the substance could be kept active in this way for at least three hours. The vials, which made a very tight fit with the end of the tube, were quickly opened and joined to the tube for the trials. The measurements for trial 8 gave a negative value of D from equation (1.21), which is of course meaningless. There seems to be no explanation for this single aberrant result, particularly in view of the conformity of the companion trial with the previous results.

Comparing these results with those for three-second exposure, we see that the substance is quite volatile. Ignoring trials 3 and 4, the mean Q/K for three-second exposure is 715. The mean Q/K for the later trials, which we

might take as total release of the available substance, is 1,413. Assuming K is constant, this indicates that half the available substance is evolved in three seconds after the head is crushed. The mean value of D for all the trials in which it could be calculated is 0·43. Although no data were taken with respect to the onset of extreme alarm, this value of D also applies to this since there is likely only one substance at work (see Wilson, 1963). In addition, we can crudely estimate Q/K for the state of extreme alarm. In no instance was extreme alarm noted beyond the 14 cm barrier. The worker who made it through the barrier in trial 4, however, showed alarm at least 5 cm from the source. Using equation (1.19) this gives a Q/K of between 55 and 153 cm³, or roughly 1/10 that of the attraction. The threshold of the alarm, therefore, is about ten times that of the attraction.

The mandibular glands of several minor workers were measured in order to estimate the upper limit of the absolute quantity of the alarm substance, and hence some idea of the absolute values of Q and K. The average gland was found to be a prolate spheroid with major axis 0·45±0·02 mm and minor axis 0·21 mm. If a is the major axis and b the minor axis, the volume is given by

$$V = \tfrac{1}{6}\pi ab^2 = 1\cdot04 \times 10^{-5}\,\text{cm}^3$$

If we assume, not too unreasonably (see Wilson, 1963), that the alarm substance makes up the entire contents of the gland, and that it has a density roughly similar to water, there are $1\cdot04 \times 10^{-5}$ gm of the substance in a single gland. In addition, let us suppose that it has a molecular weight of the order of 200, in conformity with other known ant alarm substances. It seems unlikely that such a volatile and fast diffusing molecule could have a much greater weight, yet its specificity indicates that it is likely to be larger and more complex than the simplest molecules. Under these assumptions, the gland would be expected to contain $5\cdot20 \times 10^{-8}$ gm molecular weights or about $3\cdot13 \times 10^{16}$ molecules, so that an average worker might have about $6\cdot26 \times 10^{16}$ molecules of the substance. Given that Q/K for total release of the substance is about 1,400, the threshold density of the substance is

$$K = \frac{6\cdot26 \times 10^{16}}{1400} = 4\cdot47 \times 10^{13}\,\text{mol/cm}^3$$

The threshold for extreme alarm then should be about $4\cdot47 \times 10^{14}$ mol/cm³.

The results may be easily extended to the description of the natural three-dimensional situation. Let us assume that the maximum quantity of the substance is released, as when an ant is crushed in some way, so that Q/K is 1,413. From (1.5) the maximum radius over which other ants will be attracted, barring secondary relay of the message, is about 6 cm. This maximum will be reached in thirteen seconds and after about thirty-five seconds the signal

will have faded out completely. Using a Q/K of 150 for the extreme alarm effect, we find its maximum range of effect to be only about 3 cm and its fade-out time is about eight seconds. The extreme short range of action of the substance points out the importance of the principal design feature of an alarm communication system, that is, that it be of very short duration. The threshold must be very high, or Q/K correspondingly low to avoid persistence of the signal after the period of danger has passed. The short range of action, of course, might also be desired in the alarm system. There would be no need to alert others at long distances to a very local danger sufficient to activate but one worker. The range of the *Pogonomyrmex* alarm, however, seems almost too short. It is possible to reduce the persistence of the alarm without reducing Q/K and hence the range of the system. One way is to have a large value of D. This certainly has been used in this case as the 0·43 cm²/sec value at 31°C would seem to be a maximum (if not beyond as mentioned earlier) coefficient of diffusion for a molecule in still air. A variable threshold for the substance could be used to render continuing high densities of the substance ineffectual. The related solution, also beyond the scope of the present analysis, would be to have the receiving animals respond not to absolute densities but to certain threshold gradients of the density through time. Another straightforward solution, which the *Pogonomyrmex* seem to be using, is the relay of the signal by the receiving animals. This has the effect of spreading out the source in space so that wide areas of the ground can be a little above threshold, but the density nowhere so high that a long time is required for it to diffuse to below the threshold. It also spreads the release out in time, an effect to be considered in the next case.

We have so far considered only the problem of notifying the receiving workers of the alarm situation. Since the initial behavioral response to the communication is attraction toward the source we might examine the possibility of the receiver being oriented with respect to the source by the concentration gradient of the pheromone. Using the approximate values obtained for Q and K, the gradient at the maximum range of the threshold sphere is, from (1.8)

$$\left. \frac{dU}{dr} \right|_{R_{max}} = 1·95 \times 10^{13} \, cm^{-4}$$

and the relative gradient is, from (1.9),

$$\left. \frac{\frac{dU}{dr}}{U} \right|_{R_{max}} = 0·436 \, cm^{-1}$$

Over the distance, about 0·5 cm, that the workers might sample with their

antennae while resting there is an absolute difference in concentration of about $9 \cdot 75 \times 10^{12}$ cm^{-4}, a relative change of about $21 \cdot 8\%$, on a line toward the source and, of course, no difference perpendicular to the direction of the source. This would seem to be a sufficient gradient to orient them toward the source.

Case 2: Continuous Emission in Still Air

As in the previous case, assume that the source is at $x = y = z = 0$ and there is an impervious plane at $z = 0$. Let us suppose that the substance, instead of being released in an instantaneous puff, is released at constant rate through time of $Q(t)$ mol/sec. The density function is given by

$$U(r, t) = \int_0^t \frac{2Q(t^*)}{(4\pi D(t - t^*))^{3/2}} e^{-r^2/4d(t - t^*)} \, dt^* \tag{2.1}$$

With the substitution

$$v^2 = \frac{r^2}{4D(t - t^*)}$$

this is simplified to

$$U(r, t) = \frac{1}{Dr\pi^{3/2}} \int_{\frac{r}{\sqrt{4Dt}}}^{\infty} Q\left(t - \frac{r^2}{4Dv^2}\right) e^{-v^2} \, dv \tag{2.2}$$

We will consider here only the simplest case of the rate of release being constant. This would be expected to apply, at least approximately, to many attraction and territorial systems.

If $Q(t) = Q$, the density function from (2.2) becomes

$$U(r, t) = \frac{Q}{2D\pi r} \frac{2}{\sqrt{\pi}} \int_{\frac{r}{4Dt}}^{\infty} e^{-v^2} \, dv$$

The integral

$$\frac{2}{\sqrt{\pi}} \int_x^{\infty} e^{-v^2} \, dv$$

is known as the complementary error function, and is commonly written *erfc*(x). The density function then is

$$U(r, t) = \frac{Q}{2D\pi r} \, erfc\left(\frac{r}{\sqrt{4Dt}}\right) \tag{2.3}$$

The complementary error function is tabulated in Carslaw & Jaeger (1947), National Bureau of Standards Mathematical Table 8 (1941, reissued as

Applied Mathematics series, No. 41, 1954), and other places, while the error function $erf(x)$, where

$$erfc(x) = 1 - erf(x)$$

is tabulated in nearly all collections of mathematical tables.

As the source continues for a long time the density function approaches the limit

$$U(r) = \frac{Q}{2D\pi r} \tag{2.4}$$

If $K\,mol/cm^3$ is the threshold density, the radius of the sphere above threshold surrounding the source tends in time to the limit, and maximum,

$$R_{max} = \frac{Q}{2K\pi D} \tag{2.5}$$

For any Q/K, D, and t, equation (2.3) has a unique solution for r. This solution unfortunately cannot be expressed in terms of any elementary function. If $t(p)$ is the time that it takes for the threshold sphere to reach some proportion, p, of its limiting radius, and $p*$ is such that $erfc(p*) = p$, then

$$t(p) = \left(\frac{pQ}{p*4\pi K D^{3/2}} \right)^2 \tag{2.6}$$

Using (2.6) the ratio R/R_{max} as a function of time in units $Q^2/K^2 D^3$ is graphed in Fig. 5. From (2.5) and the graph the radius through time of the threshold sphere in any particular system can be determined.
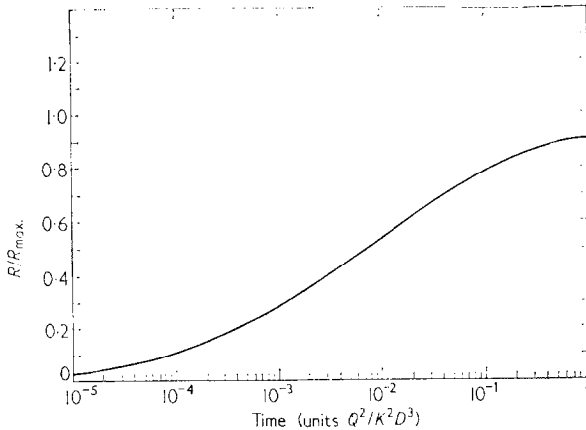

FIG. 5. The radius of the threshold sphere around a continuous point source through time. The radius is given as a proportion of its limiting value and time is in units $Q^3/K^2 D^3$, where Q is the rate of release of the substance in mol/sec, K is the threshold density in mol/cm^3, and D is the coefficient of diffusion.

For a one-dimensional system, such as was used in the analysis of the previous section, the density function from a continuous constant source of Q mol/sec is

$$U(x, t) = \int_0^t \frac{2Q}{A\sqrt{4\pi D(t - t^*)}} e^{-x^2/4D(t - t^*)} \, dt^*$$

$$= \frac{2Q}{A} \sqrt{\frac{t}{\pi D}} e^{-x^2/4Dt} - \frac{Qx}{AD} \, erfc \, \frac{x}{\sqrt{4Dt}}$$

$$= \frac{2Q}{A} \sqrt{\frac{t}{D}} \, ierfc \left(\frac{x}{\sqrt{4Dt}} \right) \tag{2.7}$$

Carslaw & Jaeger (1947, Appendix 11) give values of 2 $ierfc(x)$, twice the integral of the complementary error function. If K is the threshold density, and D is known, the ratio Q/K can be computed from a single measurement of time and distance to onset of the response as

$$\frac{Q}{K} = \frac{A\sqrt{D}}{2\sqrt{t} \, ierfc \, \dfrac{x}{\sqrt{4Dt}}} \tag{2.8}$$

To apply these results to a real case, let us reconsider the *Pogonomyrmex badius* alarm system analyzed in case 1. When a worker is alarmed it emits the alarm substance which attracts nearby workers. As the others attain the original source they begin releasing the substance themselves. If the arrival of the other workers is fairly uniform in time we might assume the total emission near the original source is approximately continuous and constant. As a hypothetical example, suppose workers are reaching the alarm zone at the rate of one every five seconds. The ratio Q/K for an individual releasing most of the available substance in a puff was found to be about 1,400 cm^3 so that the Q/K for this continuous case is 280 cm^3/sec. Taking D as 0·43 cm^2/sec as before, the maximum radius of the sphere surrounding the alarm zone which is above the attraction threshold of the pheromone is, by equation (2.5),

$$R_{max} = \frac{280}{2\pi(0·43)} = 104 \text{ cm}$$

From Fig. 5 we see that half this radius is reached in

$$t(0·5) = 0·0065 \frac{Q^2}{K^2 D^3} = 6400 \text{ sec} = 1 \text{ hr } 47 \text{ min}$$

The spread of the alarm call by the workers is certainly more complicated

than presented here, but the maximum range of 104 cm and rate of spread of 52 cm in 1 hr 47 min are probably reasonable estimates of the limits of the system.

Case 3: Chemical Trails

The odor trail, laid in relatively calm air, is a common form of communication. The source is thus continuously emitting and moving through space. The trail substance diffuses outward from the line of travel in such a manner that a cross-section at a given point perpendicular to the line of travel forms a semicircle, the radius of which increases through time to a maximum and then decreases to zero. This is the same pattern that would obtain ideally if the emitting source animal were fixed in space and its pheromone were transported by a steady wind (Roberts, 1923). However, the classical solution does not hold for sources within several hundred meters of the ground; and for most natural situations nearer the ground the fourth case, to be taken up shortly, applies.

In some trail-following ants, such as *Atta*, the trails lead to persistent food sources and are themselves persistent. In many cases, however, the trails lead to ephemeral objects, such as limited food sources, and are designed to be short-lived. In the fire ant *Solenopsis saevissima* the trail lasts an average of only 104 seconds (on a glass surface), and this rapid fade-out is important as a cut-off device to halt the outward flow of ants when the food is exhausted (Wilson, 1962).

The essential goals of a short-lived recruitment trail have been intuited as follows. The amount of material emitted at any instant of time must not be very great, because in a typical circumstance the material must be emitted over a relatively long distance out of a reservoir of finite capacity. The effective width attained through diffusion must not be great, or otherwise the orientating function of the trail will be impaired. In order to achieve greater accuracy in trail-following, the ants might use the gradient of concentration of the trail substance to aid in staying near the center of the trail; the accuracy of the fire ant trail following compared to the total width of the trail indicates that some mechanism of this kind is used. In such a case it is important that the gradient of concentration near the effective boundary of the diffusing trail substance be large so as to strongly correct erring followers. Finally, the fade-out must be moderately quick in order to prevent excessive response as well as confusion due to overlapping trail systems, but not too quick; for then the effective range of the trail will be shortened to ineffectiveness. Parenthetically, we may note that any behavioral device that shortens the response time to the trail and hence increases the average distance over which the trail is followed, will improve the system. The fire ants, and many

other types of ants, have contrived just this improvement by making the trail substance an attractant, so that no intermediate signals are necessary to initiate trail following (Wilson, 1962).

Suppose an ant lays a trail of some volatile substance for an indefinitely long time in a straight line. At any instant of time assume the ant is at the origin of a cartesian-coordinate system and is proceeding in a negative direction on the x axis; the ground surface is the plane $z = 0$. In the analysis of empirical results to follow, the surface is a glass plane. The density of the trail substance in mol/cm^3 above the plane $z = 0$ is approximately given by

$$U(x, y, z) = \frac{Q}{2\pi Dx} e^{-u(y^2+z^2)/4Dx} \tag{3.1}$$

where Q is the rate at which the substance is laid in mol/sec, u is the rate of locomotion of the ant in cm/sec, and D is the coefficient of diffusion of the substance in cm^2/sec. This result was obtained by Sutton (1953) for the isomorphic situation of a constant point source in a steady wind.

If we assume there is some threshold density, K, below which the follower ants cannot detect the trail, the boundary of the trail is the surface given by

$$K = \frac{Q}{2\pi Dx} e^{-u(y^2+z^2)/4Dx}$$

for $z > 0$ and closed by its intersection with the plane $z = 0$. A cross-section through the trail perpendicular to the x axis is a semicircle of radius R_x given by

$$R_x = \sqrt{\frac{4Dx}{u} \log \frac{Q}{2K\pi Dx}} \quad \text{for } 0 \le x \le \frac{Q}{2K\pi D} \tag{3.2}$$
$$= 0 \text{ otherwise}$$

From this we see that the maximum length of a trail at any time is

$$X_{\max} = \frac{Q}{2K\pi D} \tag{3.3}$$

The maximum trail radius occurs at

$$X = \frac{Q}{2K\pi De} = \frac{X_{\max}}{e} \tag{3.4}$$

and is

$$R_{x,\max} = \sqrt{\frac{2Q}{eK\pi u}} \tag{3.5}$$

The final measure of importance is the gradient of concentration of the trail substance with respect to r, the deviation from the trail center, particularly at the boundary of the trail R_x. From (3.1) and (3.2)

$$\frac{dU}{dr}\bigg|R_x = \frac{-Qur}{2\pi D^2 x^2}e^{-ur^2/4Dx}\bigg|R_x$$

$$= -K\sqrt{\frac{u}{Dx}\log\frac{Q}{2K\pi Dx}}$$

(3.6)

This gradient becomes large for large values of Q, for very small values of D and is maximized with respect to K for

$$K = \frac{Q}{e\pi Dx}$$

or

$$\frac{Q}{K} = e\pi Dx$$

(3.7)

In the practical case the trail is not laid for an indefinite time but only along a track from the bait to the nest entrance. By considering an actual trail to be a section cut out of an infinite trail, however, the above formulae may be taken to apply approximately except near the boundaries, that is, near the nest entrance and the bait.
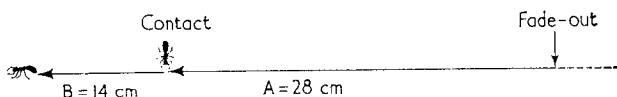

FIG. 6. Determination of the maximum trail length. Assume a worker contacts another laying a trail and follows the trail outward for distance A before losing it. Since the trail layer moves at only about one-half the rate of the trail follower, she has laid the trail distance B past the point of contact when the follower reaches the far end. The total trail length is $A + B$.

We can now use equations (3.3) and (3.5) to compute the parameters Q/K and D, given values of X_{max} and $R_{x,\,max}$ for the fire ant trail. Wilson (1962) gives 10 mm as the maximum distance over which an ant can detect the trail. The turnback points, where ants lose the trail, fall within this 1 cm limit which will therefore be used as $R_{x,\,max}$. Wilson gives 28 cm as approximately the maximum length of a trail, the length such that the outer part of the trail disappears before workers from the nest can reach it. Since follower workers move at about twice the velocity of trail layers, we might assume that an ant laying an infinite trail on the line through the bait and nest entrance would be 14 cm beyond the nest entrance when the trail begins to die out 28 cm from the nest. Therefore, X_{max} in equation (3.3) is about

42 cm (see Fig. 6). In the laboratory, the velocity of the trail-layer is 0·4 cm/sec. From equation (3.5),

$$1·0 = \sqrt{\frac{Q}{K}\frac{2}{0·4e\pi}}$$

or
$$\frac{Q}{K} = 0·2e\pi = 1·71 \text{ cm}^3/\text{sec}$$

Then from equation (3.3),

$$42 = \sqrt{\frac{1·71}{2\pi D}}$$

or
$$D = 0·00649 \text{ cm}^2/\text{sec}$$

This value is probably less than the actual coefficient of diffusion of the substance in air since the material is not all initially in the gaseous state. Since the substance is quite volatile, however, the model is still acceptably accurate, with the value of D reduced by a factor due to the evaporation time.

In order to obtain an approximate value for the threshold density, K, we can make a crude estimate of Q. The volume of Dufour's gland cavity from which the substance is emitted can be calculated as about 10^{-5} cm^3 from the measurements of Callahan, Blum & Walker (1959). If the contents of the gland have a density similar to water the contents are about 10^{-5} g. Let us suppose that all of this is the trail substance, and also that the substance has a molecular weight between 100 and 600, a highly probable range (all known olfactorily acting pheromones are in this range). Dufour's gland then could contain between 10^{16} and 6×10^{16} molecules. In laying a trail 10 cm, let us assume that an ant pays out at least 1/100 of its Dufour's gland contents, because the achievement of a trail of 100×10 cm = 10 meters seems improbable; and that it pays out no more than 1/10 of the gland contents, since active trails of several hundred mm have been observed.

We predict therefore that the trail is laid at the rate of between 10^{14} and 6×10^{15} mol/cm. For a worker travelling 0·4 cm/sec, this gives a Q of between 4×10^{13} and $2·4 \times 10^{15}$ mol/sec. The range of K corresponding to this estimate is from $2·36 \times 10^{13}$ to $1·42 \times 10^{15}$ mol/cm^3.

The widths and persistence of the ant trails may be examined by computations with equation (3.2). Table 2 gives the radii of cross-sections through a very long, freshly laid trail at various distances from the nest. The trail maintains a reasonably constant width through time except near the end points. The boundaries, surfaces of isoconcentration at the threshold level, of a typical trail through time are shown in Fig. 7.

TABLE 2

Radii of cross sections through a maximum length trail, immediately upon return of the trail layer to the nest. See Fig. 7

Distance from the nest (cm)	Radius (cm)
1	0·49
2	0·64
5	0·83
10	0·97
15	0·99
15·4	1·00 (maximum radius)
20	0·98
25	0·92
30	0·81
35	0·64
40	0·36
42	0·00 (fade-out point)

These results can be compared with the intuitively expected design features of an odor trail communication system mentioned earlier. The persistence of the trail is, as expected, sufficient to permit trails of adequate length, 28 cm, but the fade-out is rapid enough, about 100 seconds after the completion of a 20 cm trail so that following of unproductive old trails is avoided. This
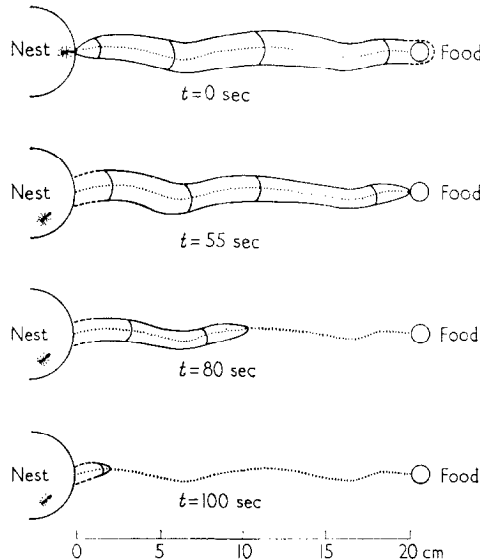

FIG. 7. The threshold volume surrounding the trail at various times, *t*, after the trail layer reaches the nest. See Table 2 for exact dimensions.

results from a proper balance of Q, which increases the persistence for higher values, and K and D, which reduce the persistence for higher values. In the case of the fire ant Q is moderate, low enough to permit adequately long trails yet large enough to maintain the persistence necessary in the longer trails. The rate of diffusion is very low, serving both to keep the persistence high and the trail narrow. The value of K is unexpectedly high. Even the lower limit of $2 \cdot 36 \times 10^{13}$ mol/cm assures that many more than a few molecules incident on the antennae are required for behavioral recognition of the trail. This, of course, ensures that a new trail will be recognized even in high background noise levels from old trails. In addition, however, the high value of K and the corresponding value of the ratio Q/K are in striking adherence to another principle design feature: the maintenance of a large gradient at the trail boundary. This gradient is increased, as noted previously, for large values of Q and small values of D. In this case we indeed have a moderate Q and a very small D. For a given Q and D, the gradient is at maximum for Q/K given by equation (3.7), that is

$$Q/K = e\pi(0 \cdot 00649)x$$

We are most interested in maximizing the gradient near the fade-out point of a long trail where it is small at best. Let us therefore set x to the maximum trail length of 42 cm. This gives

$$Q/K = e\pi(0 \cdot 00649)(42) = 2 \cdot 32 \text{ cm}^3/\text{sec}$$

which, considering the various approximations of the model and the computations, are in close agreement with the separately computed value at $1 \cdot 71$ cm^3/sec.

Case 4: Continuous Emission in a Wind

It is obvious from the examples of the previous cases that even for large rates of emission and low thresholds the diffusion process in still air allows limited communication range. In many cases, such as with the sex attractants of larger insects, it is advantageous or necessary for the communication to have a range of hundreds of meters. This is possible only by taking advantage of wind, a movement of the transporting medium. The wind does more than move the molecules of the communication substance in its direction of flow. It creates turbulence in the medium, except under the unnatural conditions of constant flow in time and space and absence of nearby boundary surfaces. In any perceptible wind this turbulent diffusivity overwhelms the diffusion properties of any particular substance, so that the diffusion constants for this case are properties of the wind structure and boundary surfaces rather than of the substance.

Roberts (1923) obtained a solution of the diffusion equation for a source

emitting at a constant rate, Q mol/sec, in a steady wind velocity u. An approximation to this solution, equation (3.1), was used previously, where the source is at $x = y = z = 0$, and the x axis is taken as the wind direction. The case of a stationary constant source in a wind is, as mentioned before, the same as a moving source in still air. All the results for the previous case may be applied in this case when the turbulent diffusivity is constant throughout space, and at any point is constant in any direction. Unfortunately, this condition is satisfied in the atmosphere only well above the ground—say at altitudes of more than several hundred meters. Roberts attempted to overcome this difficulty by assuming two components of diffusivity at any point, D_z, the vertical diffusivity and D_y the diffusivity transverse to the wind. The density function, assuming the source has been emitting for a long time, becomes in approximation

$$U(x, y, z) = \frac{Q}{2\pi x (D_y D_z)^{1/2}} e^{-u/4x(y^2/D_y + z^2/D_z)} \tag{4.1}$$

This equation, however, is still only a very crude approximation to the natural situation in which the diffusivity, both vertical and transverse, certainly varies with altitude.

A solution taking into account the normal wind profile with altitude has not yet been obtained. Sutton (1953) points out that a function of the form

$$U(x, y, z) = \frac{2Q}{\pi C_y C_z u x^{2-n}} e^{-x^{n-2}(y^2/C_y^2 + z^2/C_z^2)} \tag{4.2}$$

satisfies most of the necessary conditions, where C_y and C_z are diffusion constants determined by the wind profile and surface roughness and n is an undetermined constant. Note that if

$$n = 1, \quad C_y^2 = \frac{4D_y}{u}, \quad \text{and} \quad C_z^2 = \frac{4D_z}{u}$$

equation (4.2) reduces to (4.1).

Assuming (4.2) as the density function, and that the source has been emitting for a long time, the surface at threshold density K is defined by

$$K = \frac{2Q}{\pi C_y C_z u x^{2-n}} e^{-x^{n-2}(y^2/C_y^2 + z/C_z^2)} \tag{4.3}$$

The maximum distance downwind above threshold is

$$X_{\max} = \left(\frac{2Q}{K\pi C_y C_z u} \right)^{1/2-n} \tag{4.4}$$

The maximum height and width of the surface are reached at

$$x = \left(\frac{2Q}{K\pi C_y C_z ue} \right)^{1/2-n} \tag{4.5}$$

the maximum being

$$Z_{max} = C_z \sqrt{\frac{2Q}{K\pi C_y C_z ue}} \qquad (4.6)$$

and

$$Y_{max} = C_y \sqrt{\frac{2Q}{K\pi C_y C_z ue}} \qquad (4.7)$$

The values of Y and Z, the width and height of the threshold surface downwind, are given by

$$Y = C_y \sqrt{x^{2-n}\log\frac{2Q}{K\pi C_y C_z ux^{1/4}}} \qquad (4.8)$$

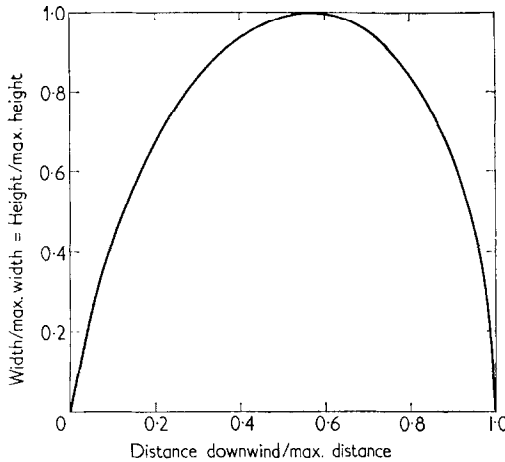$$Z = C_z \sqrt{x^{2-n}\log\frac{2Q}{K\pi C_y C_z ux^{1/4}}} \qquad (4.9)$$

FIG. 8. The height and width of the threshold volume downwind from a continuous point source in moderate wind *versus* distance downwind. All distances are given as proportions of their maximum values.

If x, y, and z in (4.8) and (4.9) are replaced by x/X_{max}, Y/Y_{max} and Z/Z_{max} respectively, the resulting equations are free of C_y, C_z, and Q/K, and for any x, Y/Y_{max} and Z/Z_{max} are identical. The function Y/Y_{max} with respect to x/X_{max} is graphed in Fig. 8 for $n = 1/4$.

The gradient of the concentration along a line directly downwind from the source is

$$\frac{dU}{dx} = \frac{2Q}{\pi C_y C_z ux^{3-n}} \qquad (4.10)$$

At the maximum range of the threshold ellipsoid this is

$$\frac{dU}{dx}\bigg|_{X_{max}} = K\left(\frac{2Q}{K\pi C_y C_z u}\right)^{-1/2-n} \tag{4.11}$$

and the relative gradient, the gradient as a proportion of the concentration at the maximum range is

$$\frac{\dfrac{dU}{dx}}{U}\bigg|_{X_{max}} = \left(\frac{2Q}{K\pi C_y C_z u}\right)^{-1/2-n} \tag{4.12}$$

Tables of C_y, C_z, and n for various types of surfaces and wind profiles are not available. Sutton, however, states that over relatively level ground in a moderate wind, say between 100 and 500 cm/sec, equation (4.2) holds quite well for $n = 1/4$, $C_y = 0.4 \, cm^{1/8}$ and $C_z = 0.2 \, cm^{1/8}$. We will use these values in the following analysis.

We can apply these results to the analysis of the sex attractant communication system of the gypsy moth, *Porthetria dispar*. The simplest method of determining Q/K is to measure the maximum distance over which the attractant is effective and using (4.4).

$$Q/K = 1/2 \, C_y C_z u \, X_{max}^{2-n}$$
$$= 0.1256 \, u \, X_{max}^{7/4} \tag{4.13}$$

Collins & Potts (1932) reported that twelve to fifteen virgin females could attract males over a distance of at least $2\frac{5}{16}$ miles, but not more than $3\frac{1}{4}$ miles. They found in separate experiments, however, that males in confinement could not fly more than several miles in the three days that they lived in captivity. It is not certain, therefore, as to whether the $3\frac{1}{4}$-mile limit is on the threshold distance of the attractant or on the ability of males to respond. For this analysis, let us assume that the maximum distance above threshold lies between $2\frac{5}{16}$ miles, or 3.72 km, and 10 miles, or 16.09 km, the latter distance being about the extreme limit of sex attraction for Lepidoptera generally. Collins and Potts experimented in summer on the New England coast, where there is a fairly persistent sea breeze of 10 miles/hr, about 450 cm/sec or more. Assuming an average wind velocity of 400 cm/sec these limits give

$$Q/K = 2.81 \times 10^{11} \, cm^3/sec, \text{ for } X_{max} = 3.72 \times 10^5 \, cm$$

and $$Q/K = 3.64 \times 10^{12} \, cm^3/sec, \text{ for } X_{max} = 1.609 \times 10^6 \, cm$$

These values, of course, are for twelve to fifteen females, so that we would expect Q/K for a single female to lie in the range $1.87 \times 10^{10} \, cm^3/sec$ to $3.03 \times 10^{11} \, cm^3/sec$.
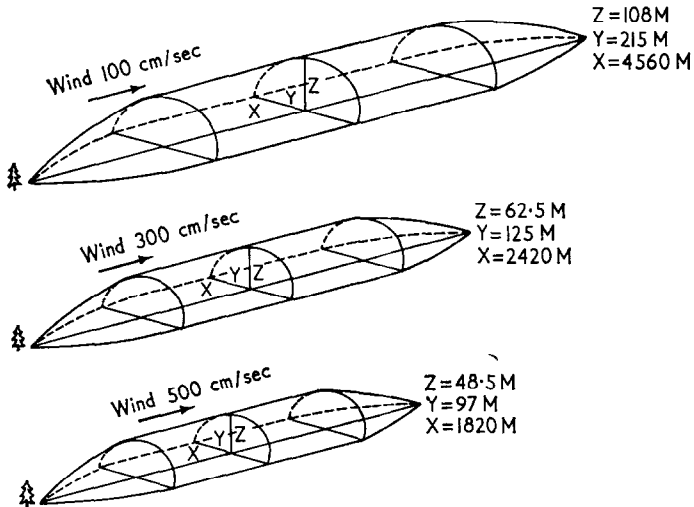
FIG. 9. The threshold volume of sex attractant downwind from a single female gypsy moth at various wind velocities. The maximum values of the dimensions are given.

Taking Q/K as about 10^{11} cm³/sec, Fig. 9 gives the dimensions of the volume over which a single female gypsy moth can attract a male in winds of 100, 300, and 500 cm/sec. Note that for the range of winds for which the formulae apply, the stronger winds reduce the range, width, and height of the volume above threshold. This is because the higher wind velocities create larger turbulent diffusivities, tending to distribute the attractant more uniformly through space, hence in threshold concentrations over a smaller volume. We can compare these turbulent diffusivities with the diffusion coefficients in still air. As mentioned earlier, the C_y and C_z in equations (4.2 to 4.10) are related to the D of equation (4.1) and the equations of previous sections by

$$D = \frac{uC^2}{4}$$

For a C of 0·4, such as used here, the equivalent D for a wind velocity of 400 cm/sec. is 16, while the coefficients of diffusion in still air are generally much less than 1.

As in the previous cases we can crudely estimate the absolute values of Q and K separately. Butenandt (1959) reported that 10^{-2}/cm³ of a 10^{-16} g/cm³ solution of the *Bombyx mori* sex attractant, or about 2,600 molecules, elicit behavioral response in half the males placed 1 cm from the source. If we treat the source as an instantaneous puff and assume 1 cm as the maximum

range of the attractant, the methods of case 1 give the threshold concentration as 192 mol/cm^3. This is probably a maximum value. By assuming the threshold for *Porthetria* to be similar to this, we see that Q, the rate of emission of a female, is about $1 \cdot 92 \times 10^{13}$ mol/sec. Jacobson, Beroza & Jones (1960) extracted 20 mg of sex attractant from 5×10^5 virgin female gypsy moths, or about 4×10^{-8} g from each female. Let us assume that the extraction technique is at least 50 % efficient so that a female probably has no more than 8×10^{-8} g. This corresponds to $8 \cdot 08 \times 10^{13}$ to $1 \cdot 616 \times 10^{14}$ molecules per female. The female, therefore, is releasing about 1/8 to 1/4 of the quantity in her reservoir each second. This predicted upper limit is surprisingly high but not *a priori* impossible.

We might now consider the question of whether or not the male gypsy moth uses the concentration gradient of the sex attractant to locate the source. At the downwind limit of the threshold ellipsoid equation (4.11) given the gradient as

$$\frac{dU}{dx}\bigg|_{X_{\max}} = 2 \cdot 50 \times 10^{-4}\ cm^{-4}$$

The relative gradient is $1 \cdot 3 \times 10^{-6}$. Flights of a meter up or downwind bring differences in concentration of $0 \cdot 013$ %, only $2 \cdot 50 \times 10^{-2}$ mol/cm^3. Differences of this order would be completely overcome by random variations in the concentration. It is therefore virtually impossible for the males to use the gradient to orient toward the female. Some other method of orientation seems necessary. As suggested by Schwink (1956) for *Bombyx mori*, anemotaxis seems the most probable alternative. That is, the males fly upwind when activated by the pheromone. When they pass out of the active zone because of their own motion or a shift in the wind, they either cease flight or commence a lateral searching motion. This procedure will ultimately bring them to the vicinity of the female.

Discussion

In this study we have made what we believe to be the first systematic analysis of the properties of communication by gaseous pheromones. Elsewhere (Wilson & Bossert, 1963) we have given reasons why we believe this kind of communication is of paramount importance in nature, especially among insects and the lower animal phyla. The equations derived are far from exhaustive, but it is hoped that with suitable minor adjustments they can be applied fruitfully to a majority of real cases. The four general cases considered (puff in still air, continuous release in still air, continuous release from a moving source, continuous release in a wind) embrace most of the conditions under which pheromones can be broadcast in the terrestrial

environment. By suitable adjustment of parameters, the same equations can be applied to the aquatic and marine environments. We then applied the equations to several of the few real cases where sufficient experimental data exist. The fact that the applications were limited to insects (moths and ants) does not mean that the models themselves are similarly limited.

The results were satisfying, in our view, for two principal reasons. First, they produced predictions concerning the exact forms of the active spaces and rates of transmission that were quite new and surprising in their biological applications. Second, by comparing the deduced properties of the several systems and considering their functions in the animal societies in which they are employed, we obtained evidence that the parameters of pheromone transmission have been adjusted in the course of evolution to obtain a high degree of efficiency. Put more exactly, support has been obtained for the following theory: that the emission rate of the pheromone and the response threshold have been adjusted in evolution to maximize efficiency with respect to a specific function. If this is true, then the study of chemical communication can fairly be said to be in the earliest stages of a rich and interesting history.

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