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A MATHEMATICAL MODEL FOR THE FLIGHT OF PEA MOTH TO PHEROMONE TRAPS THROUGH A CROP

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A model is presented that describes the average resultant track of a population of male pea moth, *Cydia nigricana* (F.), flying through a crop to a continuously emitting pheromone trap containing 100 µg (E,E)-8,10-dodecadien-1-yl acetate. This model, based on work by C. T. David, J. S. Kennedy, A. R. Ludlow, J. N. Perry and C. Wall *J. chem. Ecol.* **8**, 1207 (1982), and modified for the effect of a crop, has particular

reference to a line of interacting pheromone traps equally spaced along the mean wind direction at an emergence site. It is derived after extensive field observations. The model relates to the average flight behaviour of a population of moths, and is compatible with both the anemotactic theory and a system of integrated anemotaxis and longitudinal chemo-klinotaxis.

We give two theoretical reasons and cite observational evidence which suggest that, within a wheat crop, a discrete plume breaks up at around 10–15 m from the source and that beyond this distance pheromone exists at a non-zero concentration at all downwind positions. Close to the source moths are assumed to respond to a discrete plume as described by David *et al.* (1982) and further from it to receive pheromone continuously and fly, on average, upwind. Because of the effects of the crop we suggest that equations of atmospheric diffusion derived to predict time-averaged concentrations of pheromone may hold instantaneously. The average behaviour of a population of responding moths under these conditions is discussed. Far from the source there is a concentration of pheromone below which such moths sampling it are assumed not to respond; this is termed the threshold concentration and the positions where it occurs are termed the threshold contour. The contour is sketched for single and multiple sources. Such moths flying upwind to this contour are assumed to stop and then cast (move in a crosswind direction). This results in the moths either moving inside the contour to a region of concentration above the threshold, and resuming upwind flight, or moving outside the contour and, eventually, not responding further. Net movement in the former is therefore towards the source and such moths may eventually be caught. The model allows for random flight by non-responding moths outside the threshold contour, and for moths to 'lose' the discrete plume of one source and continue upwind flight to encounter that of the next source upwind.

The model has ten parameters, five relate directly to moth flight behaviour, one to the degree of random flight, one to meteorological conditions, two describe the number and spacing of traps and the last governs numerical accuracy. Predictions from the model of proportional catch in each of a line of traps were made using a computer program. An extensive body of 406 sets of data concerning trap interactions was collected over six years and the model provided excellent fits to this data. Throughout this paper the model is described in biological terms, formulae are provided when necessary.

1. INTRODUCTION

This paper presents a mathematical model that describes the average resultant track of a population of male pea moth, *Cydia nigricana* (F.), flying through a field crop, to a pheromone trap. Investigations of moth responses to pheromones have been stimulated by attempts to use sex-attractants to monitor and control pest species. Detailed analyses of flight in wind tunnels (Kennedy 1977*a, b*, 1978, 1982; Kennedy *et al.* 1980, 1981; Marsh *et al.* 1978, 1981) have aided an understanding of flight behaviour. It is now widely accepted that moths respond sexually to pheromone sources at least in part by optomotor anemotaxis (Kennedy 1977*a*, 1983; Kuenen & Baker 1983). Field studies involving the use of pheromones to control pests (Minks 1977) have involved many species–crop combinations. However, detailed behavioural evidence of how moths respond to pheromones in the field is scarce (but see Cardé *et al.* (1975) and David *et al.* (1983)).

The pea moth is a serious pest of peas in England (Gould & Legowski 1964; Macaulay 1977; Perry *et al.* 1981). Larvae overwinter and emerge as adults the following summer, usually in fields of wheat, which often follow peas in current agricultural rotations. Moths emerge over about ten weeks and during this period they migrate to pea fields, where gravid females oviposit.

Adult males fly between 12h00 and 21h00 B.S.T. (although the period of peak activity may only last about 1 h) at temperatures above about 18 °C (Lewis *et al.* 1975). They prefer warm, dry, cloudy weather. As far as is known neither convection nor large-scale turbulence affect moth distribution. Sexually responding males flying near to a pheromone source placed level with the top of the crop, approach it slowly in a sequence of straight but frequently interrupted trajectories through the upper levels of the crop or just above it, frequently alighting on the vegetation or hovering. Further from a source responding males fly upwind, with longer

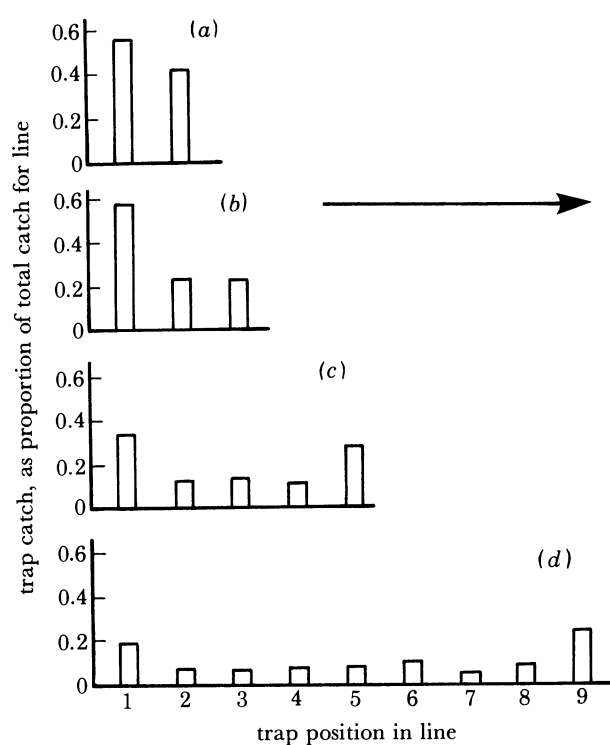


FIGURE 1. The catch in each of several equally spaced pheromone traps for the pea moth *Cydia nigricana* (F.), aligned along the mean wind direction. Each catch is expressed as a proportion of the total for the line of traps, using geometric means over several replicates. The arrow indicates the mean wind direction, trap 1 is always the extreme upwind trap. (a) Line of two traps, (b) line of three traps, (c) line of five traps (from Wall & Perry 1980); (d) line of nine traps (Perry & Wall 1982).

durations between changes of track or halts. There is yet no observational evidence for zigzagging upwind flight (Kennedy 1983) in the horizontal plane, but vertical zigzagging may occur close to the source. By contrast, flight by non-responding male moths involves short, faster movements in random directions. Flight within the crop is difficult to observe from distances greater than 10 m. Data and observations used in this paper are from experiments done in large, flat fields of wheat following peas, with no obstructions to wind such as buildings or trees.

The pheromone of the pea moth is believed to consist of a single component chemical, (E,E)-8,10-dodecadien-1-yl acetate (Greenway & Wall 1980). For experiments, synthetic lures containing 100 µg of this chemical were used in sticky (Lewis & Macaulay 1976) or water traps (Wall & Perry 1980), with the source at crop height. The pheromone is released as a vapour, which is transported to moths by the wind.

Wall & Perry (1978) provided evidence to suggest that the range of attraction of such traps

was greater than 100 m. There is now strong evidence to suggest attraction over 500 m (Wall & Perry 1980, 1984). Several traps spaced at distances less than the range of attraction may interact (Wall & Perry 1978), that is the catch in a trap may be affected by the presence of the others. Most of our data involve a line of several traps equally spaced along the mean wind direction. Although the wind direction measured instantaneously at a given position may fluctuate from moment to moment, the mean wind direction usually remains constant over several hours, and often for an entire flight period. Surprisingly, in a line of three traps, the upwind trap catch is usually larger than the other two (figure 1). A similar effect is obtained with two traps. With lines of more than three traps the catch in the extreme downwind trap is also relatively large, and often as large as the extreme upwind trap (Wall & Perry 1980; Perry & Wall 1982) (figure 1). Hirano (1976) observed similar catch profiles with *Spodoptera litura* (F.). Analysis of catches from 373 such lines, done on different occasions, has recently shown (see §7) that the proportion of the total catch for a line caught by an individual trap varies systematically within an afternoon (Perry & Wall 1984). These results and others (Wall & Perry 1980, 1981, 1982) suggest that moths are not caught in particular traps as a result of purely random processes.

Mathematical models (May 1973, 1975) are increasingly used to quantify complex biological processes (Anderson & May 1981), to highlight topics requiring further experimentation, and as a framework for discussion. Models of pheromone dispersal from point sources and resulting insect responses include those of Bossert & Wilson (1963), Nakamura (1976*a, b*), Miksad & Kittredge (1979) and Mankin *et al.* (1980). A mathematical model for bird navigation was proposed by Kendall (1974). This paper introduces a model which attempts to quantify these processes in a spatial context, by using observable facets of average moth behaviour. The model is compatible with both the anemotactic theory of orientation to a distant point source of odour (Kennedy 1977*a*) and the concept of a system of integrated anemotaxis and longitudinal chemo-klinotaxis (Kennedy 1983; Kuenen & Baker 1983). The model is used to explain experimental results.

2. MICROMETEOROLOGICAL CONSIDERATIONS

The behaviour of a moth responding to a source of pheromone in the field depends on the stimulus received, although the same stimulus may elicit different responses depending on the time of day or previous exposure (Wall & Perry 1982). The concentration of pheromone experienced depends on the release rate of the source, distance from the source and the micrometeorology of the environment. In this paper all concentrations are expressed in units of molecules per cubic metre. Warm summer afternoons result in atmospherically unstable conditions.

It is difficult to make accurate measurements of concentrations of pheromone in field conditions (Caro *et al.* 1978), especially over relatively short time periods (but see Murlis & Jones (1981)). Atmospheric physicists have derived theoretical results for the concentration of airborne material at any position downwind of a continuous point source at ground level, over open country, in near neutral conditions (see summary by Pasquill (1974)); these were confirmed by experiments (Sutton 1947; Cramer 1957). However, the models and data were time-averaged, and related to average concentrations sampled over several hours. A moth samples concentration on a much shorter time scale. Gifford (1959, 1960), Wright (1958), Murlis & Jones (1981) and others have shown that concentrations within instantaneous plumes may be very different from predictions based on time-averaged models.

An instantaneous plume over open country has a characteristic snaking shape. At a given distance downwind of the source, successive crosswind positions of such a plume swing to and fro, owing to previous changes of wind direction at the source. Over open country a gust transports material from a source in a straight line for many hundreds of metres (Davidson & Halitsky 1958; David *et al.* 1982). This implies that material can only be detected at a given position downwind if the wind direction at that position is directly from the source. David *et al.* (1982) showed how moths in such conditions may locate a source by flying upwind while detecting pheromone and casting on flying out of the plume, when the scent is lost. Casting involves crosswind flight, usually with changes in direction averaging around 180° (Kennedy 1983). This model is based on that of David *et al.* (1982) but with certain differences, because pea moth behaviour in a crop differs strikingly from that of other moths, not in crops. The effect of a crop is examined in the next section.

3. THE EFFECT OF A CROP

(a) *Physical effect*

Within wheat, or a similar crop, the vegetation near the top of the crop exerts a shearing force on a well-defined, discrete plume. Additionally, the vegetation enhances the formation of smaller-scale eddies within the crop which accelerate the plume's decay. Legg & Long (1975) and others presented normalized wind profiles for wheat; wind speeds decreased rapidly in the top half of the crop. Wilson (1980), using a split-film heat-transfer anemometer in maize, found turbulent intensities were up to five times greater within the crop than above it. Even in less dense canopies such as forests, turbulence is neither homogeneous nor isotropic (Aylor 1976; Aylor *et al.* 1976) (see also Oliver (1971) and Allen (1968)). Legg and Strange (1980) reported entrainment of nitrous oxide vapour by a mature barley crop resulting in material velocities far smaller than expected from wind velocities measured over the top of the crop.

We believe the general outcome of these physical effects of the crop is to break up the part of the discrete plume that is within the crop, at a relatively short distance (≈ 15 m) downwind of a source at crop height. Beyond this distance from a continuously emitting source at crop height there will be pheromone within the crop at indeterminate, but non-zero concentrations, at all positions.

(b) *Uptake and release of pheromone by crop*

Further evidence for this proposed effect of the crop concerns the continuous absorption and release of pheromone by the vegetation. Such vegetation acts as a potent secondary source of attractant. Although predictable from knowledge of plant biochemistry and the physicochemical properties of pheromones, this effect has only recently been quantified by entomologists (Cameron 1981; Wall *et al.* 1981; Wall & Perry 1983), but see Fabre (1937).

Results of recent field experiments (Wall & Perry 1983) show this effect to be substantial. It was shown that wheat exposed to pheromone for only 0.5 h elicited sexual responses from, and remained attractive to males for 3 h after removal of the source, so that moths were attracted to the exact position of the removed source. Also, it was not only the plants immediately next to the source that were attractive. Uptake of pheromone has also been demonstrated on peas and artificial (plastic) surfaces. We have also observed, on numerous occasions, a large increase in the attractiveness of the vacated position of a trap immediately after the trap was removed.

Therefore, the continuous absorption and release of pheromone downwind of a source may also result in non-zero concentration of pheromone at all positions. A particular molecule of pheromone may be successively absorbed and released by many plants before being perceived by a moth. The uniformity and denseness of crops aid this transmission process. In the steady-state situation, the total number of molecules available within a given volume of crop will thus be much larger than in a corresponding volume of air over open ground.

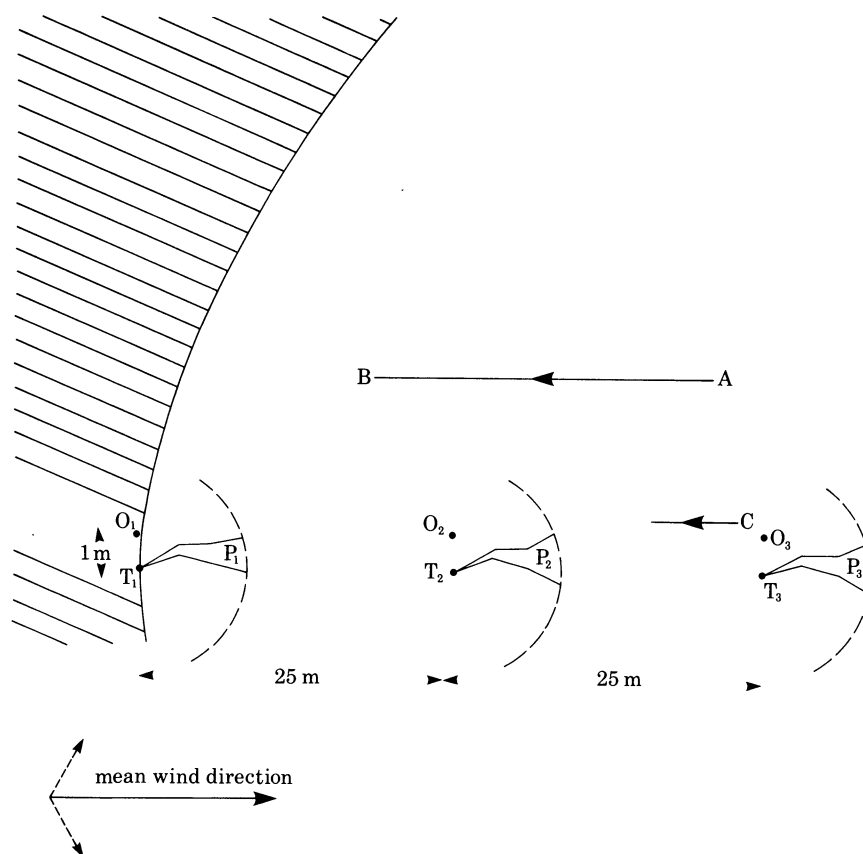


FIGURE 2. Schematic instantaneous view from above a line of three pheromone traps for the pea moth *Cydia nigricana* (F.), in a crop of wheat (not to scale). The solid arrow below the figure indicates the mean wind direction and the broken arrows the limits of fluctuation in wind direction. Three equally spaced traps: T_1 , T_2 and T_3 were aligned 25 m apart along the mean wind direction. An observer: O_1 , O_2 or O_3 stood 1 m crosswind of each trap. The circular arc (dashed line) around each trap shows the probable limit of the effective discrete plume (solid line): P_1 , P_2 or P_3 , from that trap. Moths in shaded area were assumed not to receive sufficient pheromone to respond. On occasion, the instantaneous wind direction appeared coincident with the line of traps for some time; during this period a moth, initially seen by observer O_2 at position A, subsequently flew upwind to position B, past trap T_2 . Contrast with typical moth at position C, closer to the line of traps, which encounters the discrete plume P_2 , and is caught by trap T_2 .

(c) Observational evidence

Many of our experiments have involved a line of several traps along the mean wind direction with an observer sited about 1 m crosswind of each trap. Sometimes, the instantaneous wind direction appeared to be roughly coincident with the mean wind direction, and hence with the line of traps, for periods of the order of tens of seconds. During many of these periods an observer (not sited at the extreme upwind trap) has noted moths flying upwind, parallel to

and up to about 20 m crosswind of the line of traps, past the observer's trap (moth A to position B, figure 2). The flight of these moths was against the instantaneous wind direction but was not directly towards any of the sources. Assuming the moths were responding to pheromone, this again implies non-zero concentration of pheromone at all positions downwind, and is consistent with the initial simple model of Wall & Perry (1978). Also, because these moths flew past the observer's trap, it is unlikely that they encountered the discrete plume from that trap. This too, suggests that the extent of such a plume may be relatively small (cf. moth C, figure 2). These observations have been supported by five experiments done during 1983, which showed that the average direction of moths through a 5 m × 5 m area, whose centre was 15 m crosswind of a line of three traps, was up (mean) wind.

(d) *Conclusions*

We conclude that in wheat and similar crops, moths relatively close to a source respond to a discrete plume as described by David *et al.* (1982). Further from the source, responding moths perceive pheromone continuously and, if flying, orient up (instantaneous) wind. The average ground track of such moths will be in the mean upwind direction, whether or not upwind flight in the horizontal plane has a straight or zigzagging (Kennedy 1983) track. We assume the former for pea moth following field observations, but our model is compatible with the latter since it specifies the average resultant track of a population of moths, rather than the precise mechanisms used to guide an individual. The above strategy (figure 2) is not sufficient to locate the source for those moths which are too far crosswind of the source to encounter a discrete plume. These moths require a further cue to alter upwind flight behaviour (see §5*a*, *c*).

After a source has been emitting material for some time a 'steady-state' situation will ensue in a crop downwind of the small area where the plume is well defined. The amount of pheromone passing into any given volume will approximately equal the amount leaving, so the concentration will remain roughly constant, assuming a constant wind speed. In these circumstances concentrations may approximately obey the time-averaged diffusion equations summarized by Pasquill (1974) (see §2), but these equations will apply instantaneously. Local heterogeneity ensures that these equations will never hold exactly, but the approximation is probably good enough for our purposes. Hence we may derive an expression for the concentration sampled instantaneously by a responding moth at any position.

4. EQUATIONS FOR PHEROMONE CONCENTRATIONS WITHIN A CROP

(a) *Single source, diffusion equations*

Let $\chi(x, y, z)$ be the concentration (in units of molecules per cubic metre) of pheromone measured at a position whose coordinates with respect to an origin at the source are (x, y, z) ; x and y measure the distance downwind and crosswind of the source respectively and z is the height above ground level (in metres). For a continuous point source at ground level Pasquill (1974) gave a general equation for the time-averaged concentration over open country in near-neutral conditions:

$$\chi = f(x) \exp\{-by^r - cz^s\}, \quad (1)$$

where b , c are constants and $f(x)$ is a specified function of x .

Theoretical considerations suggest $r \approx 2$ and $1 \leq s \leq 2$. Practically, the difference between

$s = 1$ and $s = 2$ is not great; the values $r = s = 2$ imply a Gaussian shape for concentration and simplify the algebra. For $r = s = 2$ it can be shown that (1) reduces to:

$$\chi = \frac{Q}{\pi \bar{u} \sigma_z \sigma_y} \exp \left\{ -\frac{1}{2} \left(\frac{y^2}{\sigma_y^2} + \frac{z^2}{\sigma_z^2} \right) \right\}, \quad (2)$$

where Q is the (constant) release rate of the source (measured in units of molecules per second), \bar{u} is the mean component of wind speed in the downwind (x) direction (in metres per second) and σ_y and σ_z (in metres) are the standard deviations of concentration measured in the crosswind and vertical directions respectively. Both σ_y and σ_z are functions of x . We shall assume throughout this paper that \bar{u} is constant, and also σ_y and σ_z for given values of x . A specific case of (2) was given by Sutton (1947) and used by Bossert & Wilson (1963) in models of insect response to sex-attractants. The functional relations generally considered between σ_y , σ_z and x are:

$$\sigma_y = \alpha_y x^\delta; \sigma_z = \alpha_z x^\delta, \quad \text{where } \alpha_y, \alpha_z \text{ are constants} \quad (3)$$

The value of δ has been estimated by Hay & Pasquill (1959) as 0.82 using data from Porton, England (Smith & Abbott 1961), and Nebraska, U.S.A. (Cramer 1957). Sutton (1947) estimated δ to be 0.88 using Porton data (but see Barad & Haugen (1959)). Bosanquet & Pearson (1936) and Calder (1952) both assumed δ to be unity but used different values for r and s from those implicit in (2). Pasquill (1974) commented that, for practical use, the different values proposed for δ gave results remarkably consistent with each other and with the observed data, for values of x up to 1000 m. Sutton (1947) noted that δ must lie between 0.5 and 1.0 on theoretical grounds and implied that $\delta \rightarrow 1$ as turbulence increases (for example, in unstable conditions). Hence for a field of wheat during an afternoon in summer $\delta = 1$ may be a reasonable approximation.

However, the accuracy of (2), derived for neutral conditions, is unknown when applied to unstable conditions. The model we shall describe is probably quite robust to deviations from (2), which is used here merely to define the shape of the volume within which moths respond. For night-flying moths no such difficulties arise because nocturnal atmospheric conditions are usually stable.

The height of a wheat crop rarely exceeds 1 m, hence the height of the source above ground level and of responding moths is negligible, compared to the maximum height to which pheromone diffuses. We therefore substitute $z = 0$ and $\delta = 1$ into (2) and (3) and obtain:

$$\chi = \frac{Q}{\pi \bar{u} \alpha_y \alpha_z x^2} \exp \left(-\frac{y^2}{2 \alpha_y^2 x^2} \right),$$

and, putting $K = Q/\pi \bar{u} \alpha_y \alpha_z$ (molecules per metre) and $\alpha = 2 \alpha_y^2$,

$$\chi = \frac{K}{x^2} \exp \left\{ \frac{-y^2}{\alpha x^2} \right\}. \quad (4)$$

We shall use (4) for the instantaneous concentration sampled by a moth at position (x, y) , as long as this is sufficiently far from a source. We assume the average distance from the source, beyond which the discrete plume is not effective is, say, ν (metres). Then (4) holds for values of x and y , for which $(x^2 + y^2)^{\frac{1}{2}} \geq \nu$. (4) may be rewritten as

$$y^2 = -\alpha x^2 \ln(\chi x^2 / K). \quad (5)$$

(b) *Single source, moth response*

For a given value of $\chi = \chi_0$, say, (5) describes the shape of a concentration contour. It is explicit for y given x , but not for x given y , the values of which must be found numerically.

The range of attraction of a pheromone source to a male moth is a finite distance which is usually difficult to determine (Wall & Perry 1978). It may be relatively great for larger moth species, and is several hundred metres even for pea moth (Wall & Perry 1984), but it has an

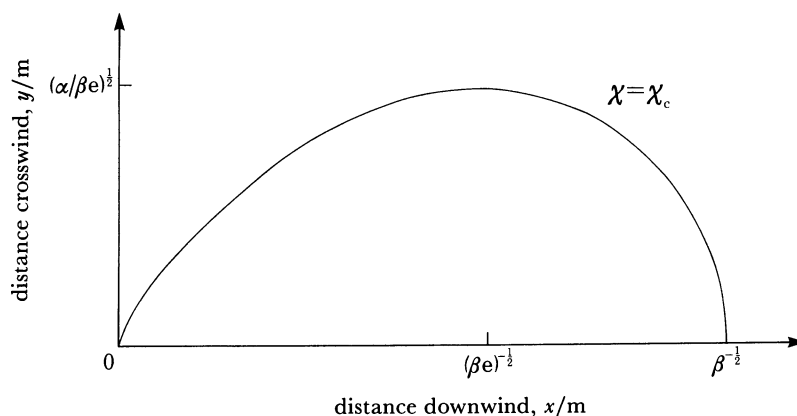


FIGURE 3. Sketch of the threshold concentration contour, $\chi = \chi_c$ molecules per cubic metre, viewed from above a crop. A single pheromone source is located at $(0, 0)$. The wind blows in the direction of x increasing, from left to right. The contour has equation $y = x[-\alpha \ln(\beta x^2)]^{1/2}$ and is symmetrical about the line $y = 0$; therefore, for simplicity, only values of $y > 0$ are shown in this and subsequent figures. The value of α used is 0.5. Only simulated moths within the area enclosed by the threshold contour are assumed to respond. The maximum width of the contour is $2(\alpha/\beta e)^{1/2}$ and its maximum length is $\beta^{-1/2}$. The shape and size of the contour are determined by α and β respectively. The line $y = 0$ is termed the mean wind axis.

upper bound. The existence of this upper bound implies that there is some concentration of pheromone so small that moths do not detect enough to initiate flight, or if previously responding do not continue to do so. Such a threshold concentration was postulated theoretically by Bossert & Wilson (1963) and demonstrated in the field by Baker & Roelofs (1981). Wilson *et al.* (1969) gave a method for estimating threshold concentrations. In a crop far from the source, such a threshold may occur where there are so few pheromone molecules in a given volume of air that the frequency of detection by a moth is too low to initiate a response (Boeckh *et al.* 1965). Alternatively, local heterogeneity in such regions, where concentrations are low, may result in a breakdown of the assumption that pheromone exists at non-zero concentrations at all positions; a moth might then sample from a local region of pheromone-free air. Our model relates to the average behaviour of a population of moths, so differences in response thresholds between individuals and within an individual through time are not modelled. However, we denote the average concentration of pheromone, below which moths are assumed not to respond by flight, as χ_c . If $\chi_c/K = \beta$, say (in units of per square metres) the threshold concentration contour has equation:

$$y = x[-\alpha \ln(\beta x^2)]^{1/2},$$

which may be sketched (figure 3) by noting $y = 0$ when $x = 0$ or $\beta^{-1/2}$, and

$$\frac{dy}{dx} = \frac{-(1 + \ln[\beta x^2]) \sqrt{\alpha}}{(-\ln[\beta x^2])^{1/2}}.$$

Hence $dy/dx \rightarrow \infty$ as $x \rightarrow 0$, $dy/dx \rightarrow -\infty$ as $x \rightarrow \beta^{-1/2}$, and $dy/dx = 0$ when $x = (\beta e)^{-1/2}$ and $y = (\alpha/\beta e)^{1/2}$.

In figure 3 the source is at position $(0, 0)$ and the mean wind direction is from left to right. The contour is symmetrical about $y = 0$, only the right-hand half, looking upwind, ($y > 0$) is shown. The range of attraction, the maximum distance from which moths respond, is $\beta^{-1/2}$. The maximum crosswind distance for response is $y = (\alpha/\beta e)^{1/2}$, at $x = (\beta e)^{-1/2}$. The maximum crosswind distance for any concentration contour lies on the line $y = x\sqrt{\alpha}$. The area bounded by the contour $\chi = \chi_c$ represents the region within which moths respond to the source. We shall denote the line, $y = 0$, as the mean wind axis.

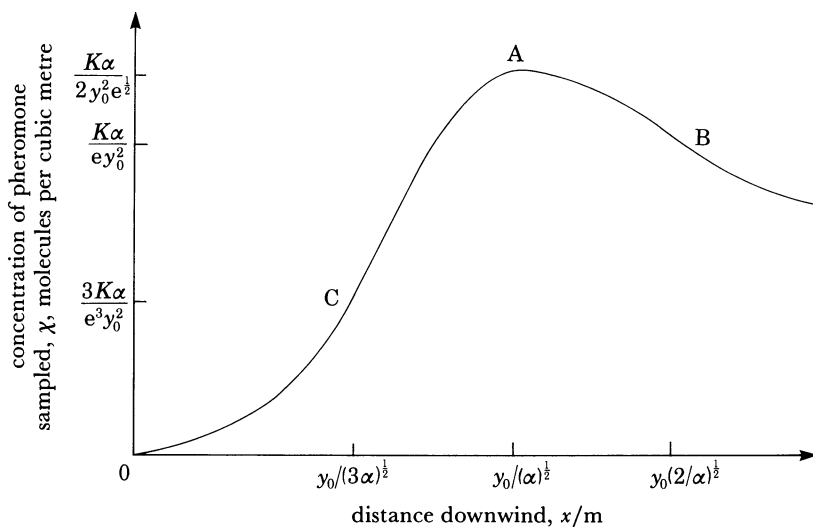


FIGURE 4. Sketch of the assumed concentration sampled by an imaginary moth flying up (mean) wind through a crop to a single source located at $(0, 0)$. The initial downwind and crosswind coordinates of the moth are assumed to be (x_0, y_0) . Its path is assumed to follow line $y = y_0$, parallel to the mean wind axis and not directly towards the source. The position on the curve corresponding to the initial position of the moth depends on the relationship between x_0 and y_0 . As it flies up (mean) wind its x coordinate decreases and it traverses the curve from right to left. The concentration curve has points of inflexion corresponding to maximum rates of increase (B) and decline (C) in concentration. The moth experiences a maximum of concentration at position A. Concentration declines because the path of the moth by-passes the source and before reaching $x = 0$ the concentration sampled will fall below the threshold for response, χ_c .

The size and shape of the threshold contour are determined in this model by the values of the two parameters β and α , respectively. The range of attraction is given by the maximum downwind distance of the threshold contour from the source. This is equal to $\beta^{-1/2}$, so, for example, a value of $\beta = 10^{-6}$ (m^{-2}) implies a range of attraction of 1000 m. The area enclosed by the threshold contour is inversely proportional to β . For example, if β is halved the area enclosed is doubled, or if the range of attraction is doubled the area enclosed is quadrupled. The value of β is related to the relative potency of the pheromone concerned (but see Baker & Roelofs (1981)). The value of α is related to the relative crosswind spread of pheromone. Where the threshold contour is furthest from the line $y = 0$, the ratio of its distance from that line to its distance downwind from the source is equal to $\alpha^{1/2}$. The ratio of the maximum width to the maximum length of the threshold contour is about $1.2(\alpha)^{1/2}$. For example, when $\alpha = 0.82$ this ratio is unity and when $\alpha = 1.3$ it is around 1.4. Relatively small values of α therefore result in relatively long, thin contours.

MODEL FOR PEA MOTH FLIGHT

Consider an average moth of the population, initially at position (x_0, y_0) , within the area bounded by $\chi = \chi_c$, and such that $y_0 > \nu$. Assume that the moth responds and flies up (instantaneous) wind (see §3*d*) and that its resultant path is up (mean) wind, along the line $y = y_0$ (constant), parallel to the mean wind axis and not directly towards the source, with x decreasing from x_0 . Equation (4), with $y = y_0$, gives the concentration sampled by such a moth at any position, x , as it flies along this path:

$$\chi = K/x^2 \exp(-(y_0^2)/(\alpha x^2)), \quad x \leq x_0. \quad (6)$$

TABLE 1. CONCENTRATION 'EVENTS' EXPERIENCED BY MOTH FLYING UPWIND

event	condition for event to be experienced	concentration, if event experienced	event experienced at position
maximum rate of increase of concentration	$x_0 \geq y_0(2/\alpha)^{\frac{1}{2}}$	$\frac{K\alpha}{2y_0^2 e^{\frac{1}{2}}}$	$([2/\alpha]^{\frac{1}{2}}y_0, y_0)$
maximum of concentration	$x_0 \geq y_0(\alpha)^{\frac{1}{2}}$	$\frac{K\alpha}{y_0^2 e}$	$(y_0/[\alpha^{\frac{1}{2}}], y_0)$
maximum rate of decline of concentration	$x_0 \geq y_0/[3\alpha]^{\frac{1}{2}}$ and $y_0 \leq [3\alpha/e^3\beta]^{\frac{1}{2}}$	$\frac{3K\alpha}{e^3 y_0^2}$	$(y_0/[3\alpha]^{\frac{1}{2}}, y_0)$

Equation (6) indicates how the concentration sampled changes as x decreases. This is sketched in figure 4. The position on the figure from which the moth starts depends on the relationship between x_0 and y_0 . The moth flies upwind, that is from right to left in the figure. The concentration curve has a maximum (A, figure 4), and also two points of inflexion, corresponding to maximum rates of increase (B, figure 4) and decline (C, figure 4) in concentration. How many of these 'events' the moth experiences depends on its initial position (x_0, y_0) (table 1 and cf. fig. 2 of Wall & Perry (1982)). The concentration experienced declines because the moth is assumed to fly on a path that by-passes the source, indeed the concentration experienced will fall below the threshold for response, χ_c , at some value of x as $x \rightarrow 0$. When this occurs the moth is assumed to cease upwind flight. This may occur before the maximum rate of decline of concentration has been experienced.

(c) *Single source, cues for cessation of upwind flight*

As discussed in §3*d* a strategy of upwind flight alone will not be sufficient to locate the source unless $y_0 < \nu$. Some cue is required to cease upwind flight and adopt a different strategy. In the model of David *et al.* (1982) the cue is loss of the discrete plume, whereupon the moth commences casting. In this crop model the cue could conceivably be any of the events listed in table 1, or the event of an encounter with the threshold contour. We have adopted the latter as the cue for cessation of upwind flight. This always occurs whatever value of (x_0, y_0) is chosen, it is analogous to the choice of David *et al.* (1982) and it is an 'on-off' mechanism that is mathematically tractable. The use of a different, or multiple cues to reflect changing response thresholds is not considered here.

(d) Multiple sources

The concentration at a position downwind of several sources, emitting simultaneously, is simply the sum of the concentrations computed for each source singly. We shall restrict our discussion to the case for which we have data: a line of several, say i , sources, equally spaced a distance, s , say, apart, and aligned along the mean wind direction. The extreme upwind trap has position $(0, 0)$, the other traps have positions $(s, 0) \dots ([i-1]s, 0)$. The concentration, χ , at position (x, y) downwind of such a line of sources is:

$$\chi = K \sum_{j=0}^{i-1} \frac{\exp \{-y^2/[\alpha(x-j s)^2]\}}{(x-j s)^2}, \quad x > (i-1)s,$$

and there is now no explicit solution for y given x (cf. (4)). Such an explicit solution is not strictly necessary, but it is useful to enable a sketch of the threshold to be made. Also, computing (see §6) is less practicable without an explicit solution. Future models might adopt a stochastic approach or use contouring routines, but in this paper we shall use a simple approximation to obtain an explicit solution.

For most of our data $s \ll \beta^{-\frac{1}{2}}$ (range of attraction). Generally $s \approx 25\text{--}50$ m, whereas we estimate $\beta^{-\frac{1}{2}}$ to be approximately 1000 m. Under these conditions we approximate the concentration at a given position downwind of the i sources, whose coordinates are $(0, 0) \dots ([i-1]s, 0)$, by that from one source with strength i times that of a single source, and coordinates $([i-1]s/2, 0)$. So

$$\chi \approx \frac{iK \exp \{-y^2/(\alpha[x - (i-1)s/2]^2)\}}{\{x - [(i-1)s/2]\}^2}, \quad x > (i-1)s, \quad (7)$$

and there is now an explicit solution for y given x . The threshold contour has identical shape to that shown in figure 3, but a different size. The range of attraction is now $([i-1]s/2) + (i/\beta)^{\frac{1}{2}}$; the maximum crosswind distance is at position $([i-1]s/2 + (i/\beta e)^{\frac{1}{2}}, (i\alpha/\beta e)^{\frac{1}{2}})$; the area enclosed by the threshold contour is approximately i times that for a single source. The approximation is generally quite good and is best for relatively large values of x .

For $x \leq (i-1)s$ the natural choice would be simply to extend the above approximation, so that for $(j-1)s < x \leq js$ we might approximate the j sources upwind of any given position by a single source of strength j at $(j-1)s/2$. Continuity conditions for the threshold contour necessitate a small modification. Hence for $(j-1)s < x \leq js$ we approximate the threshold contour by a sequence of straight lines joining $([j-1]s, y_{j-1})$ and (js, y_j) , where:

$$y_j^2 = -\frac{\alpha j^2 s^2}{4} \ln \left\{ \frac{\beta j^2 s^2}{4(j+1)} \right\} \quad \text{and} \quad y_0 = 0. \quad (8)$$

For example, the vertex of the concentration contour at $j = 1$, $x = s$ corresponds to the concentration expected from a source of double the usual strength at $(s/2, 0)$. Its crosswind distance is given by $y_1^2 = -(\alpha s^2/4) \ln \{\beta s^2/8\}$. The threshold contour may now be sketched for multiple sources; an example is given in figure 5 for $i = 4$ sources. All values on the threshold contour are known explicitly except for values of $x > (i-1)s$ given y , these may easily be found using Newton–Raphson techniques. Note the successive widening of the contour as j and x increase.

The model is quite robust to deviations from the assumptions made for multiple sources. We require only qualitative accuracy concerning the shape of the threshold contour. Turbulence and variable response thresholds in moths render very accurate determination of the threshold contour meaningless.

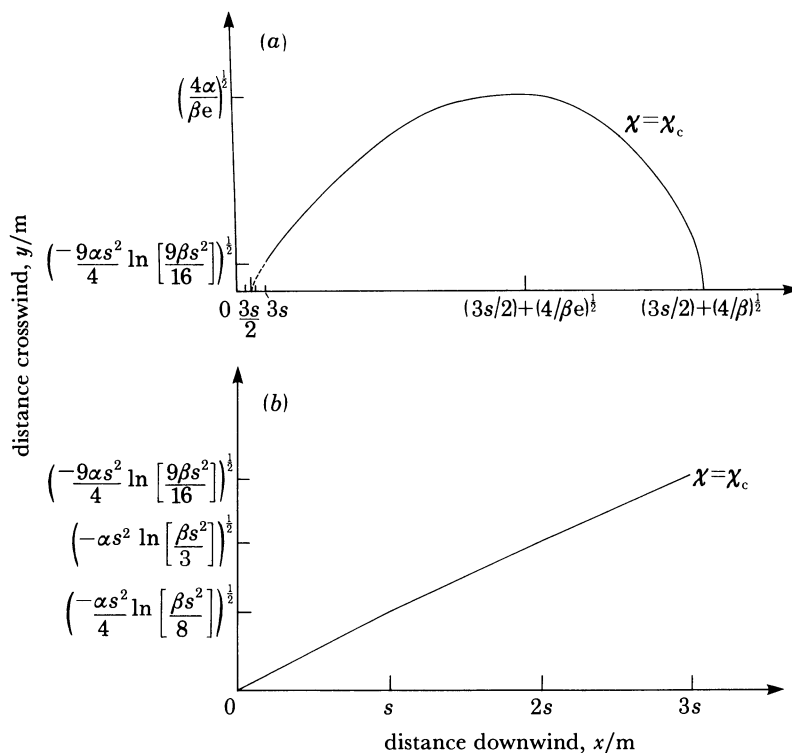


FIGURE 5. (a) Sketch of the threshold contour, $\chi = \chi_c$ molecules per cubic metre, for $i = 4$ sources and for $x > 3s$, viewed from above a crop. The pheromone sources are located at $(0, 0)$, $(s, 0)$, $(2s, 0)$ and $(3s, 0)$. The value of α used is 0.5. A larger value than usual is used for s to accommodate all of the contour on one figure. The threshold contour (bold line) is approximated by that expected from one source with strength four times that of a single source, positioned at $(3s/2, 0)$. The contour is sketched using (7). The maximum crosswind and downwind extents of the contour are indicated. The shape is identical to that of figure 3. (b) The threshold contour, with conditions as in (a), above, is shown for $x < 3s$. The contour is approximated by three straight lines given by (8). The approximation follows the same principle as that in (a), above, although a slight modification is required to ensure the contour is continuous. Note that the contour is continuous between figure 5a and b, because (7) and (8) give a common y coordinate when $x = 3s$.

5. THE MODEL

(a) Basic assumptions

Some basic assumptions on which the model is based have already been discussed. They are brought together here for convenience. 'Source' and 'trap' are now synonymous.

(i) The model refers to the average behaviour of a population of male moths, hereafter called 'moths'.

(ii) For all positions downwind of the extreme upwind trap, and not within a distance, ν , of any trap, the concentration of pheromone sampled instantaneously by responding moths is given by (6), (7) or (8).

(iii) The resultant movement (in the horizontal plane) of responding moths within the area

bounded by the threshold contour of concentration is up (mean) wind unless they are caught by a trap or encounter the threshold contour.

(iv) Moths may be caught if they pass within a distance, ν , of a trap, from the downwind side of the trap. A discrete plume is assumed to exist in this region.

(v) Moths which encounter the threshold contour immediately stop. They then cast and their resultant movement is in a cross (mean) wind direction.

(vi) Moths initially outside the area bounded by the threshold contour fly in random directions. Moths that finish casting outside the contour then fly in random directions.

(vii) Before siting the traps, moths inside the area bounded by the future position of the threshold contour are distributed uniformly in space.

(viii) For a line of traps, the inter-trap spacing is substantially smaller than the range of attraction of a single trap.

Further details are given in subsequent sub-sections. Since there is symmetry about the mean wind axis ($y = 0$) we consider only the region with positive y -values.

(b) Inner zones

The area bounded by the upwind and downwind ends of the threshold contour, the mean wind axis ($y = 0$) and the line $y = \nu$ is termed the inner zone. The inner zone may be subdivided according to which trap's discrete plume may be first encountered by moths flying upwind from positions within it. For example, when $i = 3$, the rectangular part of the inner zone between traps 2 and 3, that is, the region ($s \leq x < 2s, 0 \leq y \leq \nu$), is the inner zone of the centre trap ($j = 2$). The inner zone of the extreme downwind trap is always the largest. Simulated moths in the inner zone of trap j ($j \neq 1$) are assumed to be caught by trap j , with probability $1 - \Pi_u$, or to fly on upwind into the inner zone of trap $j-1$, with probability Π_u . This 'upwind escape' is designed to model the possibility that a real moth may not encounter, or having encountered may subsequently lose, the discrete plume from trap j , while remaining stimulated by pheromone from traps $1 \dots j-1$. Such a moth may fly on upwind rather than adopt the change in behaviour and characteristic slow, hovering, flight which usually accompanies very close approach to a source. Simulated moths in the inner zone of the extreme upwind trap ($j = 1$) are assumed to be caught always by that trap, despite the results of Wall & Perry (1981) who showed that in practice the efficiency of triangular sticky traps containing 100 μg (E, E)-8,10-dodecadien-1-yl acetate on rubber is $\approx 37\%$. No effect of trap position in the line (j) on this efficiency was found. Trap efficiency is not modelled here because we are primarily interested in predicted ratios of catches in different traps, rather than in absolute numbers.

Simulated moths may be in the inner zone initially, or may enter it through crosswind flight. Once in the inner zone it is assumed a moth will be caught inevitably.

The value of Π_u is unlikely to be large. Wall & Perry (1978) observed a line of three traps closely; the large upwind trap catch could not be explained by the relatively few moths that approached very close to other traps then flew past them and on upwind.

For simplicity ν was assumed constant for all traps. There are arguments that ν may increase or decrease with j . For $y = \nu$ (constant), χ decreases strictly with decreasing x for $x \leq (i-1)s$. To ensure an equal concentration at position ($[j-1]s, \nu$) for each trap, j , would require ν to increase with j . By contrast, real moths may alter their upwind flight behaviour because of the ratio of discrete plume concentration to background concentration, rather than in response to any particular absolute value of concentration (Sanders 1982). In that case, a decreasing function of $\nu(j)$ would be required. Little evidence exists for choice at present.

A crucial aspect in the performance of the model is that the distance between the threshold contour and the inner zone of trap j , decreases with j . This, combined with the large inner zone of the extreme downwind trap, enables the model to reflect the wide range of trap catch proportions encountered in field data.

(c) *Behaviour at threshold contour*

Casting to and fro across the wind close to a source is common in many species (David *et al.* 1982), but has never been observed in pea moth closer than 15 m to a trap. In a recent mark–release experiment (Wall & Perry 1984) male pea moth occasionally cast above the crop after release about 500 m from the source. In the same experiment crosswind flight without changes in direction was frequently observed after release, often followed by upwind flight. Distances moved during these observed, single, crosswind casts were up to 30 m; crosswind flight for longer distances may have occurred but have been obscured by the vegetation. Thus, some observed crosswind flights may have been part of wider casts, not seen in full either because moths were lost to sight or because the cast was interrupted by the onset of pheromone stimulation. These observations were made after moths were released following about 48 h captivity and 24 h after mild anaesthetic with CO₂. However, in experiments on wild individuals during 1983, casting to and fro was observed about 20 m from a source on seven separate occasions and single crosswind casts were fairly frequent.

Under the assumptions of this model, a simulated moth encountering the threshold contour from within receives no information from the instantaneous direction of the wind concerning in which crosswind direction the mean wind axis lies, so it is equiprobable that the initial leg of its simulated cast is towards or away from the mean wind axis. We assume the probability that the resultant direction of movement of simulated moths is crosswind away from the mean wind axis (y increasing) to be Π_1 . Such moths finish casting in an area in which the concentration $\chi < \chi_c$, the threshold for response, and are assumed not to respond further. These moths are then treated as indistinguishable from those outside the threshold contour that fly randomly (see §5*d*) (moth A, figure 6).

Those simulated moths whose resultant direction of movement is crosswind towards the mean wind axis (y decreasing) are assumed to move a variable distance. Their net distance moved, d , is assumed to have some probability density function, such that the probability of small values of d is relatively large and of large values of d relatively small. An exponential distribution with parameter γ , say, satisfies this condition. Hence the probability of moth B (figure 6) moving crosswind a net distance between d_1 and d_2 is $(1 - \Pi_1) (e^{-\gamma d_1} - e^{-\gamma d_2})$.

Simulated moths may move so far net crosswind that they enter the inner zone. Moth C (figure 6), distance d_3 away from the inner zone at $y = \nu$, has probability $(1 - \Pi_1) e^{-\gamma d_3}$ of moving at least this distance, into the inner zone. If such a moth flies a net crosswind distance greater than $(d_3 + \nu)$ it is assumed to remain in the inner zone, not to fly on through it. The mean net crosswind distance flown is γ^{-1} and the median is approximately $0.7 \gamma^{-1}$ (γ has units of per metre).

After a simulated moth has flown the particular net distance crosswind towards the mean wind axis it is assumed to resume upwind flight immediately. Unless such moths have flown into the inner zone they will encounter the threshold contour once again (moth D, figure 6). Net motion is therefore diagonal to the mean wind axis. The crosswind distance moved on each encounter is assumed to be independent of distances moved on previous encounters. Such moths

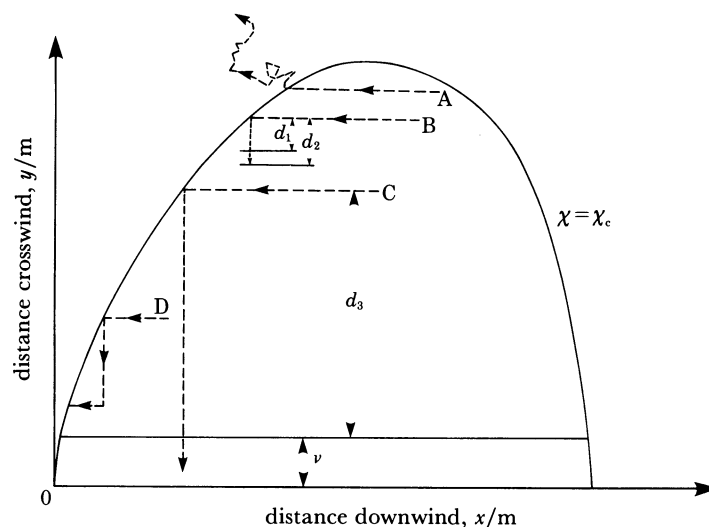


FIGURE 6. Description of assumed net movement of simulated moths which encounter the threshold contour, $\chi = \chi_c$ molecules per cubic metre, after flying up (mean) wind. After casting moth A has moved a net distance crosswind away from the mean wind axis ($y = 0$), with probability Π_1 , into an area in which pheromone concentration is below the threshold for response ($\chi < \chi_c$), and is then assumed to fly randomly. After casting moth B has moved a net distance crosswind towards the mean wind axis, with probability $1 - \Pi_1$. The net distance it moves is given by an exponential distribution with parameter γ , thus it has a relatively large probability of moving only a small distance. The probability that moth B moves a net distance between d_1 and d_2 closer to the mean wind axis is thus $(1 - \Pi_1) (e^{-\gamma d_1} - e^{-\gamma d_2})$. After casting moth C has moved into the inner zone, a net distance crosswind of at least d_3 , with probability $(1 - \Pi_1) e^{-\gamma d_3}$. After resuming upwind flight, moth C will be subsequently caught by a trap. It cannot encounter the threshold contour again. By contrast, moth D encounters the threshold contour, casts, moves crosswind towards the mean wind axis a certain net distance, resumes upwind flight and encounters the threshold contour for a second time. Moth D may subsequently encounter the threshold contour several more times; its net motion is diagonal to the mean wind axis. The units of γ are per metre.

which encounter it several times are not ‘following’ the threshold contour; in random walk terminology (Cox & Miller 1965) the contour is a reflecting barrier, and the inner zone is an absorbing barrier. All moths modelled eventually either cross the threshold contour after finishing casting or enter the inner zone of one of the traps. The probability of the latter depends on the moth’s initial crosswind position, y_0 , on Π_1 , and on γ . For large γ moths encounter the threshold contour relatively often. If such moths do not cross the contour after finishing casting on any of, say, m occasions the net crosswind distance moved has a Gamma distribution with parameters m and γ . The probability of this occurring is $(1 - \Pi_1)^m$, which decreases rapidly with m . For example, if $\Pi_1 = 0.6$ and $m = 5$, $1 - \Pi_1 = 0.4$ but $(1 - \Pi_1)^m \approx 0.01$. In simulations of the model with reasonable parameter values and $\Pi_1 = 0.5$, fewer than 5% of moths initially responding may enter the inner zone. We believe this reflects field situations well.

• (d) *Random flight outside the threshold contour*

Real moths, in regions of sufficiently low concentration may be active but not responding to pheromone from the traps. There are extensive observations of pea moth engaging in such behaviour. Some moths observed may have been females, but the proportion of females engaging in such flight is likely to be very small (J. C. Graham, unpublished data). We have never observed any systematic directional drift in flight, which always appears random in direction. Observers in control and treatment areas of experiments described by Wall & Perry

(1983) never reported directional flight in non-responding moths. Such downwind drift is not the cause of large catches in the extreme upwind of a line of interacting traps; Wall & Perry (1981) demonstrated that interactions occurred between traps when the attractant (E)-10-dodecen-1-yl acetate was used, but there was no difference between the catch in the upwind, centre or downwind traps. Pea moth is known to aggregate in the headlands around emergence sites and in the middle of fields, but no systematic preference with respect to wind direction can be shown (J. C. Graham, unpublished).

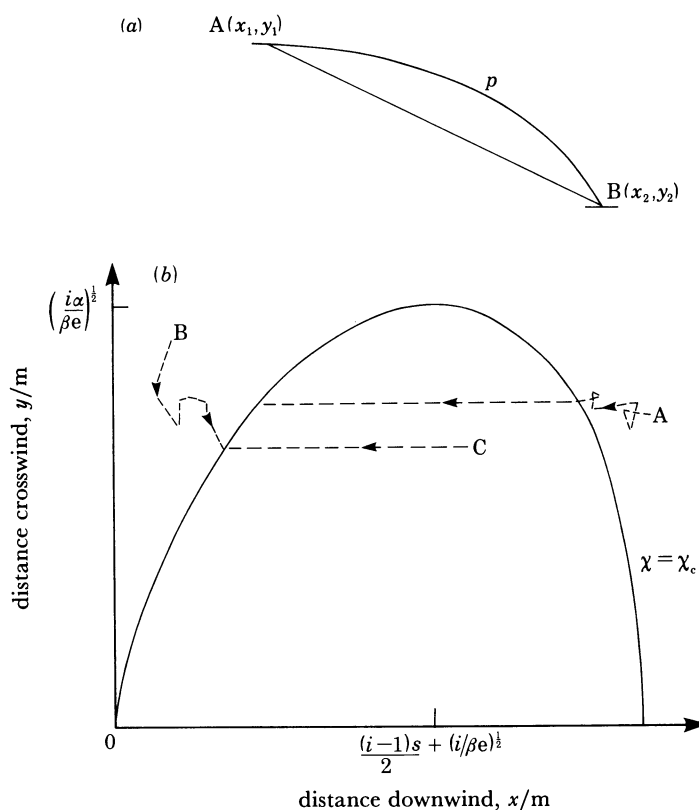


FIGURE 7. (a) A small element of the threshold contour, $\chi = \chi_c$ molecules per cubic metre, between A (x_1, y_1) and B (x_2, y_2) , with length p approximated by the length of the straight line AB, which is $[(x_1 - x_2)^2 + (y_1 - y_2)^2]^{1/2}$. (b) Description of assumed behaviour of a randomly flying simulated moth which flies inside the threshold contour, $\chi = \chi_c$, by chance. For several, i , sources the maximum crosswind extent of the contour occurs when $x = [(i-1)s/2] + (i/\beta e)^{1/2}$. Moth A crosses the contour where $x > [(i-1)s/2] + (i/\beta e)^{1/2}$ and is assumed to behave identically to a moth initially inside the contour, that is, it flies upwind until it encounters the threshold contour. Moth B crosses the threshold contour where $x < [(i-1)s/2] + (i/\beta e)^{1/2}$ and is assumed to behave identically to moth C, which encounters the same position on the contour after flying upwind from a position inside it. Each moth casts and moves a net distance crosswind, either out of the area bounded by the threshold contour or towards the mean wind axis ($y = 0$).

The model allows a simulated moth flying randomly outside the threshold contour to cross to its interior, and assumes it then responds in the same way as one initially inside. Hence such a moth may subsequently be caught in a trap (Cardé 1979). There is evidence that this occurs extensively for pea moth. Real moths are caught by a trap throughout a far longer period (afternoon) than is required by responding moths to reach a trap, even from hundreds of metres away. Additionally, we have never had any indication that running a trap over several successive days has reduced the number of moths in the area.

To estimate accurately the number of moths, say M , crossing the threshold contour requires knowledge of the average values of the velocity of random flight and the distance moved before a change in direction, and the length of time the trap is operating. Consider a small element AB of the threshold contour (figure 7a) between A(x_1, y_1) and B(x_2, y_2), with length p , say. We assume that m simulated moths enter through AB and denote the total perimeter of the threshold contour by P , then the assumption of random flight implies $E[m] = Mp/P$.

Now

$$p = \int_{x_1}^{x_2} \left\{ \frac{-\alpha}{\ln(\beta x^2)} + (1-2\alpha) - \alpha \ln(\beta x^2) \right\}^{\frac{1}{2}} dx,$$

which has no explicit solution. We therefore approximate AB by a straight line and

$$p \approx \sqrt{[(x_2 - x_1)^2 + (y_2 - y_1)^2]}. \quad (9)$$

The value of P is found by splitting the entire threshold contour into similar small elements and summing them. Hence m may be found if M is given. The value M is not input explicitly but is expressed in the model through N , the total number of moths initially assumed to be inside the threshold contour, and λ , where $\lambda = M/N$. Therefore

$$E[m] = \lambda N p / P. \quad (10)$$

Hence λ is the average number of moths crossing the threshold contour from outside, expressed as a proportion of the number initially present inside. Note that λ may be larger than unity. Model outcomes seem not very sensitive to changes in λ within the range $\lambda = 0$ to $\lambda = 1/2$.

Simulated moths crossing inside the threshold contour on its downwind side ($x \geq [i-1]s/2 + [i/\beta e]^{\frac{1}{2}}$) (moth A, figure 7b) are assumed to fly upwind as previously described. Those crossing the contour on its upwind side ($x < [i-1]s/2 + [i/\beta e]^{\frac{1}{2}}$) (moth B, figure 7b) are assumed to behave exactly as they would if they had encountered the threshold contour by flying upwind (moth C, figure 7b) (see §5c), that is, they cast and move a net distance crosswind, either out of, or further into the area bounded by the threshold contour.

No record is kept in the model of the coordinates of any moth outside the threshold contour. These moths are merely assumed to make up a population each of which independently moves in a simple random walk with the threshold contour as an absorbing barrier.

This argument emphasizes the difficulty in defining the area from which actual moths are caught. Bossert & Wilson (1963) defined the volume within which moths respond as the 'active space'. For successive positions of an instantaneous plume the boundary of the active space is not constant in time. For our crop model it is, and that boundary is the threshold contour. Wall & Perry (1978) attempted to include the initial positions of randomly flying moths, which crossed the threshold contour and subsequently were caught, in their definition of a 'trapping zone'. This definition was unclear with respect to the concepts discussed in this section and requires revision.

(e) Techniques

This section seeks to explain how the various facets previously discussed are integrated into a coherent working model. We are concerned with the average behaviour of a moth population, therefore the probability assigned to an individual moth of behaving in a certain way is synonymous with the proportion of the population that behave in that way.

Insects generally have spatially aggregated populations (Taylor *et al.* 1978; Perry *et al.* 1980; Perry 1981). However, since the initial aggregation (before the traps are operating) is not systematically related to the positions of the traps, there is no advantage to building it into

the model, although it should be allowed for in interpreting the data. Additionally, s is small, so the model should be fairly robust to deviations from the assumption that, before siting the traps, moths are distributed uniformly. Hence, aside from a scaling factor relating to the population density, moth number is equivalent to crop area. For a single trap, the area, $A(x_1, x_2)$ bounded by the mean wind axis ($y = 0$), the threshold contour and two arbitrary x -values, x_1 and x_2 , (figure 8) may easily be calculated.

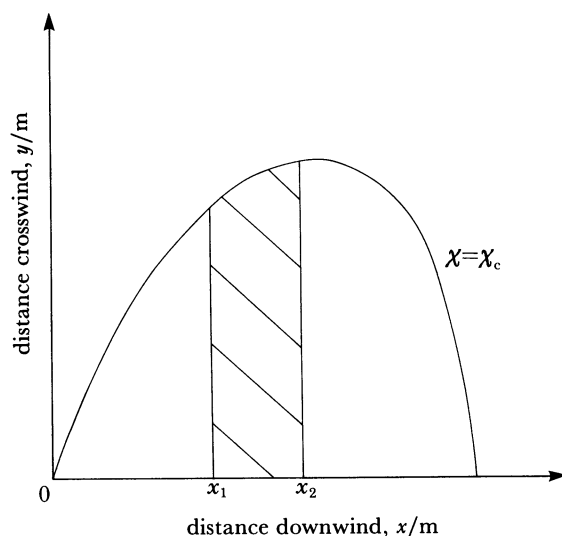


FIGURE 8. The shaded region represents $A(x_1, x_2)$, the area bounded by the mean wind axis ($y = 0$), the threshold contour $\chi = \chi_c$ molecules per cubic metre, and the lines $x = x_1$, $x = x_2$.

$$A(x_1, x_2) = \int_{x_1}^{x_2} \{-\alpha x^2 \ln(\beta x^2)\}^{\frac{1}{2}} dx.$$

Put $u^2 = -\ln(\beta x^2)$ and let $u_1^2 = -\ln(\beta x_1^2)$, $u_2^2 = -\ln(\beta x_2^2)$, then

$$A(x_1, x_2) = -\beta^{-1} \sqrt{\alpha} \int_{u_1}^{u_2} u^2 e^{-u^2} du.$$

The normal probability integral is usually written:

$$\phi(y) = \int_{-\infty}^y e^{-y^2/2} dy.$$

Integration by parts then gives

$$A(x_1, x_2) = \frac{\sqrt{\alpha}}{2\beta} \{u_1 e^{-u_1^2} - u_2 e^{-u_2^2} - \pi^{\frac{1}{2}} \phi(u_1 \sqrt{2}) + \pi^{\frac{1}{2}} \phi(u_2 \sqrt{2})\}. \quad (11)$$

Values of ϕ are widely tabulated and available as standard functions in many computer programs, so $A(x_1, x_2)$ may be computed easily. Other areas required may be derived using (11). Results for multiple sources follow easily. Since the data usually involves ratios of catches, rather than absolute numbers, a scaling factor is rarely needed.

Because of the complex procedures discussed in §5c no explicit solution is possible for the number of simulated moths that finally occupy the inner zones of each particular trap. Hence the solution is obtained numerically, using a semi-stochastic approach. To achieve this the area bounded by the threshold contour and the line $y = \nu$ (that is, not including the inner zone,

figure 9) is subdivided into narrow strips, of width w , whose long edges are parallel to the mean wind axis. The short edges comprise small elements of the threshold contour conforming to the approximation required in §5*d*. Each strip is then considered separately, but to allow moth movement into, out of and between strips a coherent temporal ordering is required for movement. This is available, since simulated moths never move from a given strip to one further from the mean wind axis. Hence strips are considered consecutively, starting with that furthest from the mean wind axis.

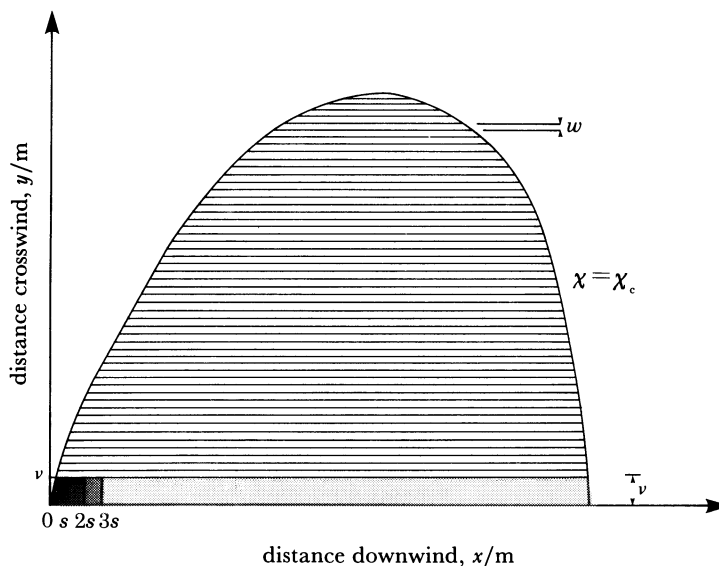


FIGURE 9. The lower part of this figure indicates the inner zone of each of four traps. The area bounded by the threshold contour, $\chi = \chi_c$ molecules per cubic metre, excluding the inner zone is subdivided into small strips of width w , parallel to the mean wind axis ($y = 0$). The length of the upwind and downwind edges of each strip is approximated by (9) and the area of each strip is found using Newton–Raphson techniques and (11). Note that the assumptions of the model preclude simulated moth movement from any given strip to one further from the mean wind axis.

The following procedure is adopted.

Step 1. The area of the inner zone of each trap, say $A_I(j)$ is calculated, and the number of moths in each inner zone, denoted $I(j)$, computed as $cA_I(j)$, where c is a scaling factor. The area of each strip $A(k)$, $k = 1 \dots n_s$, and the number of moths within it, denoted $S(k)$, are computed similarly, using (11). The total number of moths, N , initially inside the threshold contour is computed as:

$$N = \sum_{j=1}^i I(j) + \sum_{k=1}^{n_s} S(k).$$

Step 2. The perimeter of the upwind edge of each strip, say $p_u(k)$, and that of the downwind edge, $p_d(k)$, are computed using the approximation given in (9). The perimeter of the threshold contour bounding the inner zone of the extreme upwind trap, p_1 , and the perimeter of the threshold contour bounding the inner zone of the extreme downwind trap, p_i , are computed similarly. The total perimeter of the threshold contour, P , is approximated as:

$$P = p_1 + p_i + \sum_{k=1}^{n_s} \{p_u(k) + p_d(k)\}.$$

Step 3. For each element of the threshold contour involved in step 2 the number of moths entering owing to random flight are calculated using (10), and each of the values of $S(k)$ and $I(j)$ updated to $S^*(k)$ and $I^*(j)$ by computing:

$$S^*(k) = S(k) + \frac{\lambda N}{P} \{p_u(k) + p_d(k)\}, \quad I^*(1) = I(1) + \frac{\lambda N}{P} p_1 \quad \text{and} \quad I^*(i) = I(i) + \frac{\lambda N}{P} p_i.$$

Note that for most values of β , ν and α commonly used, only the inner zone of the extreme upwind and extreme downwind traps have a boundary which is an element of the threshold contour, so $I^*(j) = I(j)$ for $j = 2 \dots (i-1)$. Now we consider successive strips, k , starting with $k = 1$, the furthest strip from the mean wind axis. Put $k = 1$.

Step 4. $S(k)$ is replaced by $S^*(k)$, for all $k = 1 \dots n_s$, and $I(j)$ by $I^*(j)$, for all $j = 1 \dots i$.

Step 5. The number of moths in the current strip that encounter the threshold contour and fly crosswind a net distance towards the mean wind axis is computed as $(1 - \Pi_1) S(k)$. Of these, the number flying into strip t , where $t = (k+1) \dots n_s$ is computed as

$$(1 - \Pi_1) S(k) \{e^{-\gamma w(t-k-1)} - e^{-\gamma w(t-k)}\},$$

and the number flying into the inner zone as $(1 - \Pi_1) S(k) e^{-\gamma w(n_s-k)}$. If the minimum x -value on the upwind edge of the current strip is denoted as x^* then the appropriate inner zone will belong to trap j^* , where $j^* = \text{Int} [x^*/s] + 1$ for $x^* < (i-1)s$, and $j^* = i$ otherwise. The remaining number of moths in the current strip area, $\Pi_1 S(k)$, represents those which finish their casts on the outside of the threshold contour and are not subsequently caught by a trap. The numbers of moths in strips and inner zones are then updated to $S^*(t)$, $t = (k+1) \dots n_s$, and $I^*(j)$ by computing:

Step 6.

$$\begin{aligned} S^*(t) &= S(t) + (1 - \Pi_1) S(k) \{e^{-\gamma w(t-k-1)} - e^{-\gamma w(t-k)}\}, \quad t = (k+1) \dots n_s, \\ S^*(k) &= 0, \\ I^*(j^*) &= I(j^*) + (1 - \Pi_1) S(k) e^{-\gamma w(n_s-k)}, \end{aligned}$$

and

$$I^*(j) = I(j), \quad j \neq j^*.$$

The value of k is increased by one, and we return to step 4, unless the value of k has now reached $n_s + 1$.

Step 7. Replace $I(j)$ by $I^*(j)$, for all $j = 1 \dots i$. The effect of steps 4–7 is to redistribute all moths in the strips either to the area outside the threshold contour or among each of the inner zones of the i traps. These moths do not leave the inner zones without being caught by a trap as detailed in §5*b*. The number of moths caught by each trap, $T(j)$, $j = 1 \dots i$, is computed from:

Step 8.

$$\begin{aligned} T(j) &= (1 - \Pi_u) \sum_{q=j}^i \Pi_u^{q-j} I(q), \quad j = 2 \dots i, \\ T(1) &= \sum_{q=1}^i \Pi_u^{q-1} I(q). \end{aligned}$$

The total catch for the line of traps is $\sum_{j=1}^i T(j)$. We are usually interested in the proportion of this total caught by any trap, j , which is $T(j)/\sum_{j=1}^i T(j)$. Note that this proportion is independent of the scale factor c . This completes the description of the techniques used in the model.

6. PARAMETERS AND COMPUTING

The model has ten parameters: α , β , γ , ν , λ , Π_u , Π_1 , w , i , s . The last two merely fix the configuration of the traps and are constant for a given set of data. Changes in w merely affect the accuracy of model predictions, in practice w is set small enough to give accurate results but not so small that computer time is wasted. A workable compromise is given by setting $w = 1/\gamma$. The seven remaining parameters determine the model outcome; α is determined solely on micrometeorological grounds and β , γ , ν , λ , Π_u and Π_1 are governed by different aspects of moth flight behaviour. If only relative proportions, $T(j)/\sum_{j=1}^i T(j)$, of the total catch for

TABLE 2. LIKELY RANGES FOR PARAMETER VALUES

parameter	description	typical value	likely range	strength of evidence
α	measures relative extent of crosswind spread of pheromone; governs shape of threshold contour, for example $\alpha = 1.3$ implies contour is almost half as wide again as it is long.	1.3	0.1–1.5	fairly strong
β/m^{-2}	measures relative potency of pheromone; governs size of threshold contour; β is the reciprocal of the square of the range of attraction.	10^{-6} (m^{-2})	10^{-7} – 10^{-5} (m^{-2})	strong
γ/m^{-1}	parameter of the exponential probability density function governing the net crosswind distance moved by a moth encountering the threshold contour; for example $\gamma = 0.03 \text{ m}^{-1}$ implies 50% of moths move less than 23 m and the mean distance moved is 33 m.	0.03 (m^{-1})	0.01–0.5 (m^{-1})	fair
ν/m	measures the mean distance from a trap within which a discrete plume is effective; ν is width of inner zone; moths passing within ν metres of a trap may be caught, moths passing at greater distances cannot.	10 (m)	5–10 (m)	fairly strong
λ	measures relative activity of non-responding randomly flying moths; represents the number of moths entering the threshold contour, expressed as a proportion of those initially inside.	0.5	> 0	fair
Π_u	measures probability that a moth may pass close to one of the downwind traps ($j = 2 \dots i$) without being caught and continue upwind to the next trap; represents chance of moth not encountering, or losing, the discrete plume.	0.1	0.0–0.2	fairly strong
Π_1	measures probability that a moth may fly upwind, encounter the threshold contour, finish casting outside it (further from the mean wind axis), where the concentration is below the threshold for response, and fly randomly thereafter, outside the threshold contour.	0.5	0.1–0.8	very weak

a line are of interest then the model is slightly overparametrized. This is because identical outcomes will arise from $\alpha = \alpha_1$, $\nu = \nu_1$, $\gamma = \gamma_1$, as from $\alpha = k^2\alpha_1$, $\nu = k\nu_1$, $\gamma = \gamma_1/k$, when all other parameters are held constant.

The degree of observational evidence for likely values of the seven parameters ranges from strong to very weak. Likely ranges of values are given in table 2. Sometimes inferences may be made from field data when no direct observations are available. Pasquill (1974) and others gave values corresponding to a range of values for α between 0.003 and 0.07, for open country. For a crop these values are likely to be up to 20 times larger (Wilson 1980). On many separate occasions during field experiments moths have been observed approaching close to a trap at an angle subtending up to 60° with the mean wind axis. This occurred from both sides of the mean wind axis ($y > 0$ and $y < 0$) almost simultaneously (Wall & Perry 1978). Such observations are consistent with a value of α of roughly 1.3. The range of attraction, $\beta^{-\frac{1}{2}}$, for pea moth has been shown by mark-recapture experiments (Wall & Perry 1984) to be at least 160 m and stimulation has been demonstrated at 500 m, hence 1000 m has been adopted as a working value, although this will be an underestimate for other species. The value of γ does not imply an amplitude of to and fro casting, since the model allows the single, crosswind casts often observed in pea moth. Low values of γ might be used to represent motion towards the mean wind axis, possibly in response to some cue received before an encounter with the threshold contour (see §4c). Values of ν and Π_u have been chosen from direct observation. It is unlikely that λ is small, except on cool days when it has been observed that moths may respond sufficiently to be caught by pheromone traps even though random flight is minimal; degrees of activity of responding and randomly flying moths are not necessarily associated (Wall & Perry 1982, 1983). The upper bound for λ is unknown. A value of 0.5 for Π_1 might imply a random choice on behalf of a moth at the threshold contour, although other interpretations are possible. By using field data, particularly those concerning the ratio between total catches in separate lines of traps with differing values of i , we may infer that Π_1 usually lies between 0.2 and 0.7.

The program to simulate the model was written using the statistical package Genstat (Alvey *et al.* 1979). The program uses 17 macros and has 809 lines of code. The iterative scheme described in §5e necessitates a relatively large store and time for each run. This could be reduced if the program were converted to FORTRAN.

7. DATA

Data for use with the model concerns catches in a line of traps along the wind. Data from 406 such lines has been collected. In some experiments, which had a latin square design (Perry *et al.* 1980), comparisons were possible between catches in each trap of several separate lines with different values of i . In these experiments traps were left to operate for an entire afternoon before the catch was recorded. In other experiments catches were recorded, simultaneously at each trap, after traps had been running for a known duration. In some of these, catches were recorded at the end of consecutive two- or five-minute replicates, several replicates were therefore collected within an afternoon for each single line of traps, and a more detailed analysis was possible. The data are summarized in table 3. The analysis of much of this data will be published elsewhere and only the main results are summarized here. The only comparable data known for other species is that of Hirano (1976) (see Nakamura 1976a).

TABLE 3. DATA FOR MODEL: NUMBER OF REPLICATES FOR CATCHES OF PEA MOTH IN A LINE OF PHEROMONE TRAPS ALONG THE WIND

type of experiment	i	s	number of replicates	reference
single-line, timed, non-consecutive replicates	3	25	7	Wall & Perry (1978)
	3	50	3	Wall & Perry (1981)
	3	2	4	Perry & Wall (1982)
	3	10	10	
	3	50	4	
	2	25	6	
	2	100	9	Wall & Perry (1980)
	2	150	9	
	2	200	6	
	4	25	4	
	5	25	2	Perry & Wall (1982)
	5	100	2	Wall & Perry (1980)
9	25	2	Perry & Wall (1982)	
single-line, consecutive, two- or five-minute replicates	3	25	213	Perry & Wall (1982, 1983)
	2	100	12	Wall & Perry (1980)
	2	150	14	
	2	200	12	
comparable lines, untimed, complete afternoon replicates	1, 3	25	6	Wall & Perry (1978)
	1, 3	100	4	
comparable lines, untimed, complete afternoon replicates	1, 2, 3	50	4	Wall & Perry (1980)
	1, 2	25, 75, 125, 150, 175, 200	7	

When $i = 3$, data concerning the proportion of the total catch for the line, $T(j)/\sum_{j=1}^3 T(j)$ may conveniently be shown on a barycentric triangle (Gower & Barnett 1971). Figure 10 shows such data from the 42 timed non-consecutive and complete afternoon replicates. The data vary widely between replicates and values of $T(j)/\sum_{j=1}^3 T(j)$, $j = 1 \dots 3$, range from 0.75, 0.17, 0.08 to 0.11, 0.37, 0.52. Generally proportions in the centre trap ($j = 2$) were smaller than those in the upwind ($j = 1$) or downwind ($j = 3$) traps, the mean values being 0.43, 0.25, 0.32. The wide range of proportions obtained on different afternoons were not, however, caused by purely random processes, as shown by the data from the six afternoons on which consecutive catches were recorded. For these data, within an afternoon, the centre trap proportion remained constant. The catch in the other two traps (upwind and downwind) may be considered independently of that in the centre trap. The proportion of the total for these two traps that was caught up in the upwind trap, that is $T(1)/[T(1) + T(3)]$, varied systematically throughout the afternoon, showing noticeable upward or downward trends and autocorrelation through time (Perry & Wall 1984). Similar results were obtained with only two traps ($i = 2$). The proportion of the total catch for the two traps that was caught in the upwind trap, that is $T(1)/[T(1) + T(2)]$, was different for non-consecutive data taken on different occasions, but varied systematically within an afternoon for consecutive replicates (figure 11). These results emphasize that interactions between pheromone traps reflect real, changing, behavioural responses, and are caused by changes in flight behaviour, micrometeorological conditions or both. The model can reflect such results, and details of fits are given in the next section.

For the limited data we have collected so far concerning lines with $i = 4, 5$ or 9 , our results are similar to those of Hirano (1976) with *Spodoptera litura* (F.) and his lines of $i = 4$ and 8 . Proportions in the extreme upwind and downwind traps are roughly equal, and relatively larger than those in the other traps. Examples are given in the next section.

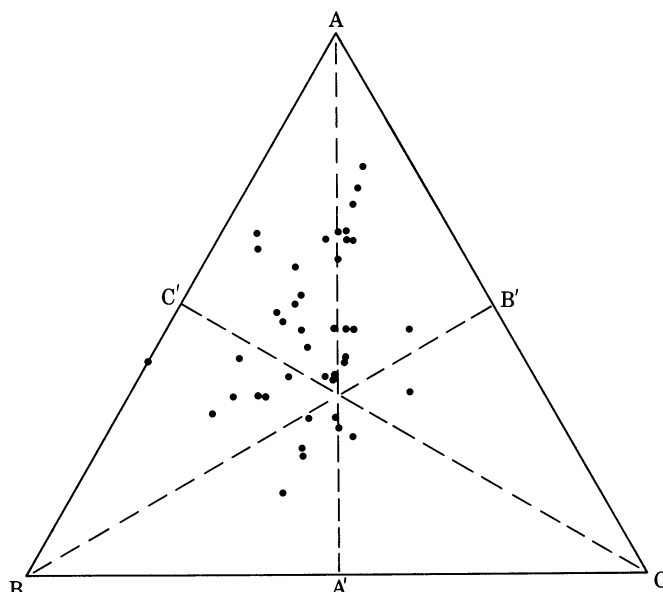


FIGURE 10. A barycentric triangle, representing data concerned with proportions in each of three categories (trinomial data), is an equilateral triangle with each side representing one category (Gower & Barnett 1971). Data points are located so that the ratio of the distances of a point from each side is the same as the ratio of the proportions in the corresponding categories. Here, each data point represents the observed catch of the pea moth *Cydia nigricana* (F.) in a single replicate line of $i = 3$ pheromone traps. The three sides of the triangle BC, AB and AC represent the proportion of the total for the line caught by the upwind, centre and downwind traps respectively. For example, the data point closest to the apex, A, of the triangle represents a replicate in which 0.75 of the total catch was in the upwind trap, 0.17 in the centre trap and 0.08 in the downwind trap. The dashed lines are for reference, for example data points to the left of line AA' represent a greater catch in the downwind than in the centre trap. A data point exactly at C' would represent a zero catch in the centre trap, a data point exactly at C would represent a zero catch in both the upwind and downwind traps. The data here represent replicates well separated in time. A wide range of proportions are demonstrated (data of Wall & Perry (1978, 1980), see table 3.)

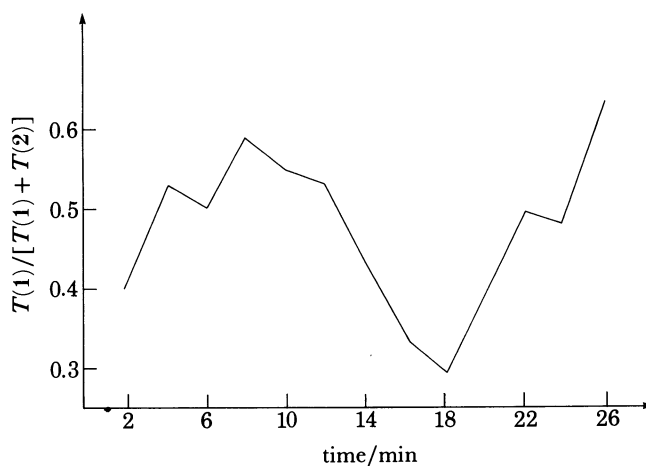


FIGURE 11. The proportion of the total observed catch for a line of $i = 2$ traps that was caught by the upwind ($j = 1$) trap (that is, $T(1)/[T(1) + T(2)]$) is plotted against time. The proportions are from consecutive timed 10 min replicates (data of Wall & Perry (1980), $s = 200$ m, see table 3) and vary systematically with time in a roughly cubic cycle, emphasizing that trap interactions are not caused by purely random processes.

8. FITTING

In this section we demonstrate that the model is capable of reproducing observed patterns in data to a tolerable accuracy. A full description of the behaviour of the model, including sensitivity analyses, will be published elsewhere. No attempt has been made here to obtain the best possible fit to a given set of data, we only demonstrate that fairly good fits are obtainable with reasonable parameter values.

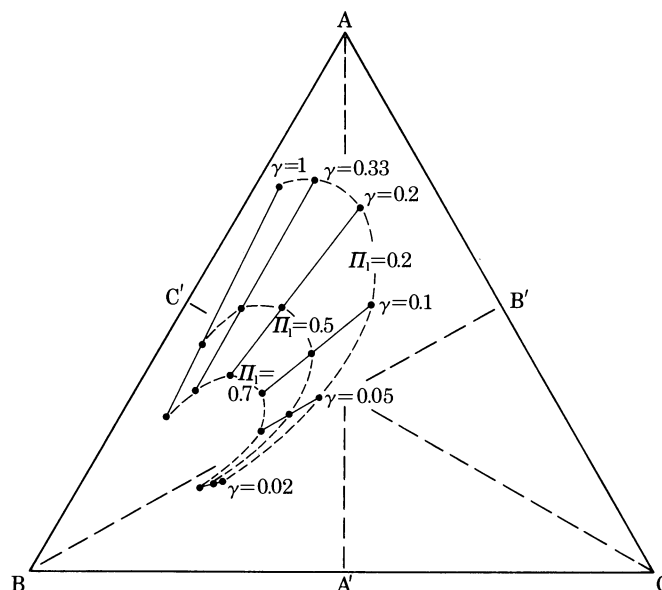


FIGURE 12. Model outcomes for $i = 3$ traps with inter-trap spacing $s = 25$ m plotted on a barycentric triangle (see figure 10). This figure demonstrates that the range of data shown in figure 10 may be reproduced by the model with all parameters held at constant values except two. Parameters with constant values are $\alpha = 0.1$, $\beta = 10^{-6} \text{ m}^{-2}$, $\nu = 5 \text{ m}$, $\lambda = 0.5$, $\Pi_u = 0.1$. Contours are shown for two parameters: Π_1 at three values, $\Pi_1 = 0.2$, 0.5 and 0.7 ; γ (m^{-1}) at six values, $\gamma = 1.0$, 0.33 , 0.20 , 0.10 , 0.05 and 0.02 . Note that for γ constant, variation in Π_1 moves the model outcome along contours roughly parallel to side AB, that is, the proportion in the centre trap is roughly constant when γ is constant.

Figure 12 demonstrates that the range of data shown in figure 10 is reproducible with all parameters held constant except Π_1 and γ . When γ is held constant too the predicted proportion caught in the centre trap, $T(2)/[T(1) + T(2) + T(3)]$, is approximately constant. This reflects observed data within an afternoon. Variation in parameter Π_1 , when γ is constant, leads to model outcomes which mimic the systematic fluctuations in $T(1)/[T(1) + T(3)]$ observed during an afternoon. Variation in parameter Π_u , instead of Π_1 , has a similar effect.

A further, important, test of the model is that it should provide a reasonable fit to data from comparable, separate lines of traps which have different values of i . Table 4 shows the fit to three of the four sets (table 3) of such data. Observed catches are means over the replicates. Fairly good fits are obtained. Four of the seven parameters allowed to vary took constant values over the three sets of data. The other three took constant values over two sets of data. Hence reasonable fits to different sets of data were obtained with little change in parameter values. The value of α is smaller for one set of data. Such values of α may reflect conditions during cooler afternoons when mean wind speeds are relatively large and fluctuations in direction relatively small.

The model also mimics data from lines with a large number of traps. Table 5 shows the fit

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TABLE 4. FIT OF MODEL TO THREE SETS OF DATA COMPRISING CATCHES IN COMPARABLE

data	LINES OF TRAPS		observed catch	fitted catch	parameter values		
	number of traps in line (<i>i</i>)	trap number in line (<i>j</i>)			Π_1	α	Π_u
<i>s</i> = 50: Wall & Perry (1980)	1	1	281.3	298.5	0.5	1.30	0.0
	2	1	220.3	217.3			
	2	2	160.8	163.3			
	3	1	294.0	291.1			
	3	2	97.7	113.8			
<i>s</i> = 25: Wall & Perry (1978)	3	3	119.6	106.4	0.2	0.144	0.17
	1	1	87.4	93.4			
	3	1	79.0	79.8			
	3	2	57.3	52.2			
<i>s</i> = 100: Wall & Perry (1978)	3	3	54.8	53.2	0.5	0.144	0.17
	3	3	76.4	78.9			
	3	2	70.4	64.8			
	3	3	76.4	78.9			

$\nu = 15$
 $\beta = 10^{-6}$
 $\gamma = 0.0167$
 $\lambda = 0.5$

TABLE 5. FIT OF MODEL TO SETS OF DATA COMPRISING CATCHES IN A LINE OF MANY TRAPS

data	trap number in line (<i>j</i>)	observed catch	fitted catch	parameter values		
				α	γ	ν
<i>i</i> = 5: <i>s</i> = 25: Wall & Perry (1980)	1	68.9	62.0	0.144	0.0167	1
	2	32.6	39.5			
	3	32.5	32.5			
	4	28.6	36.7			
	5	102.4	94.3			
<i>i</i> = 9: <i>s</i> = 25: Perry & Wall (1982)	1	85.5	78.1	0.25	0.0111	5
	2	32.3	60.4			
	3	29.6	48.0			
	4	35.0	38.9			
	5	39.6	31.9			
	6	51.7	26.6			
	7	20.4	24.0			
	8	36.2	32.0			
	9	106.7	97.1			

$\lambda = 0.5$
 $\beta = 10^{-6}$
 $\Pi_u = 0.17$
 $\Pi_1 = 0.5$

to two sets of data, for $i = 5$ and $i = 9$. The model predicts relatively large catches in the extreme upwind and downwind traps, as required. Parameter values again differ little between sets of data, or from those given in table 4.

Limited unpublished data of J. C. Graham suggest the density of male pea moth in unusually severely infested emergence sites is around 0.1 m^{-2} . This accords with estimates made by Lewis *et al.* (1975). Assuming a trap efficiency of 40% and that all males respond, the model predicts a catch of about 4000 moths. This accords with evidence; Wall & Perry (1980) recorded catches of over 2000 in a single water trap during an afternoon, at a moderately infested site in Begwary, Bedfordshire. A catch of 100–200 is more usual and this accords with density estimates obtained by J. C. Graham (unpublished) at less heavily infested sites.

Model outcomes seem sensitive to all parameters except λ .

9. DISCUSSION

The aims of modelling include the provision of a framework for discussion and identification of areas requiring further study. This model represents a first attempt to include behavioural parameters; the values of some of these require more precise measurement. Initial indications suggest the model fits well to our field data, but interpretation requires care because of the large number of parameters.

Females under laboratory conditions do not call continuously (T. Lewis, unpublished), and in field conditions probably only sporadically (Lewis *et al.* 1975). Females remain on vegetation while calling and the absorption and release of pheromone by the vegetation, as a secondary source, favours a strategy of sporadic calling. Our data have remained consistent over many experiments, despite the presence of wild virgin females which might be thought to affect the approach of males to synthetic sources. Additionally, females may well be mated very soon after they commence calling. Assuming a moderate male density of 0.004 m^{-2} , mark-recapture data suggests the duration of flight from male to calling female may be less than 12 s. Females are not easily observed in the field; however, their effect on the data described here is unlikely to have been substantial.

Limited similar experiments with another chemical attractant, (E)-10-dodecen-1-yl acetate (Wall & Perry 1981), showed that interactions occurred, but proportions of catches in lines of three traps did not differ significantly. The range of attraction of (E)-10-dodecen-1-yl acetate is almost certainly less than that of (E,E)-8,10-dodecadien-1-yl acetate, which implies β is larger for the former attractant. Model outcomes with relatively large values of β give results which conform with this data.

There are many possible applications of this model. Much pheromone research concerns pests of crops. The importance of the effects of the crop on flight for pea moth may have analogues in many other studied species. The patchy success and unpredictable performance of control measures involving mating disruption and mass trapping is partly owing to lack of study of behaviour in the field. This model may provide insight into possible control measures and, we hope, encourage similar field work on different species.

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