Chemical communication: does odor plume shape matter?

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Many insects use chemical information to gather information about their environment. Infochemicals are spread into the environment as the wind disperses the odor molecules from the source. The structure of an odor plume around a food source is complex and time-dependent. At a large scale, it meanders as it moves with the wind. At a smaller scale, patches with odors are interspersed with regions of clean air. In this study, we compare a plume model that takes the features of a real odor plume into account, a so-called filamentous plume model, with a simplified, time-averaged model, which is commonly used in the literature, and we investigate by simulation their effect on a modeled fruit fly population. During foraging *Drosophila melanogaster* is attracted to food odors and its aggregation pheromone. Ample knowledge on the attraction to these infochemicals in an experimental set-up exist in the literature. The comparison of the plumes in a simulation study clearly showed that the filamentous plume attracted more fruit flies towards the source than the time-averaged plume. We discuss the results in the light of experimental findings.

Keywords: Drosophila melanogaster, filamentous plume, Gaussian plume, settlement, spatial model

In insects, chemical information is widely used to gather information about the environment (Bell & Cardé 1984, 1995, Cardé & Minks 1997, Schoonhoven *et al.* 2005). The chemical cues involved are termed infochemicals (Dicke & Sabelis 1988). Upon release by an individual, infochemicals induce specific behavior in other individuals. In principle, any organism can exploit the information once it has been released (Vet & Dicke 1992).

The attraction of insects to chemicals and the searching behavior of insects in odor plumes have been studied in the laboratory and in the field (Cardé 1984, Murlis *et al.* 1992). In addition, mathematical models for odor plumes and plume tracing models for individual insects or autonomous robots have been developed (Sutton 1953, Yamanaka *et al.* 2003, Farrell *et al.* 2002). Though, much research efforts have already been spent on how individual insects respond to aggregation pheromones, there is still a strong need to study the spatial aspects of infochemicals on population dynamics.

In this paper, we study the spatial aspects of infochemical use by adopting a spatio-temporal approach that incorporates odor plume dynamics and the evoked responses of organisms. We take *Drosophila melanogaster* as a model organism. Drosophilid fruit flies breed in various decaying materials such as fermenting fruits, fungi or sap streams (Janssen *et al.* 1988). These resources are ephemeral. Therefore, the life of an adult fly generally starts with the task of locating a substrate that is suitable for feeding, mating and subsequently ovipositing. Additionally, the substrate must contain enough food for the development of the larvae. Chemical attraction towards odors from the food source (blend of fermentation products and yeast odor) and aggregation pheromone (cis-vaccenyl acetate) in combination with sight plays a directive role in the selection of these resources (Hutner *et al.* 1937, Bartelt *et al.* 1985, Wertheim *et al.* 2006, Kellogg *et al.* 1962).

Infochemicals are distributed into the environment as the wind disperses the odor molecules from the source. The structure of odor plumes is complex. Seen from a distance, plumes exhibit a sinuous pattern as they move with the wind. At a smaller scale, within the plume shape, patches with odors are interspersed with regions of clean air, so-called intermittency. In this study, we compare a filamentous plume model that takes these features of a real odor plume into account with a simplified, time-averaged model, by investigating their effect on a modeled fruit fly population. In both cases, we assume that the fruit flies detect a food source only by chemotaxis. The main question to be investigated is; do the different odor plume models affect the spatial distribution of the simulated fruit fly population? If so, does this difference affect the rate of settlement of the fruit flies on the resource? Our goal is to find the odor plume model that gives the most realistic prediction of the spatial distribution of a fruit fly population. As both plumes have a comparable time-average plume structure and the fruit flies use the same behavioral mechanism to find the odor source, we hypothesize that both odor plume models give the same results for the spatial distribution of fruit flies. To assess the realism of the prediction of the models, we discuss the results in the light of the experimental results by Wertheim *et al.* (2002).

DESCRIPTION OF THE MODEL

Odor distribution and the insects' responses to infochemicals are spatial processes. Therefore, a spatio-temporal model is used. We assume that *D. melanogaster* only responds to a concentration gradient, and does not use sight, to find the odor source. Therefore, we can use a chemotaxis model for the dispersal of *D. melanogaster*.

Odor distribution

First, we introduce a simple diffusion advection model in which the odor concentration is averaged over time. The odor distribution of this plume model, the Gaussian plume, is described by the dispersal kernel K_G

$$K_G(x,y)=\frac{1}{4\pi\sqrt{D_{Gx}}\sqrt{D_{Gy}}\,t}\exp\left(-\frac{1}{4t}\left(\frac{(x-\overline{u}t)^2}{D_{Gx}}-\frac{y^2}{D_{Gy}}\right)\right)$$

Here, D_{Gx} and D_{Gy} are the diffusivity constants of the infochemicals in the longitudinal (with the wind direction) and the transversal (perpendicular to the wind) direction, respectively. The time averaged wind velocity with magnitude $\bar{u}$ is here taken along the x-axis.

Second, in contrast to the model above, an important characteristic of a real odor plume is that it meanders and has an intermittent internal structure. The meandering is caused by turbulent eddies that are much larger than the odor puffs that are released at the source and transport the puff as a whole, causing the ensemble of puffs to appear as a sinuous plume. Farrell *et al.* (2002) developed a plume model that incorporates these important characteristics of a real odor plume. The plume consists of odor filaments with an instantaneous odor concentration. In this model, the velocity vector of an odor particle is decomposed into three components: v_a, the transport of the plume as a whole (advection), v_m, the transport within the body of the plume (centerline relative diffusion), and v_d, the changing shape of the filament. Advection, with components $v_a = [\bar{u},\bar{v}]$ is in this model described by (Farrell *et al.* 2002)

$$\frac{\partial\overline{u}}{\partial t}=-\overline{u}\frac{\partial\overline{u}}{\partial x}-\overline{v}\frac{\partial\overline{u}}{\partial y}+\frac{1}{2}D_{Fx}\frac{\partial^2\overline{u}}{\partial x^2}+\frac{1}{2}D_{Fy}\frac{\partial^2\overline{u}}{\partial y^2}\ ,$$

$$\frac{\partial\overline{v}}{\partial t}=-\overline{u}\frac{\partial\overline{v}}{\partial x}-\overline{v}\frac{\partial\overline{v}}{\partial y}+\frac{1}{2}D_{Fx}\frac{\partial^2\overline{v}}{\partial x^2}+\frac{1}{2}D_{Fy}\frac{\partial^2\overline{v}}{\partial y^2}\ ,$$

where $\bar{u}$ and $\bar{v}$ are the mean velocities of a turbulent flow, in respectively x and y direction, and D_{Fx} and D_{Fy} represent the diffusivity in the longitudinal and transversal direction. Solving these equations numerically for boundary conditions generated by a constant mean flow plus a (stochastic) colored noise process yields a continuous, spatio-temporal varying wind field. For a detailed description of the model and the parameter values used, we refer to Farrell *et al.* (2002).

Dispersal of fruit flies

While in absence of an odor (*e.g.* food odors and its aggregation pheromone) the dispersal of fruit flies is random, the presence of an odor attracts the fruit flies on average towards the odor source. Powell *et al.* (1998) developed a general format for chemotactical movement in biology. We use this to model the response of the population as a function of the concentration gradient of the food odor. This is described by the following equation

$$\frac{\partial P}{\partial t} = -D_P \nabla \cdot \left[\kappa \, P \, \nabla f(F,A) - \nabla P\right],$$

where P is the spatial distribution of the *Drosophila* population, D_P is the dispersal constant (or the so-called diffusion constant) of the population, F and A denote the concentrations of food odors and aggregation pheromone, respectively. The function $f(F,A)$ is a sensory index function modeling the relation between the odor concentrations and the sensory perception of the flies, and is to be specified later on. The parameter κ models a property of fruit flies, weighting the relative strength of their sensory perception of infochemicals as compared to the random dispersal (D_P). If there is no sensory perception of infochemicals, then the movement is at random and $\kappa = 0$. On the other hand, a strong influence of the sensory perception in comparison to the random dispersion corresponds to high values of κ. In that case, the movement is directed towards the odor source.

METHODS

Integro-difference approach for population dispersal

The partial differential equation for the chemotactic dynamics of the population is approximated using the integrodifference approach (Neubert *et al.* 1995, Powell *et al.* 1998, Etienne *et al.* 2002). In this approach, the dispersal of the population is calculated by taking the convolution product of the population density and the dispersal probability function. According to Powell *et al.* (1998), the time evolution of P is governed by

$$P(x,y,t+\Delta t) = N e^{\kappa(F,A)} \cdot K_{RD} * \left\{ e^{-\kappa(F,A)} P(x,y,t) \right\}.$$

Here, the convolution product is indicated with an asterisk, and N is a normalization constant. The random dispersal kernel K_{RD} (a two-dimensional normal distribution) for the population of fruit flies is given by the Gaussian distribution

$$K_{RD}(x,y) = \frac{1}{4\pi D_P t} e^{-\frac{x^2+y^2}{4 D_P t}},$$

where D_P is the dispersal constant of the fruit fly population. For a detailed description of the simulation model, see Lof *et al.* (submitted).

Sensory index

Bartelt *et al.* (1985) showed for the response of *D. melanogaster* towards its aggregation pheromone and food odors, that (1) the aggregation pheromone is only attractive when food odors are also present, and (2) *D. melanogaster* is about four times more attracted to the combination of its aggregation pheromone and food odors, than to food odors alone. A description of the response of *D. melanogaster* to infochemicals that is consistent with these findings is:

$$f(F,A) = \frac{F}{F_0 + F} + \eta \frac{FA}{F_0 A_0 + FA} \; .$$

F_0 and A_0 are the half saturation values for food odors and aggregation pheromones, respectively, and η represents the attraction ratio of food odor in combination with aggregation pheromones (F+A) relative to the attraction to food odor alone (F).

Parameter estimation of Gaussian plume

For a fair comparison between the Gaussian and filamentous plume models, we must take into account that the filamentous plume is stochastic in nature, while the Gaussian plume is deterministic. Therefore, we first generated 10 replicates of 10 min time-average filamentous plumes with an advective wind velocity v_a=[0.5,0]. Next, we fitted our Gaussian plume on the average plume of the 10 replicates; in practice, this number of replicates appeared to be sufficient. The realized mean wind speed in the x-direction was 0.51 m s^{-1} for the filamentous plume. Therefore, we set the velocity within the Gaussian plume in the x-direction to 0.51 m s^{-1}. We estimated the diffusivity constants D_{Gx} and D_{Gy} of the Gaussian plume, by using a non-linear least square optimization (in MATLAB 7.3). The Gaussian plume and the filamentous plume fitted best for D_{Gx}= 0.02596 and D_{Gy}= 0.017307.

Simulation

In Fig. 1, some simulation results are compared. We note that the odor source is in all cases positioned at (7.5, 15.0). At the start of the simulation, we released 800 fruit flies downwind, always at a distance of 1 m from the odor source. In subsequent simulations, this initial position was varied over different angles (−45°, −22.5°, 0°, 22.5°, 45°) with respect to the mean wind direction. We looked at the dispersal patterns after 30 minutes, realized with a time step of 0.01 s for the odor dispersal and of 1 s for the chemotactic dispersal of the population.

Parameter values

We used the parameter values as given in Table 1. We adopted the parameter values for the diffusivity constants of the filamentous plume (D_{Fx}, D_{Fy}) from

Table 1. Description and values of parameters used in simulations

parameter	description	value	unit
D_{Gx}	Diffusity of the constant Gaussian plume in x-direction	0.02596	$m^2 s^{-1}$
D_{Gy}	Diffusity of the constant Gaussian plume in y-direction	0.01731	$m^2 s^{-1}$
$\bar{u}$	Mean velocity advection infochemicals in x-direction	0.51	$m s^{-1}$
$\bar{v}$	Mean velocity advection infochemicals in y-direction	0	$m s^{-1}$
D_{Fx}, D_{Fy}	Diffusivity of the filamentous odor plume	1	$m^2 s^{-1}$
D_P	Dispersal constant of the fruit fly population	0.000965	$m^2 s^{-1}$
κ	Relative strength of movement towards infochemicals compared to random dispersal	5	-
F_0	Saturation parameter for food odors	10	$ng m^{-2}$
A_0	Saturation parameter for aggregation pheromones	0.04	$ng m^{-2}$
η	Attraction ratio of food odors in combination with aggregation pheromones relative to food odors alone	2.51	-

Farrell *et al.* (2002). Fruit flies prefer to disperse during wind free days. They stop flying at a wind speed of 0.9 m s^{-1} (Kellogg *et al.* 1962). Therefore, we chose a (mean) wind speed ($\bar{u}$) of 0.51 m s^{-1} to ensure that the realized wind speed is realistic. The parameters values for the diffusivity constants of the Gaussian plume (D_{Gx}, D_{Gy}) resulted from of parameter estimation (see above). The dispersal constant for the fruit fly population (D_P) was set on 0.000965 $m^2 s^{-1}$ based on field data of Timofeeff-Ressovsky and Timofeeff-Ressovsky (1941) on the spread of *D. melanogaster* in a park. No specific estimate was available for relative strength of the chemical attraction towards food odors and aggregation pheromone as compared to the random dispersal for *D. melanogaster*. Powell *et al.* (1998) used κ=10 for mountain pine beetles. As the population dynamics in our system take place at a smaller spatial scale than the dynamics of the mountain pine beetle, we assumed κ to be smaller and chose κ=5. The odor production parameters (Φ_F,Φ_A) are based on the field experiment of Wertheim *et al.* (2002). They applied 4.5 μg synthetic pheromone on a substrate, taking into account that only a small part evaporates into the air. Converting from a substrate to 1 m^2, gives a pheromone production of 10.68 ng s^{-1} m^{-2}. In a field experiment comparing the attractiveness of substrates with food odors only to substrates with food odors and aggregation pheromone combined, Wertheim *et al.* (2006) found a 1:4.5 ratio of settled fruit flies. No information was present on the production of food odors in the experiment. By using a simulation with the same set-up as the field experiment by Wertheim *et al.* (2002), using the above-mentioned ratio, the production of food odors could be estimated as 8.74 ng m^{-2}. For a more detailed description of the parameter values used, we refer to de Gee *et al.* (submitted).

RESULTS

The results presented in Figures 1 and 2 clearly show that the two odor plume models compared in this paper dramatically affect the calculated spatial distributions of the fruit flies. As shown in these figures, in the case of the time-varying filamentous plume the fruit flies are much more effectively attracted to the odor source than in case of the Gaussian plume model. Apparently, the gradient of the odor concentration in the time-averaged Gaussian plume is not high

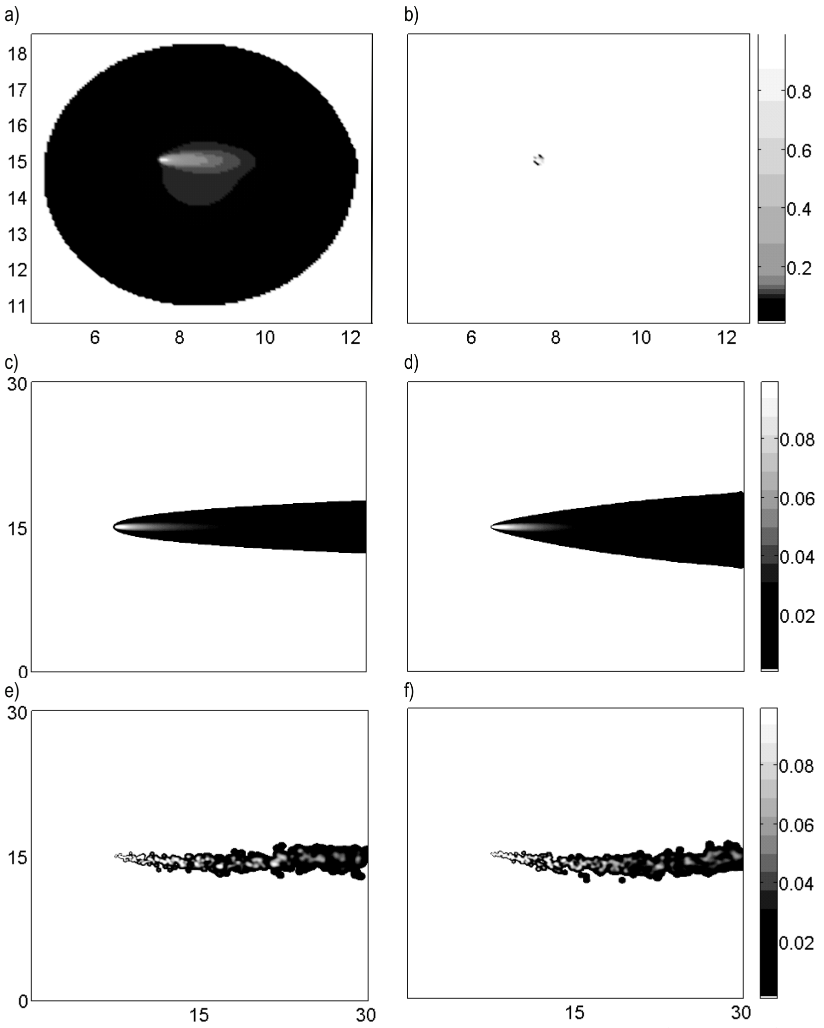

Figure 1. Spatial distribution of the fruit flies near the odor source (position (7.5, 15)) after 30 minutes of dispersal for a) the simulation with the Gaussian plume model and b) the filamentous plume model. Graphs of the complete spatial domain for c) the Gaussian plume model, d) a 10 min-average of the filamentous plume, e-f) two snapshots of a filamentous plume, taken 10 seconds apart. The darker shades denote low population (a-b) or odor (c-f) concentrations, the lighter shades high concentrations. Note that the background (conc. = 0) is also colored white.

enough to attract the fruit flies sufficiently. The resulting dispersal of the fruit flies is mostly random, as the large almost circular distribution, with high concentrations in the center and lower concentrations further away, in Fig 1a clearly shows. Only a small part of the population is attracted to the source of the infochemicals, the plume shape in the center. The instantaneous odor concentration in an odor filament can be far higher than the time-averaged mean concentration (compare Fig. 1 e-f with c-d). Therefore, in the simulations with the filamentous plume the fruit flies were able to find the odor source, resulting in much higher settlement. Not only the settlement was higher, but the fruit flies also could find the source much faster, within half a minute the first fruit flies settled on the source, while for the Gaussian plume first settlement started after 1.5 minutes (Fig. 2b).

The position of the initial population, compared to the mean wind direction, did not affect the spatial distribution or the settlement of the fruit flies.

To investigate the dependence of these findings on odor concentration we varied this concentration for both models. We found that for the Gaussian model a higher odor concentration led to a better attraction, as expected, while for the filamentous plume, increase in odor concentration, first led to better attraction up to a concentration with maximum effect, further increasing the odor concentration caused a decrease in attraction due to satiation. Essentially the overall conclusion is not affected: the Gaussian plume model is much less effective than the filamentous one.

COMPARISON WITH THE EXPERIMENT

To evaluate which odor plume model gives the most realistic results, we compare our model results with the outcome of an experimental study by Wertheim *et al.* (2002). They studied the behavioral responses of *D. melanogaster* to pheromone-treated and control substrates in an outdoor population cage. To make this comparison possible, we based the pheromone production in our model on the pheromone concentration used in this experiment. We multiplied

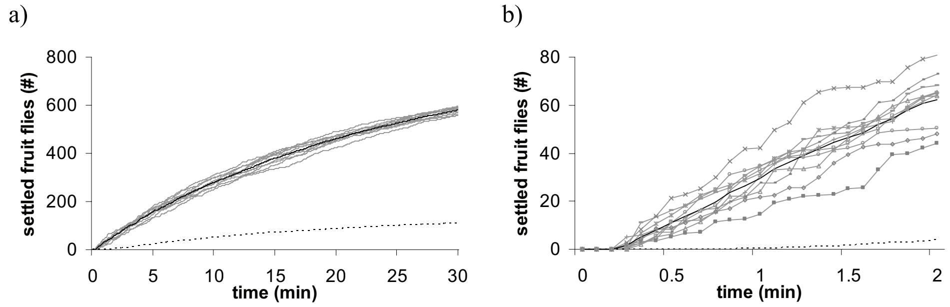

Figure 2. A time plot of the number of fruit flies that settled on the resource for the different replicates of the filamentous plume (grey lines) the average of which is given by the black solid line and for the simulation with the Gaussian plume (black dotted line).

the average number as given in Figure 4a in the paper by Wertheim *et al.* (2002) with the number of pheromone treated substrates (4), thereby we deduced that in their experiment, after 5 minutes already 60 fruit flies found the substrate and after 30 minutes approximately 140 fruit flies were settled on the substrate. A large part of the 400 to 800 fruit flies remained in their holding pot the first hour of the experiment (Wertheim *et al.* 2002). Under the assumption that in the first 30 minutes 300 fruit flies dispersed in the population cage, in our model approximately 160 fruit flies should have settled at the food source after 5 min and 375 fruit flies after 30 min. From comparison with these experimental data, we conclude that the settlement for the simulation with the Gaussian plume is much too low (Fig. 2). The settlement for the simulations with the filamentous plume is approximately the same as in the experiment after 5 minutes, while after 30 minutes the settlement in our simulation is much higher than in the experiment. However, this discrepancy can be explained, since in the experiment the fruit flies could choose between pheromone-treated substrates and control substrates. In our simulation model, we only have one odor source, containing both food odors and aggregation pheromone. Thus, all fruit flies could potentially settle down on the odor source, while in the experiment a part of the population settled down elsewhere.

CONCLUSION

In conclusion, the filamentous plume model gives much more realistic results than the Gaussian plume model. The use of a time-averaged plume model for odor distribution results in a strong underestimation of the number of fruit flies that settle down on a resource, whereas the filamentous plume model leads to the results that reasonably agree with the experimental evidence.

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