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MODELISATION DU COMPORTEMENT DU SUIVI DE LA PISTE CHEZ LES FOURMIS

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RESUME: De nombreux travaux ont été consacrés à l'identification des glandes et des phéromones impliquées dans la formation des pistes chez les fourmis. Cependant la compréhension du suivi de la piste et des capacités de cette dernière à transmettre une information passe par l'étude de ses charactéristiques physico-chimiques et des mécanismes de perception-orientation de l'insecte. Un modèle simulant le mouvement de l'insecte et prenant en compte la souplesse de sa réponse, nous a permi de tirer des conclusions concernant l'efficacité du suivi de la piste. Le modèle reproduit qualitativement les résultats experimentaux actuellement disponibles.

Mots clés: Fourmis, osmotropotaxie, suivi de la piste, modèle mathematique;

SUMMARY:

Modelling trail following behaviour in ants.

A model of osmotropotactic orientation is presented that determines the behaviour of ants following an idealised trail. The model concentrates on the level of the ants' behaviour. Computer simulations reproduce qualitatively experimental results. The influence of a parameter that tunes the flexibility of the ants' response to a chemical stimulus is investigated, giving some clues to the conditions required for effective trail following.

Key words: Ants, osmotropotaxis, trail following, mathematical model;

Introduction:

Osmotropotaxis is one of the main mechanisms of trail following in ants and termites (Hangartner, 1967; Leuthold, 1975). In osmotropotaxis it is believed that the ant determines the actual pheromone concentration with both antennae and tries to minimise the concentration difference between the two antennae by changing its direction (Kühn, 1919; Fraenkel & Gunn, 1940; for a recent discussion see Bell & Tobin, 1982). Few experiments have been performed to support this theory (Hangartner, 1967; Leuthold, 1975) and even less is known from a theoretical point of view.

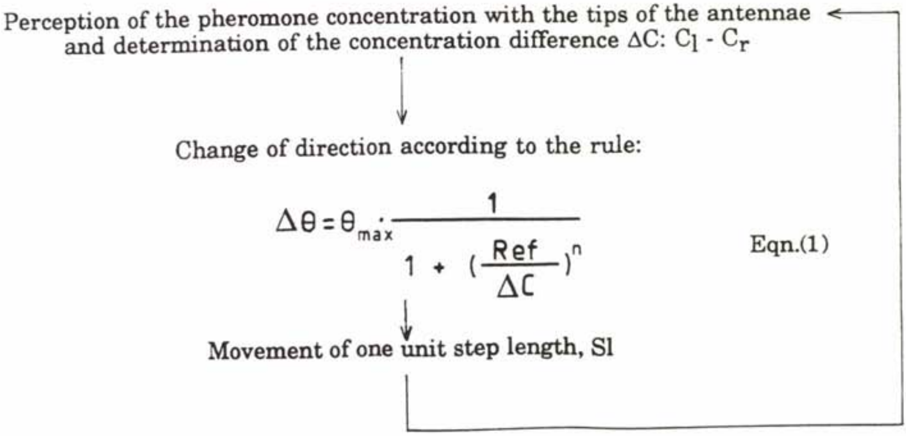
Trail following can be viewed as a complex interplay between the response of the ant and the chemical environment determined by diffusion, adsorption-desorption, evaporation etc... At the behavioural level a lot of questions arise immediately. For example, do the ants behave deterministically, i.e., are they following the path wiggling from left to right, always changing their direction the same way?

A simple model is presented that allows us to answer some of these questions. It must be emphasised, however, that our model is phenomenological in that it determines the behavioural response of the animal to a chemical stimulus. Physiological or neurobiological aspects are not explicitly considered.

Trail following experiments are usually performed on circular trails. Thus our computer simulations were performed for circular and linear trails. For the time being there are two experimental results (Pasteels et. al., 1986) that could be reproduced by our simulations and that are used to determine whether a model can be accepted or rejected. These are the straight line obtained when plotting the logarithm of the fraction of ants still following the trail as a function of the distance (survival curve) and the peaked curve obtained for the mean distance followed on the trail as a function of the pheromone concentration

The model:

We assume that the ants start at the center of the trail, Fig. (1), (since we are interested here in the trail following fidelity and not in the trail recognition abilities) heading in a certain direction (starting angle). The movement is then determined by the following algorithm performed every time step:



Perception of the pheromone concentration with the tips of the antennae and determination of the concentration difference ΔC: $C_l - C_r$

Change of direction according to the rule:

$$\Delta\theta = \theta_{max} \cdot \frac{1}{1 + \left(\frac{Ref}{\Delta C}\right)^{n}}$$

Eqn.(1)

Movement of one unit step length, Sl

θ_{max} is the maximal turning angle, Ref is a reference value with units of concentration, and n is an integer or non-integer valued number. The exponent n tunes the flexibility of the response. By adjusting its value the model can be tuned from a smooth and flexible response corresponding to a low value of n, to a rigid and inflexible behaviour for large n (= 8, 9, 10). The higher the exponent the more the answer resembles a yes-or-no step function. All three steps are assumed to be performed in one unit time step.

The diffusion of the pheromone is assumed to obey Fick's law. To present only the basic features of the model we restrict ourselves to a fixed diffusion profile in time.

External disturbances like wind or turbulence caused by the movements of the ants, behavioural fluctuations due to the vibrations of the antennae and physiological noise are lumped together in one noise representation, where fluctuations are imposed on the concentration of the pheromone at the point of perception. If C_l (or C_r) is the mean concentration, given by Fick's law, perceived by the left antenna, $C_l(1 + \varepsilon)$ shall be used in the calculation of ΔC. ε has a value that lies with equal probability between $-\varepsilon_{max}$ and $+\varepsilon_{max}$ which correspond to the maximally allowed fluctuations.

Thus the model contains the following parameters:

Geometrical parameter:	- distance between the antennae, d;
Behavioural parameters:	- flexibility exponent n; - reference concentration Ref; - maximal turning angle; - steplength, Sl;
Physico-chemical parameters:	- amount of pheromone laid; - diffusion coefficient of the pheromone; - diffusion time;
Noise:	- ε_{max}, maximal fluctuation allowed;

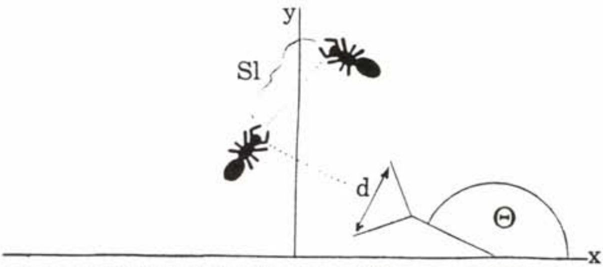


Fig. (1): Geometry of the model and movement; for parameters see text ;
Géométrie du modèle et du mouvement; paramètres voir texte;

Results:

For a plot of the logarithm of the number of ants still on the trail as a function of the distance travelled, reasonably straight lines are obtained for a large number of parameter combinations, Fig. (2). A plot of the mean distance travelled on the path as a function of the concentration gives a peaked curve, Fig.(3), when a flexible response is used, (small n). Both results are obtained for linear and circular trails. The straightness of the survival curve and the peaked nature of the concentration dependence of the mean distance followed seem not to be linked necessarily. That is to say that not all the points of the concentration/mean distance curve correspond to a situation where the probability of leaving the trail is constant.

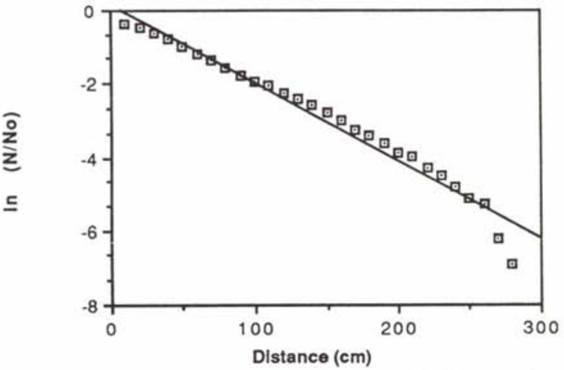


Fig. (2): Natural logarithm of fraction of ants still following the path as a function of distance; linear trail;
$ln(N/N_o) = 0.197 - 0.021r$; *r=distance;*
Parameters:
Concentration profile fixed after 10s Diffusion;
Diffusion coefficient= $0.01 cm^2/s$; *Sl=* $0.15 cm$; *d=* $0.5 cm$;
amount of pheromone laid= $1.2 \times 10^{-11} g/cm$; *Ref=* $5.0 \times 10^{-12} g/cm^3$;
maximal turning angle= 30°; $\varepsilon_{max} = 0.85$; *flexibility exponent n= 1;*
number of ants used for simulation= 1000; starting angle= 20°

Logarithme néperien de la fraction des fourmis qui suivent toujours la piste en fonction de la distance courue; piste linéaire;
$ln(N/N_o) = 0.197 - 0.021r$; *r=distance;*
Paramètres:
Profile de la concentration fixée après 10s de diffusion;
coefficient de diffusion= $0.01 cm^2/s$; *Sl=* $0.15 cm$; *d=* $0.5 cm$;
quantité de phéromone déposée= $1.2 \times 10^{-11} g/cm$; *Ref=* $5.0 \times 10^{-12} g/cm^3$;
angle de déviation maximal= 30°; $\varepsilon_{max} = 0.85$; *exponent de flexibilité n= 1;*
nombre de fourmis utilisées pour la simulation= 1000; angle de départ= 20°

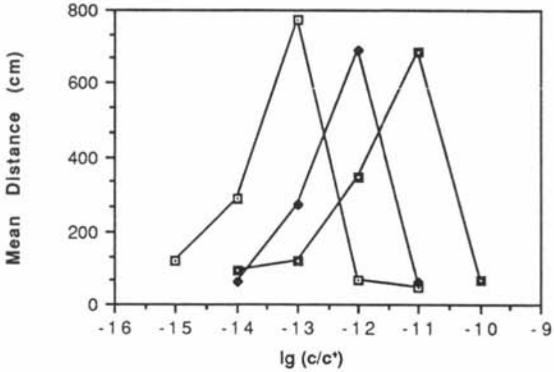


Fig. (3): Mean trail distance followed as a function of the amount of pheromone ; linear trail; Ref values: ⊡ = $5 \times 10^{-13}\, g/cm^3$; ◆ = $5 \times 10^{-12}\, g/cm^3$; ■ = $5 \times 10^{-11}\, g/cm^3$; *Parameters: idem fig.(2), except: number of ants used for each simulation = 100; equiprobable distribution of starting angles*

Distance moyenne suivie sur la piste en fonction de la quantité de pheromone déposée; piste linéaire;
valeurs de Ref: ⊡ = $5 \times 10^{-13}\, g/cm^3$; ◆ = $5 \times 10^{-12}\, g/cm^3$; ■ = $5 \times 10^{-11}\, g/cm^3$;
Paramètres: idem fig.(2), sauf: nombres des fourmis utilisées pour la simulation= 100; distribution equiprobable des angles de départ

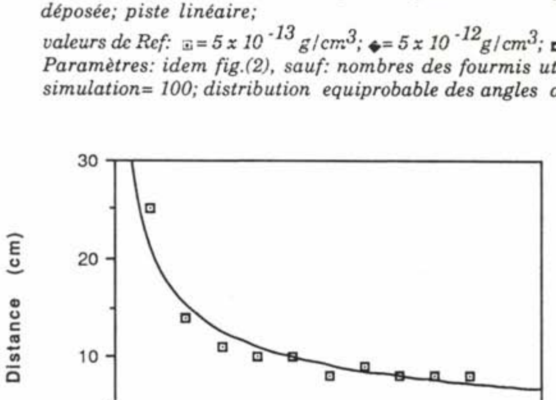


Fig.(4): Mean trail distance followed as a function of the flexibility exponent n; linear trail; Parameters: idem fig.(2), except: Sl= 0.35cm; equiprobable distribution of starting angles

Distance moyenne suivie sur la piste en fonction de l'exponent de flexibilité n; piste linéaire; Paramètres: idem fig.(2), sauf: Sl= 0.35cm; distribution equiprobable des angles de départ

The two experimental results are thus reproduced by the model. A detailed description of the influence of the different parameters will be given in a forthcoming paper. By increasing the parameter n in eqn.(1) the model can be tuned from a smooth and flexible response to a rigid and unflexible one. For all parameters fixed and for a given concentration, as the response becomes more and more rigid, the mean distance travelled decreases very rapidly, Fig.(4).

Discussion:

Despite its remarkable simplicity the model is able to reproduce given experimental data and to give us some answers to the questions raised in the introduction. The diffusion conditions are surely oversimplified. A large number of results remain correct, however, under more realistic conditions (Calenbuhr and Deneubourg, in preparation).

Note that the rule used to determine the change of direction should not be regarded as THE rule. Other functions that have similar properties are conceivable and are being tested.

The given function eqn.(1) works well for a large number of parameter combinations. Nevertheless, for the time being the results can only be considered as qualitative. This might indicate that the influence of noise on the level of the behaviour of the ants is still underestimated in the model. For the time being we don't know what kind of stochastic process can be mapped onto the behaviour of an individual moving in a homogeneous field, and if this behaviour is more or less constant or variable depending on certain external conditions or on the individual's internal disposition. Investigations to determine the statistical properties of the ants' movements are under way.

We have discussed here only the influence of two parameters: the reference concentration and the flexibility exponent. The first interesting result concerns the reference concentration. Different numerical values don't affect the general form of the mean distance as a function of the concentration. Moreover, the mean distance for the optimal answer is independent of the value of Ref. The second interesting result concerns the flexibility exponent: lower values result in a much greater trail fidelity and show clearly that a flexible and smooth reaction is preferable.

It is interesting to note that the mean distance travelled on a linear path is considerably longer than the mean distance on circular paths (one order of magnitude or more). This has been confirmed by experiments conducted on Pheidole pallidula (Detrain, in prep.), and should be kept in mind when discussing experimental results obtained on circular trails. This difference is certainly due to the geometry of the problem which deserves more attention, both theoretically and experimentally.

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