

EXPERIMENTAL STUDY AND MODELLING  
OF FOOD RECRUITMENT  
IN THE ANT *TETRAMORIUM IMPURUM* (HYM. FORM.)

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Reçu le 28 décembre 1982.

Accepté le 23 mars 1983.

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SUMMARY

A study of global recruitment in *Tetramorium impurum* has shown its main characteristics.

The growth of population in the neighbourhood of the food source is a logistic curve. Damped oscillations are observed. These oscillations are the result of time delay in recruitment and crowding around the food source.

A mathematical model is able to reproduce these different effects and it allows one to identify and give quantitative values to pertinent parameters.

RESUME

**Etude expérimentale du recrutement global chez *Tetramorium impurum*  
(Hym. Form.)**

Une étude du recrutement global, menée chez *Tetramorium impurum*, a mis en évidence ses principales caractéristiques.

La croissance de la population participant au recrutement est de type logistique. De plus, des oscillations amorties sont observées. Celles-ci ont deux origines : les délais temporels dans les recrutements et l'effet de l'encombrement à la source.

Un modèle mathématique permettant de reproduire ces différents effets et de quantifier les paramètres pertinents est présenté.

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INTRODUCTION

The mechanisms by which the ant societies manage to assemble great quantities of ants around food sources constitute the food recruitment.

It is necessary here to distinguish between individual and global recruitment. Individual recruitment is the behavioural sequence which allows the recruiter to bring a given number of ants towards the food source. The succession of these individual recruitments constitutes the global recruitment. Several kinds of individual food recruitment are known today (HÖLLDOBLER, 1978; MASCHWITZ, 1975).

*Tetramorium impurum* uses mainly the group recruitment strategy, which however evolves toward mass recruitment at the end of the recruiting process (VERHAEGHE, 1982).

However, global recruitment is not a simple accumulation of individual recruitments because individual interactions and peripheral phenomena (i.e. crowding at the food source, trophallactic flows, ...) are involved which further increase the complexity of the process. Mathematical models are good ways to study such phenomena. The models presented here are based on individual behaviours and allow us to bridge the individual and the collective level. These models are free from any optimisation concept but the "cost/benefit" may be computed subsequently from the models' dynamics.

This article is divided into two parts: an experimental study of the global recruitment, and the development of a mathematical model describing this recruitment and its confrontation with the experimental data.

## EXPERIMENTAL STUDY OF THE GLOBAL RECRUITMENT

### Material and methods

All the experiments were performed on societies gathered in the neighbourhood of Treignes (Belgium). The societies were held in a large nest (VERHAEGHE, 1982) connected by a tube (T) to a foraging arena (A I) (*fig. 1*). A I is connected by a narrow bridge to a second arena (A II) in which the food (F) is offered (0.1 ml of 1 M sucrose) on a glass cover slide.

This experimental design allows measurement of the incoming and outgoing flux of ants in arena II. These two measures allow us to determine the number of ants present in arena II at each moment of the experiment. A camera connected to a time lapse device (functionning every 4 minutes) allows an estimation of the number of ants around the food source and of its exhaustion. Among the numerous parameters which may rule the global recruitment, we have chosen to study the influence of the size of the nest and the fact that the substratum in which the recruitment occurs is or is not familiar to the ants. Consequently, societies of two sizes (nest A: 750 workers, nest B: 1500 workers) were each studied in two experimental conditions: unknown substratum (arena II and the bridge were unknown to the ants) and known substratum (arena II and the bridge were connected to the arena I 4 days before the experiments). These two societies are the result of the division of one colony, using aleatory sampling. Each combination (large/small colonies, known/unknown substratum) was the subject of 2 or 3 experiments (*table 1*).

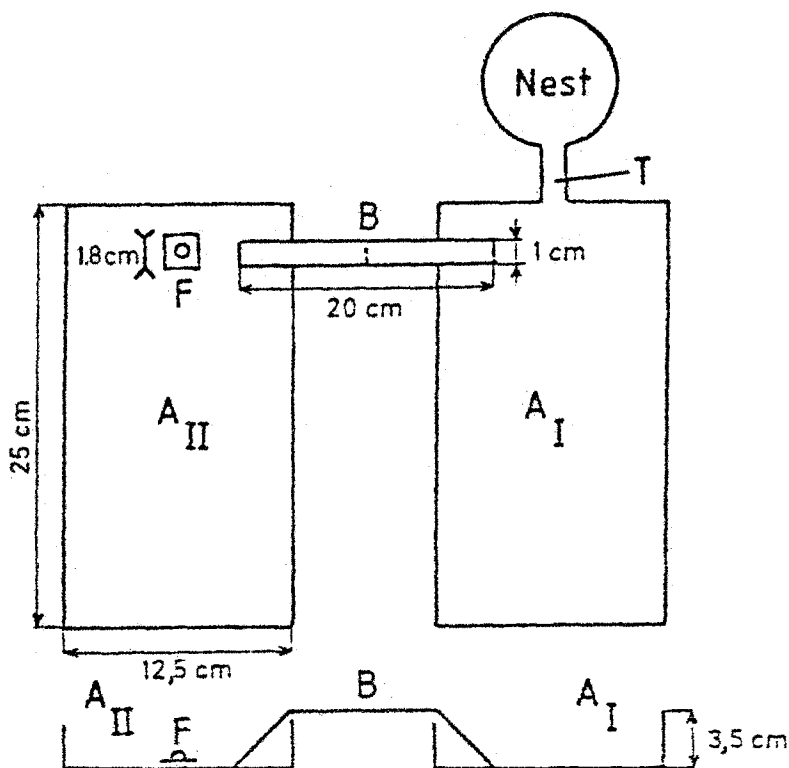


Fig. 1. — Experimental device used to study the global recruitment. A I arena connects to the nest by the tube T, B bridge, A II arena with the food source F.

Fig. 1. — Dispositif expérimental pour l'étude du recrutement global. Le nid est connecté à une aire (A I) par un tube (T). Le pont (B) la connecte à l'aire (A II) où la source de nourriture (F) est déposée.

## Results

Three types of recruitment curves were observed (summary in *table I*):

- 1) slow, non oscillatory, with a plateau (*fig. 2*);
- 2) fast, oscillatory, with a plateau (*fig. 3*);
- 3) explosive recruitment, without a plateau (*fig. 4*).

The results can be summarized as follows:

— The nest size influences the growth phase of the recruitment curve, the height of the plateau and the presence of oscillations in it. The slow

Table I. — (1) A: 750 workers, B: 1500 workers, — unknown substratum, + known substratum; (2) number of workers entering the arena A II per min. and per worker already present in the arena measured for the first 10 min.; (3) number of workers leaving the arena A II per min. and per worker present in the arena, measured for the first 10 min.; (4) measured on the first 10 min.; (5) maximum number of ants in A II; (6) time when the maximum is reached (min.); (7) I: logistic growth, II: logistic growth with oscillations, III: explosive recruitment.

Tableau I. — (1) A: 750 ouvrières, B: 1500 ouvrières, — substrat inconnu, + substrat connu; (2) nombre d'ouvrières entrant dans A II par min. et par ouvrière présente dans A II mesuré sur les 10 premières min.; (3) nombre d'ouvrières quittant A II par min. et par ouvrière présente sur l'aire mesuré sur les 10 premières min.; (4) mesuré sur les 10 premières min.; (5) nombre maximum de fourmis sur A II; (6) temps où il est atteint (min.); (7) I: croissance logistique, II: croissance logistique avec oscillations, III: recrutement explosif.

Nest	Entry rate	Exit rate	Slope at the origin	Max.	T max.	Type of curve
(1)	(2)	(3)	(4)	(5)	(6)	(7)
A—	$1,6 \cdot 10^{-1}$	$5,9 \cdot 10^{-2}$	3,3	186	50	I (fig. 2)
A—	No recruitment		—	—	—	—
A+	No recruitment		—	—	—	—
A+	$2,1 \cdot 10^{-1}$	$2,3 \cdot 10^{-2}$	4	244	46	I
B—	$2,1 \cdot 10^{-1}$	$3,7 \cdot 10^{-2}$	7,4	303	49	II (fig. 3)
B—	$1,7 \cdot 10^{-1}$	$5 \cdot 10^{-2}$	18,1	270	36	II
B+	$2,5 \cdot 10^{-1}$	$2,3 \cdot 10^{-2}$	16,5	598	44	III (fig. 4)
B+	$3,4 \cdot 10^{-1}$	$4,6 \cdot 10^{-2}$	26,7	420	34	III
B+	$3,8 \cdot 10^{-1}$	$3,9 \cdot 10^{-2}$	20,7	394	18	III

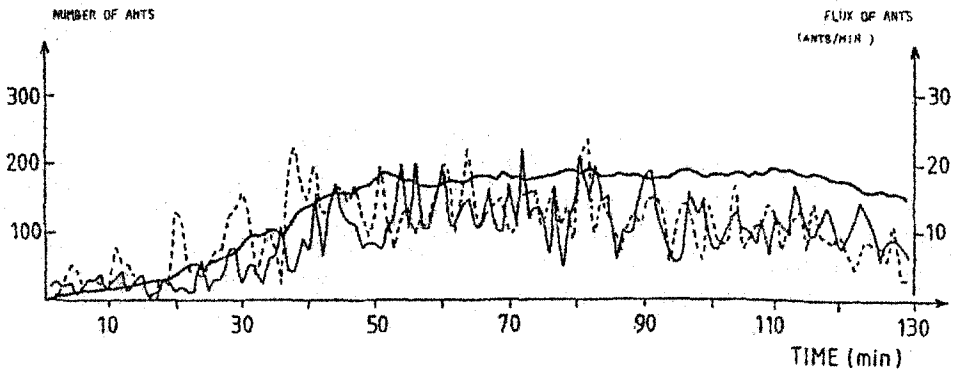


Fig. 2. — Slow, non oscillatory recruitment with plateau. Food source: 0.1 ml of 1 M sucrose, nest A, unknown substratum. Population of ants in A II: heavy line. Flux of incoming: dashed line. Flux of outgoing: light line.

Fig. 2. — Recrutement lent, sans oscillation avec plateau. Source de nourriture: 0,1 ml de sucrose 1 M, nid A, substrat inconnu. Population en A II: trait épais continu. Flux d'entrée: trait discontinu. Flux de sortie: trait fin continu.

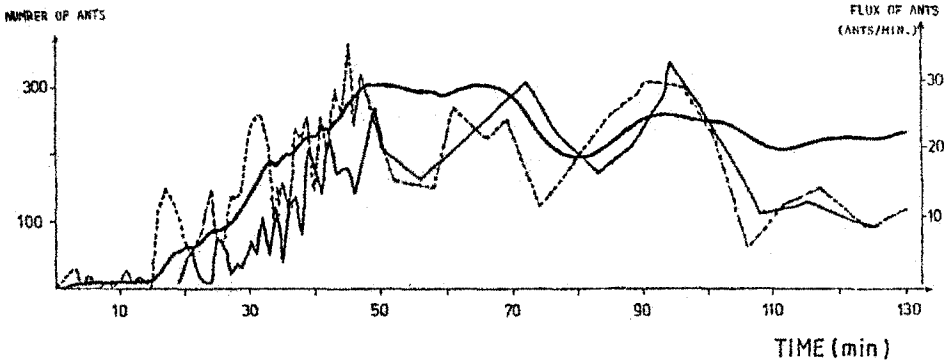


Fig. 3. — Fast, oscillatory recruitment, with plateau. Food source: 0.1 ml of 1 M sucrose, nest B, unknown substratum. Same symbols as in 2.

Fig. 3. — Recrutement rapide avec oscillations et plateau. Source de nourriture: 0,1 ml de sucrose 1 M, nid B, substrat inconnu. Mêmes symboles qu'en 2.

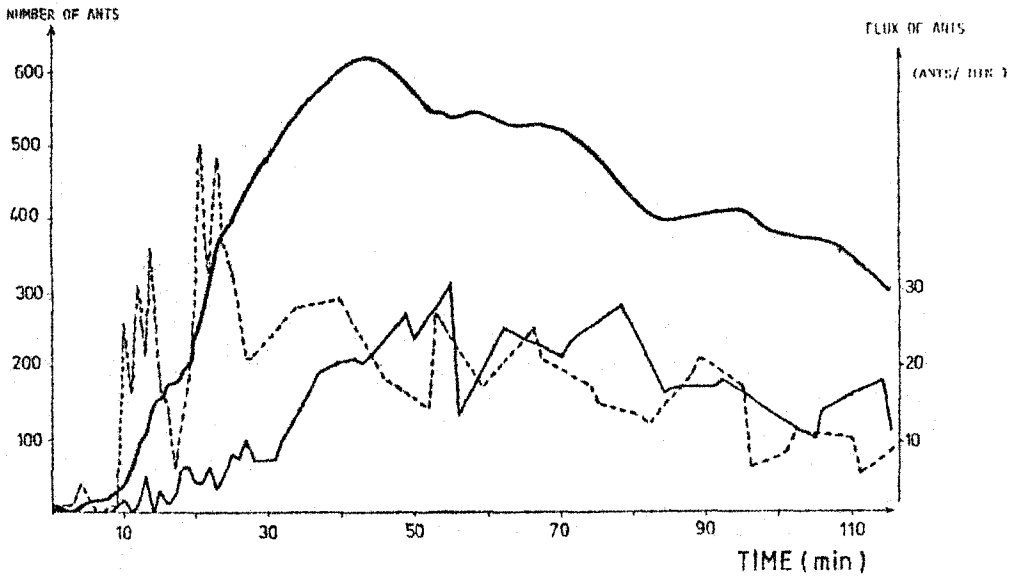


Fig. 4. — Explosive recruitment. Food source: 0.1 ml of 1 M sucrose, nest B, known substratum. Same symbols as in 2.

Fig. 4. — Recrutement de type explosif. Source de nourriture: 0,1 ml de sucrose 1 M, nid B, substrat connu. Mêmes symboles qu'en 2.

recruitment observed with nest A (low population) is due to the small worker-force. Moreover these curve shows no oscillations.

— The recruitment is slower when it is performed on an unknown substratum than on a familiar one because in the first case, either the ants were lost in arena II or they were more involved in exploratory activities.

— In the explosive recruitment (type III), the food source is exhausted before the recruitment reaches the plateau as confirmed by our direct observations on the food source itself.

Similar results have been observed by WILSON (1962) and SUDD (1960) in experiments with other species. We intend to reproduce our results with the aid of the mathematical models which are developed in the next section.

### LOGISTIC TYPE MODELS OF GLOBAL RECRUITMENT

#### Basic model

The sigmoidal growth of the population around the food source suggests that the recruitment is ruled by a logistic-type equation. This equation is one of the more simplest examples of an autocatalytic process. Except for the very beginning, in any recruitment, the arrival of an ant at the food source is obviously determined by the fact that it has been recruited, thus finally by the presence in the near past of other workers near the food source.

We assume that starvation is constant during the experiments. The quantity of food involved reasonably allows such an assumption.

Accordingly, the general equation can be described as :

$$\dot{X} = a X (N - X) - b X \quad (1)$$

where  $X$  is the population at the food source,  $N$  the total population able to participate to the recruitment,  $a$  the recruitment rate and  $b$  the departure rate. When the food source is discovered by chance, we are in the situation where  $X$  begins to be different from zero but still small. Afterwards, the population around the food source increases. This growth is only possible if :

$$a N - b > 0. \quad (2)$$

This relation shows that the recruitment can only be possible if the size of colony  $N$  and the recruitment rate  $a$  are sufficient (2 is not everytime verified for the small colony A, see *table I*). The temporal evolution of  $X$  is described by :

$$\dot{X} = \frac{(N - b/a)}{1 + C \cdot \exp(- (a N - b) t)} \quad (3)$$

$$\text{with } C = \frac{N - b/a - X(0)}{X(0)} \quad X(0) : \text{initial population in A II}$$

*Figures 5 and 6* show the fitting of the experiments illustrated in *figures 2 and 3*. These curves have been fitted by eye as well as the following. However the first estimation of the values of the parameters have been computed from *table I*.

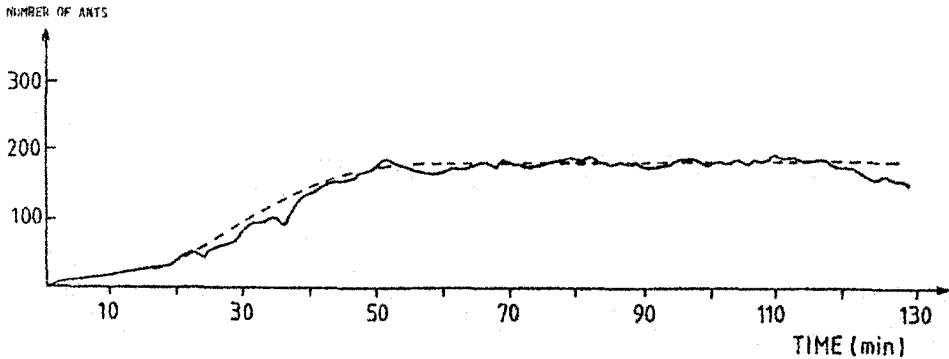


Fig. 5. — Fitting of experiment (*fig. 2*) with equation 1. Value of parameters:  $N = 270$ ,  $a = 8 \cdot 10^{-4}$ ,  $b = 72 \cdot 10^{-3}$ . Experiment: heavy line. Fitting: dashed line.

Fig. 5. — Ajustement de l'expérience (*fig. 2*) avec l'équation 1. Valeur des paramètres:  $N = 270$ ,  $a = 8 \cdot 10^{-4}$ ,  $b = 72 \cdot 10^{-3}$ . Expérience: trait continu. Ajustement: trait discontinu.

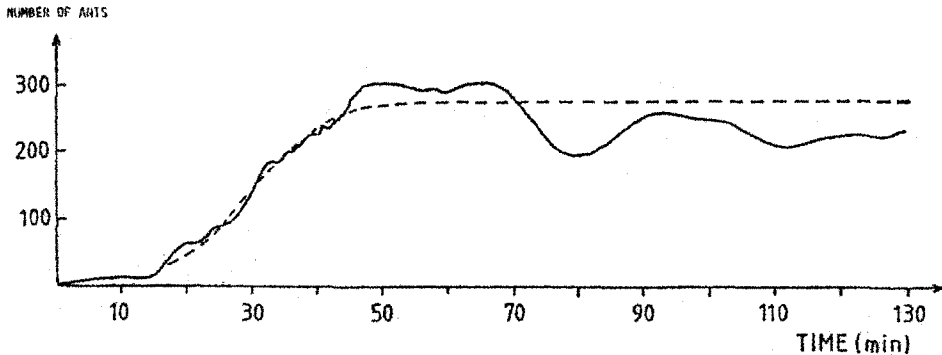


Fig. 6 a

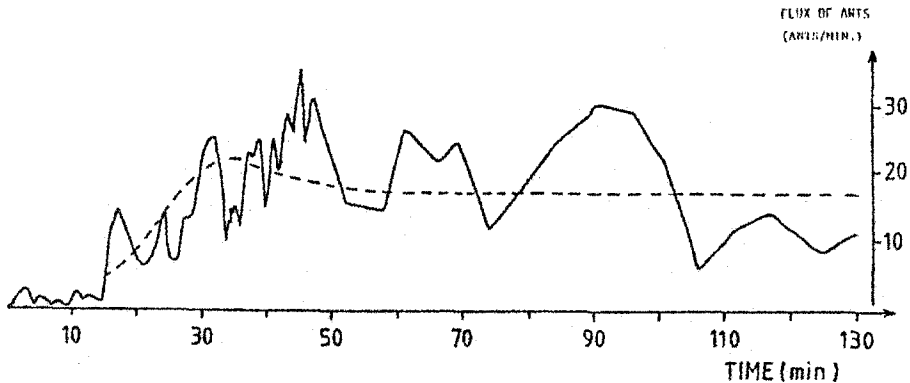


Fig. 6 b

Fig. 6. — Fitting of experiment (*fig. 3*) with equation 1. 6 a) Population around the food source. 6 b) Incoming flux. Value of parameters:  $N = 370$ ,  $a = 5.5 \cdot 10^{-4}$ ,  $b = 65 \cdot 10^{-3}$ . Experiment: heavy line. Fitting: dashed line.

Fig. 6. — Ajustement de l'expérience (*fig. 3*) avec l'équation 1. 6 a) Population à la source. 6 b) Flux d'entrée. Valeur des paramètres:  $N = 370$ ,  $a = 5,5 \cdot 10^{-4}$ ,  $b = 65 \cdot 10^{-3}$ . Expérience: trait continu. Ajustement: trait discontinu.

These examples show that it is possible to determine the range value of the part of the colony involved in the recruitment  $N$  and also the approximate values for  $a$  and  $b$ .

#### Model with food exhaustion

The model previously described is correct up to the point when the food is exhausted. Afterwards the evolution of the system is only described by the flow of departing animals:  $-bX$ . Such an assumption is only correct for tandem and group recruitment. For mass recruitment, the memory effect of the trail allows the recruitment to persist after the exhaustion of the food. Taking these effects into account, the system becomes:

$$\dot{X} = aX(N - X) - bX \quad \text{Food source} > 0. \quad (4.a)$$

$$\dot{X} = -bX \quad \text{Food source} = 0. \quad (4.b)$$

So the system follows, the equation (3) as a solution between the discovery of the food source and its exhaustion  $T_f$  which is given by:

$$T_f = \frac{\text{Ln}(\exp(aD/zb)(1+C) - C)}{a(N - b/a)} \quad (5)$$

where  $C$  is the same as in (3),  $z$  is the amount of food transported by an ant and  $D$  is the initial dimension of the food source.

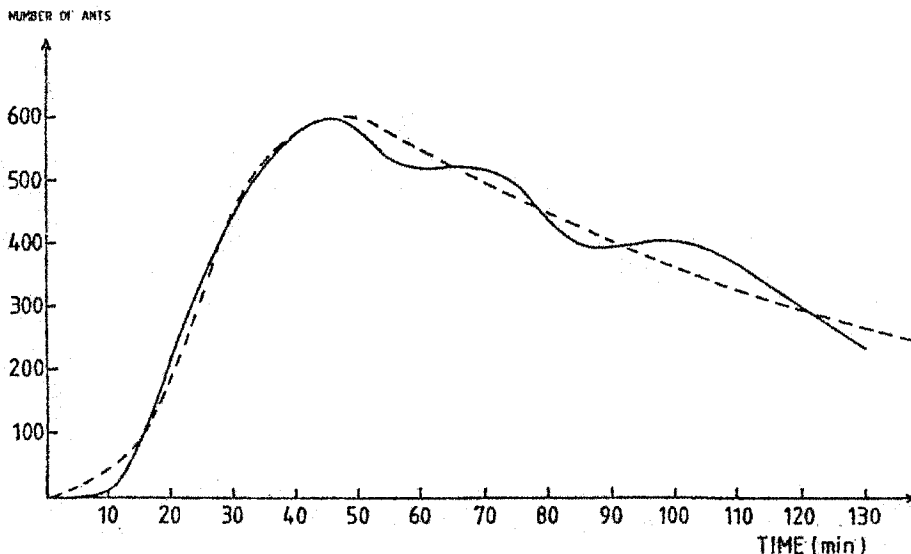


Fig. 7. — Fitting of experiment (*fig. 4*) with equations (10). Value of parameters:  $N = 650$ ,  $D = 0.1$  ml,  $a = 3.2 \cdot 10^{-4}$ ,  $z = 0.39$  mm<sup>3</sup>,  $b = 16 \cdot 10^{-3}$ . Experiment: heavy line. Fitting: dashed line.

Fig. 7. — Ajustement de l'expérience (*fig. 4*) avec les équations (10). Valeur des paramètres:  $N = 650$ ,  $D = 0,1$  ml,  $a = 3,2 \cdot 10^{-4}$ ,  $z = 0,39$  mm<sup>3</sup>,  $b = 16 \cdot 10^{-3}$ . Expérience: trait continu. Ajustement: trait discontinu.

Afterwards the system follows an exponential decay. *Figure 7* shows the fitting of the experiment illustrated in *figure 4*, in which the food is rapidly exhausted. The model assumes the disappearance of the input flow. The experimental curve does not show this phenomenon (cf. *fig. 4*, dashed line): in *Tetramorium*, group recruitment is followed by mass recruitment when the trail is strong enough.

The comparison of the fitting illustrated in the *figures 6 and 7* shows that the value of  $N$ , for the same colony, is much more large on a known area than on an unknown.

Analysing experimental data with the help of this model allows one to quantify the influence of the experimental conditions (i.e. quantity, size, location of the food source...) as far as the more significant parameters are concerned (i.e. recruitment rate, number of possible recruits). Such studies should give quantitative bases for the comprehension of how each species modulates its individual and global behaviour according to the circumstances, and for the comparison of strategies in different species.

## OSCILLATIONS DURING THE RECRUITMENT

Two kinds of oscillations were observed in the recruitment :

- 1) High frequency oscillations (a few min. between two peaks) in the incoming and outgoing flux which appear essentially during the growth phase of the recruitment (*fig. 2, 3, 4*).
- 2) Low frequency oscillations (30-40 min. between two peaks) which are only observed during the recruitments in which a high number of ants are involved (compare the *figures 2 and 3*).

### Oscillations of high frequency

We assume that these oscillations are induced by the time-delay  $\beta$  between the moment a recruiter drank and the moment when a group of recruits reached the food source. To take this time-delay into account, the equation for the flow of arriving ants (see 1) becomes a  $X(t - \beta)(N - X)$  and the evolution time of  $X$  becomes :

$$\dot{X} = a X(t - \beta)(N - X) - b X \quad (6)$$

The properties of equation (6), which is more realistic than (1), are very similar, except for the presence of damped oscillations (AGUR and DENEUBOURG, in preparation).

The fitting of the experimental data to this model gives good agreement for the evolution in time of  $X$  but not for the flows between the nest and the food source. The fitting could be improved if we replace  $\beta$  by a distribution of the time delay.

### Oscillations of low-frequency

WILSON (1962) in recruitment experiments on *Solenopsis invicta* (= *sævis-sima*) has postulated the importance of the interaction between crowding around the food source and the recruitment. He showed that the crowding induces a gap in the recruitment because an ant which does not test the food does not recruit [this statement verified by WILSON for *Solenopsis*, and by JAFFE and HOWSE (1979) for *Atta* is also true for *Tetramorium*, VERHAEGHE (1982)]. We assume that the low-frequency oscillations observed in *Tetramorium* are the result of the interaction between crowding around the food source and recruitment in the nest.

In the model, we have made the following simple assumptions :

- The evolution of the recruitment follows equation (1), but now  $a$  is replaced by a function of  $S$  which is the part of the border of the food source occupied by the ants.
- $S$  is controlled by two terms, namely the flow towards the food source ( $u X$ ) and the departure of ants from the food source ( $g S$ ).  $g$  is defined as an ant's drinking time.

(1) is now replaced by a system of two equations, one for the ants, and one for  $S$  :

$$\dot{X} = \frac{a X}{1 + (S/P)^n} (N - X) - b X \quad (7,a)$$

$$\dot{S} = u X - g S \quad (7,b)$$

$P$  is a measure of the number of ants able to drink at the food source at the same time. The dependence of the rate of recruitment on crowding increases with  $n$ . A small  $n$  means that the ants spend a short time seeking a free place at the food source.

The non-trivial stationary state is given by :

$$S = \frac{u X}{g} \quad (8,a)$$

where  $X$  is the real positive root of the equation :

$$-q X^n - X + (N - \frac{b}{a}) = 0, \quad \text{where } q = \frac{b u n}{a g n n} \quad (8,b)$$

If  $a N - b > 0$ , there is one and only one real positive root of  $X$ . We see from (8,b) that when  $P$  is large, crowding does not affect the stationary state which is then the same as that of equation (1). Linear stability analysis shows that this state is always stable (NICOLIS and PRIGOGINE, 1977).

If the following condition is verified :

$$W = \left( g - \frac{a X}{1 + (S/P)^n} \right)^2 - \frac{4 g b n (S)^n}{(1 + (S/P)^n)^2 P n} < 0 \quad (9)$$

the state is a stable focus and thus is reached with damped oscillations. The rate of damping and the frequency of this oscillation are respectively :

$$0.5 \left( g + \frac{a X}{1 + (S/P)^n} \right) \tag{10,a}$$

$$0.5 (-W)^{0.5} \tag{10,b}$$

If (9) is not verified, the stationnary state is a stable node and it is reached monotonically (no oscillations).

The results obtained with this model are in satisfactory agreement with the experiments shown in *figure 3* (see *fig. 8* for the simulation) but new experiments are needed to make more precise assessments of the values of *n* and *P* in this particular experimental situation.

NUMBER OF ANTS

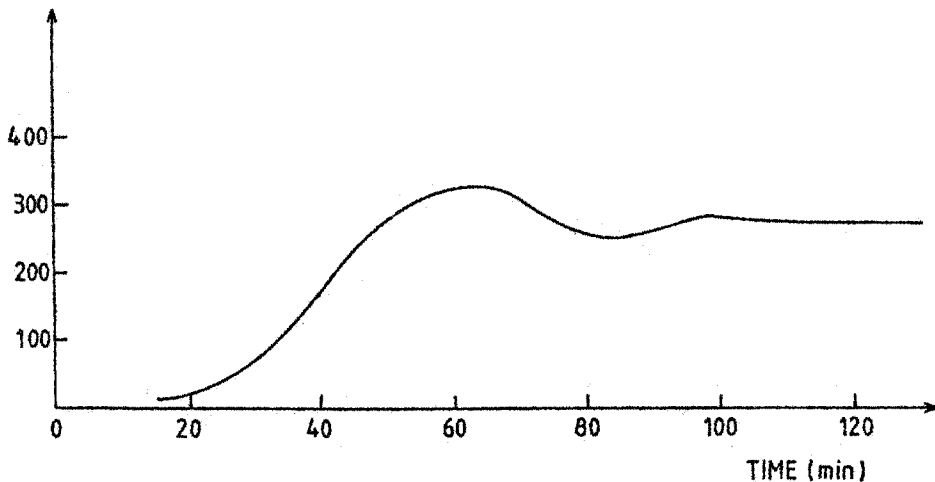


Fig. 8. — Recruitment with damped oscillations (equations 8). Value of parameters :  $N = 500, a = 4 \cdot 10^{-4}, b = 60 \cdot 10^{-3}, u = 5 \cdot 10^{-2}, g = 7 \cdot 10^{-2}, P = 200, n = 20.$

Fig. 8. — Recrutement avec oscillations amorties (equations 8). Valeur des paramètres :  $N = 500, a = 4 \cdot 10^{-4}, b = 60 \cdot 10^{-3}, u = 5 \cdot 10^{-2}, g = 7 \cdot 10^{-2}, P = 200, n = 20.$

The relation (9) shows that when *P* becomes large in comparison with *N*, the oscillations disappears. The period increases when *N* decreases, and for low values of *N*, there are no oscillations. These two effects are verified in the experiment illustrated in *figure 2*. Similarly, when the maximum rate of recruitment *a* is low, the oscillations do not appear. From this result, it is clear that low-frequency oscillations should not occur in colonies characterized by either being of small size or having a low rate of recruitment as with the species which use tandem recruitment.

This model confirms basic's hypothesis : the low frequency oscillations are induced by the interplay between crowding and recruitment. Moreover the model clarifies the relations between the different parameters (rate of recruitment, colony size, food source dimension, behaviour of ants at the food source) and the characteristics of the oscillations. These oscillations themselves are of lesser interest but as they are a consequence of homeostatic mechanisms which allow the society to adapt its recruit-force to the characteristics of food sources, we think they deserve a special study. The efficiency of the homeostatic mechanisms could be test with the help of this model.

### DISCUSSION AND PERSPECTIVES

De BRUYN (1977) and BARONI-URBANI (1979) published equation (1) as a model for food recruitment but without comparison with experimental data. MAEBELIS (1979) assessed the existence of a recruitment process in the emigration of *Formica polyctena* by using a similar model to simulate field observations.

JAFFE (1980) uses computer simulation in his work on recruitment in *Atta cephalotes* which is based on a preliminary experimental work by JAFFE and HOWSE (1979). One of their results, in striking contrast to our work and the other authors, is that the number of ants recruited to the food source is not dependent on the number of ants which leave the food source and return to the nest to recruit nestmates. For JAFFE and HOWSE the mass recruitment mechanism probably includes the following components: an ability of ants to detect the concentration of pheromone on the trail and to relate it to the attractiveness of the food; feed backs of the food quality, of the degree of starvation, of the trail concentration and of the density of ants on the trail on the individual trail laying activity.

TAYLOR (1977, 1978) proposes a model of foraging behaviour in which the society tends to maximise its net energy intake as a function of the characteristics of the trophic area.

The models discussed above as well as those presented in this paper deal with simple situations. However, they can be the primer for more complex and realistic developments.

A multiple food-source situation is frequent in the field. In this case the equation (1) is replaced by a system of  $n$  equations: one equation per population of ants exploiting each food source. The exploitation of each food source is characterised by one  $a_i$  and one  $b_i$ , which have the same meaning as that of  $a$  and  $b$  in (1). If the distance between food and nest diminishes or the food source is richer, the ratio  $a : b$  will be higher. From the properties of the logistic equation the source which possesses the best  $a : b$  ratio will be selected. So by this simple mechanism of communication-

competition the colony will be able to exploit the "best" source. This has been verified experimentally by PARRO (1981).

The optimal exploitation of the whole trophic field is a compromise between two antagonistic requisites. The first is the necessity to perform an efficient recruitment. The better mechanism is the more deterministic. If a worker loses its way on the trail it cannot participate in the exploitation of the food source. The second is the ability to discover a new food source. In this case, the more noise in the recruitment process, the better. A worker, having lost its way, is now able to discover a new food source and hence to extend the resources of the society. A model dealing with these two requisites is published in separate papers (PASTEELS *et al.*, 1982; DENEUBOURG *et al.*, 1983).

Another problem, exemplified by some authors (De VROEY, 1979; BARONI, URBANI and KANNOVSKI, 1974), lies in the study of the competition for a trophic field by colonies belonging to different species. The continuous or alternative occupation of food sources observed by these authors could possibly be explained in terms of competition of different adaptive recruitment strategies and could be described by systems of equations of type (1).

ACKNOWLEDGEMENTS. — We would like to thank Professors NICOLIS, PASTEELS and FRIGOGNE, Dr. D. KAHN and Dr. Goss for their suggestions and constant interest, and Mr. KINET for helping us to prepare figures.

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