



Emerging Patterns and Food Recruitment in Ants: an Analytical Study

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A model of food recruitment by social insects accounting for the competition between trails in the presence of an arbitrary number of sources is developed and analysed in detail. Both the case of identical environmental characteristics and the case where one source and the corresponding trail are different from the others are considered. Different collective responses depending on the environmental conditions, and without change of individual behaviour, are shown to exist, associated with the possibility that the colony may be led to exploit one source or a group of sources preferentially. The full bifurcation diagram of steady-state solutions is constructed from which the dominant exploitation patterns are identified. The biological relevance of the results is discussed and suggestions are made for their experimental testing in connection with the recruitment behavior of species using trail recruitment. The same phenomenological model can be used for different trail-laying species since the predictions are generic and not restricted to a given species, except for the parameter values used.

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1. Introduction

Amplifying communications occupies an important place in the organization of animal societies and, most particularly, in social insects. From a theoretical point of view, amplification implies interaction between at least two individuals and is therefore expected to introduce to the dynamics a nonlinear element (Nicolis & Prigogine, 1977) that could in principle be manifested at the level of the society as a whole in the form of complex collective spatio-temporal phenomena. Since nonlinearity generally implies multiplicity, these phenomena cannot in principle be predicted without appealing to mathematical modeling linking the characteristics of individual behavior to the collective response (Deneubourg

& Goss, 1989; Bonabeau *et al.*, 1997; Theraulaz & Spitz, 1997; Camazine *et al.*, 1999; Detrain and Deneubourg, 1999).

One of the most intensely studied cases of communication is food recruitment. Depending on the species, different processes may be involved. In bees, it implies direct interactions between individuals (Camazine & Sneyd, 1991; Seeley *et al.*, 1991; Seeley, 1995). In ants, recruitment is primarily ensured by chemical means (Sudd, 1957; Wilson 1962, 1971; Hölldobler & Wilson, 1991; Robson & Traniello, 1995). In the present paper, we will be concerned by recruitment in ant societies associated with foraging. Here a scout having discovered a food source returns to the nest, laying a pheromonal trail which stimulates the inactive foragers waiting in the nest (Fig. 1). These recruits can become recruiters in their turn.

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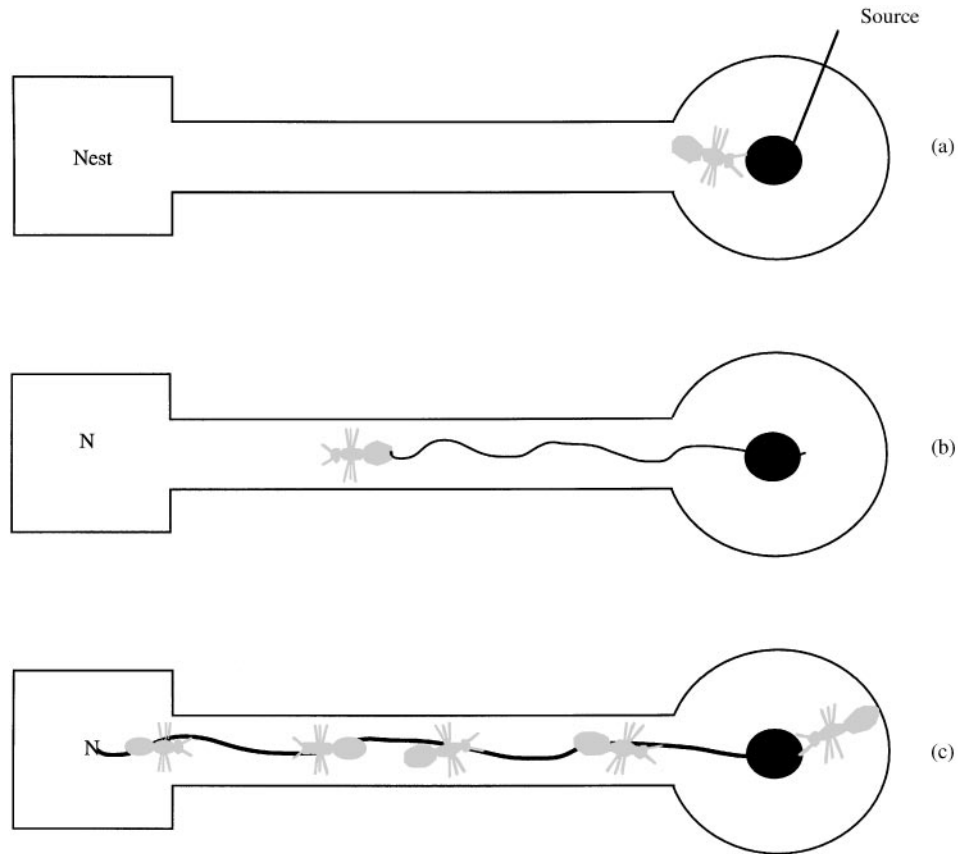


FIG. 1. Schematic representation of the recruitment process: (a) discovery of the source, (b) return to the nest while laying a trail, (c) trail stimulates individuals to leave the nest toward the source.

Roughly speaking, two types of phenomena are at work during this type of recruitment:

- A first mechanism, where the recruiter and/or the trail stimulate the inactive foragers waiting in the nest to leave it (worker ant recruitment).
- A second mechanism, only due to the trail, which guides the recruited ants and transmits the information concerning the location of the food source (trail recruitment).

As recruits can become recruiters in their turn, both mechanisms are gradually amplified.

It has been shown that a pheromone trail alone is able to stimulate forager ants to leave their nest (Wilson, 1962), but in most cases, both recruiters and trail are involved. On the other hand, for the orientation to be followed, the situation is much more simple: the trail alone is involved and the recruiter is not needed to guide the recruits.

An important step in the understanding of recruitment behaviour has been the design of experiments in deliberately idealized situations, in which many of the complications present in the real world can be eliminated. This has also facilitated the development of mathematical models in which the parameters can be determined directly from the experiment. In this context, detailed experimental studies reported by several authors (Pasteels *et al.*, 1987; Beckers *et al.*, 1992b; Robson & Traniello, 1995; Detrain & Deneubourg, 1997) showed unexpected behavior when two food sources—or two paths—were simultaneously made available. In particular, the competition between the two chemical trails leading to the sources gave rise to a bifurcation phenomenon, in which one of the trails attracted most of the population and pre-dominated clearly over the other.

Several models aiming to study the influence of different parameters on this behaviour have been

proposed in the literature. Different methods of analysis have been applied, such as numerical solutions of the differential equations describing the evolution of the relevant variables or Monte Carlo type of simulations (see e.g. Edelstein-Keshet *et al.*, 1995; Watmough & Edelstein-Keshet, 1995; Stickland *et al.*, 1992, 1993, 1995). In the present paper, a model capable of accounting for the competition between trails in the presence of an *arbitrary* number of sources is proposed and analysed in detail. The model extends that previously proposed and tested experimentally by Beckers *et al.* (1992a), Deneubourg *et al.* (1990) and Goss *et al.* (1989) for species using trail-laying recruitment, which was limited to two food sources or two paths. In particular, the different types of steady-state solutions are identified and their stability properties studied. This allows us to construct the full bifurcation diagram. As will be shown, the colony may be led to exploit only a subset of sources. The model accounts not only for the environmental features such as the number and quality of sources but also for social and physical parameters such as the flux of individuals, the quantity of pheromone deposited on a trail, and its rate of evaporation. We will be interested both in the case of a homogeneous environment and in the case where one of the sources is different from the others.

The model is introduced in Section 2 where the problem of stability is also formulated in the most general case. In Section 3 the steady-state solutions and their stability are studied in the case where the physical and chemical characteristics of the sources and trails leading to them are identical. In Section 4, the case where the characteristics of one of the sources and of the corresponding trail are different from the others is considered. On the basis of the results obtained, a number of concrete, quantitative predictions are made in these two sections for recruitment behavior of ants using trail recruitment, using, as an example, experimentally determined parameter values for the species *Lasius niger*. The procedure also applies to other ant species undergoing similar types of recruitment, the only difference being the parameter values. The main conclusions are summarized in Section 5.

2. The Model

We concern ourselves only with the case of trail recruitment (see Introduction). We analyse the traffic among these trails and, in particular, identify those that will be followed in a preferred manner. One may reasonably expect that the direct interaction between individuals is then superseded by their response to the pheromone concentration present in a given trail. Thus, in the framework of such a “macroscopic”, description the principal variables will be the pheromone concentration rather than the number of individuals present on the various trails, at a given time. A schematic representation of the setup and the associated processes is given in Fig. 2(a). The outgoing flux from the nest [$\phi(R, c)$], depending of the nest size, is a function of the quantity of trail pheromone (c) and the number of recruiters (R) inside the nest. However, these two variables are strongly correlated because if a recruiter comes back, it adds automatically pheromone on the trail, and we shall consider that the flux is only a function of the concentration of pheromone, $\phi = \phi(c)$. An empirical equation which seems to fit well with experimental data is (Beckers *et al.*, 1992a)

$$\phi(c) = \frac{a + bc^2}{a' + b'c^2}. \quad (1a)$$

Beckers *et al.* observed that ants lay a pheromone trail only after ingesting food. The recruited ants thus do not lay a trail on their first trip between the nest and the food source, but ants which leave the nest for their subsequent foraging also lay trail between the nest and the food source. To increase still the complexity of the problem, after a certain number of trips ants may stop laying trail, despite the fact that they are still foraging (Beckers *et al.*, 1993). It follows that between a departure from the nest and an increase of pheromone there is a time delay τ (one round trip plus time in the nest plus loading time). The increase of trail concentration at time t is then the proportional to the flux at time $t - \tau$. As it turns out, taking into account this delay does not change the basic features of the dynamics but may merely give rise to damped

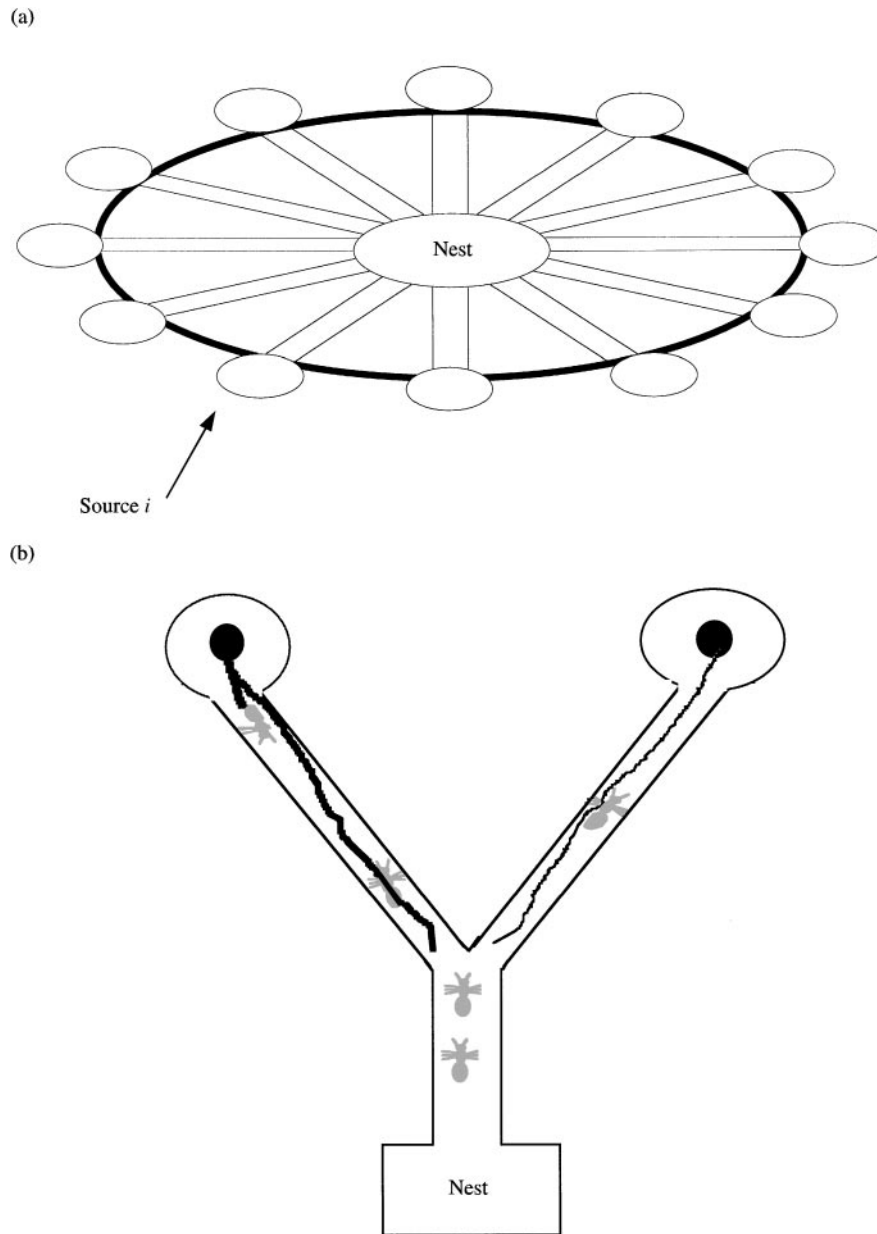


FIG. 2. (a) Setup proposed for experimental test of the model. The sources are placed around the nest and are accessible through paths of identical texture. (b) Schematic representation of the choice between two identical paths, once the individuals left the nest.

oscillations under certain conditions (see, e.g. Verhaeghe & Deneubourg, 1983). Since time delays (min) are negligible compared to the time-scale of the dynamics (hr), in the rest of this paper we will assume that the flux parameter ϕ is a constant. One may check that there are no effects on

stationary solutions and their stability resulting from this simplification.

Under natural conditions or in experimental setups, ants have a choice between trails [Fig. 2(b)]. The model is mainly devoted to this orientation choice, for which the trail alone is

involved and the recruiter is not needed. Let c_i be the pheromone concentration on trail $i = 1, \dots, s$. The rate of change of c_i with time can be decomposed into two parts. A first, positive contribution reflecting the “birth” of trail i through the deposition of pheromone by the individual provided the food source is suitable; and a second, negative contribution describing the “death” of the trail via progressive disappearance of the pheromone through evaporation

$$\frac{dc_i}{dt} = \phi \sigma_i F_i(\{c_i\}) - v_i c_i, \quad i = 1, \dots, s. \quad (1b)$$

Here ϕ is the total ant flow from the nest toward the trails (taken to be a constant as discussed above), σ_i the quantity of pheromone deposited on the trail i (in turn, an increasing function of the quality of the food source), v_i the corresponding evaporation rate and $F_i(\{c_j\})$ a function describing the relative attractiveness of trail i over the others. It is reasonable to assume that this function increases with increasing values of c_i and eventually saturates at a plateau value as c_i gets very large. The particular form chosen here is (Deneubourg *et al.*, 1990)

$$F_i = \frac{(k + c_i)^l}{\sum_{j=1}^s (k + c_j)^l}. \quad (1c)$$

Here s is the total number of sources and k , a concentration threshold beyond which the pheromone laid on a trail begins to be effective. The parameter l measures the sensitivity of the process of choice of a particular trail on the pheromonal concentration c_i present, and will be therefore be referred to hereafter as “cooperativity parameter”. This function has been applied and quantified in the case of different species, in particular *Lasius niger* (Beckers *et al.*, 1992a,b, 1993), *Linepitema humile* (Deneubourg *et al.*, 1990; Goss *et al.*, 1989), army ants (Franks, 1986; Franks *et al.*, 1991) and *Messor pergandei* (Rissing & Wheeler, 1976; Goss & Deneubourg, 1989), and tested in different situations. It is a generic function to describe the choice between paths in terms of the concentration of pheromone. Recall that the interactions among recruits in the trails do not figure in the model.

This model accounts for three types of feedback:

- A positive, nonlinear feedback of trail i onto itself through the function F_i .
- A negative, linear, feedback of trail i onto itself through the evaporation of the pheromone.
- A negative, nonlinear feedback of trail $j \neq i$ onto trail i associated with competition.

It is convenient to introduce scaled variables and parameters through the transformation

$$C_i = \frac{c_i}{k}, \quad q_i = \frac{\sigma_i}{k}, \quad \Phi = \frac{\phi}{v}.$$

Furthermore, we assume that the environment and the substrate are homogeneous. We thus subsequently set all v_i equal to a common value v which, by normalizing time, can be set to $v = 1$. Equations (1b) and (1c) reduce then to the system

$$\frac{dC_i}{dt} = \Phi q_i \frac{(1 + C_i)^l}{\sum_{j=1}^s (1 + C_j)^l} - C_i. \quad (2)$$

In the sequel, the parameter l will be fixed to a value $l = 2$ compatible with the experiment (Beckers *et al.*, 1992b, 1993). The solutions of eqn (2) will therefore depend entirely on the parameters Φq_i and on s .

We shall be especially interested in the steady-state solutions. Setting the time derivative to zero and dividing the equations as applied to the trails i and j one obtains

$$\frac{q_i(1 + C_i)^2}{q_j(1 + C_j)^2} = \frac{C_i}{C_j} \quad (3a)$$

and

$$\sum_{j=1}^s (1 + C_j)^2 = \Phi q_i \frac{(1 + C_i)^2}{C_i}. \quad (3b)$$

Typically, these equations admit multiple solutions $\{C_{i, st}\}$. In what follows, we shall therefore be led to test the stability of these different branches in order to determine the state that will actually be chosen by the system. Setting $C_i = C_{i, st} + \delta C_i$ and linearizing eqns (2) with

respect to the perturbations δC_i , we obtain the following set of equations:

$$\frac{d\delta C_i}{dt} = \sum_k A_{ik} \delta C_k, \tag{4a}$$

with

$$A_{ik} = -\frac{2C_i^2(1 + C_k)}{\Phi q_i(1 + C_i)^2} + \frac{C_i - 1}{1 + C_i} \delta_{ik}^{kr} \tag{4b}$$

where we used eqn (3). For simplicity, we have dropped the index “st” from C_i since it is understood that all these coefficients are to be evaluated in the steady state.

As well known (Nicolis, 1995), the characteristic exponents determining the stability of the stationary state are given by the eigenvalues of the Jacobian matrix $\{A_{ik}\}$ or, equivalently, by characteristic equation

$$\det|A_{ij} - \omega \delta_{ij}^{kr}| = 0. \tag{4c}$$

The stability condition is $\text{Re } \omega_i < 0$ for all i . Notice that for $l = 1$ there is only one steady-state solution of eqns (2), which is always stable.

3. The Case of Identical Sources and Trails

We shall first deal with the case where the food sources presented to the colony are identical and the trails leading to them have the same physical characteristics, $q_i = q$ for all i . Equations (2) admit then a first type of stationary solution, the *homogeneous* solution, in which all sources are exploited in an identical manner:

$$C_i = \frac{\Phi q}{s} = C. \tag{5}$$

To test the stability of this solution we introduce these relations along with $q_i = q$ into eqn (4b). One checks then easily that the elements of the Jacobian matrix $\{A_{ik}\}$ in eqn (4) can only take two different values

$$A_{ii} = a = \frac{-2\Phi q}{s(\Phi q + s)} + \frac{\Phi q - s}{\Phi q + s},$$

$$A_{ij} = b = \frac{-2\Phi q}{s(\Phi q + s)}.$$

The characteristic equation (4c) takes the form

$$(\omega - (a + (s - 1)b))(\omega - (a - b))^{s-1} = 0.$$

We obtain a first solution

$$\omega_1 = a + (s - 1)b = -1 < 0 \tag{6a}$$

which is always stable, and a group of $s - 1$ degenerate ones

$$\omega_{2 \dots s} = a - b = \frac{\Phi q - s}{s + \Phi q}. \tag{6b}$$

We conclude that the homogeneous solution may lose its stability, the instability condition being $\Phi q > s$. When this happens new stationary solutions must take over, which are necessarily non-homogeneous.

It is easy to show from eqns (2) that the only such solutions are *semi-inhomogeneous* ones in which j trails having a concentration C_1 are exploited in a different manner with respect to the other $s - j$ ones having a concentration C_2 . These steady-state concentrations are given by

$$C_1^\pm = \frac{\Phi q}{2j} \pm \frac{1}{2} \sqrt{\left(\frac{\Phi q}{j}\right)^2 - 4\left(\frac{s-j}{j}\right)} \tag{7a}$$

with

$$C_2^\mp = \frac{1}{C_1^\pm} = \frac{\Phi q - jC_1^\pm}{(s-j)}, \quad j = 1, \dots, s/2$$

$$\text{for } s \text{ even or } (s + 1)/2 \text{ for } s \text{ odd.} \tag{7b}$$

Here the superscripts $+$ and $-$ correspond, respectively, to a trail that is more heavily or less heavily marked by the individuals. These solutions exist as long as

$$\Phi q \geq 2\sqrt{(s-j)j}. \tag{8}$$

To determine stability we consider separately the cases $j = 1$ and $j > 1$.

3.1. THE CASE $j = 1$

The elements of the Jacobian matrix $\{A_{ik}\}$ in eqn (4a) can now take five distinct values

$$\begin{aligned}
 A_{11} = a_1 &= \frac{2(s-1)}{\Phi q(1+C_1)} - 1, \\
 A_{ii} = a_2 &= \frac{2\left(C_1 + \frac{(s-2)}{C_1}\right)}{\Phi q(1+C_1)} - 1, \\
 A_{1i} = b_1 &= -\frac{2C_1}{\Phi q(1+C_1)}, \\
 A_{i1} = b_2 &= \frac{b_1}{C_1}, \\
 A_{ij} = c &= \frac{2}{\Phi q(1+C_1)C_1}, \\
 & i, j > 1, \quad i \neq j. \tag{9}
 \end{aligned}$$

The characteristic equation takes the form

$$\begin{aligned}
 (\omega - a_2 + c)^{s-2}(\omega^2 - (a_1 + a_2 + (s-2)c)\omega \\
 + a_1a_2 + a_1c(s-2) - (s-1)b_1b_2) = 0. \tag{10}
 \end{aligned}$$

A numerical evaluation of the roots of this equation reveals that the high concentration C_1^+ is always stable while the low concentration C_1^- is always unstable.

3.2. THE CASE $j > 1$

There are now six distinct elements of the Jacobian matrix $\{A_{ik}\}$ in eqn (4a):

$$\begin{aligned}
 A_{ii} = a_1 &= -\frac{2C_1^2}{\Phi q(1+C_1)} + \frac{C_1-1}{1+C_1}, \\
 A_{kk} = a_2 &= -\frac{2}{\Phi qC_1(1+C_1)} + \frac{1-C_1}{1+C_1}, \\
 A_{ik} = b_1 &= -\frac{2C_1}{\Phi q(1+C_1)},
 \end{aligned}$$

$$\begin{aligned}
 A_{ki} = b_2 &= -\frac{2}{\Phi q(1+C_1)}, \\
 A_{ii'} = c_1 &= -\frac{2C_1^2}{\Phi q(1+C_1)}, \\
 A_{kk'} = c_2 &= -\frac{2}{\Phi qC_1(1+C_1)}, \\
 & 1 \leq i, i' \leq j; i \neq i', \\
 & j+1 \leq k, k' \leq s; k \neq k'. \tag{11}
 \end{aligned}$$

After some manipulations of the characteristic determinant, one finds that the characteristic equation possesses the following two j and $s-j$ degenerate roots:

$$\begin{aligned}
 \omega_1 = a_1 - c_1 &= \frac{C_1-1}{1+C_1}, \\
 \omega_2 = a_2 - c_2 &= \frac{1-C_1}{1+C_1}. \tag{12}
 \end{aligned}$$

The stability conditions $\omega < 0$ for each of these roots are, clearly, mutually incompatible. We conclude that at least one root of the characteristic equation is positive and hence that the semi-inhomogeneous solutions with $j > 1$ are always unstable.

In summary, the homogeneous solution [eqn (5)] loses its stability at a threshold value of the parameter $\Phi q = s$. As regards the inhomogeneous solutions, only the branch C_1^+ and the corresponding branch C_2^- of the case $j = 1$ are stable. These solutions emerge at critical parameter values given by eqn (8). For $j = 1$ and $s > 2$, each of these values corresponds to a *limit point bifurcation*, one branch of which goes in the (C, q) diagram through the critical point $\Phi q = s$. For s even and $j = s/2$, there is a pitchfork bifurcation of unstable branches emerging from $\Phi q = s$, otherwise all other bifurcations are limit point ones originating on the left of this criticality.

As an illustration, Fig. 3(a) depicts the bifurcation diagram in the case of $s = 4$. The homogeneous state loses its stability at $(\Phi q)_c = 4$, which is

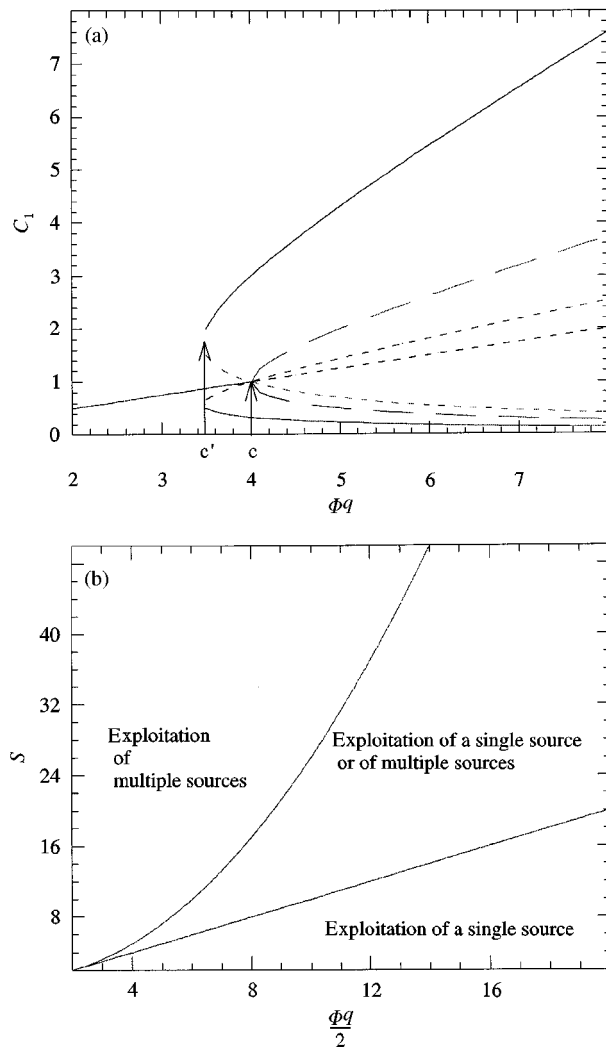


FIG. 3. (a) Bifurcation diagram of the steady-state solutions of eqns (2) in the case of four sources. $(\Phi q)_c$: pitchfork bifurcation point where the homogeneous branch loses its stability. $(\Phi q)_c$: limit point bifurcation. (b) State diagram representing the parameter regions of different modes of exploitation of resources in the case of $\Phi = 10$.

also the locus of a pitchfork bifurcation of two unstable branches (branches corresponding to $j = 2$). The limit points are located at $(\Phi q)_c = 3.5$, generating four semi-inhomogeneous solutions, two of which are stable (the upper and lower branches). In the domain $3.5 < \Phi q < 4$, one therefore has three simultaneously stable solutions whereas for $\Phi q > 4$ only two states are stable.

Figure 3(b) depicts the “state diagram” of the system, showing the range of parameter values corresponding to one or multiple solutions. In

the upper part of the graph, the homogeneous solution is stable and the semi-inhomogeneous ones do not exist, which means that one has equal exploitation of multiple resources. In the lower part, the homogeneous solution is unstable and the semi-inhomogeneous ones exist; in other words, the colony exploits preferentially one resource of the s available, the others being equally visited but nevertheless overwhelmed by the dominant one. Finally, the middle part corresponds to coexistence of multiple source and one preferred source exploitation modes.

3.3. BIOLOGICAL RELEVANCE

We now propose to exploit the results of Sections 3.1 and 3.2 to give ideas of experiments that could lead to the observation of the patterns predicted and summarized in Fig. 3.

It has been shown (Hahn & Maschwitz, 1985) that *Messor rufitarsis* changes its mode of exploitation with the number of sources and their distribution. Both a single heavily marked trail and a more diffuse exploitation can be observed when several sources are present. These results are in qualitative agreement with our predictions, but the situation to which they refer is not identical to ours. It would therefore be important to undertake laboratory experiments creating deliberately the idealized conditions stipulated in the model. A first question to be asked would then be whether there exists a critical number s_c marking the passage from uniform to inhomogeneous exploitation. In terms of the original parameters and variables, this number is given by [cf. eqn (6b)]

$$s_c = \frac{\phi \sigma}{vk}.$$

For the values characteristic of *Lasius niger* (Beckers *et al.*, 1993) ($k = 6$, $1/v = 1500$ s, $\sigma = 1$ (for a good concentration in sucrose of 1 M), $\phi = 0.1$ s $^{-1}$) this gives $s_c = 25$, indicating that the inhomogeneous exploitation will prevail up to this number. In terms of Fig. 3(a), this value of s_c is the intersection of the abscissa $\Phi q = 25$ with the lower curve. It marks the limit between an exploitation of a single preferred source and a mixed exploitation (exploitation of a single

preferred source or an equal exploitation of multiple sources). The intersection of the same abscissa with the upper curve of the figure gives [see eqn (7a)] $s_c = (\phi\sigma/2vk)^2 + 1 \approx 157$, which is very high. We conclude that for these values of Φq , the transition between exploitation of a single source and mixed exploitation is experimentally accessible, whereas the transition between mixed exploitation and equal exploitation of multiple sources is not. Conversely, for a given number of sources, the transition is facilitated by decreasing the size of the colony (parameter ϕ) or the quality of the sources (parameter σ). For parameter values $\phi = 0.05 \text{ s}^{-1}$ and $\sigma = 0.5$ (which correspond to a food source concentration of 0.1 M, in sucrose), we see that the corresponding transition values are respectively $s_c = 6$ and $s_c \approx 11$. This last value, which corresponds to the transition towards the homogeneous exploitation, becomes now experimentally accessible.

Let us comment in some detail on mixed exploitation (region between c and c'). According to Fig. 3(b), mixed exploitation occurs when Φq lies between the limit point bifurcation and the point of loss of stability of homogeneous solution. For these critical points we have [eqns (5)–(7)]

loss of stability of homogeneous solution:

$$\begin{cases} C = \frac{\Phi q}{s}, \\ (\Phi q)_c = s; \end{cases}$$

onset of semi-inhomogeneous solutions:

$$\begin{cases} C_1 = \frac{\Phi q}{2}, \\ C_2 = \frac{2}{\Phi q}, \\ (\Phi q)_i = 2\sqrt{s-1}. \end{cases}$$

We observe that as s increases, C decreases, and C_1 and C_2 remain unchanged. This implies that the distance between the homogeneous branch and the high concentration semi-inhomogeneous branch increases while it decreases for the lower semi-inhomogeneous branch. On the other hand, as s increases, $(\Phi q)_c$

increases faster than $(\Phi q)_c$. As a result, the range of values of Φq where there is coexistence between two modes of exploitation increases. Nevertheless, as pointed out above, the homogeneous branch and the lower semi-inhomogeneous one tend to be indistinguishable. In other words, the passage between an exploitation of one preferred source and an equal exploitation is blurred. In conclusion, in the case of *Lasius niger*, the homogeneous exploitation shall not be often observed except in small colonies and food sources that induce a low trail-laying activity.

4. One of the Sources is Different

We now turn to the more realistic situation where the food sources and/or the physical characteristics of the trails leading to them are not identical. To identify the new features brought about by this change, we limit our analysis to the case where only one of the trails (say 1) is different, all other $s - 1$ trails being identical, $q_2 = \dots = q_s = q$, $q_1 \neq q$. It then follows straightforwardly from eqn (3) that two different types of pheromone concentration C_2, \dots, C_s in the $s - 1$ identical sources can be envisaged, just like in Section 3, eqn (5) and (7): either all of them are identical, $C_2 = \dots = C_s = C_2$, or there are j trails having a concentration $C_2 = \dots = C_{j+1} = C_2$ and $s - j - 1$ trails having a concentration $C_{j+2} = \dots = C_s = C_3$, with $C_3 = 1/C_2$. We hereafter analyse these two cases separately.

4.1. THE CASE $C_2 = \dots = C_s = C_2$

We obtain after some straightforward manipulations a cubic equation for C_1 :

$$\begin{aligned} & \left(1 + \frac{q^2}{(s-1)q_1^2}\right)C_1^3 \\ & + \left(2 - \Phi q_1 - \frac{2\Phi q^2}{(s-1)q_1} - \frac{2q}{q_1}\right)C_1^2 \\ & + \left(2\Phi q + s - 2\Phi q_1 + \frac{\Phi q^2}{(s-1)}\right)C_1 - \Phi q_1 = 0 \end{aligned} \tag{13}$$

with, for C_2 ,

$$C_2 = \dots = C_s = \left(\Phi - \frac{C_1}{q_1} \right) \frac{q}{(s-1)}. \quad (14)$$

Regarding stability, one sees, not unexpectedly, that the Jacobian matrix has just five different elements as in the case $j = 1$ of Section 3:

$$\begin{aligned} A_{11} &= a_1 = \frac{C_1 - 1}{1 + C_1} - \frac{2C_1^2}{\Phi q_1(1 + C_1)}, \\ A_{k1} &= c = -\frac{2(1 + C_1)C_2^2}{\Phi q(1 + C_2)^2} \\ A_{1k} &= b = -\frac{2(1 + C_2)C_1^2}{\Phi q_1(1 + C_1)^2}, \\ A_{kj} &= d = -\frac{2C_2^2}{\Phi q(1 + C_2)}, \\ A_{kk} &= a_2 = \frac{C_2 - 1}{1 + C_2} - \frac{2C_2^2}{\Phi q(1 + C_2)}, \end{aligned} \quad (15)$$

$k, j > 1, \quad k \neq j.$

The characteristic equation has the same structure as in eqn (10). No general statement concerning its solutions can be made, and one has to resort to a numerical evaluation in which the explicit value of C_1 given by eqn (13) is inserted in the expressions (15) from which the ω 's can be computed. This can be done explicitly for $s = 3$ and 4, but for $s > 4$ integration of the full equations in time is also performed, as discussed further below. In all cases considered only the solution branch in which C_1 is dominant turns out to be stable.

Figure 4I(a)–(d) depict, for the parameter value $q_1 = 1$, the bifurcation diagrams of C_1 as a function of the parameter $\varepsilon = q/q_1$ for the values $s = 3, 5, 10$ and 20. We observe an s -shaped curve but no hysteresis, since only one branch (the upper one) is stable. As s increases further the s -shape disappears, and one obtains a monotonic dependence of C_1 on ε : this unique branch of solutions is stable for all values of ε , implying that the richer source always takes over.

Curiously, under the same conditions, the value of C_1 at a given ε steadily decreases. A closer analysis shows that there is no optimal value of s in which the richer source both takes over and is visited by a sizable part of the total population.

4.2. THE CASE $C_3 = 1/C_2$

We obtain now a quartic equation, which is most easily expressed in terms of C_2 rather than C_1 :

$$\begin{aligned} &j \left(j + \frac{q^2}{q_1^2} \right) C_2^4 - \left(2j \frac{q}{q_1} \left(\Phi q_1 + 1 - \frac{q}{q_1} \right) + \Phi \frac{q^3}{q_1^2} \right) \\ &C_2^3 + \left(\frac{q^2}{q_1^2} (s + q_1^2 \Phi^2) + 2j(s - j - 1) + 2\Phi \frac{q^2}{q_1} \left(1 \right. \right. \\ &\left. \left. - \frac{q}{q_1} \right) \right) C_2^2 - \left(2 \frac{q}{q_1} (s - j - 1) \left(\frac{q}{q_1} - 1 + \Phi q_1 \right) \right. \\ &\left. - \Phi \frac{q^3}{q_1^2} \right) C_2 + (s - j - 1) \left(s - j - 1 + \frac{q^2}{q_1^2} \right) = 0 \end{aligned} \quad (16)$$

with, for C_1 ,

$$C_1 = q_1 \left(\Phi - j \frac{C_2}{q} - \frac{(s - j - 1)}{q C_2} \right). \quad (17)$$

Regarding stability, there are now 11 different elements of the Jacobian matrix, given by

$$\begin{aligned} A_{11} &= a_1 = -\frac{2C_1^2}{\Phi q_1(1 + C_1)} + \frac{C_1 - 1}{1 + C_1}, \\ A_{k'k'} &= a_2 = -\frac{2C_2^2}{\Phi q(1 + C_2)} + \frac{C_2 - 1}{1 + C_2}, \\ A_{1k'} &= b_1 = -\frac{2C_1^2(1 + C_2)}{\Phi q_1(1 + C_1)^2}, \\ A_{k''k''} &= a_3 = -\frac{2}{\Phi q(1 + C_2)} + \frac{1 - C_2}{1 + C_2}, \\ A_{1k''} &= b_2 = -\frac{2C_1^2(1 + C_2)}{\Phi q_1(1 + C_1)^2 C_2}, \end{aligned}$$

$$\begin{aligned}
 A_{k'l'} = d_1 &= -\frac{2C_2^2}{\Phi q(1+C_2)}, & 2 \leq k', l' \leq j+1; \\
 & & k' \neq l', \\
 A_{k'1} = c_1 &= -\frac{2C_2^2(1+C_1)}{\Phi q(1+C_2)^2}, & j+2 \leq k'', l'' \leq s; \\
 & & k'' \neq l''.
 \end{aligned}
 \tag{18}$$

As in Section 3, one now has to distinguish between $j > 1$ and $j = 1$. In the first case, by performing the same type of transformation as in Section 3.2, one identifies two roots of opposite sign of that characteristic equation, entailing that this type of solution is always unstable. We may therefore restrict our attention to the case $j = 1$. In this situation, we have zero, two, or four physically acceptable solutions (real positive). Furthermore one can identify, by similar

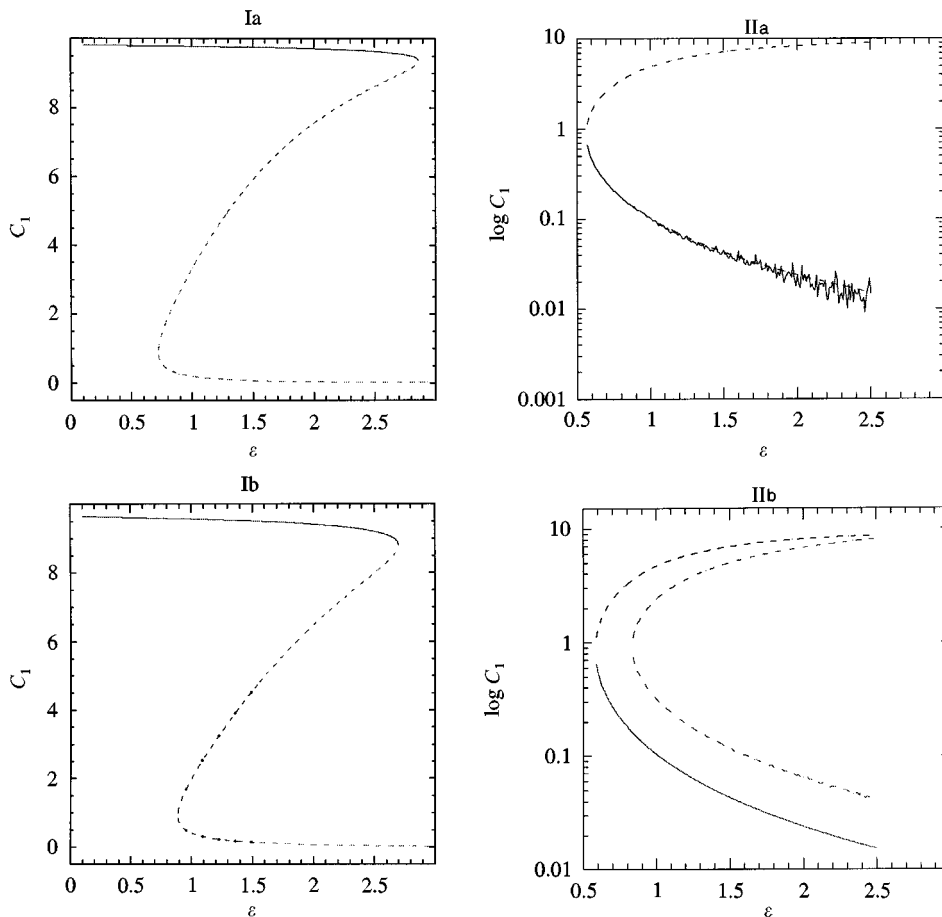


FIG. 4. Bifurcation diagrams of C_1 [eqns (13), (16), (17)] as a function of the parameter $\epsilon = q/q_1$ for 3 sources (a); 5 sources (b); 10 sources (c); and 20 sources (d). The case $C_2 = C_3$ (I) and the case $C_2 = 1/C_3$ (II) are shown in the left and the right panels, respectively. Parameter Φq is equal to 10.

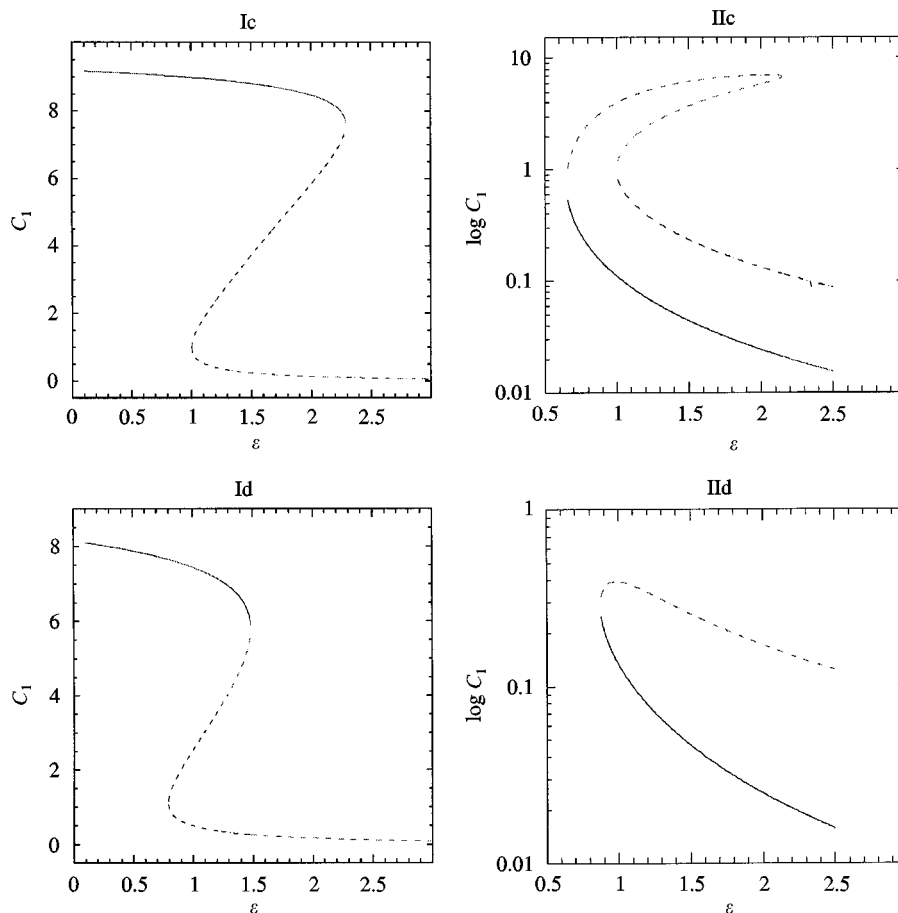


FIG. 4. (Continued)

manipulations as above, one root of the characteristic equation equal to

$$\omega = a_3 - d_2 = \frac{1 - C_2}{1 + C_2}.$$

This implies that the branches with $C_2 < 1$ and hence with large C_1 are always unstable, but does not suffice to guarantee that the branches with $C_2 > 1$ are stable. One must therefore resort again to numerical evaluations, showing that of all the solution branches available only the one with the smallest C_1 (the greatest C_2) is stable.

Figure 4II(a)–(d) depict, for the parameter value $q_1 = 1$, four representative bifurcation diagrams illustrating this behavior corresponding respectively to $s = 3, 5, 10$ and 20 . As s increases further the bifurcation diagram reduces to

a single limit point bifurcation starting at $\epsilon > 1$ with the upper branch unstable and the lower one stable.

Figure 5 shows the “state diagram” of the system with respect to the parameters s and ϵ . The four curves, drawn for four different values of Φ separate the region of one solution of the cubic equation [eqn (13)] and no solution of the quartic equation [eqn (16)] (left part of the curves) from the region of one solution of the cubic equation physically acceptable solutions of the quartic equation (right part of the curves). In more physical terms, these regions correspond, respectively, to exploitation of a preferred source (a single stable solution) and to exploitation of multiple resources (two coexisting stable solutions). We see that as Φ increases, the region of exploitation of a preferred source shifts towards increasing values of ϵ .

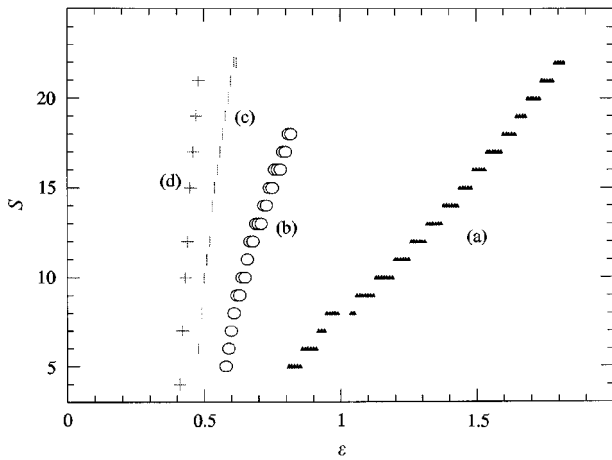


FIG. 5. State diagram representing the parameter regions in the case of $\Phi = 5$ (a); $\Phi = 10$ (b); $\Phi = 15$ (c); $\Phi = 20$ (d) of different modes of exploitation of the resources. The region on the right of the curves corresponds to the exploitation of multiple sources and on the left, to the exploitation of preferential source.

As mentioned above, to confirm the stability of the high and low C_1 branches of Fig. 4I and II in the case of several sources, integration of the full set of eqns (2) in time is also necessary. Figure 6 illustrates two typical outcomes of such an integration for $s = 5$, carried out using a second-order Runge–Kutta method. One starts with initial conditions in which the value of C_1, C_2 and C_3 are close. In the left-hand figure, the parameter ε is such that the solution $C_2 = C_3$, is favored. We see that after a short lapse of time, C_1 takes over and tends to a high value, whereas

C_2 and C_3 tend both to the same low value after a slight overshoot in intermediate times. In contrast, in the right-hand figure, the parameter ε is such that $C_3 = 1/C_2$ is favored. We see that C_2 now takes over, whereas C_1 decreases towards a very small value, even less than the value attained by C_3 after an overshoot in intermediate times. These results show that selection is very sharp, in the sense that there is no induction period during which the choice of the trails is undecided.

In the above analysis, we have taken the parameter $q_1 = 1$, a value corresponding, in the identical sources case, to the exploitation of a single preferred source [inhomogeneous solutions: eqns (7)]. Actually, eqns (13) and (16) display not only the ratio q/q_1 but also q_1 itself. One may therefore wonder how the situation would change by shifting q_1 towards the range of values corresponding, in the identical sources case, to a mixed exploitation, i.e., exploitation of a single source [semi-inhomogeneous solutions, eqn (7)] and exploitation of multiple sources [homogeneous solution, eqn (5)].

Figure 7(a) shows the bifurcation diagram in the case of three sources under these conditions. We have taken the parameter $q_1 = 0.291$ and varied q in the vicinity of this value. One observes a similar situation as the identical sources case: a coexistence of three stable solutions, although the range is now more limited than in Section 3 (Fig. 3).

As q_1 decreases further the situation again changes. To be specific, consider the value

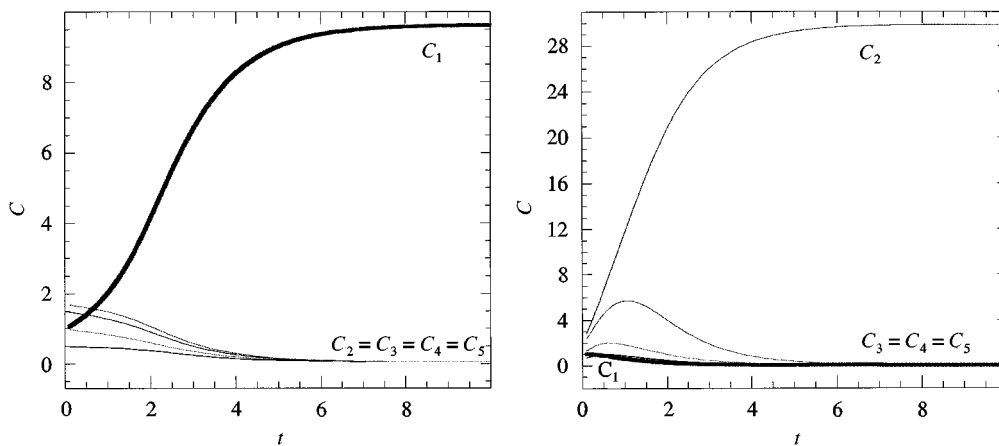


FIG. 6. Time evolution of pheromone concentrations as obtained from integration of eqns (2) in the case of $s = 5$. The left graph corresponds to the case $C_2 = C_3$ with $\varepsilon = 0.5$ and the right graph to the case $C_3 = 1/C_2$ ($\varepsilon = 3$).

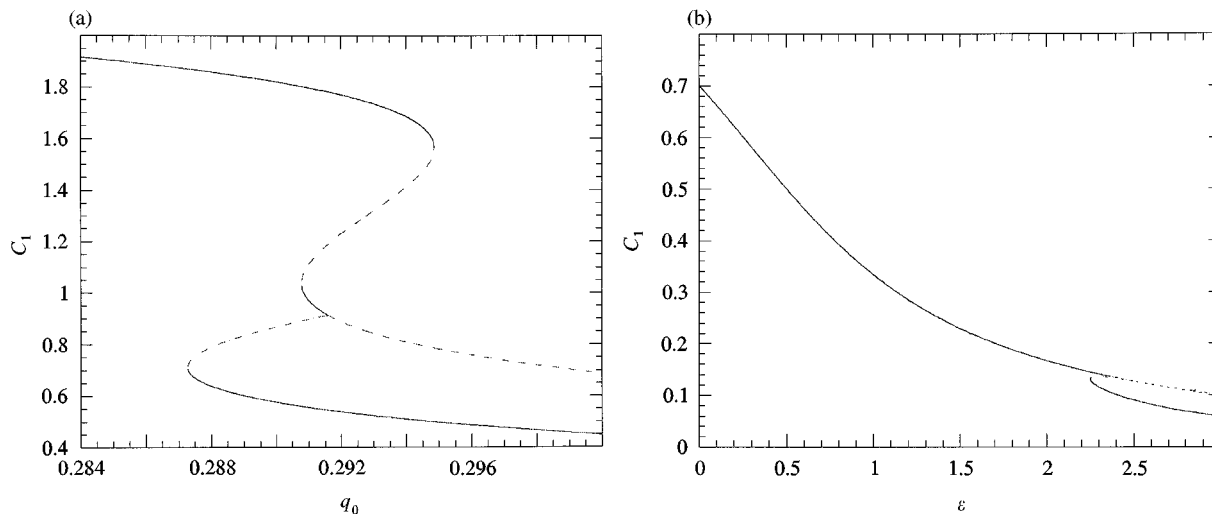


FIG. 7. (a) Bifurcation diagram of C_1 [eqns (13), (16), (17)] as a function of parameter $\epsilon = q/q_1$ for $s = 3$ and $q_1 = 0, 291$. (b) As in (a) but for $s = 5$ and $q_1 = 0, 167$ (corresponding to the species *Lasius niger*).

$q_1 = \sigma/k = 0.167$ associated to *Lasius niger* in the presence of a source of 1 M in sucrose. The numerical solution of eqns (13) and (16) complemented by stability analysis leads, for $s = 5$, to a bifurcation diagram depicted in Fig. 7(b). We observe that the high C_1 branch continues in a stable way well beyond $q = q_1$. For the critical value of ϵ corresponding to the loss of stability, one observes a subcritical bifurcation of an unstable solution which is stabilized through a limit point bifurcation. In the region between the limit point and the instability point of the high C_1 branch one has two simultaneously stable state solutions. Notice that the limit point is shifted toward higher values of ϵ as s increases.

So far, the bifurcation diagrams of Figs 4–7 have been obtained by keeping Φ at a fixed value, $\Phi = 10$. In *Lasius niger* where v is equal to $1/1500 \text{ s}^{-1}$, this corresponds to a physical flux $\phi = \Phi v = 0.0067$ (one ant per 150 s), a very low flux indeed. Increasing this value to about 0.1, leads to a modification of Fig. 7b, resembling the situation described in Fig. 4I and II.

4.3. BIOLOGICAL RELEVANCE

One of the predictions coming out of the analysis of Sections 4.1 and 4.2 is that a high C_1 branch can remain stable even for parameter values for which source 1 is poorer and that a low

C_1 branch can remain stable even for parameter values for which source 1 is richer. There are, however, limits to this inertia, defined by critical values of s and Φq [Fig. 4I and II and Fig. 7(a)]. This prediction should also be amenable to experimental testing. Notice, however, that it concerns only the final state of the system. Before reaching this state, a variety of transient exploitation patterns may be possible. They could be observed under suitable initial conditions corresponding to various distributions of the ants in the trails.

Let us now focus on the biologically relevant case where one source is richer than the others. The prediction that for the parameter values of *Lasius niger* there exist different modes of exploitation of the sources present as the flux of individuals is varied, is directly amenable to experimental testing. We have seen [Fig. 7(b)] that for small flux values the colony has no choice but to exploit preferentially the richest source. To show this experimentally it would suffice to present to a small colony a few sources poor in sucrose along with a rich one. The prediction is, then, that, whatever the time sequence in which the sources are introduced, the rich source will be overwhelmingly exploited.

On the other hand, we have seen that if the flux is increased different solutions can be reached. The colony has the choice between a preferred exploitation of the rich or of one of the poor

sources. To observe this, we suggest to introduce a delay in the discovery of some of the sources. Specifically, let first the colony exploit for some time (typically some minutes) a few poor sources. We next introduce the rich source. The prediction is, then, that one of the poor sources will still be exploited in a preferential manner. If one further introduces a few poor sources, one will observe after a transient period, in view of the comments at the end of Section 4.1 on the role of the parameter s , switching to the other stable mode, the preferential exploitation of the rich source. Notice that in this latter experiment the time sequence in which the sources are introduced is crucial, contrary to the previous case.

5. Conclusions

In this work a mathematical model of food recruitment in the presence of an arbitrary number of sources, applicable to trail laying ants, was developed and analysed in detail. Two cases were considered: all the sources are identical; and one of the sources is different. In both instances, it has been possible to cast the problem in terms of two key parameters, the rate of the pheromone deposition on the trail and the number of sources. We have identified the role of these parameters on the global behavior, particularly in connection with the possibility of different modes of exploitation of resources by the colony.

Another important parameter turned out to be the flux Φ , providing a measure of the size of the colony. In actual fact, as pointed out in the Introduction Φ should be allowed to be time dependent, owing to the existence of a time lag between the discovery of the source and the recruitment at the nest. But if one limits oneself to the steady-state regime one is entitled to replace Φ by a constant value, the only difference being a slight modification of the transient behavior prior to the establishment of the steady state (see Introduction). Among the other parameters present, the pheromone disappearance rate ν was shown to play a "trivial role", serving merely to normalize the time scale. The model can be applied to all trail laying species, provided the parameter values are appropriately adapted. As an example, we have illustrated our predictions for the specific set of parameters of the species *Lasius niger*.

In the case where all sources are equal, the most unexpected result was undoubtedly the possibility of competition between trails, leading to a semi-inhomogeneous distribution of pheromone between them. Interestingly, it turned out that under the assumptions of the model, at most two groups of sources could be exploited in a different manner, one consisting of a single preferred source and a second consisting of all other sources exploited on equal footing.

These results show that the colony may focus its activity preferentially on one particular source rather than on another, even if the sources are identical. This type of collective response may partially explain some aspects of the complex foraging patterns of species present in large colonies and being individually good trail layers, such as *Solenopsis*, *Pheidole*, *Messor*, (Hölldobler & Wilson, 1991; Beckers *et al.*, 1990). Confronted to a multiplicity of choices, these species have the capacity to focus on one activity.

Such strategies are expected to be selected for in species which need a cooperation between foragers or possess different specialized individuals such as minor and major as in the case of *Pheidole* (see, e.g. Detrain & Deneubourg, 1997).

Throughout our analysis, we have assumed that the food sources are not exhausted during one recruitment. Some sources in natural conditions, such as aphids colonies or *Lycaneid caterpillars* (Hölldobler & Wilson, 1991), are close to this situation. *Lycaneid caterpillar* provide food to ants in return for protection from predators (Pierce *et al.*, 1987). It is also known that *Lycaneid* butterflies prefer to oviposit on bushes already containing caterpillars and their attendant ants. Our model suggests that a local ant colony may select, with a certain probability one of the aphids colonies or bushes (that are all identical) and that this probability increases with the population of aphids or caterpillars. As a consequence, small colonies may remain ignored and exposed to predator. Moreover, the productivity of ant-attractive or ant-nutritive substances may increase with the number of insects as it has been shown in the *Lycaneid caterpillars* (Leimar & Axen, 1993). Such situations where the productivity of the source depends on the number of ants introduces a new positive feedback, which accentuates the phenomenon.

Our result provides also a partial justification of the idea advanced in the literature that the use of a limited number of preferred paths rather than of several diffuse ones is likely to have an adaptive significance. First, a strong heavily marked pheromone trail is easier to follow and hence fewer ants lose their way (Pasteels *et al.*, 1987). Moreover, there is likely to be safety in numbers: competition from other ants may influence the effective profitability of a food source, hence defense against potentially interloping foragers from other colonies, may prove necessary at food source (Hunt, 1983; Franks & Partridge, 1993). A single dense traffic column is also probably better able to defend itself against predators than a sparse column, since isolated ants can easily fall prey to predators. The defense of ants on a trail or the defense of a food source may thus be viewed as a cooperative phenomenon, and a semi-inhomogeneous exploitation of identical sources may facilitate such a cooperative defense (the probability to win increases when the number of individuals implied increases).

Similarly to defense, attack may also be viewed as an example of inhomogeneous exploitation of resources induced by cooperativity. An example is provided by army ants (Franks, 1986) which extensively lay trail and use trail recruitment to food sources (Chadab & Rettenmeyer, 1974; Franks *et al.*, 1991). They are present in large colonies and are capable to attack and immobilize big preys, thereby focusing collectively on one activity. Another situation in which focalization on one activity is observed is the case of species capable to attack colonies of social insects (Hölldobler & Wilson, 1991): one can argue that their capacity to attack efficiently is due to their strong cooperativity.

Intuitively, one expects a strong correlation between the ability to change defense strategy and the environmental parameters. Our results fully corroborate this idea by showing that as the number of sources increases, the colony switches to a homogeneous exploitation (all the sources are exploited identically), this mode being observed also for a small colony. In other words, the colony changes its exploitation strategy as an environmental or a social parameter changes as Hahn & Maschwitz (1985) showed that *Messor*

rufitarsis changed its mode of exploitation when the number of sources increased. A better way to defend and to avoid conflicts when the size of the colony is small or the number of sources present is large is dispersion, since a small colony does not have the capacity to have sufficient cooperativity to defend itself since defense is itself a cooperative process. Our model accounts for these different situations without invoking changes in the individual behavior. We can expect then that natural selection will favor species able to defend and thus enhance asymmetric exploitation.

In the situation where one source is different, strong selection rules were also shown to hold. For s not very large either the concentration of pheromone in all $s - 1$ trails other than the one leading to the differentiated food source (say 1) are identical, in which case the stable state corresponds to a high C_1 concentration; or there is one trail among those leading to the $s - 1$ identical sources that has different pheromone concentration, in which case, the stable state corresponds to a low C_1 concentration. This holds true both if the differentiated source is richer or poorer than the other $s - 1$ sources. The origin of this behavior is in the occurrence of a s -shaped bifurcation diagram, as a result of which the stable solution branch continues until the closest limit point bifurcation.

On the other hand, beyond some value of s the rich source always takes over: the model predicts then that the increase of the number of poor sources will facilitate the exploitation of one richer source. This result allows us to understand the situations where there is a large choice between different sources and yet, the colony focuses on one source (Vasconcelos, 1997).

This preference results from the amplification of the trail: a small difference between the parameters of pheromone deposition q and q_1 , strongly correlated in our model to the richness of the sources is sufficient to focus the activity. We notice that other characteristics affecting the pheromone deposition (decreasing the number of trail-laying individuals returning to the nest, returning and discovering time, etc.) can lead to the same result.

We have seen in this paper a typical example of competition among trails induced by amplifying

interactions, but many other phenomena found in insect societies, such as nest-moving or building behavior (Rasse, 1999), are following a similar logic. Furthermore, spatial aggregation can be viewed as a result of the competition between different, possibly identical attractive sites. The selection of one site depends on the size of the population, the number of sites present and their characteristics. In particular, if the size of the colony is large, one site will be selected. On the contrary, if it is small, the colony will not have the ability to be cooperative and will be dispersed, no single site being preferred.

A major theoretical problem that remains open is to account more properly for the variability of the system. This variability may be of internal origin, the discovery of the sources being random rather than deterministic. External factors constitute an additional source of variability in space (complex terrain, etc.) as well as in time (temperature or humidity variabilities, predation, etc). One way to account for these effects is to view the process as a probabilistic game and assign transition probabilities associated with the choice of each trail. This could be implemented numerically by a Monte Carlo type of simulation. Another possibility would be to augment eqns (1) or (2) by noise terms. In the white-noise limit, this would lead to a Fokker-Planck equation for the probability density (Van Kampen, 1981) whose stationary solution would provide the relative probabilities of occupation of the various trails.

As noticed above, the pheromone disappearance rate ν plays a trivial role in the present model. This may be an oversimplification since, after all, the nature of the substrate should definitely influence the overall process. Probabilistic analysis and Monte Carlo simulations should, again, provide the adequate framework for tackling this problem.

In natural conditions, the parameters pertaining to each of the food sources are, typically, different. On the other hand, our simplified model (all sources are identical or one is different) is easy to test in laboratory and allows to sort out the underlying mechanisms and analyse the influence of the parameters. One may reasonably expect that in the real world (i.e. when the parameters associated to the different sources are different)

the foraging patterns, though more complex, will be built according to the same mechanisms.

Finally, throughout this study, it has been assumed tacitly that increased pheromone concentration has, invariably, an attractive effect and that the trail laying is constant for each source. There is evidence that many other effects influence the trail laying during recruitment, such as crowding around the food source (Wilson, 1971; Verhaeghe & Deneubourg, 1983), suppression of trail laying after a certain number of foraging trips (Beckers *et al.*, 1983) or saturation effects (Aron *et al.*, 1989). Nevertheless, these negative feedback mechanisms mainly affect the recruitment in its late stage. They slow down the amplifying action of the pheromone and their main contribution is to reduce the range of parameters or the conditions for which heterogeneities or asymmetrical exploitations are observed. Incorporating these possibilities would confer further complexity to the dynamics than the one found in the present work, and would undoubtedly be worth attempting in the future.

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