Resource exploitation strategies in the presence of traffic between food sources

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ABSTRACT

A mathematical model of food recruitment and resource exploitation in group-living organisms accounting for direct traffic of individuals between the available sources is developed. It is shown that traffic between sources gives rise to the enhancement of the range of stability of the homogeneous mode of exploitation and of the range of coexistence of homogeneous and semi-inhomogeneous ones, as well as the appearance of symmetry breaking transitions leading to fully inhomogeneous exploitation modes.

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1. Introduction

One of the most intensely studied cases of communication in animal societies and, most particularly, in social insects is foraging recruitment. It has been shown (Camazine et al., 2001; Dussutour et al., 2004; Vittori et al., 2006; Detrain and Deneubourg, 2006, 2008; Dussutour et al., 2009a,b) that this phenomenon often involves collective decision making leading to different resource exploitation strategies, through a mechanism of self-organization induced by amplifying interactions between individuals. Depending on the species these may imply direct interactions as it happens in bees (Camazine and Sneyd, 1991; Seeley et al., 1991; Seeley, 1995) or indirect ones via chemical trails as it happens in ants (Sudd, 1957; Wilson, 1962; Hölldobler and Wilson, 1990; Robson and Traniello, 1995).

The mechanism of recruitment via chemical trails for mass recruiting ants can be summarized as follows: An individual discovers one food source, eats and returns to the nest laying down a chemical substance known as pheromone. The resulting "pheromone trail" has two functions: to alert the other individuals to get out of the nest and to lead them to the food source. On each trip ants reinforce the trail and the selection of a particular source can thus be viewed as the result of a collective decision.

Ant colonies are usually confronted with the choice between alternative food sources. An important step in understanding of recruitment behavior under these conditions has been the design of experiments in deliberately idealized situations. This has also

facilitated the development of mathematical models in which the parameters can be determined directly from the experiment. A by now classical scheme considered in this context is the case of two sources connected to the nest by a bridge-like device involving two simultaneously available branches of adjustable lengths (Robson and Traniello, 1995; Beckers et al., 1992b, 1993; Detrain and Deneubourg, 1997; Dussutour et al., 2004, 2009a,b; Vittori et al., 2006). Here the competition between the two chemical trails formed by depositing pheromone on the branches gives rise to a variety of nonlinear phenomena associated with different modes of traffic between the nest and the sources. Specifically, for the case of equivalent sources, there is an equal exploitation of the two sources for small amounts of pheromone deposit per time unit, reflected by the prevalence of symmetric (homogeneous) states. After a threshold value of this parameter the system switches to a preferred exploitation of one or other source through a pitchfork bifurcation marking the prevalence of asymmetric (inhomogeneous) states. For different sources there is a preferred exploitation of the richest source for small values of pheromone deposition. After a threshold value corresponding to a limit point bifurcation, the system switches to the possibility to exploit the richest source or the poorest one. These results have been amply corroborated by experiment for the species *Lasius niger* (Beckers et al., 1992a,b, 1993).

In the present paper a model accounting for direct traffic of individuals between the available sources in addition to indirect one through the nest as above, as well as for the presence of more than two sources, is reported and analyzed in detail. Emphasis is placed on the role of some key properties, such as of the number and geometry of the spatial arrangement of the sources, in the types of solutions generated by the model equations. The general formulation is presented in Section 2. Sections 3–5 are devoted to the

analysis of some prototypical case studies pertaining to different numbers and configurations of the sources relative to the nest. The role of direct traffic between sources in the exploitation strategies is brought out and some new, traffic-induced effects are identified. The main conclusions along with suggestions on experiments to be undertaken in order to check the theoretical predictions are summarized in Section 6.

2. Formulation

In the following we will be concerned exclusively with food recruitment by chemical trails. Let $\{N_i\}$ $(i = 1, \ldots s)$ be the population densities around a source i and $\{c_i\}$ the pheromone concentrations in the trails $1, \ldots s$ leading from the nest to the sources. At the level of a macroscopic (mean-field) description we express their rate of change with time as follows:

$$\frac{dN_i}{dt} = \phi \bar{q}_i F_i(\{c_j\}) - \nu_i N_i + \sum_{j \neq i} J_{ij} \tag{1a}$$

$$\frac{dc_i}{dt} = a_i N_i - b_i c_i \quad i = 1, \ldots, s \tag{1b}$$

The first (positive) contribution in Eq. (1a) displays a choice function F_i, describing the relative attractiveness of trail i by a single ant over the others. ϕ is the total ant flow from the nest and $\bar{q}_i$ the quantity of pheromone deposited on trail i. The second (negative) term corresponds to the spontaneous loss of activity of a fraction of individuals initially engaged on source i. The third term accounts for the traffic of individuals between source i and sources $j(1, \ldots, i-1, i+1, \ldots s)$ as expected to arise in realistic situations. Finally the two terms in Eq. (1b) describe the production of pheromone by the foraging individuals and the disappearance of pheromone through, for instance, evaporation.

The mathematical form used in the sequel for the choice function has been derived and tested for various species, in particular *Lasius niger* (Deneubourg and Goss, 1989; Beckers et al., 1992a,b, 1993):

$$F_i(\{c_j\}) = \frac{(k + c_i)^\ell}{\sum\limits_{j=1}^{s} (k + c_j)^\ell} \tag{2a}$$

where k is a concentration threshold beyond which the pheromone is effective and ℓ measures the degree of cooperativity in the process of choice. The mathematical expression of the traffic term J_{ij} is, on the other hand, not well established. The idea advanced in this paper is that traffic between sources reflects primarily (a), individual-level randomness; (b), the exploration of the environment by individuals having attained the sources and moving subsequently, with some probability, in the part of space outside the trails joining them with the nest; and (c), crowding effects in the sense that if the density of individuals (and hence of pheromone) around a particular source is very high, individuals will have a tendency to move away from it and explore other possibilities. To a first approximation, it appears reasonable to model the motion resulting from the conjunction of the foregoing elements by a random walk. In the continuous space limit this would give rise to a process of diffusion described by a Fick type law. In the discrete representation adopted in the present work one is on the other hand led to the expression:

$$J_{ij} = D_{ij}(N_j - N_i) \tag{2b}$$

where the transfer coefficients D_{ij} depend on the length and texture of the channel through which sources i and j communicate and are assumed to define a symmetric, positive definite matrix.

We emphasize that the processes described by Eqs. (2a) and (2b) coexist at each stage of evolution of the variables N_i and c_i. Process (2a) is predominantly cooperative and, if expressed in terms of the differences $\delta c_i = c_i - c_j$ $(j \neq i)$ leads to the first order in δc_i to an expression reminiscent of chemotactic motion, in the sense that c_i would tend to grow further in time if initially δc_i happened to be positive. In principle random motion should also be present in the traffic manifested, for instance, by U-turns performed by the individuals and directing them from high to low concentration regions. This is, simply, neglected in Eq. (2a) as it may reasonably be expected to be the case if the density is sufficiently large. In contrast to (2a) process (2b) is predominantly random/passive, in the sense that N_i tends to decrease in time if initially $\delta N_i = N_i - N_j$ happens to be positive. Cooperative transport effects may also be present and can in principle be incorporated as corrections to the passive traffic terms, considered to be the dominant ones. In this work they are neglected to first approximation. The situation is different in certain species as, for instance, social caterpillars which as they move build complex networks of trails that subsequently affect their mobility, in which case transport is expected to be cooperative to the dominant order (Nicolis et al., 2008).

In the following it will be assumed that the characteristic times of pheromone production and evaporation, a_i^{-1} and b_i^{-1} in Eq. (1b) are much shorter than those implied in the recruitment and transport processes in Eq. (1a), in other words, pheromone concentration depends on time predominantly through the time dependence of the numbers of individuals present. Accordingly, after a short initial time period a quasi steady-state regime is expected to be established whereby the two terms in the right hand side of Eq. (1b) will balance each other,

$$N_i \approx \frac{b_i}{a_i} c_i$$

Substituting the above "equation of state" into Eq. (1a) one obtains then a closed set of equations for the c_i's,

$$\frac{dc_i}{dt} = \phi q_i F_i(\{c_j\}) - \nu_i c_i + \sum_{j \neq i} D_{ij}\left(c_j - c_i\right)$$

where we have set $q_i = \bar{q}_i a_i / b_i$.

In the sequel the parameter ℓ will be fixed to a value $\ell = 2$ compatible with experiments carried out for the ant species *Lasius niger* (Beckers et al., 1992a,b), and the c_i's will be normalized such that k can be set equal to unity. Furthermore, we assume that the sources presented to the colony and the trails linking the sources to the nest have identical characteristics, and thus set all ν_i's and q_i's to a common value $\nu_i = \nu$, $q_i = q$. Under these conditions, the following results can be established for the solutions of Eqs. (1) in absence of traffic terms J_{ij} (Nicolis and Deneubourg, 1999):

There exists a unique homogeneous steady-state solution in which all sources are exploited in an identical manner:

$$c_i^0 = \frac{\phi q}{s \nu} = c^0 \tag{3a}$$

where the superscript indicates the absence of communication between sources. This solution loses its stability beyond a critical value of parameter $\phi q / \nu$,

$$\left(\frac{\phi q}{\nu}\right)_c = s \tag{3b}$$

Beyond the instability threshold Eqs. (1) admit semi-inhomogeneous solutions in which j trails having a common concentration c_1^0 are exploited in a different manner with respect to the other $s - j$ ones having a common concentration $c_2^0 = 1/c_1^0$,

with

$$c_{1,\pm}^0 = \frac{\phi q}{2\nu j} \pm \frac{1}{2}\sqrt{\left(\frac{\phi q}{\nu j}\right)^2 - 4\left(\frac{s-j}{j}\right)}$$

$$j = 1\ldots\frac{s}{2}, \quad s\text{ even}$$

$$j = 1\ldots\frac{s+1}{2}, \quad s\text{ odd} \tag{4}$$

Among these solutions, only branch c_{1+}^0 and $c_{2+}^0 = 1/c_{1+}^0$ of the case $j = 1$ are stable. All solutions cross the homogeneous branch (3a) at the critical value (3b) of the bifurcation parameter $\phi q/\nu$ and merge, typically, pairwise through limit point bifurcations corresponding to the vanishing of the argument of the square root in Eq. (4). Notice that for $s = 2$ and $j = 1$ there are two stable branches bifurcating symmetrically at the critical value (3b) (pitchfork bifurcation) corresponding to trails that are more or less heavily marked and thus to a fully inhomogeneous solution. For $s > 2$ symmetric pairs of branches still exist as mathematical solutions, but they are all unstable.

Our objective in this work is first, to determine how the above results are modified by the presence of the traffic terms J_{ij} in Eqs. (1) and second, to explore the possibility of new, transport-induced effects. On inspecting Eqs. (1), (2b) and (3a) one sees straightforwardly that the homogeneous state in the presence of traffic is still given by (3a),

$$c_i = \frac{\phi q}{s\nu} = \bar{c} \tag{5a}$$

To assess its stability we linearize (1) around $\bar{c}$,

$$\frac{d\delta c_i}{dt} = \sum_k A_{ik}\delta c_k \tag{5b}$$

with

$$A_{ii} = \frac{2\phi q(s-1)}{s(s+(\phi q/\nu))} - \left(\nu + \sum_{k\neq i}D_{ik}\right) \equiv a$$

$$A_{ij} = \frac{-2\phi q}{s(s+(\phi q/\nu))} + D_{ij} \equiv b \tag{5c}$$

The stability condition of the homogeneous solution is, then, $Re\,\omega_\alpha < 0$ for all α, where the ω_α's are solutions of the characteristic equation:

$$\det|A_{ij} - \omega\delta_{ij}^{kr}| = 0 \tag{5d}$$

At criticality itself and in absence of time-periodic solutions (as is the case in the present problem) Eq. (5d) admits the solution $\omega_c = 0$ and

$$\det|A_{ij}| = 0 \tag{5e}$$

In the next sections we derive the explicit form of the stability condition along with the structure of the bifurcating solutions in a number of representative situations.

3. Two identical communicating sources

The traffic term J_{12} reads

$$J_{12} = D(c_2 - c_1) = -J_{21} \tag{6}$$

We have from (5a) and (5c):

$$c_1 = c_2 = \bar{c} = \frac{\phi q}{2\nu}$$

$$A_{11} = A_{22} = \frac{\phi q}{2+(\phi q/\nu)} - (\nu + D) \tag{7}$$

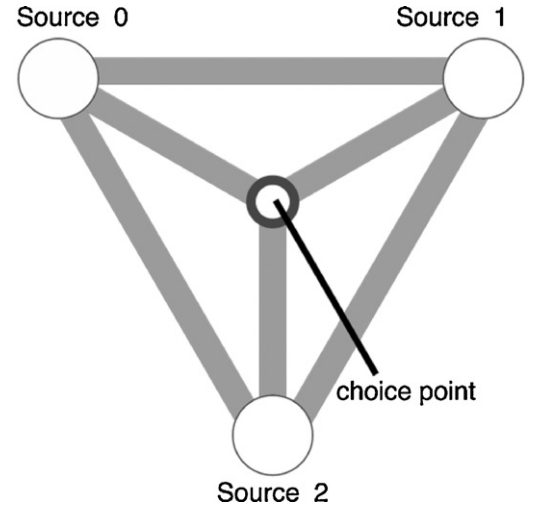$$A_{12} = A_{21} = \frac{-\phi q}{2+(\phi q/\nu)} + D$$

Fig. 1. Schematic representation of three identical equidistant food sources surrounding the nest. Ants arrive at the choice point from the nest located beneath the plan of the figure.

The criticality condition (5e) yields after a straightforward calculation,

$$\left(\frac{\phi q}{\nu}\right)_c = \frac{4(D/\nu)+2}{1-2(D/\nu)} \tag{8}$$

For $D = 0$ we recover condition (3b). As coupling is gradually strengthened on the instability threshold increases monotonously, entailing that bifurcation is postponed owing to the stabilizing action of the coupling on the homogeneous state. Eventually, beyond the value $D/\nu = 1/2$ bifurcation is suppressed and the homogeneous state remains stable thereafter. To obtain the inhomogeneous steady-state solutions in the range of D/ν values less than $1/2$ we use the property $c_1 + c_2 = \phi q/\nu$ and write the steady-state form of Eqs. (1) for $s = 2$ as:

$$\frac{(1+c_1)^2}{(1+c_2)^2} = \frac{-D(\phi q/\nu)+(\nu+2D)c_1}{-D(\phi q/\nu)+(\nu+2D)c_2} \tag{9}$$

We obtain in this way a closed equation for c_1,

$$(\nu+2D)c_1^2 - (\nu+2D)\frac{\phi q}{\nu}c_1 + \nu + 2D + 2D\frac{\phi q}{\nu} + D\left(\frac{\phi q}{\nu}\right)^2 = 0 \tag{10}$$

giving rise to a symmetric pair of stable inhomogeneous solutions born at the threshold value (8) and bifurcating beyond this value, as the uniform steady-state solution loses its stability.

4. Three identical and equidistant communicating sources

Fig. 1 provides a sketch of the configuration considered in this section. The traffic term J_{ik} now reads

$$\sum_{k\neq i}J_{ik} = D(c_{i+1} + c_{i-1} - 2c_i) \tag{11}$$

where all indexes are taken mod 3. Eqs. (1) still admit the homogeneous steady-state solution

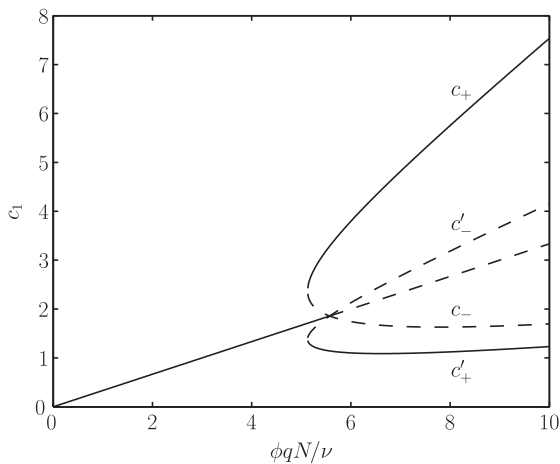$$c_1 = c_2 = c_3 = \bar{c} = \frac{\phi q}{3\nu} \tag{12}$$

Fig. 2. Bifurcation diagram of steady-state solutions of Eqs. (1) in the geometry of Fig. 1. $c_{\pm}$ and $c'_{\pm}$ represent the semi-inhomogeneous states as given by Eq. (15a) and (15b) while the central branch stands for the homogeneous state. Full and dashed lines denote stable and unstable solutions, respectively. Parameter values: $D/\nu = 0.1$.

To obtain the full set of steady state solutions we divide the steady state form of these equations by pairs. We obtain (cf. also Eq. (9)):

$$\frac{(1+c_1)^2}{(1+c_2)^2} = \frac{-D(\phi q/\nu) + (\nu+3D)c_1}{-D(\phi q/\nu) + (\nu+3D)c_2}$$
$$\frac{(1+c_1)^2}{(1+c_3)^2} = \frac{-D(\phi q/\nu) + (\nu+3D)c_1}{-D(\phi q/\nu) + (\nu+3D)c_3} \qquad (13)$$

In addition to state (12) these equations admit the three semi-inhomogeneous solutions

$$c_i = c, \quad c_{j_1} = c_{j_2} = c'; \qquad i, j_1, j_2 = 1, 2, 3 \quad j_1, j_2 \neq i \qquad (14)$$

where c satisfies the equation (to be compared with Eq. (10)):

$$\frac{\nu+3D}{2}c^2 - \frac{\phi q}{2\nu}(\nu+2D)c + \nu + 3D + 2D\frac{\phi q}{\nu} + \frac{D}{2}\left(\frac{\phi q}{\nu}\right)^2 = 0 \quad (15a)$$

and

$$c' = \frac{1}{2}\left(\frac{\phi q}{\nu} - c\right) \qquad (15b)$$

For $D = 0$ the solutions of Eq. (15a) reduce to the result of Eq. (4). Our objective is here to determine the dependence of c on the coupling parameter D and to assess the range of stability of the semi-inhomogeneous states. Of special interest will also be the possibility of coexistence of simultaneously stable homogeneous and semi-inhomogeneous states.

We first note that among the two solutions of Eq. (15a) there is one branch cutting the homogeneous solution $\bar{c}$, Eq. (12), at a value of parameter $\phi q/\nu$ obtained by setting $c = \bar{c}$:

$$\left(\frac{\phi q}{\nu}\right)_1 = \frac{3(1 + 3(D/\nu))}{1 - 3(D/\nu)} \qquad (16a)$$

This branch extends on both sides of this particular state and eventually merges with the other non-negative branch through a limit point bifurcation at parameter values corresponding to the vanishing of the discriminant of Eq. (15a):

$$\left(\frac{\phi q}{\nu}\right)_2 = \frac{2(4(D/\nu) + \sqrt{2})(1 + 3(D/\nu))}{1 - 8(D/\nu)^2} \qquad (16b)$$

For each value of c there is also the corresponding value of c' given by Eq. (15b). The set of four values of c and c' represents, then, the number of values that each of the variables c_1, c_2, c_3 can take as the parameters are varied.
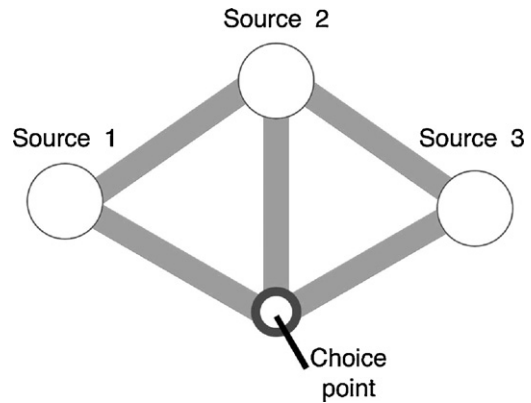

Fig. 3. Schematic representation of three linearly disposed food sources. Ants arrive at the choice point from the nest located beneath the plan of the figure.

Fig. 2 depicts the corresponding bifurcation diagram. Stability analysis using Eq. (5) shows that the homogeneous solution loses its stability beyond the threshold value $(\phi q/\nu)_1$. The stability of the semi-inhomogeneous states can be analyzed along similar lines, with the elements A_{ij} of the linearized operator (Jacobian matrix) being now given by

$$A_{ii} = \phi q \frac{2(1+c_i)\sum_{j \neq i}(1+c_j)^2}{[(1+c_1)^2 + (1+c_2)^2 + (1+c_3)^2]^2} - (\nu + 2D) \qquad (17)$$

$$A_{ij} = \phi q \frac{-2(1+c_i)^2(1+c_j)}{[(1+c_1)^2 + (1+c_2)^2 + (1+c_3)^2]^2} + D \quad (i \neq j)$$

As it turns out there is a range of values of $s = (\phi q/\nu)_1 - (\phi q/\nu)_2$ in which semi-inhomogeneous states coexist and are simultaneously stable with the homogeneous one. This range tends to increase as D is gradually increased, but eventually for large D's one witnesses the disappearance of both the crossing and the limit points.

5. Three identical non-equidistant communicating sources

Fig. 3 illustrates a typical "quasi-linear" configuration, in which the distance between sources 1 and 3 is larger than the distances between 1–2 and 2–3, supposed to be equal. Expression (11) is
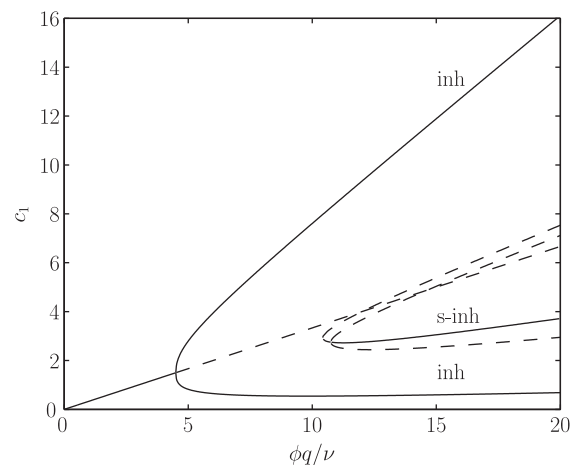

Fig. 4. Bifurcation diagram of the steady-state solutions of Eqs. (1) in the geometry of Fig. 3. Full and dashed lines denote stable and unstable solutions, respectively. Parameter values: $D/\nu = 0.2$.
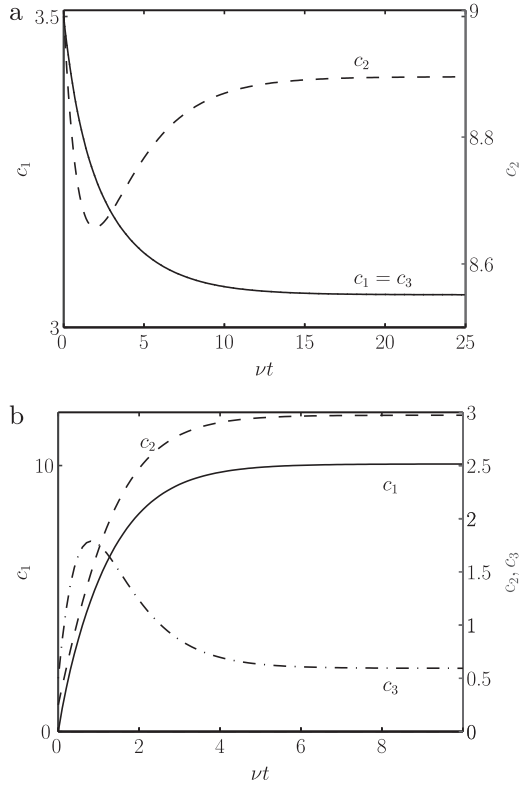
Fig. 5. Evolution of c_i's in time (normalized by the evaporation rate ν) for $\phi q/\nu = 15$ and $D/\nu = 0.2$ and for different initial conditions. (a) $c_1(0) = c_3(0) = 3.5$, $c_2(0) = 9$, the evolution leads to a semi-inhomogeneous state. (b) $c_1(0) = 1$, $c_2(0) = 0$, $c_3(0) = 0.5$, the evolution leads to a fully inhomogeneous state. Right ordinates in (a) and (b) stand for c_2 and for c_2, c_3, respectively.

replaced by

$$\sum_{k \neq i} J_{ik} = D(c_2 - c_i) \quad i = 1, 3$$

$$\sum_{k \neq 2} J_{2k} = D(c_1 + c_3 - 2c_2) \tag{18}$$

The evolution equations still admit the homogeneous steady-state solution (12) as well as the semi-inhomogeneous solutions

$$c_2 = c, \quad c_1 = c_3 = c' = \frac{1}{2}\left(\frac{\phi q}{\nu} - c\right) \tag{19}$$

where c now satisfies a cubic equation,

$$\frac{3}{2}(\nu + 3D)c^3 - (2\phi q + \frac{9\phi q D}{2\nu})c^2$$

$$+ \left\{ (\nu + 3D)[1 + 2(1 + \frac{\phi q}{2\nu})^2] + D\left(\frac{\phi q}{\nu}\right)^2 - 2\phi q \right\} c \tag{20}$$

$$- D\frac{\phi q}{\nu}\left\{ 1 + 2(1 + \frac{\phi q}{2\nu})^2 \right\} - \phi q = 0$$

A new point is that in addition to solutions (19) and (20) the equations may now admit fully inhomogeneous solutions, in which $c_1 \neq c_3$. To determine them we divide the steady-state solutions for c_1 and c_3,

$$\frac{(1 + c_1)^2}{(1 + c_3)^2} = \frac{(\nu + D)c_1 - Dc_2}{(\nu + D)c_3 - Dc_2} \tag{21a}$$

and eliminate c_3 through the sum condition

$$c_1 + c_2 + c_3 = \frac{\phi q}{\nu} \tag{21b}$$

One arrives in this way at an equation linking c_2 to c_1,

$$Dc_2^2 - \left\{ 2D + \frac{D}{\nu}\phi q + (D + \nu)c_1 \right\} c_2 + (D + \nu)c_1 \left(\frac{\phi q}{\nu} - c_1\right)$$

$$- (D + \nu) = 0 \tag{22}$$

Solving formally for c_2 and substituting into one of the original steady-state equations yields a closed equation for c_1, from which c_2 and c_3 can also be deduced. Fig. 4 summarizes the main results in the form of a bifurcation diagram for the variable c_1. Stability analysis along similar lines as in the previous sections shows that there is a pair of stable fully inhomogeneous solutions bifurcating at parameter value for which the homogeneous solution loses its stability. We are thus here in presence of a transport-induced, symmetry-breaking transition reminiscent of the Turing instability (Turing, 1952) arising in wide classes of reaction-diffusion systems. Furthermore, in certain ranges of parameter values these inhomogeneous branches may coexist and be simultaneously stable with a semi-inhomogeneous solution as illustrated further in Fig. 5, in which the results of a direct time integration of the full nonlinear equations for the $c_{i's}$ are depicted. Notice that as long as time is scaled by the evaporation rate ν the evolution is fully controlled by the two parameters $\phi q/\nu$ and D/ν.

Finally, one can handle along the same lines the more general case where all distances between sources are unequal, a feature that can be accounted for by introducing different values of the pairwise transfer coefficients. In this setting, the only non-homogeneous states are fully inhomogeneous solutions of the evolution equations.

6. Conclusions

In this paper a mathematical model of self-organization in social insects, associated with recruitment in the presence of direct traffic of individuals between food sources has been developed. The analysis brought out some new features arising from the existence of additional communication channels as compared with the more limited communication between each individual source and the nest ordinarily considered in the literature, such as: enhancement of stability of the homogeneous state, enhancement of the domain of coexistence of homogeneous and semi-inhomogeneous states, and transport-induced symmetry breaking transitions leading to fully inhomogeneous states that can be in stable coexistence with semi-inhomogeneous ones in certain ranges of parameter values.

The coexistence of homogeneous and semi-inhomogeneous exploitation modes in mass recruitment, for the same parameter values, was already reported in Nicolis and Deneubourg (1999). The enhancement of the coexistence domain as well as of the domain of stability of the homogeneous mode found in the present work implies that in the presence of intersource traffic these regimes are more robust towards perturbations and thus biologically more significant. The emergence of fully inhomogeneous states through symmetry-breaking instability is potentially even more significant, as it heralds the onset of a new mode of organization in which a highly non-trivial "division of work" is installed between the individuals even though they are undistinguishable and non specialized at the outset. So far this type of regime remains unexplored in the food recruitment literature per se, but has been found experimentally to exist and has been analyzed theoretically in the context of certain forms of collective behavior associated with the uptake, transport and deposition of material (Theraulaz et al., 2002). Furthermore, beyond the social insect literature the resource exploitation patterns found in slime molds (Nakagaki et al., 2004) are studied in a setting that allows automatically for traffic between the sources.

The results derived in this work bring also the recruitment problem closer to the context expected to arise in real world situations, where individuals can circulate freely around and between the food sources. They can be exploited to design controlled experiments that could lead to the observation of the patterns predicted and summarized in Figs. 2, 4 and 5. The idea would be, first to link the sources by additional bridges and test the adequacy of Eq. (2b) in describing the nature of traffic between sources in the absence of nest, by releasing individuals in randomly selected parts of these bridges. The next step would be to carry out the experiment in the presence of nest and monitor the frequency of visits of the trails linking the nest to the sources as a function of the total flux of individuals for various spatial arrangements of the sources, as in the geometries adopted in Figs. 1 and 3. Depending on the length and texture (Detrain et al., 2001) of the source-to-source trails different values of the effective coupling coefficient D can be achieved whose influence on the type and stability of the state that can be realized can then be assessed (see also (Aron et al., 1990) for a somewhat analogous study in which traffic between different parts of a nest linked by a network of trails was instead considered).

On the theoretical side, it would be worth extending the analysis beyond the range of validity of the adiabatic elimination procedure outline in Section 2 using the full set of Eqs. (1a) and (1b). The question would then be whether the stability properties of the various solution branches will be affected, being understood that the steady state solutions themselves will be left unaffected.

In natural conditions the parameters pertaining to each of the food sources and to the texture of the different trails are, typically, different. Furthermore, the sources become eventually exhausted. Our simplified model (all sources and trails are identical and constantly replenished) allows to sort out the underlying mechanisms, analyze the influence of the parameters and dispose thus of a reliable reference point in the perspective of a comparison with experiment along the above envisioned lines. Still, it would be interesting to augment the model by introducing some of these real-world complications. A different type of extension would be to account for the variability inherent in individual behavior, the discovery of the sources being typically the result of random exploration rather than of a deterministic process.

By their generic character the models developed and analyzed in this work should apply if suitably adapted to a wide range of situations involving collective decision-making and resource exploitation in insect societies beyond mass recruitment and foraging, such as aggregation and building-related activities. Finally, in higher group-living organisms individuals dispose of far more advanced mobility and more generally communication capabilities than social insects. It may thus be expected that they will make non-trivial uses of the extra flexibility afforded by the availability of direct linkages between available options in their decision making.

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