

Self-organization, collective decision making and resource exploitation strategies in social insects

S.C. Nicolis^{1,a} and A. Dussutour²

¹ Department of Zoology, University of Oxford S. Parks road, OX1 3PS Oxford, UK

² School of Biological Sciences, University of Sydney New South Wales 2006, Australia

Received 16 January 2008 / Received in final form 29 May 2008

Published online 22 August 2008 – © EDP Sciences, Società Italiana di Fisica, Springer-Verlag 2008

Abstract. Amplifying communications are a ubiquitous characteristic of group-living animals. This work is concerned with their role in the processes of food recruitment and resource exploitation by social insects. The collective choices made by ants faced with different food sources are analyzed using both a mean field description and a stochastic approach. Emphasis is placed on the possibility of optimizing the recruitment and exploitation strategies through an appropriate balance between individual variability, cooperative interactions and environmental constraints.

PACS. 05.65.+b Self-organized systems – 05.10.Ln Monte Carlo methods

1 Introduction

In this work we show how collective decision making leading to different resource exploitation strategies may arise in social insects through a mechanism of self-organization. Emphasis will be placed on the link between the characteristics of single individuals, the response at the population level and the environmental constraints. As a corollary, conditions under which the collective response can be optimized will be identified.

The basic mechanisms underlying the phenomena to be considered are (a) competition between different sources of information; and (b) the occurrence of amplifying interactions between constituent units as reflected by the presence of feedback loops. They confer a markedly nonlinear character to the evolution of the system. A key point of our approach will be mathematical modelling, in close synergy with experiment, using techniques of nonlinear science such as stability and bifurcation theories. This will allow us, in particular, to identify the key variables and parameters as well as the principal mechanisms responsible for the behaviour. A mean field analysis in which fluctuations and other sources of variability are discarded is first carried out in Section 2. It is complemented by an analysis incorporating the effects of variability in Sections 3 and 4, where it is shown that variability may be the origin of qualitatively new effects. The main conclusions are summarized in Section 5.

^a *Present address:* Mathematics department, Uppsala University Box 480 751 06 Uppsala, Sweden.
e-mail: snicolis@math.uu.se

2 Collective decision making associated with food recruitment: mean field analysis

Our first case study is collective decision-making associated with food recruitment in ant colonies. The mechanisms of recruitment can be summarized as follows. An ant discovers one food source, eats and returns to the nest laying down a chemical substance known as a pheromone. The resulting “pheromone trail” has two functions: it tells other individuals to leave the nest and it leads them to the food source. Ants reinforce the pheromone trail on every trip and the source ends thus being exploited in a collective manner.

Ant colonies are usually confronted with choice and competition between multiple food sources. We first neglect individual and environmental variability and focus on the nature of the “traffic” established along the trails leading to the food sources. The key point allowing us to model this situation is to recognize that direct contacts between individuals can be ignored when compared to an individual’s response to the pheromone concentration present in a given trail. The principal variables are thus the pheromone concentrations C_i rather than the number of individuals present on the various trails i at a given time. A generic model capturing the main features of competition between the sources can then be written as [1,2].

$$\frac{dC_i}{dt} = \phi q_i \frac{(k + C_i)^\ell}{\sum_{j=1}^s (k + C_j)^\ell} - \nu_i C_i \quad i = 1, \dots, s \quad (1)$$

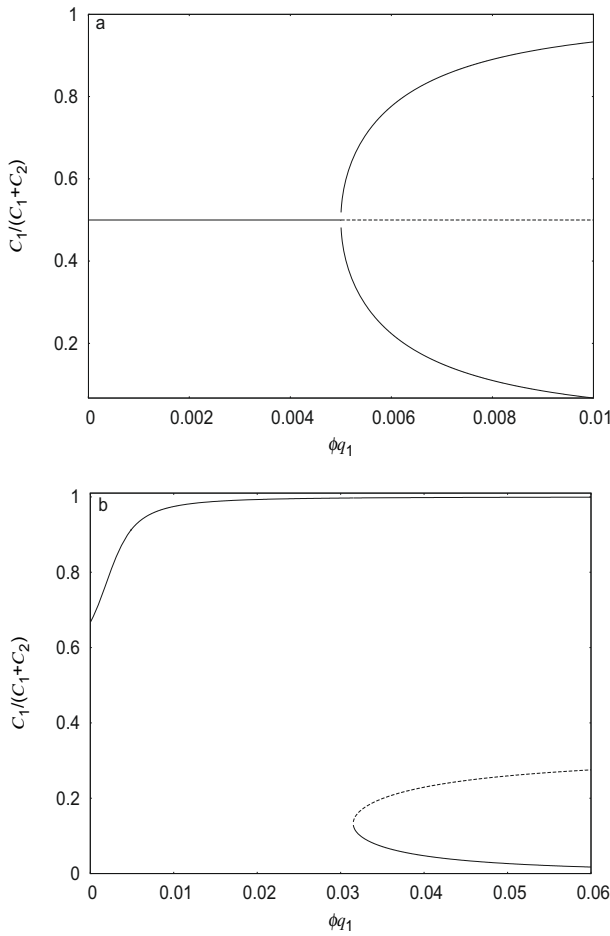


Fig. 1. Bifurcation diagrams of the steady-state solutions of equation (1) as a function of ϕq_1 in the case of $q_2/q_1 = 1$ (a), and $q_2/q_1 = 0.5$ (b). Parameter values $k = 6$, $\nu_1 = \nu_2 = 1/2400s^{-1}$ and $s = 2$.

The first, positive, term corresponds to the attractiveness of trail i over the others. Its mathematical expression has been quantified and tested for various ant species, in particular *Lasius niger* [3–5], *Linepitema humile* [1,6], army ants [7,8] and *Messor pergandei* [6,9]. Here, ϕ is the flux of individuals leaving the nest (related to the size of the colony), q_i is the quantity of pheromone laid down by an ant on the trail i whose magnitude reflects the quality of source i , s is the total number of sources visited by the ants, k is a concentration threshold beyond which the pheromone is effective and ℓ measures the sensitivity of the choice. The latter parameter can also be viewed as the strength of cooperativity between individuals. In the following, the value $\ell = 2$ will be adopted, which seems to fit experimental data for the ant species *Lasius niger*. The second, negative term corresponds to the disappearance of the pheromone on the trail i through, for instance, evaporation (parameter ν_i).

Resolving equation (1) in the simplest case of two sources in competition, using the parameters associated with the species *Lasius niger*, leads to the bifurcation diagrams depicted in Figures 1a, 1b, according to whether

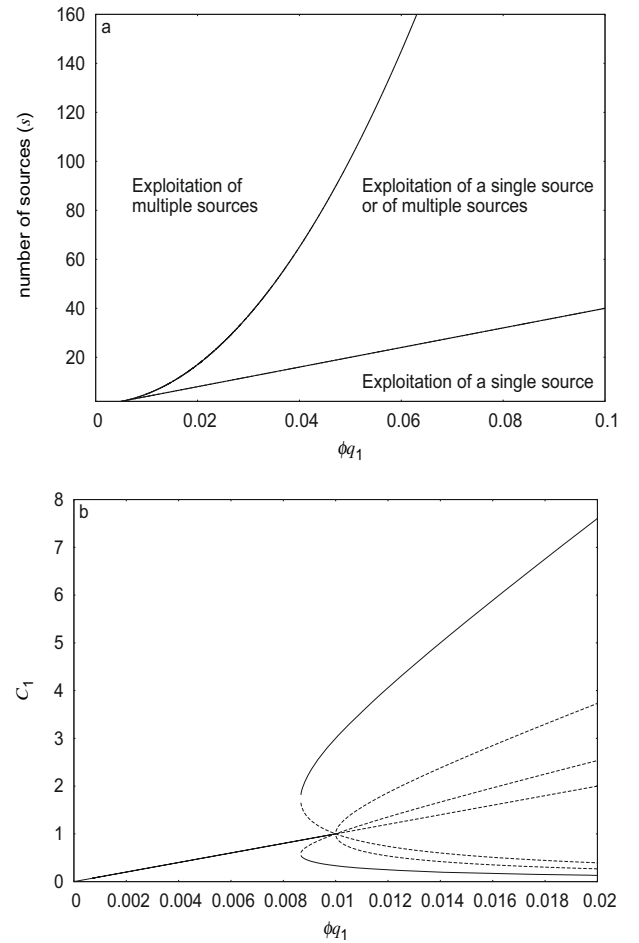


Fig. 2. State diagram representing the parameter regions of different modes of exploitation resources as a function of ϕq_1 . Parameter values as in Figure 1a. (b) Bifurcation diagram of the steady-state solutions of equation (1) as a function of ϕq_1 in the case of four equal sources in competition. Parameter values as in Figure 1a.

the two sources have the same or different quality. For the case of equivalent sources, we see that there is an equal exploitation of the two sources for small values of pheromone deposition. After a threshold value the system switches to a preferred exploitation of one or other source. For different sources there is a preferred exploitation of the richest source for small values of q_1 . After a threshold value, the system switches to the possibility to exploit the richest source or the poorest one. These results have been corroborated by experiment for the species *Lasius niger* [2–5,10,12]

In the more realistic situation where more than two sources are present, it is useful to build a “state diagram” summarizing the different strategies of exploitation. Figure 2a shows the number of sources against the parameter ϕq , keeping $q_1 = q_2$. We see that for small values of ϕ and a high number of sources there is equal exploitation of all the sources. In intermediate values of ϕq and a high number of sources the colony selects with some probability either one source or all sources. For still higher values

of ϕq but a low number of sources, the colony finally selects one source preferentially. As an example, the bifurcation diagram in the presence of four sources is shown in Figure 2b. These predictions are in qualitative agreement with experimental results showing that *Messor rufitarsis* [11] changes its mode of exploitation with the number of sources and their distribution. To gain a more quantitative agreement it is important to undertake laboratory experiments using conditions stipulated in the model.

So far an “idealized” static environment has been deliberately considered, in order to characterise some generic trends that could otherwise be blurred by noise. Real world environments are quite different. They are subjected to imperfections of different kinds and to evolutionary processes in their own right, imposing on the system a variety of stresses that may elicit unexpected responses and behavioural modes. In the rest of this section we present some results based on an extended form of equation (1) emulating a “dynamic” environment. Specifically, we consider the case of $s = 2$ sources and allow for the possibility that one may be unavailable during a certain period of time, adopting the following scenarios:

- (i) the two sources are available during the time interval $0 \leq t \leq T$. At the level of the model, equation (1) (for $s = 2$) is run in its full form with both q_1 and q_2 being non-zero;
- (ii) source 1 becomes unavailable during the time interval $T < t \leq 2T$. At the level of the model, in equation (1) (for $s = 2$) one takes $q_1 = 0$ and q_2 as in (i);
- (iii) source 1 becomes again available for $t > 2T$, we determine the response of the system at $t = 3T$. At the level of the model, equation (1) (for $s = 2$) is run during $2T < t \leq 3T$ for q_i values as in (i) and with an initial condition corresponding to the state reached at $t = 2T$ in stage (ii).

Figures 3a, 3b summarize the new effects arising from the dynamic environments described above. To emulate the experimental set-up, the evaporation rates ν_1 and ν_2 are set to different values. In both cases the time interval T is taken to be considerably longer than the intrinsic time scales associated with the parameters ν_i or ϕ in equation (1). As can be seen, running the system with fixed parameter values and two slightly different initial conditions may lead an initial population visiting predominantly source 1 to switch to source 2 (Fig. 3a) or, on the contrary, after an intermediate stage of “hesitation” (cf. dip in Fig. 3b) maintain the same mode of exploitation. A similar sensitivity is encountered when the value of parameter ν_1 is changed relative to ν_2 with identical initial conditions, as depicted in Figures 4a, 4b. It is important to conduct experiments to confirm these predictions.

3 Accounting for variability: Monte Carlo approach

We now extend the above scheme to account for variability. The question is, by incorporating fluctuations in

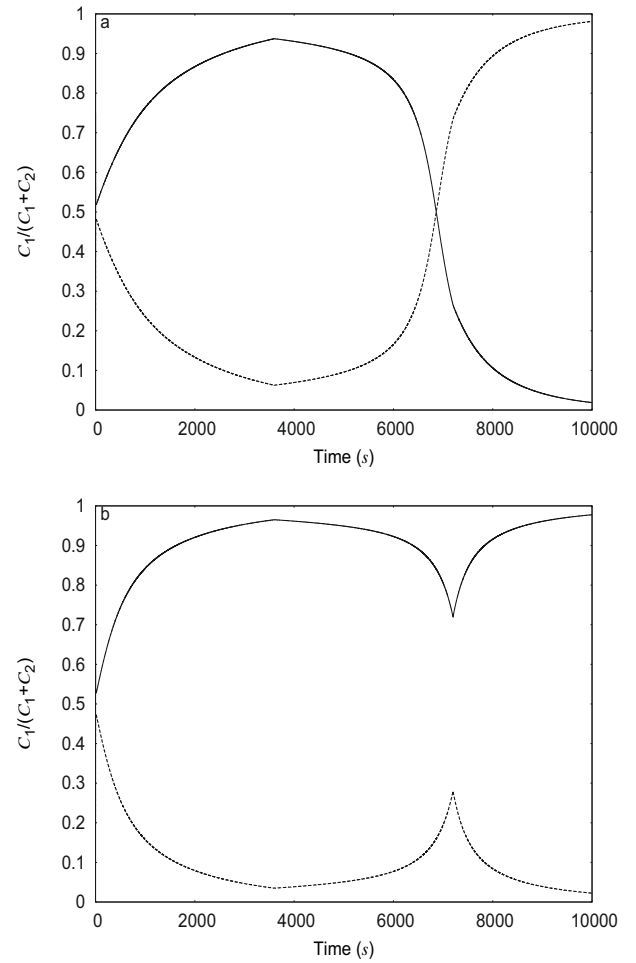


Fig. 3. Foraging in a dynamic environment: evolution of the reduced pheromone concentrations according to the scenario defined in Section 2. Source 1 becomes unavailable ($q_1 = 0$) in the time laps $3600 < t < 7200$. Integration of equation (1) (for $s = 2$) and for two slightly different initial conditions: $C_1(0) = 0.01$ (full line) and $C_2(0) = 0.03$ (dotted line) (a) and $C_1(0) = 0.01$ (full line) and $C_2(0) = 0.04$ (dotted line) (b). Parameter values $\phi = 0.2s^{-1}$, $q_1 = q_2 = 1$, $\nu_1 = 1/1600s^{-1}$, $\nu_2 = 1/2400s^{-1}$ and $k = 1$.

the framework of a situation where we have food sources in competition, do we obtain access to behaviours not amenable to a mean-field description? To this end we adopt a Monte Carlo approach [12,13]. The advantage of this type of approach is that we can directly simulate the process of interest rather than solving equations that model it at a probabilistic level, such as the Fokker-Planck equation [14]. In such a numerical experiment the random aspects of the process are thus automatically incorporated. We can summarize the different steps as follows: (Fig. 5)

- a. *Initial conditions.* The pheromone concentrations and number of ants over each trail are fixed to zero.
- b. *Decision process.*
 - (i) The first decision concerns the arrival of an ant to the choice point. This probability is given by the

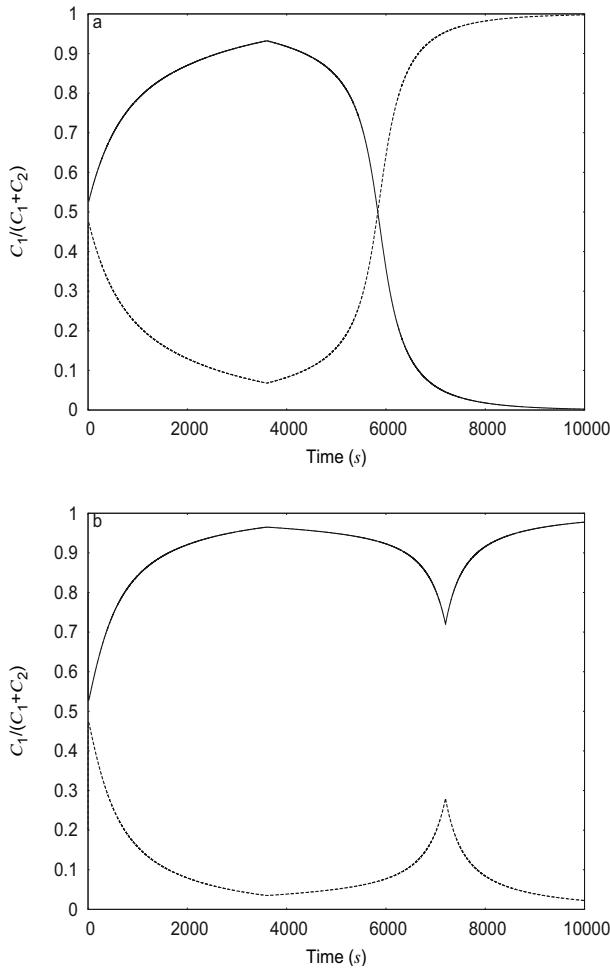


Fig. 4. As in Figure 3 but for identical initial conditions $C_1(0) = 0.01$ (full line) and $C_2(0) = 0.04$ (dotted line) and $\nu_1 = 1/1200s^{-1}$, (a), $\nu_1 = 1/1600s^{-1}$, (b).

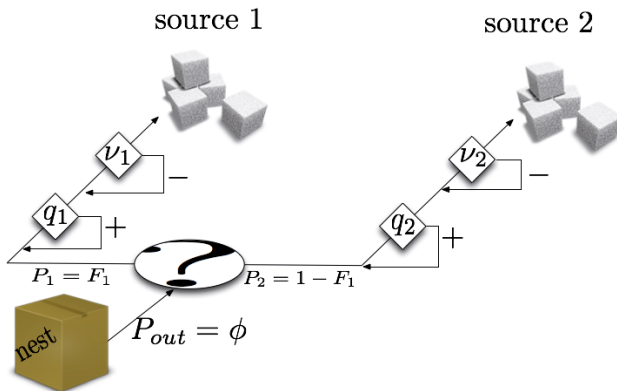


Fig. 5. Organigram of the Monte Carlo simulation.

normalized value of the flux parameter ϕ . A random number is sampled from a uniform distribution between 0 and 1. If its value is less than or equal to ϕ , an ant comes to the choice point.

- (ii) The second decision is the choice of the trail. The trails will initially have the same probability of being followed, but will differentiate as soon as

at least one individual has adopted a trail and laid a quantity of pheromone. The choice of a specific trail is governed by the nonlinear function $F_i = \frac{(k+C_1)^2}{(k+C_1)^2 + (k+C_2)^2}$ used in the analytical formulation of the model (Eq. (1)). It is implemented by sampling a second random number from a uniform distribution. If it is less than or equal to the function F_1 , the ant will follow and lay pheromone on trail 1. If it is between F_1 and $F_1 + F_2$, it will follow and mark trail 2, and so on.

- c. *Time evolution.* When an ant chooses a trail i it lays a quantity q_i of pheromone that gradually disappears through the parameter ν . Hence, the probabilities represented by function F_i are updated at each simulation step according to the actual pheromone concentrations. The process is repeated for a number of steps sufficient to reach the stationary state, where the total quantity of pheromone over both trails is constant.

We first extend the mean-field model of equation (1) by running the simulation with the parameters used in Figure 1. Figure 6 summarizes the result. The plots represent the probability that an ant has chosen a particular trail in the time interval considered. Clearly, the bimodal character of these histograms constitutes the probabilistic signature of the bifurcation phenomena predicted by the mean-field analysis (Fig. 1).

We next apply the Monte Carlo simulation to the case of a dynamic environment as defined in the second part of Section 2. To establish a connection with the results of the mean-field analysis (Figs. 3 and 4) we perform a large number of runs and average over these individual realizations. Adopting the same conditions as in Figure 4 we find that the average trajectory will invariably tend to a state favouring source 2. The cross-over behaviour found when switching from Figures 4a to 4b is thus not realized, owing to the smoothing action of the averaging over the initial conditions. We here have an interesting example of the important role of stochasticity, where the dynamics present an intrinsic sensitivity towards the initial conditions or the parameters. If on the other hand, source 1 (when available) is richer than source 2, crossover becomes possible (Fig. 7).

4 Optimizing the exploitation of resources: the role of randomness

We start with the simplest case of a single food source. Let N be the number of individuals exploiting this source. We denote the inactive individuals I (for example, those still confined to the nest or performing a random walk back to it). W describes the workers and X the individuals engaged in the trail leading to the food source. We stipulate that an inactive individual I can become a worker W when encountering a recruiter. A worker W , with a certain probability, can become a recruiter. Finally, a recruiter can become inactive, for example by losing the trail.

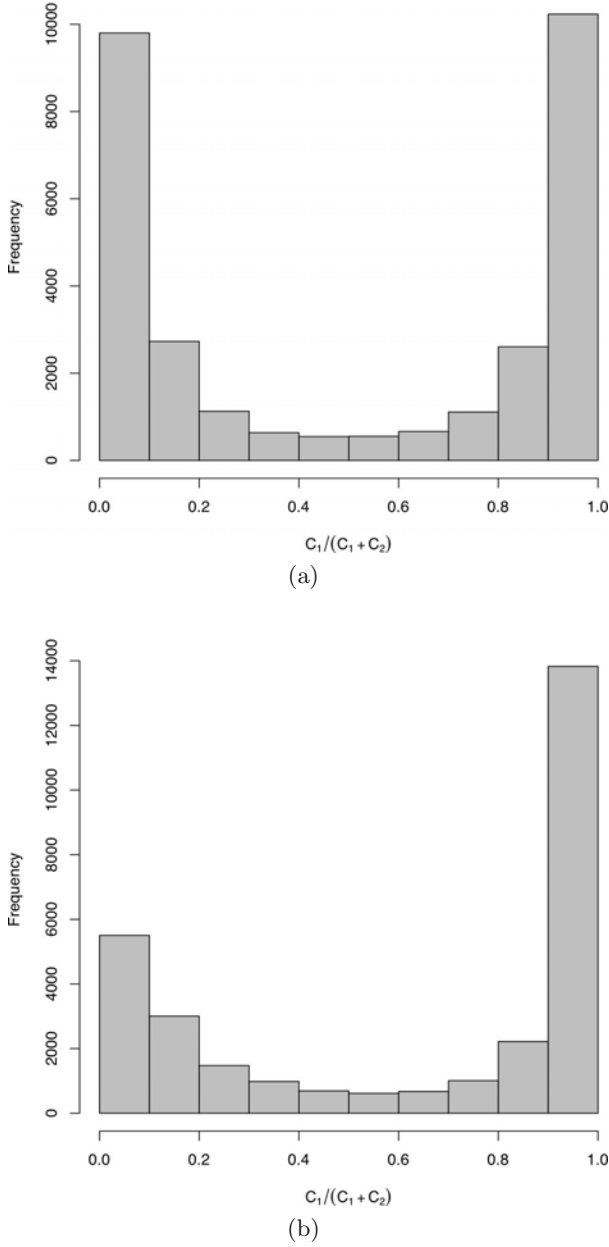


Fig. 6. Probability histograms corresponding to (a) sources of equal richness and (b) unequal richness, as obtained from a Monte Carlo simulation. In (b), the left source is the richest one. Other parameter values as in Figure 1b.

The evolution equations thus take the form

$$\begin{aligned} \frac{dW}{dt} &= qIX - kW \\ \frac{dX}{dt} &= kW - rX \\ \frac{dI}{dt} &= -qIX + rX. \end{aligned} \quad (2)$$

Here q has the same interpretation as in equation (1). k is the probability per unit time for a worker to become a recruiter and r corresponds to the probability that a

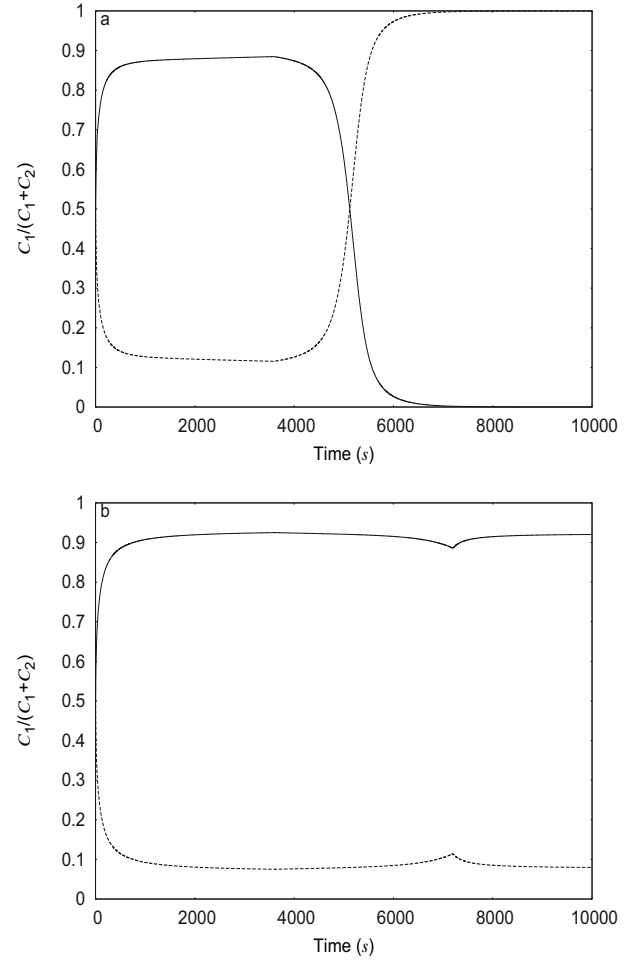


Fig. 7. Foraging in a dynamic environment: evolution of the reduced pheromone concentrations averaged over 15 000 realizations as obtained from a Monte Carlo simulation. The two sources are asymmetric. From $t = 0$ to $t = 3600$ and from $t = 7200$ to the end, $q_1 = 2$ and $q_2 = 1$. From $3600 < t < 7200$, $q_1 = 0$ and $q_2 = 1$. (a) $\nu_1 = 1/600s^{-1}$, (b) $\nu_1 = 1/1200s^{-1}$. Other parameter values $\phi = 0.2s^{-1}$ and $\nu_2 = 1/2400s^{-1}$.

recruiter will lose the trail and become inactive. Note that the following conservation relation is satisfied identically:

$$I + W + X = N = \text{constant}.$$

At the steady state, equation (2) gives the trivial solution:

$$\begin{aligned} X_s &= W_s = 0 \\ I_s &= N \end{aligned} \quad (3a)$$

and the non-trivial solution:

$$\begin{aligned} W_s &= \frac{Nr - \frac{r^2}{q}}{r + k} \\ X_s &= \frac{Nk - r\frac{k}{q}}{r + k} \\ I_s &= \frac{r}{q}. \end{aligned} \quad (3b)$$

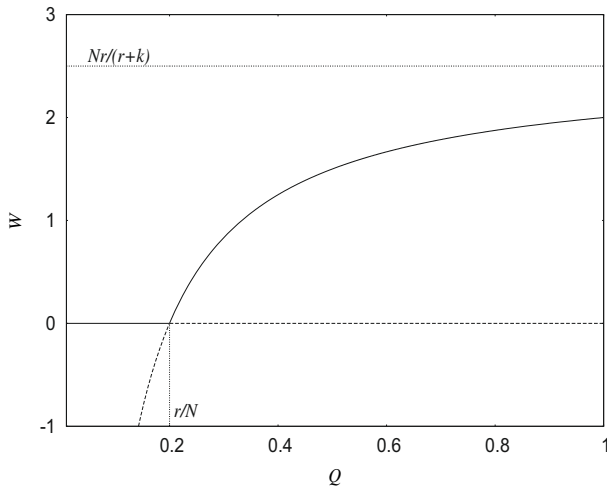


Fig. 8. Bifurcation diagram of the steady-state solutions (Eq. (3)) of the model of equation (2).

Figure 8 shows the bifurcation diagram of these solutions and their stability. We see that there is a transcritical bifurcation at a threshold value $q_c = r/N$ of parameter q . For $q > q_c$ the trivial state loses its stability and the non-trivial state becomes stable. Notice that this guarantees at the same time that W_s and X_s are non-negative and thus physically acceptable.

We now seek the conditions, if any, of optimal exploitation of the resources. As can be seen, no optimal W_s exists with respect to q or N for fixed r, k . There exists, however, an optimal W_s for some r , for given q and N . To compute this we take the extremum of W_s with respect to r , in equation (3b), and see that $dW/dr = 0$ at

$$r^* = -k + \sqrt{k^2 + kNq}. \quad (4)$$

Since r reflects the randomness at an individual level, we may interpret this result as the existence of optimal randomness at which recruitment is the most intense. Randomness ensures the “recycling” or “reshuffling” of the population, since individuals I are eventually bound to return to the nest whereupon they will again be recruited through the first step (which is the only cooperative step) of our scheme. It can be checked that the value of W at the optimum increases with both N and q .

We next consider the case of two competing food sources. To account for the role of variability in the process of competition we again augment the deterministic model (Eq. (1) for $s = 2$) and carry out a Monte Carlo simulation, as in Section 3. We raise the question of the existence of parameter ranges for which the selection of the richest source can be optimized, when two sources of different richness are offered to the colony. First let us see the role of the size of the colony, parameter ϕ in equation (1). Figure 9 shows a plot of the selection of the richest source against ϕ . We see that individuals from small colonies have to lay down more pheromone to select the richest source. On the other hand, individuals from big colonies may lay down less pheromone to select the richest

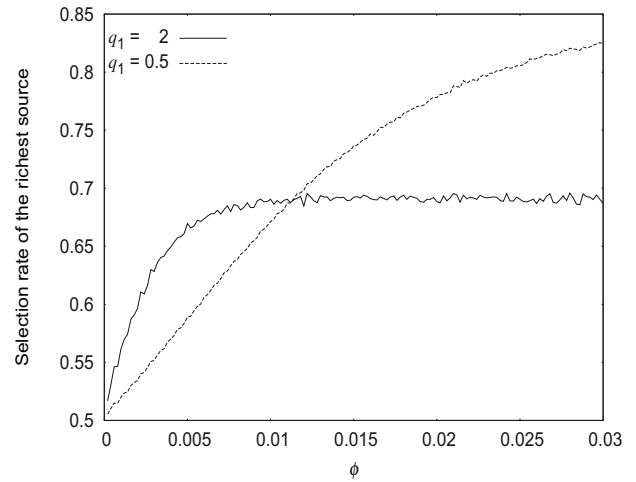


Fig. 9. Selection rate of the richest source as a function of the parameter ϕ for $q_2/q_1 = 0.75$. Other parameter values as in Figure 1.

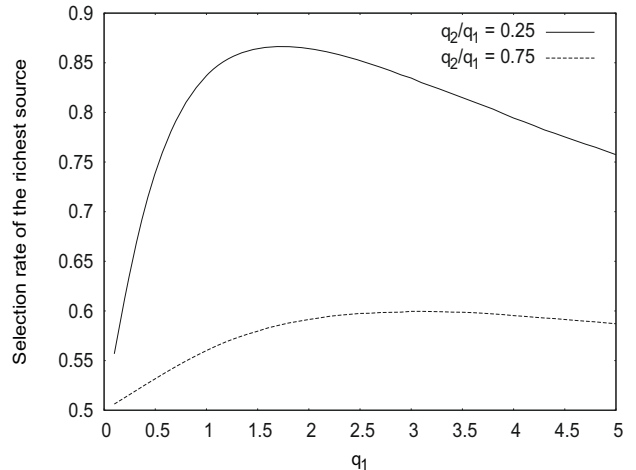


Fig. 10. Selection rate of the richest source as a function of the parameter q_1 for $\phi = 0.1s^{-1}$. Other parameter values as in Figure 1.

source and, moreover, in a better way. This may provide a rationale for the well known fact that trail recruitment mainly occurs in large ant colonies.

The key parameter of this study is the pheromone deposition. In the graph of Figure 10 where the selection of the richest source is plotted against the pheromone deposition, we see the existence of an optimal value of the parameter for which the exploitation is maximal. We can see that the maximal exploitation is higher when the difference between the source qualities is large. This reflects the fact that in this scenario competition is less pronounced.

The existence of an optimal q shows that there is a noise level that maximizes the response in terms of efficiency – at first sight, a counter-intuitive result. It opens some tantalizing perspectives that would be worth implementing experimentally in the future by deliberately tuning the values of the parameters involved.

5 Conclusions

In this paper some generic features of the self-organizing patterns associated with resource exploitation in social insects have been addressed. Emphasis was placed on the transition from individual behaviour where only local information is available, to the collective scale where the colony as a whole becomes capable of choosing between the different options afforded by the multiplicity of the solutions of the underlying evolution laws.

On the one hand, the process of choice leads to robust modes of exploitation, as reflected by the stability of each of the resulting solutions beyond its bifurcation points. But on the other, the response has a marked plasticity conferred by the conjunction of multiplicity, individual variability and environmental constraints associated, for instance, with heterogeneities or to the temporary unavailability of certain resources. In particular (cf. Figs. 3, 4 and 7), the response may switch between the options available in an unexpected way, depending on the initial conditions and the ranges of parameter values considered.

A further manifestation of the far reaching role of variability analyzed in this paper has been the existence of optimal responses, attained when randomness exceeds a finite level (Eq. (3) and Figs. 9, 10). Again, such responses can only arise in the presence of cooperativity and non-linearity, which provide the necessary amplification mechanisms.

Although obtained in the context of social insect biology, our results are in many aspects paradigmatic. As such, they are expected to apply to a variety of other biological processes [10] or artificial systems [15]. For instance, aggregation involves a logic similar to that of food recruitment, as a colony has the choice of different relative attractive sites to aggregate. It can therefore be expected that fluctuations are at work and that there exists an optimal value of amplification and interactions between animals.

Of special interest is the possibility of building mixed societies composed of animals and of artificial agents [16,17]. An exciting possibility is the control of the behaviour of a population. If realizable, this could have far reaching applications in a variety of fields including agriculture. For instance, one could take advantage of amplifying interactions to induce synchronization through an artificial agent in a population of farm animals. In a different vein, data analysis complemented by modelling could lead to the identification of environmental conditions and

stresses that cause the onset of undesirable abnormal behaviours such as aggression or high mortality, which could be subsequently avoided.

SCN was supported by a post doctoral fellowship of University of Oxford. We thank the referees for their helpful comments.

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