



Optimality of Collective Choices: A Stochastic Approach

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Amplifying communication is a characteristic of group-living animals. This study is concerned with food recruitment by chemical means, known to be associated with foraging in most ant colonies but also with defence or nest moving. A stochastic approach of collective choices made by ants faced with different sources is developed to account for the fluctuations inherent to the recruitment process. It has been established that ants are able to optimize their foraging by selecting the most rewarding source. Our results not only confirm that selection is the result of a trail modulation according to food quality but also show the existence of an optimal quantity of laid pheromone for which the selection of a source is at the maximum, whatever the difference between the two sources might be. In terms of colony size, large colonies more easily focus their activity on one source. Moreover,

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the selection of the rich source is more efficient if many individuals lay small quantities of pheromone, instead of a small group of individuals laying a higher trail amount. These properties due to the stochasticity of the recruitment process can be extended to other social phenomena in which competition between different sources of information occurs.

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1. INTRODUCTION

Amplifying communication is a characteristic of group-living animals, such as social arthropods (Hölldobler and Wilson, 1991; Fitzgerald, 1995; Seeley, 1995; Theraulaz and Spitz, 1997; Bonabeau *et al.*, 1999; Detrain *et al.*, 1999; Camazine *et al.*, 2001), one common type of such communication being recruitment. The nature of interactions implied in this phenomenon depends on the species and can involve chemical means and/or physical contacts (Camazine and Sneyd, 1991; Seeley *et al.*, 1991; Visscher and Camazine, 1999; Miller and Koehler, 2000; Costa and Louque, 2001; Ruf *et al.*, 2001). Mathematical modelling of these amplifying processes then leads to coupled nonlinear differential equations linking the characteristics of individual behaviour to the collective response (Nicolis and Deneubourg, 1999; Beekman *et al.*, 2001; Camazine *et al.*, 2001).

The present study is concerned with food recruitment by chemical means, known to be associated with foraging in most ant colonies but also with defence or nest moving (Hölldobler and Wilson, 1991; Traniello and Robson, 1995). In particular, we study cases of competition between food sources leading to trail selection and choice of a particular source by the colony. There is evidence that ants are able to optimize their foraging behaviour by selecting the most rewarding source, due merely to a modulation of the quantity of pheromone laid on a trail (Hangartner, 1969; Hölldobler and Wilson, 1991; Traniello and Robson, 1995). The study of the mechanisms at the origin of such a modulation is hindered by a number of practical difficulties. In particular, it is not clear how one can identify experimentally or by mathematical modelling based on the traditional mean field approach the parameters that can optimize the selection of a source. It is therefore important to resort to other methods. In the present paper a stochastic method of simulation of the trails system is developed to account for the fluctuations inherent to the trail recruitment process due, for example, to the variable frequency of individuals leaving the nest and/or coming to the point of choice between the trails. By taking into account this kind of fluctuation we complete a mean field type of analysis and give key information of statistical nature such as the frequency of visits of an ant in one or other trail or the selection rate of a particular trail i , which are inaccessible in the traditional approach. Furthermore, fluctuations in the number of individuals are expected to be important in small size colonies.

The model is developed in Section 2. Section 3 is devoted to our main results. The main conclusions and the connection with experimental results are presented in Section 4.

2. THE MODEL

2.1. Mean field formulation. Ordinarily in the mathematical modelling of competition processes involving living organisms it is assumed that the effect perceived by a given individual in the population at any time reflects the overall interactions undergone by it with all other individuals present. In this averaged view, referred to as the mean field description, fluctuations arising from individual or external variability—reflecting essentially local effects—are simply neglected.

We now consider, within the framework of such a description, a model describing the evolution of the concentration of trail pheromone and the resulting traffic of the ants over each trail. The analytical formulation of the model and its experimental validation have been already carried out in the case where two sources are present [Beckers *et al.* (1992a), for other models, see Edelstein-Keshet (1994), Stickleland *et al.* (1995)], while a general modelling accounting for a great number of sources has been developed by Nicolis and Deneubourg (1999).

The differential equations describing the time evolution of the concentration of pheromone (c_i) on the trails possess two terms. The first, positive part reflects the ‘birth’ of the trail i , $\phi q_i F_i$ and the second, negative part describes the ‘death’ of the trail i through progressive disappearance of the pheromone by evaporation, $-vc_i$. The flux of foragers from the nest (ϕ) to the trails is related to the colony size. The quantity of pheromone laid on trail i (q_i) is related to the richness of the sources i and v is the evaporation rate of the pheromone. The function F_i describes the relative attractiveness of trail i over the others. The form taken here is (Deneubourg *et al.*, 1990)

$$F_i = \frac{(k + c_i)^\ell}{\sum_{j=1}^s (k + c_j)^\ell} \quad (2.1)$$

k acting like a concentration threshold beyond which the choice of a trail begins to be effective. The parameter ℓ stands for the sensitivity of the process of choice of a particular trail on the pheromonal concentrations c_i present. In the sequel it will be fixed to a value $\ell = 2$, drawn from the experiments made in the *Lasius niger* species (Beckers *et al.*, 1992b, 1993). The model equations can now be written in the form

$$\frac{dc_i}{dt} = \phi q_i \frac{(k + c_i)^2}{\sum_{j=1}^s (k + c_j)^2} - vc_i \quad i = 1, \dots, s \quad (2.2)$$

s being the number of sources present.

Figure 1 summarizes the main results of analytical work previously performed on these equations in the case where two sources are present [for a discussion

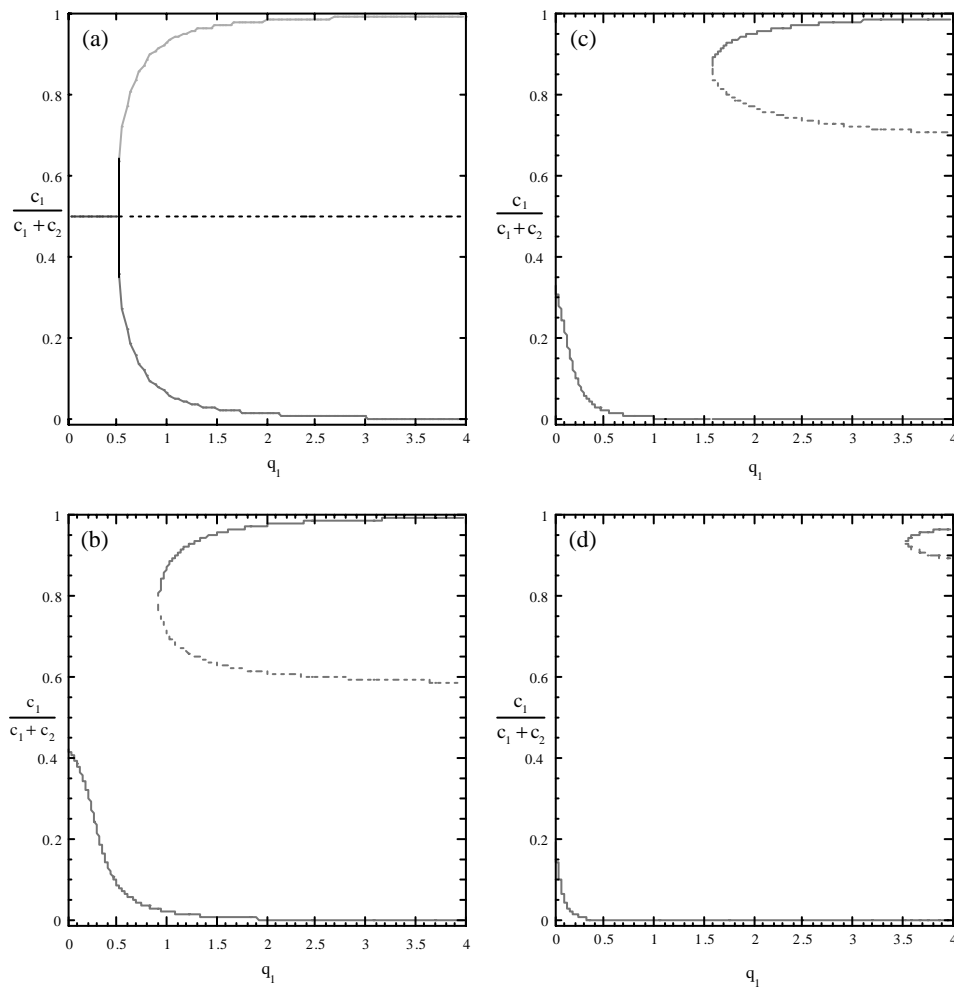


Figure 1. Bifurcation diagrams of the steady-state solutions of equation (2.2) as a function of q_1 in the case $q_2/q_1 = 1$ (a); $q_2/q_1 = 0.75$ (b); $q_2/q_1 = 0.5$ (c); $q_2/q_1 = 0.25$ (d). Parameter values $k = 6$, $\phi = 0.01 \text{ s}^{-1}$ and $\nu = 1/2400 \text{ s}^{-1}$.

of s sources, see Nicolis and Deneubourg (1999)]. It shows the bifurcation diagram of $c_1/(c_1 + c_2)$ with respect to the parameter q_1 . As can be seen when $q_1 = q_2$ [Fig. 1(a)] we have a typical pitchfork bifurcation diagram, meaning that the homogeneous state (equal exploitation of the two sources) becomes unstable at a particular value of the parameter ($q_1 = \frac{2\nu k}{\phi}$). As q_1 becomes different from q_2 one witnesses the breaking of the pitchfork bifurcation. In particular, for increasing differences between the two food sources [Fig. 1(b)–(d)], the colony is led to exploit preferentially one particular source, since only one stable inhomogeneous solution subsists in a wide region of parameter values. Moreover, in the domain of coexistence of two states, the attraction basin around one of the inhomogeneous solutions is greater than that of the other.

In the above picture the exploitation of a particular source, be it the richer or the poorer one, is determined entirely on whether the initial conditions belong to the attraction basin of the corresponding steady states. The question of transitions between states in view of taking advantage of the existence of the rich source and choosing the corresponding adequate strategy does not arise.

In order to incorporate this important aspect we now enlarge the mean field description. Specifically we investigate in the sequel the effects of stochasticity in the process and, in particular, how fluctuations of the number of individuals at the choice point (ϕ) and of the choice itself influence the frequency of collective selection.

2.2. Principle and implementation of a Monte Carlo simulation. In order to sort out the main effects arising from the fluctuations we appeal to Monte Carlo simulations (Gillespie, 1992). The advantage of this type of approach is that one can simulate directly the process of interest rather than solve master type equations (van Kampen, 1981) modeling it at a probabilistic level. In such a numerical experiment the random aspects of the process are thus automatically incorporated. We can summarize the different steps as follows.

a. Initial conditions. The pheromone concentrations and numbers of ants over each trail are fixed to zero.

b. Decision process.

- The first decision concerns the coming or not of an ant to the choice point. This probability is given by the normalized value of the flux parameter. 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.
- The second decision is the choice of the trail. The trails will have initially the same probability to be 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 F_i [see equation (2.1)] used in the analytical formulation of the model. 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 on the trail 1. If it is between F_1 and F_2 , it will follow and mark on 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 (2.1) 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.

The simulations are run for 30 000 realizations and we calculate the mean selection percentage for these simulations, that is, the average value of the fractions

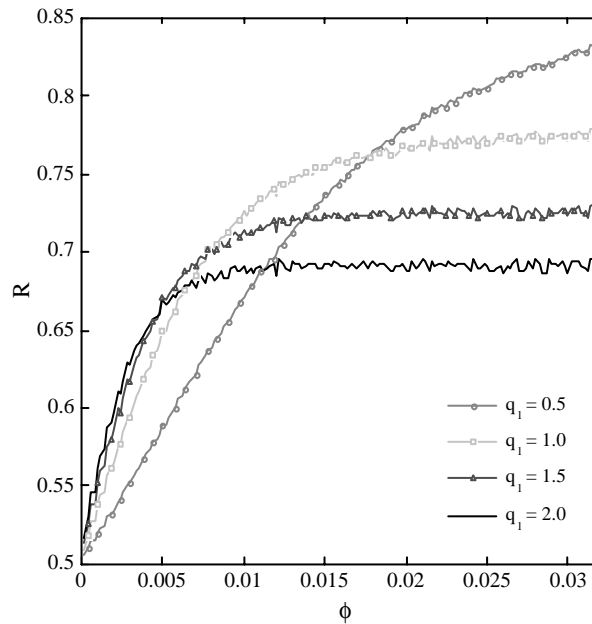


Figure 2. Selection rate vs. parameter ϕ for different values of q_1 and $q_2/q_1 = 0.75$. Parameter values are $k = 6$ and $\nu = 1/2400 \text{ s}^{-1}$.

associated to the richest source [equation (2.2)] at the stationary state (in the following, this will be referred as the index R). The choice of other indicators (ratio of the total number of passages, ratio of the quantity of pheromone deposited, food retrieved on the different paths, ...) leads to similar results.

3. RESULTS

We consider two distinct cases. First we study the role of the colony size in the selection of the richest source. Next we show the existence of an ‘optimum’ absolute value of q_i in the selection of the richest source and the corresponding choice of a foraging path. Finally we study the role of the distribution of the total quantity of pheromone among the individuals of the colony. The following results correspond to the situation where two sources are simultaneously offered to the colony.

3.1. The role of the colony size. We are interested in how the parameter ϕ —the ants flux, known to be related to the size of the colony—plays a role in the selection rate [ratio of the frequencies in equation (2.1)] of the richest source. Figure 2 gives the selection rate of a trail leading to the richest source with respect to ϕ , for different absolute values of q_1 and for q_2/q_1 fixed to the value 0.75. One sees that for small values of q_1 most individuals focus on the trail leading to the richest

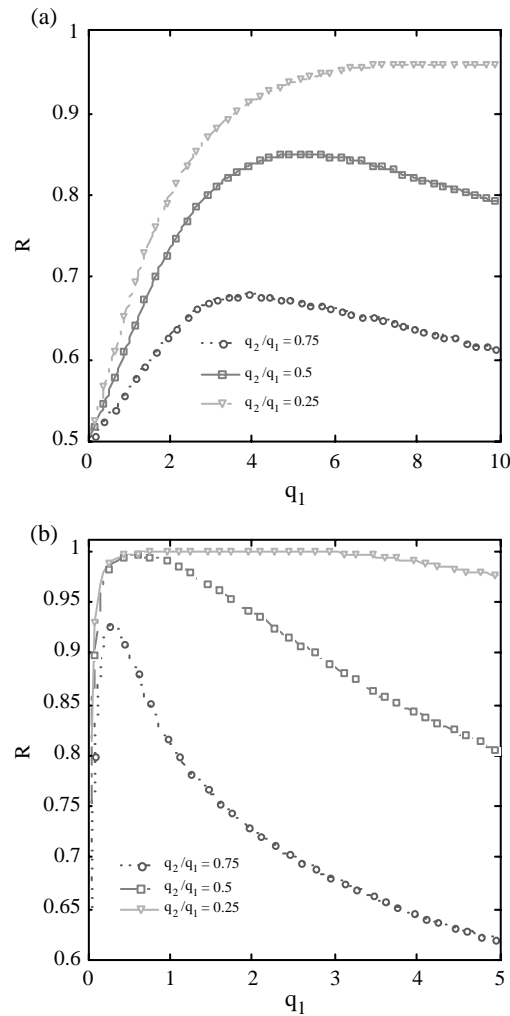


Figure 3. Selection rate [ratio of the frequencies [equation (2.1)] at the end of the process] vs. parameter q_1 for different values of q_2/q_1 with $\phi = 1/600 \text{ s}^{-1}$ (a); and $\phi = 1/10 \text{ s}^{-1}$ (b). Parameter values as in Fig. 2.

source for large colonies, even if the selection rate is less sensitive for small values of the flux. In other words, ants from small colonies have to lay large quantities of trail pheromone to reach a good selection rate while individuals from large colonies can lay smaller quantities per passage and reach a better global selection rate.

3.2. Optimization of the selection. We now study the influence of the absolute values of q_1 and q_2 on the selection rate for a given colony size and ratio q_2/q_1 . As seen in Fig. 3, there exists an optimized value of q_1 (and thus of q_2) for which the selection of the richest source reaches a maximum at the stationary state. The maximum is higher if the difference (ratio q_2/q_1) between the two sources is larger.

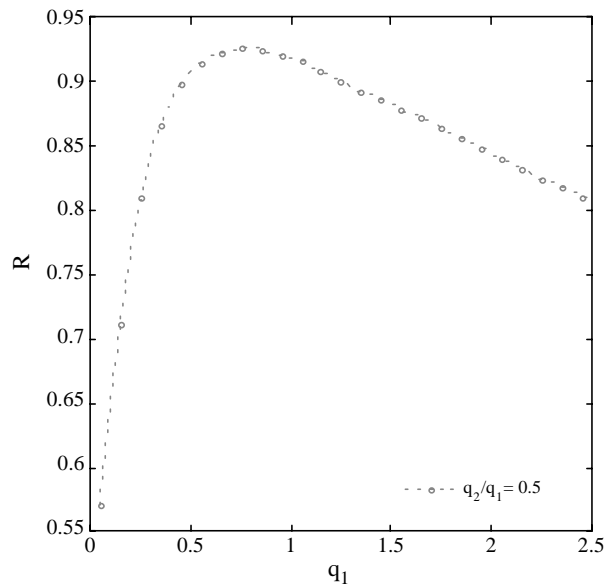


Figure 4. Selection rate vs. parameter q_1 for $q_2/q_1 = 0.5$ after 1 h of exploitation. Parameter values are $k = 6$, $\nu = 1/2400 \text{ s}^{-1}$ and $\phi = 0.1 \text{ s}^{-1}$.

This can be intuitively understood since the competition is less marked as the increasing difference between sources leads to less marked competition between trails (inducing the selection of the richest source). Indeed, higher differences in trail modulation according to the food quality imply a higher determinism in the choice of the richest source.

We also see that, for increasing values of the flux parameter, the maximum is shifted to smaller absolute values of q_1 . This is to be related to our previous results in Section 3.1 showing how large colonies are capable of reaching a high selection rate with small values of q_1 . Remarkably, the notion of optimized selection of the richest source holds true in the transient regime as well. This is shown in Fig. 4, where the selection after 1 h of exploitation vs. the parameter q_1 is plotted.

These results mean that the optimized selection of a trail leading to the richest source is not only due to the relative modulation of trail laying according to food quality (q_2/q_1) but also to the intrinsic capability of individuals to lay a certain quantity q of trail pheromone. A natural question is whether the existence of such a maximum is due to the bifurcation (multistationarity) underlying the process of choice (Fig. 1), but there is no current evidence that there is a one-to-one link between the two phenomena. Still, it is worth noting that in a situation where the parameter ℓ is equal to 1 [applicable to bees, see e.g., Seeley *et al.* (1991)], meaning that there is no bifurcation and that the probability to select one source is directly proportional to the relative number of recruiters, the maximum remains but has a very weak amplitude [Fig. 5(a)]. On the other hand, Fig. 5(b) depicts

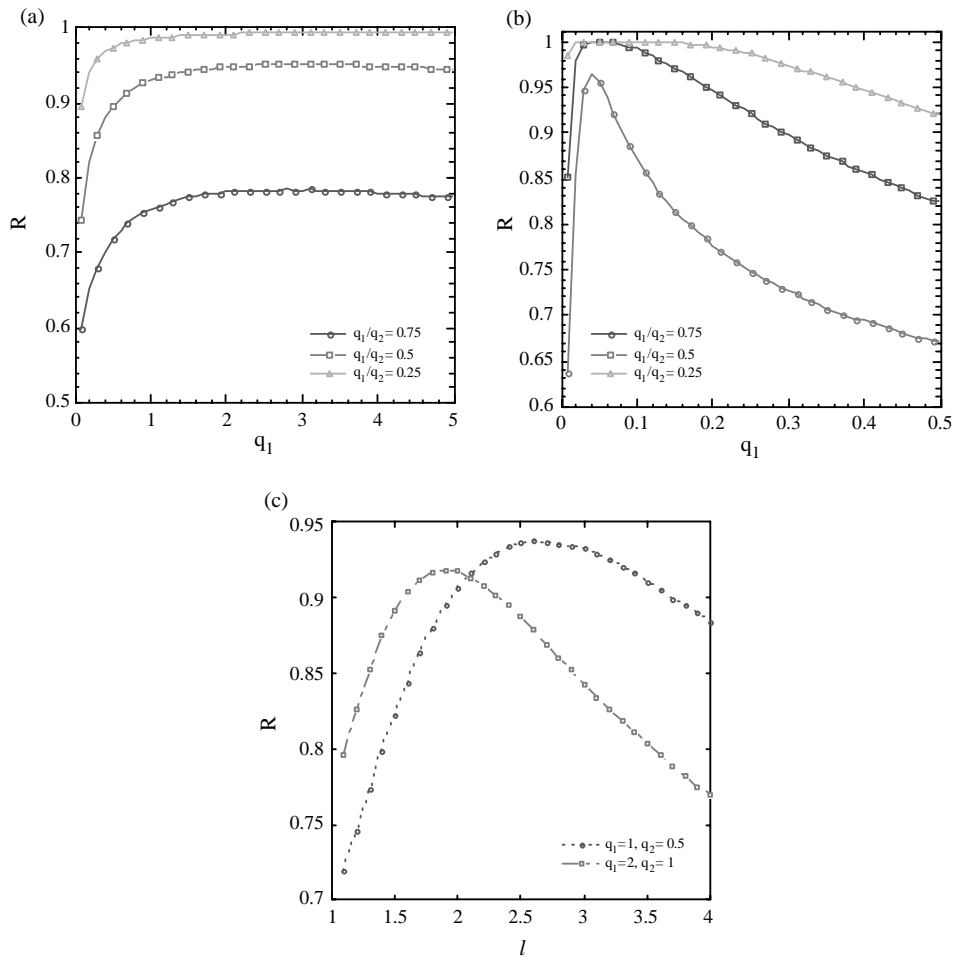


Figure 5. Selection rate vs. parameter q_1 for different values of q_2/q_1 in the case of parameter value $l = 1$ (a) and $l = 5$ (b). (c) stands for the selection rate vs. parameter l for $q_2/q_1 = 0.5$ for two different absolute values of q_1 and q_2 . Parameter values are $\phi = 1/10 \text{ s}^{-1}$, $k = 6$ and $\nu = 1/2400 \text{ s}^{-1}$.

the hypothetical case of ℓ equal to 5, implying a stronger nonlinearity (but giving otherwise rise to the same bifurcation properties as $\ell = 2$) that is to say a higher sensitivity to the pheromone, associated to a marked amplification effect. The maximum again subsists but is now sharper than for smaller values of parameter ℓ . Moreover, there is a value of the parameter ℓ for which the selection is optimized. Figure 5(c) gives the selection rate of the richest source ($q_2/q_1 = 0.5$) for two different (given) values of q_1 and q_2 with respect to the parameter ℓ . It should be noted that the ℓ values which optimize the selection are between 1.9 and 2.6 (this range includes the experimental value of the parameter for the species *Lasius niger*, $\ell \approx 2$). Moreover, it can be shown that if we decrease the flux of individuals the maximum is shifted to higher values of ℓ , suggesting that if a colony possesses a

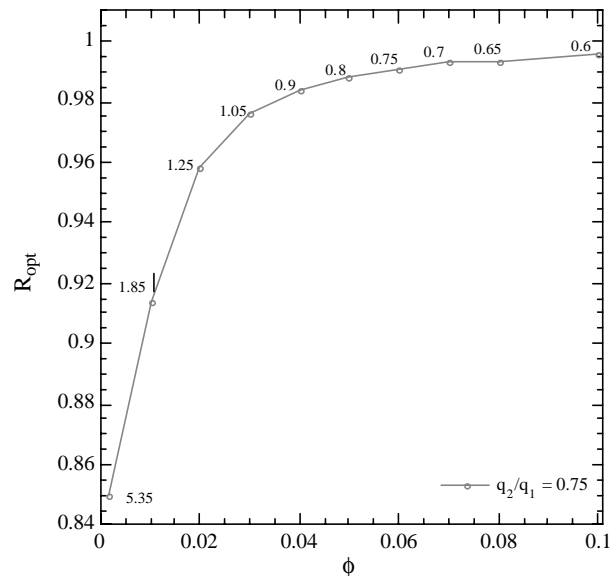


Figure 6. Optimal selection rate vs. parameter ϕ . The numbers written next to the points stand for the values of q_1 which optimizes the selection.

small number of individuals the ants need to have a more deterministic behaviour (close to an all or nothing response).

3.3. High trail laying vs. being numerous. Figure 6 shows the optimal selection (maxima in Fig. 3) vs. the parameter ϕ . The corresponding q_1 are explicitly indicated. We see that the optimal value is always bigger for high values of ϕ and small values of q_1 . These results show thus clearly that it is more efficient for an ant colony to have more individuals who lay small quantities of pheromone rather than to have few individuals laying large quantities of pheromone.

We have considered until now a simplified case where there is only one behavioural category of ants that were all engaged in trail laying. However, in nature ants colonies are composed of different groups of individuals among which some are specialized in trail laying. Hence we need to address the situation in which the colony is composed by active (laying) ants and inactive (nonlaying) ones. In this case the parameter ϕ stands only for the flux of active ants, the size of the colony being constant. For a given total amount of trail quantity, ant societies have the choice to allocate this task to a large number of individuals or to restrain this activity to a small number of individuals laying a large quantity q of trail pheromone. More specifically, we are interested in how the ‘distribution’ of the total quantity of pheromone in the colony can imply a higher selection of the richest source. We thus consider the situation where the product of the parameters ϕ (flux of active ants) and q_1 is constant but absolute values of parameters are changing, meaning that there exists a modulation between the number of laying

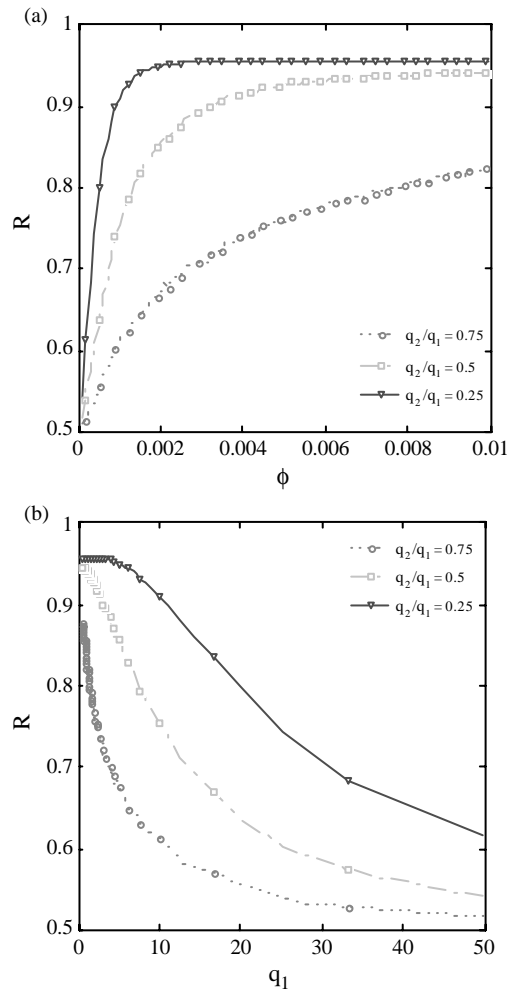


Figure 7. Selection rate vs. ϕ (a) and q_1 (b) for different values of q_1/q_2 , the product ϕq_1 being constant and equal to 0.001. Parameter values as in Fig. 3.

ants and the quantity of pheromone laid down per individual. Figure 7 shows the selection rate with respect to the parameter ϕ (a) and q_1 (b). While in a mean field approach all these situations would lead to identical global responses we see that, in the presence of fluctuations, the selection of one trail becomes more marked for large ϕ 's and low q_1 . This suggests that colonies with more laying individuals that allow themselves to lay less pheromone are more capable to focus on one trail than colonies with fewer active ants. The figures also show that the selection is better when the difference between the sources is larger (parameter q_2/q_1). Notice that since in our setting the final choice is only sensitive to the concentration of pheromone and thus to the effect of active ants, our previous results remain true.

4. DISCUSSION

An approach accounting for the fluctuations in the number of foragers and the stochasticity in the process of decision has been carried out here in the case where an ant colony is confronted with the possibility to follow trails leading to food sources of different quality. The simulation extends the analytical mean field type of formulation previously studied by giving access to some additional results of statistical nature.

We first showed the existence of a preferred quantity of laid pheromone for which the selection of a trail is at the maximum, whatever the difference between the two sources might be. Moreover, in terms of size of the colony, we saw that large colonies can more easily focus on one trail but also that focusing is sharper if the individuals lay small quantities of pheromone. This is especially clear from the results of Section 3.3, where we took the product of the parameters ϕ and q_1 constant, each of them having been varied. It strongly suggests that the selection is the result of not only a modulation of trail laying according to food quality but also of the intrinsic capacity of individuals to lay a certain quantity of pheromone. Furthermore, small colonies (or small groups of ants specialized in trail laying) are less able to take advantage of the trail recruitment than large colonies (or large groups of trail-laying foragers).

It is well known that trail recruitment in ants mainly occurs in large societies. Different hypotheses have been formulated to explain the positive correlation between cooperativity through trail recruitment and colony size (Beckers *et al.*, 1989; Hölldobler and Wilson, 1991; Anderson and McShea, 2001). Our results provide further insights on this matter by showing that large numbers of trail-laying ants enhance the optimality and the efficiency of collective choices.

Our results also suggest that optimal responses are reached when during a recruitment the majority of the foragers are involved in trail laying. Experimental results on the mass-recruiting ant *Lasius niger* seem in agreement with our prediction (Mailleux *et al.*, 2000). These authors show that close to 90% of the foragers lay down a trail pheromone at the beginning of the recruitment. One can expect the decisions during the beginning of the recruitment play an essential role in the final collective choice. This is confirmed by the analysis of the dynamics of our model [e.g., after 10 min, in the case of $q_1 = q_2 = 0.1$ (0.2) and a flux equal to 0.1 s^{-1} , 75% (85%) of simulations have already made a choice]. This result could mean that a high percentage of laying individuals is needed to optimize the selection of a source. Later when the choice is made, the percentage of trail-laying ants may decrease without affecting the foraging efficiency of the colony as experimentally observed through extinction of trail-laying behaviour over successive trips (Mailleux *et al.*, 2000; Geissles and Roces, 2001).

As pointed out in the Introduction, the results obtained in this paper in the specific biological context of trail recruitment can be generalized to other decision processes involving different competing options (Bonabeau *et al.*, 1999;

Camazine *et al.*, 2001). For instance, aggregation can be described by similar mathematical models when individuals of a colony have the choice between different relative attractive sites to aggregate themselves (Rivault *et al.*, 1999; Lioni *et al.*, 2001). It can therefore be expected that since the mechanisms underlying this phenomenon (as well as other phenomena implying competition) are similar to recruitment, the same kind of fluctuations are at work and there exists an optimized value of amplification and interaction between animals.

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