

Most self-organised decisions and patterns arise as a result of a competition between different sources of information that are amplified through different positive feedbacks. In contrast, negative feedbacks often arise 'automatically' as a result of the system's constraints (e.g. limits on the supply of food, the food reserve and the number of available workers). Amplifying communication is a characteristic of group-living animals (Deneubourg and Goss, 1989; Parrish and Keshner-Edelstein, 1999). One common type of such communication is recruitment to multiple food sources in social arthropods, but also in vertebrates and many others groups. The nature of interactions implied in these phenomena depends on the species and can involve chemical communication and/or physical contacts (Hölldobler and Wilson, 1991; Fitzgerald, 1995; Seeley, 1995; Costa and Louque, 2001; Ruf *et al.*, 2001). Many parameters may influence the patterns of food exploitation as well as foraging efficiency. Indeed, in natural conditions,

In animal societies, collective decisions and patterns emerge through self-organised processes, from a variety of interactions among individuals. The rules specifying these interactions are executed using only local information, that is, without reference to the global pattern. Thus collective decisions can be made that, at the individual level, require only limited cognitive abilities and partial knowledge of the environment (Camazine *et al.*, 2001; Hemelrijk, 2002). Simple behavioural rules lead to behavioural flexibility of the society depending on its characteristics (e.g. demography, starvation and kinship) and on its environment (e.g. food distribution and presence of competitors).

Introduction

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J. L. DENEUBOURG, S. C. NICOLIS AND C. DETRAIN

Optimality of communication in self-organised social behaviour

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colonies have to choose between several food sources that are not identical: some are close to the nest, some are large, some contain nutrients of higher energetic value.

Many experimental and theoretical studies deal with the link between the collective response and the capacity of single individuals, such as the variables which they are able to assess to tune their communication (Detrain *et al.*, 1999). However, several questions remain open because they cannot be validated easily by experiments. In this respect, models are useful tools to explore the role of each behavioural component on the emergence of collective patterns. Moreover, they give the opportunity to better understand why a behaviour or value of a parameter has been selected and to extrapolate its evolutionary implications.

This paper presents a theoretical analysis of the role of some parameters involved in self-organised collective choices: the number of amplifications or competing resources, the intensity of the communication and the individual sensitivity to a signal. Optimisation is a main question in the study of social organisation and individual decision-making (Oster and Wilson, 1978; Krebs and Davies, 1997) but very few studies deal with the efficiency of communication and information transfer. Therefore, we will investigate how the communication can be optimised to generate the most efficient collective response and how these optimal values of communication depend on the characteristics of the society and of the environment. These questions will be addressed in the context of ants' recruitment by chemical means, known to be associated with foraging mostly but also with defence or nest-moving (Hölldobler and Wilson, 1991; Traniello and Robson, 1995). A mathematical model of food recruitment applicable to trail-laying ants is used to perform this analysis.

The model

The model describes the development of the concentration of trail pheromone and as a consequence, the traffic of the ants over each trail. 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 , $\phi_i q_i I_i$, 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):

$$F_i = \frac{(k + c_i)^i}{(k + c_1)^1 + \dots + (k + c_s)^s} \quad i = 1, \dots, s \quad (2.1)$$

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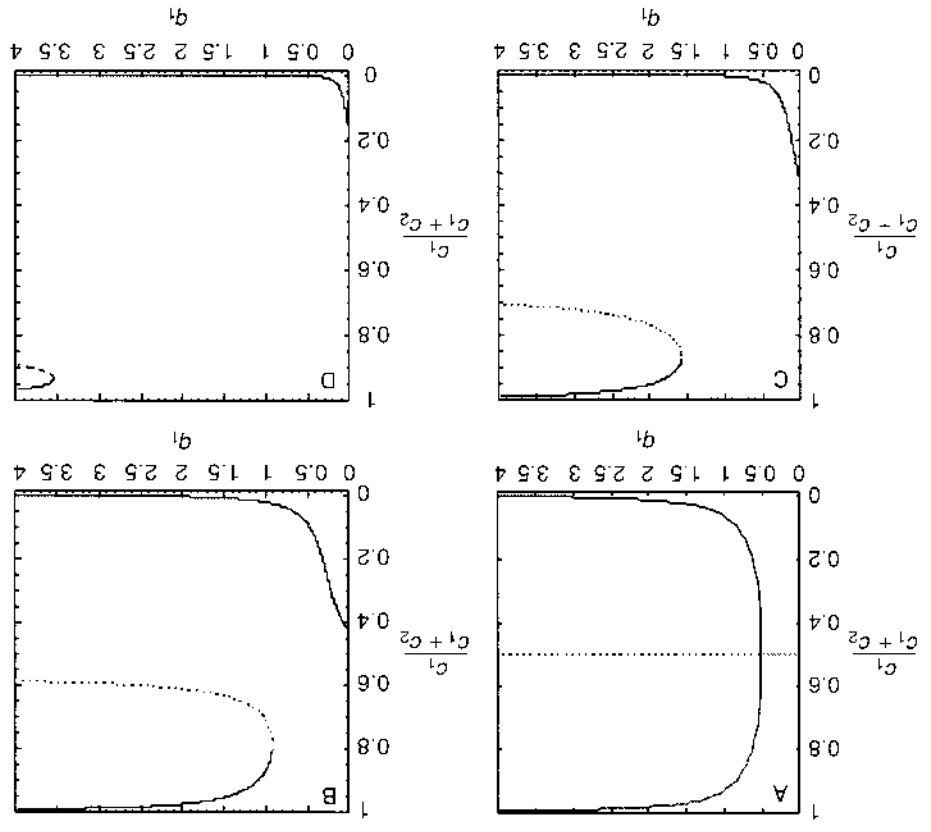
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Figure 2.1 summarises the main results of analytical work previously performed on these equations in the case where two sources are present. It shows the bifurcation diagram of $c_1/(c_1 + c_2)$ with respect to the parameter q_1 . As can be seen, when $q_1 = q_2$ (Fig. 2.1A) we have a typical pitchfork bifurcation diagram,

$$\frac{dc_1}{dt} = \phi q_1 - v c_1 \quad l = 1, \dots, s \quad (2.2)$$

in the form
niger species (Beckers et al., 1992a, 1993). The model equations can be now written it will be fixed to a value $l = 2$, drawn from the experiments made in the *Lasius* pheromonal concentrations q_1 present. Large values of l correspond to a detrainment for the sensitivity of the process of choice of a particular trail on the old beyond which the choice of a trail begins to be effective. The parameter l where s is the number of sources present and k acts as a concentration thresh-

Figure 2.1 Bifurcation diagrams of the steady-state solutions of Eq. (2.1) for two sources) as a function of q_1 : (A) $q_2/q_1 = 1$; (B) $q_2/q_1 = 0.75$; (C) $q_2/q_1 = 0.5$; (D) $q_2/q_1 = 0.25$. Parameter values $k = 6$, $\phi = 0.01 \text{ s}^{-1}$ and $v = 1/2400 \text{ s}^{-1}$.



meaning that the homogeneous state (equal exploitation of the two sources) becomes unstable at a particular value of the parameter ($q_1 = 2rk\phi^{-1}$). 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. 2.1B, C, 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 solution is greater than that of the other.

In order to sort out the main effects arising from the fluctuations, we used Monte Carlo simulations where the random aspect of the process is automatically incorporated. The simulations are based on the same mechanisms defined in the differential system of Eqs (2.2). We can summarise the different steps of the simulations as follows. When an ant chooses a trail i , it lays a quantity q_i of pheromone that gradually disappears through the evaporation parameter v . 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 experimental validation of the model has been already carried out in the case where two sources are present (Beckers *et al.*, 1992b; Nicolis and Deneubourg, 1999; Camazine *et al.*, 2001).

This validated model is then used to discuss how the differences in communication and information transfer alter the collective patterns that will emerge.

Optimality of collective choices: the influence of the number of food sources

Let us consider the case where, in natural conditions, ants have to choose between several competing resources. Models give the opportunity to isolate the influence of the number of food sources (s) on the food choices of the colony related to trail recruitment.

We consider s identical sources (where $q = q_1 = q_2 = \dots = q_s$). Using (2.1), it can be shown that the behaviour of this system is more complex than the one in which there are only two food sources. Figure 2.2 summarises the behaviour of the model. Keeping all the parameters constant (q, ϕ, v, k), for $s < s_{c1}$, we observe stable stationary states in which one food source is preferentially exploited and the others are less but equally exploited. For $s_{c1} < s < s_{c2}$, we found two stable stationary states: the previous one and a second state (the homogeneous state) in which all food sources are equally exploited. When $s < s_{c2}$, the model predicts only one stable stationary state: the homogeneous state. To summarise, for a small number of food sources ($s < s_{c2}$), the foragers focus on one source, for a

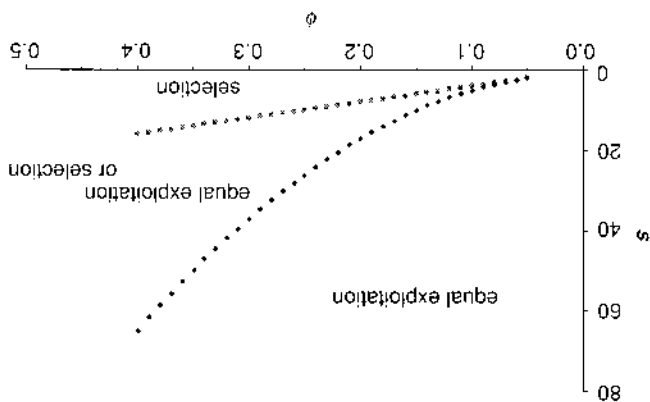


Figure 2.2 Pattern of exploitation in a multiple source situation as a function of the number of sources (s) and ϕ ($s = 1$). Parameter values $k = 6$, $q = 0.1$ and $\nu = 1/2400 \text{ s}^{-1}$.

large number ($s > s_{c1}$), all the sources are equally exploited. Between s_{c1} and s_{c2} ,

both patterns are observed. The randomness of the discoveries will determine the selection of one of the patterns. If by chance one source is discovered a long time before the others, the probability of observing the pattern 'selection' of one source will be high. If most of the sources are discovered simultaneously, we will observe the equal exploitation of the different sources. Keeping s constant, when ϕ (that is related to the colony size) grows, we switch from an equal exploitation of food sources to the state where one source is preferentially exploited. Similarly, when the quantity of pheromone laid on trail q (related to the richness of the sources) is large, one source is also preferentially exploited. The critical values s_{c1} and s_{c2} (for $l = 2$) are:

$$s_{c1} = 2Z \tag{2.3}$$

$$s_{c2} = 1 + Z^2 \tag{2.4}$$

where $Z = q\phi(2k\nu)^{-1}$.

The sensitivity to the trail, the parameter l , also affects the chance of observing the selection of one source: higher values of l will elicit higher s_{c1} and s_{c2} values. Moreover, a critical value of $l = 1$ exists for which the model predicts that a colony will never focus on a single source independently of the colony size, the number of food sources or the trail laying intensity.

To summarise, the plasticity in the pattern of choice between several food sources may result without any requirement for qualitative changes in the information exchanged between nestmates nor any change in the individual behaviour of the ants. This plasticity has important consequences when direct

of the two sources) $(q_1 = 2\nu k\phi^{-1})$. As q_1 the pitchfork bifurcation the two food sources, the particular source, the region of parameter space, the attraction, er than that of the mechanism defined process is automatic- different steps of it lays a quantity q_1 ration parameter ν . updated at each sim- ions. The process is ordinary state, where already carried out 1992b; Nicolis and differences in communication will emerge. The sources ants have to opportunity to food choices of sing (2.1), it an the one in behaviour of we observe exploited and two stable was state) in it predicts for a re, for a re, for a

competition frequently occurs between colonies. Indeed, the defence is a highly cooperative activity, meaning that the probability of winning a fight increases non-linearly with the number of workers (Tranks and Partridge, 1993). Our model suggests that a large colony, able to fight efficiently and exclude competitors at a food site, will more often adopt a pattern where one source is preferentially exploited. A small colony unable in most cases to monopolise a source will tend to scatter the workers on several sources without trying to concentrate its whole foraging force on one site. By doing so, small colonies minimise agonistic interactions and reduce the loss of workers.

Besides colony size, the quality of food sources also influences the pattern of food choice. Knowing that trail intensity increases with food quality, the model predicts that the selection and the monopolisation of one source is automatically favoured when high quality food sources are discovered. At the evolution-ary level, the value of the parameters will be selected depending in part upon whether there is a selective advantage in concentrating the colony's efforts on a single site or whether it is better to distribute one's workforce more widely.

Optimality of collective choices: the influence of the recruitment intensity

In this section, we show the existence of an 'optimum' absolute value of q_1 in the selection of the richest source and the corresponding choice of a foraging path. Simulations are used to account for the fluctuations inherent to the trail recruitment process. The following results correspond to the situation where two sources are simultaneously offered to the colony. We 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 . The percentage of simulations leading to the selection of the richest source, R , is the index of efficiency. As seen in Fig. 2.3, there exists an optimised 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. 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 . The optimal value is always bigger for high values of ϕ and small values of q_1 . This shows that large colonies are capable of reaching a high selection rate with small values of q . These results mean that the optimised selection of a trail leading to the richest source is not

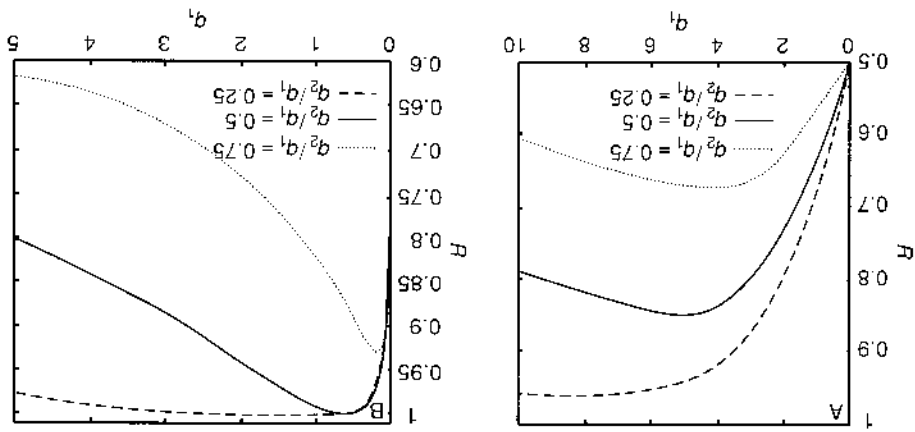


Figure 2.3 Selection rate (ratio of the frequencies (2.1) at the end of the process) versus parameter q_1 for different values of q_2/q_1 with (A) $\phi = 1/600 \text{ s}^{-1}$ and (B) $\phi = 1/2400 \text{ s}^{-1}$. Parameter values are $k = 6$ and $n = 1/2400 \text{ s}^{-1}$.

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. 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.

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 efficiency of collective choices.

Optimality of collective choices: the influence of the sensitivity to the trail

The parameter l stands for the sensitivity of the process of choice between l trails of pheromonal concentrations q_i . There is a value of the parameter l for which the selection is optimised (Fig. 2.4). It should be noted that the l values, which optimise the selection, are between 1.9 and 2.6 (this range includes the experimental value of the parameter for the species *Lasius niger*, $l \approx 2$). 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

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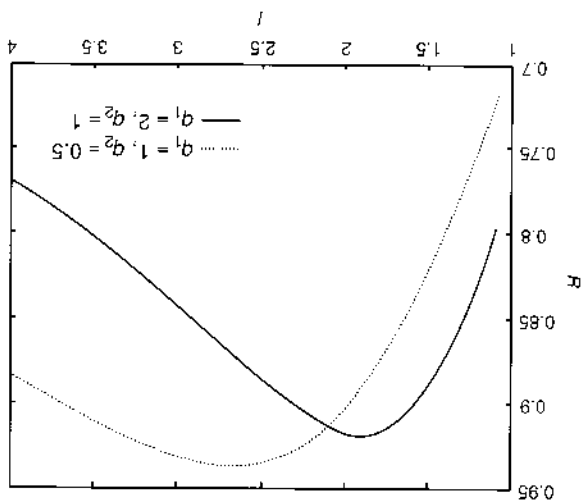


Figure 2.4 Selection rate (k) versus parameter l for $q_2/q_1 = 0.5$ for two different absolute values of q_1 and q_2 . Parameter values are $\phi = 1/10 \text{ s}^{-1}$, $k = 6$ and $\nu = 1/2400 \text{ s}^{-1}$.

a small number of individuals, the ants need to have a more deterministic behaviour.

Discussion

The results above demonstrate that changes in the dynamics of information transfer, environmental and social parameters can be responsible for shifts between different collective responses. By increasing the number of sources in competition or by decreasing the number of workers, the colony shifts from a heterogeneous exploitation to an equal exploitation of all sources. The trail intensity (q) and the sensitivity to the trail (l) also act upon this shift with large values of both parameters favouring the heterogeneous exploitation of the environment.

We show the existence of a quantity of laid pheromone and a sensitivity for which the foraging efficiency reaches a maximum, whatever qualitative differences between the two sources might be. Moreover, in terms of colony size, the model shows that large colonies easily focus on the richest source, this selection being sharper if the individuals lay small quantities of pheromone and respond to the trail in a more deterministic way. One should also notice that even for optimised values of communication (q and l), small colonies always perform less efficient food retrieval in terms of energetic return. In other words, small-sized

colonies seem less able to take advantage of trail recruitment properties than large ones.

From a stochastic point of view, the quantity of pheromone q and the parameter l have similar effects. Indeed, higher values of both parameters lead to more deterministic behaviours of the ants. The existence of an optimal value for both q and l show that there is a level of noise that maximises the collective response in terms of efficiency and selection of the most rewarding site.

Selected parameter values of recruitment enable animal societies to respond adaptively to the diversity of the environment, despite some simplicity of decision rules at the individual level. It is rather trivial to claim that species-specific parameter values have been selected as trade-off responses to multiple and sometimes opposite constraints. For example, for a small colony, intercolonial competition contributes to selecting low values of trail sensitivity while, by contrast, the optimal exploitation of the most rewarding sources favours high sensitivity values. As we cannot experimentally disentangle these different selective effects, modelling gives us the opportunity to isolate and assess their respective contributions to the shaping of communication.

Results obtained in the work described in this paper in the specific biological context of food recruitment can be generalised to other decision processes involving different competing options (Camazine and Sneyd, 1991; Seeley *et al.*, 1991; Visscher and Camazine, 1999; Camazine *et al.*, 2001; Hemelrijk, 2002). Recruitment systems are used for others purposes such as nest defence or swarming (Hölldobler and Wilson, 1990). Moreover, recruitment has also been shown in numerous gregarious species such as social caterpillars (Fitzgerald, 1995), or vertebrates such as Norway rats (Galef and Buckley, 1996) and naked mole rats (Judd and Sherman, 1996). Furthermore, aggregation can be viewed as a result of the competition between different attractive sites. Aggregation can be described by similar mathematical models when individuals of a colony have the choice between different relative attractive sites to aggregate themselves (Rivausti *et al.*, 1999; Liont *et al.*, 2001; Ame *et al.*, unpubl. data). It can therefore be expected that since the mechanisms underlying all phenomena implying competition are similar to recruitment, the same kind of collective plasticity and optimised value of amplification could be observed.

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