

## RANDOM BEHAVIOUR, AMPLIFICATION PROCESSES AND NUMBER OF PARTICIPANTS: HOW THEY CONTRIBUTE TO THE FORAGING PROPERTIES OF ANTS

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Two major types of foraging organisation in ants are described and compared, being illustrated with experimental data and mathematical models.

The first concerns large colonies of identical, unspecialised foragers. The communication and interaction between foragers and their randomness generates collective and efficient structures. The second concerns small societies of deterministic and specialised foragers, rarely communicating together.

The first organisation is discussed in relation to the different recruitment mechanisms, trail-following error, quality and degree of aggregation of food-sources, and territorial marking, and is the key to many types of collective behaviour in social insects. The second is discussed in relation to spatial specialisation, foraging density, individual learning and genetic programming. The two organisations may be associated in the same colony.

The choice of organisation is discussed in relation to colony size and size and predictability of food sources.

### 1. Introduction

The analysis of ant foraging activity is a good approach towards the analysis of the mechanisms involved in their social organisation. We will discuss here how collective foraging patterns can emerge from the interplay between a) random events, from the environment and inherent to animal behaviour; b) amplification processes due to communication or memory; and c) the number of participants. The discussion will be to a large extent theoretical with references to idealistic conditions, and will aim to focus on mechanisms which deserve more experimental investigations.

### 2. Collective foraging and recruitment

The foraging strategies can be classified following different axes. If we consider the foraging behaviour of their workers, most of the species fall into one of the three following categories [1]:

i) Purely individual foraging;

ii) individual foraging + recruitment;

iii) individual + recruitment + permanent trail.

In the first case, the foragers explore the foraging area individually and if one discovers a food source it exploits it on its own and does not or cannot inform its nestmates of its discovery (e.g. *Cataglyphis bicolor* [2]; *Neoponera apicalis* [3]).

In the second case, the workers forage individually, but if one encounters an important food source it recruits nestmates which initiate the food source's exploitation. Recruitment is a collective name for the behavioural mechanisms which enable the growth of the number of individuals in a particular place, in this case the food source's location (examples in [4-6]).

Different recruitment mechanisms exist. In mass recruitment a scout (the recruiter) discovers the food source and returns to the nest, laying a chemical trail. In the nest, some of its nestmates (the recruited) detect the trail and follow it to the food source. There they ingest food and return to the nest reinforcing the trail. In tandem recruitment the scout invites ants at the nest to accom-

pany her back to the food. One recruit succeeds in following the leader, the two animals being in close contact. In group recruitment, the recruiter leads a group of recruits to the food source by means of a short-range chemical attractant. After food ingestion, in each recruitment type, the recruited become recruiters. This typically autocatalytic process is the basis of many activities in the ants' society.

In the third case (iii), the foragers come and go on stable "roads" joining the nest to the food source, using chemical trails and visual memory (e.g. *Formica rufa* [7]).

### 2.1. Reliability and rate of information transmission during food recruitment

Mass recruitment allows the fastest growth of the number of ants at the source, whereas tandem recruitment is the more reliable system, the recruiter being careful about the communication of its discovery (invitation and guiding). Moreover some species using tandem have a feed-back that reduces loss of information [8]. Should the tandem be broken and the recruited ant lose contact with the recruiter, the latter stops and emits a pheromone which attracts the recruited ant. The tandem moves off when the recruit is once more in physical contact with the leader.

Available data indicate that tandem recruitment is more characteristic of small colonies, as opposed to mass recruitment which is found in large societies. These observations suggest that there could be a conflict between the rate of recruitment and its reliability, and that the development of specific mechanisms may depend on parameters such as the number of ants. Small societies have a greater chance of losing information than large colonies, which can use mechanisms that allow mass diffusion of information without being too careful about its reliability.

This idea is supported by a second observation. Some species use a mixed tandem or group-mass recruitment technique. At the beginning of the recruitment, tandem or group leading is frequent,

but when the recruitment is well developed, trail following takes over. The loss of information at the beginning of the recruitment is the dominant constraint: few workers possess the information. As the recruitment proceeds, more workers possess the information and this constraint disappears, allowing the development of the more rapid mass recruitment.

### 2.2. Accuracy and quantification of recruitment

The number of ants ( $Z$ ) around the food source grows logistically [9–11]. Initially growth is exponential, expressing the autocatalytic nature of the process. Later on a decline of the growth rate is observed, there being less and less ants ( $Y$ ) that have not yet been recruited, (the population of the society is finite  $Z + Y = N$ ). The number of ants at the source reaches a plateau value when the rate of recruitment ( $aZY$ ) is equal to the rate of departure from the food source ( $bZ$ ), and the time evolution of the recruitment (fig. 1) may be adequately described by the following equation:

$$\dot{Z} = aZY - bZ,$$

where  $a$  and  $b$  are rate constants.

However, the above description of recruitment is highly idealized, and the individual ants' behaviour is far from being so deterministic. In the first place, the recruiter may interrupt its recruitment cycle with a number of activities sometimes apparently unrelated to the "job" in question [12], i.e. grooming behaviour. In the second place, only a certain proportion of the recruited ants (which leave the nest) arrive at the source, this accuracy varying from species to species. At the very beginning of a recruitment in *Tapinoma erraticum*, which uses mass recruitment, ~ 75% of recruited ants arrive at the food-source, compared with ~ 20% for the sympatric species *Tetramorium impurum*, which uses group and mass recruitment [13].

The trail following error decreases greatly during the course of a mass recruitment. For a given

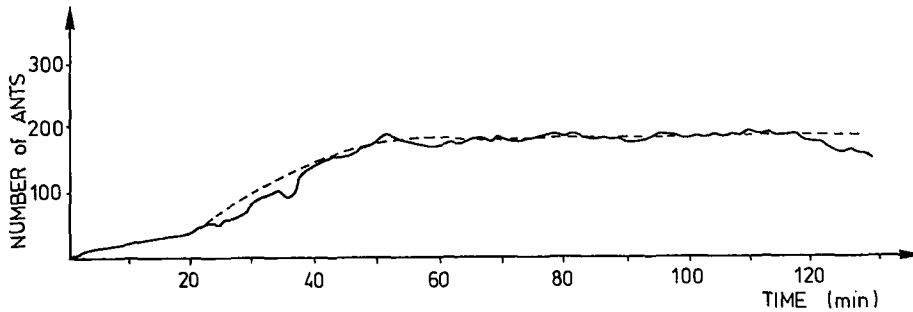


Fig. 1. Fitting of experiment with eq. (1). Value of parameters:  $N = 270$ ,  $a = 8 \times 10^{-4}$ ,  $b = 72 \times 10^{-3}$ . Experiment: heavy line. Fitting: dashed lines.

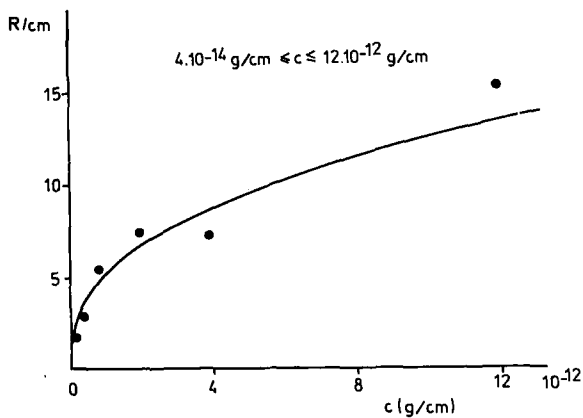


Fig. 2. Mean distance followed on trail as a function of trail concentration.

trail pheromone concentration, the proportion of ants that follow a given length is an exponential function of this length (within a certain range) [14]. The mean distance followed is proportional to the trail concentration at the power 0.36 (fig. 2). As the mass recruitment develops, the ants that have fed reinforce the trail, and thus the trail-following accuracy increases. Furthermore in some species the reinforcement is proportional to the food quality, allowing an adaptive response to food-sources of differing quality [15–17].

The error rate is thus dependent on the species, the quality of the food source, and the nature and the different phases of a recruitment. To what extent may these differences be seen as different

degrees of perfection of recruitment and to what extent as an adaptive response to different environmental constraints? In other terms, can error be anything but a disadvantage?

### 2.3. The function of lost ants

Lost recruits, i.e. those that have lost the trail, search the foraging ground for a period of time before returning to the nest. Their essentially random walk gives rise to a bell-shaped distribution centered around the trail [14]. A species with a low level of noise (high accuracy) presents a narrow distribution, and one with a high level of error presents a more open one (cf. *T. impurum* and *T. erraticum*, see 2.2). Although they do not exploit the already known food source, lost ants searching the area may discover new food sources. What then is the best balance between low accuracy allowing new discoveries, and high accuracy favouring immediate exploitation? This was investigated with the help of a mathematical model in which an ant society exploits a quantity of food divided into different numbers of sources. Different ants “species” with different trail-following accuracy levels were compared (fig. 3). With one source the more deterministic the ant, the better its performance, as lost ants serve no purpose. With more than one source, however, the lost ants enable the discovery of other sources and there is an optimal error level which minimises the global

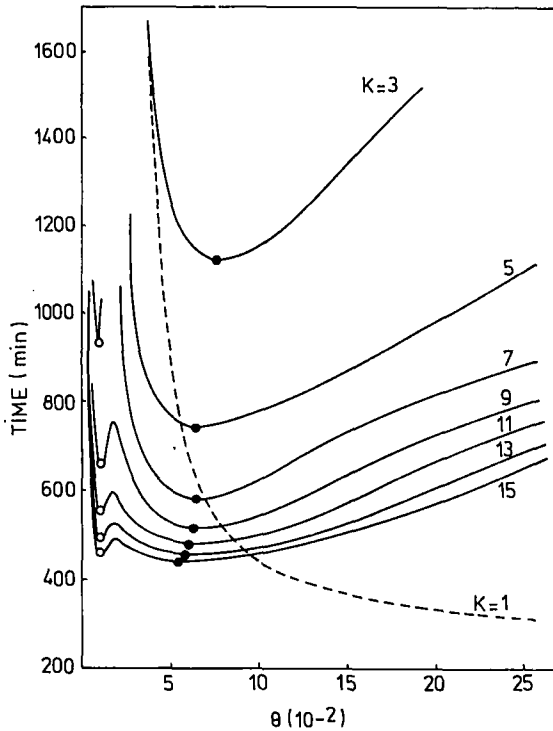


Fig. 3. Collection time for different number of food sources ( $K$ ), as a function of the trail-following accuracy parameter. All food offered is collected (1 ml). Value of parameters;  $N = 650$ ,  $a = 10^{-3}$ ,  $b = 16 \times 10^{-3}$ ,  $2d = 1.4$  cm.

exploitation time. There is also a sub-optimal solution, and an error level above which collective exploitation is not possible [19, 20].

Some inaccuracy during mass recruitment could therefore be functional when food sources are aggregated, and at least in theory the level of accuracy could be tuned to the natural distribution of the food sources. Gould [21] suggests a similar process concerning bees' dance language.

The role of the lost ants is illustrated by the following series of experiments [22, Pasteels et al., in prep.]. A  $10^{-1}$  M sucrose solution is offered to an ant society. The source is discovered, recruitment begins and the number of ants around the source increases. When exploitation of this source is well under way a second, 1 M solution food source is introduced. This source is discovered by lost ants which then recruit to the 1 M source with

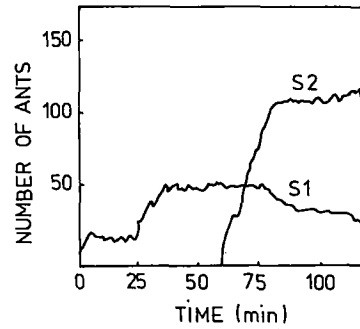


Fig. 4. Evolution of the number of *Tetramorium caespitum* workers around a 1 M (S1) sucrose solution and a 0.1 M (S2) solution introduced after 60 min.

a higher accuracy (stronger trail-pheromone concentration, see above). The number of ants grows rapidly around the 1 M solution and falls off around the first,  $10^{-1}$  M source and the collecting effort shifts to the new more rewarding source. There is thus competition between the two sources of information, the best one being selected via exploitation of the first (fig. 4).

This experiment can be easily described with a system of equations in which we consider that the trail following error is constant for each food source, but higher for the  $10^{-1}$  M than for the 1 M source. However, the following experiment clearly invalidates such an explanation.

If two identical food sources are offered at the same time to the society, the number of ants

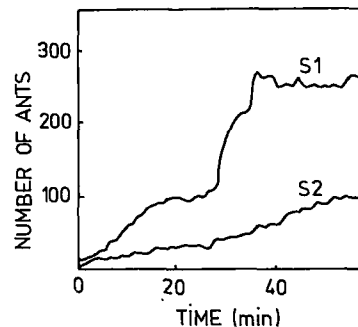


Fig. 5. No. of ants at two 1 M sucrose sources introduced simultaneously.

around each source grows symmetrically until an abrupt change in the kinetics occurs, one of the sources becoming more exploited than the other (fig. 5). This asymmetry does not appear if small colonies are used or when the experimental set-up is manipulated so as to increase the error-level, providing a classical example of a bifurcation phenomenon: below a certain critical value exploitation is symmetrical, above the critical value asymmetry appears, resulting from the interaction between the random and deterministic aspects of the communication involved. The dynamics may be summarised as follows:

$$\dot{X}_1 = aX_1f(N - X - E) - bX_1 + cE,$$

$$\dot{X}_2 = aX_2f(N - X - E) - bX_2 + cE,$$

$$\dot{E} = aX(1 - f)(N - X - E) - pE - 2cE,$$

with  $X_1 + X_2 = X$ , where  $X_1$  and  $X_2$  represent the number of ants at source 1 and 2 respectively.  $E$  is the number of lost ants,  $N$  is the number of potential and actual foragers and  $a$  is the number of ants recruited per ant at the source per potential forager, per minute.

Of the  $aX(N - X - E)$  newly recruited ants, a fraction  $f$  arrive at the food-source and the complement  $(1 - f)$  become lost. The successful ants,  $X$ , remain on average  $b^{-1}$  minutes at the source. The lost ants,  $E$ , have a probability  $c$  of finding a source per minute, or else return to the nest after an average  $p^{-1}$  minutes.

In recruitment where trail following is an important factor (mass recruitment), one may consider that  $f$  increases with the number of ants ( $X_i$ ) exploiting the source and thus reinforcing the trail. With the following function  $f(X_i) = X_i/(g + X_i)$ , the model is able to reproduce the experimental asymmetry unobtainable with a constant error function. Fig. 6 shows how the bifurcation appears as the colony size increases. With small  $N$ , the two food sources are exploited symmetrically. When a critical colony size is reached, the symmetry is broken.

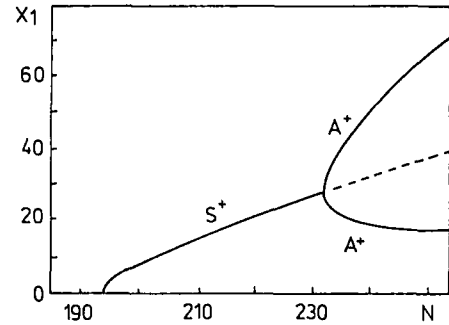


Fig. 6. Steady state solution for the two source model, giving the number of ants at one source as a function of the number of potential recruits.  $S^+$  represents the symmetrical solution and  $A^+$  the asymmetrical one. The solid curves are stable solutions and the dashed curves unstable ( $g = 24.3$ ,  $b = 0.1$ ,  $p = 0.033$ ,  $a = 0.001$ ,  $c = 0.018$ ).

The change in the error level during the course of the recruitment thus makes this foraging “structure” possible. The symmetry breaking could well be adaptive, as it allows the society to concentrate the exploitation on one source which is then better defended than if the foragers were divided around several sources. It also diminishes the error level. Small societies or species using a recruitment system with constant error level would be unable to exhibit this regulation.

#### 2.4. Discovery versus recruitment

So far, we have spoken only about the interplay between discovery and exploitation in the case of food sources that are aggregated in space and time.

However, the tuning between the rate of discovery and the rate of exploitation is a permanent feature of foraging activity. Indeed, many ant species exploit food sources that arrive more or less randomly in the foraging area. What, for these societies, would be the optimal ratio between the number of animals outside the nest, able to make discoveries but competing with each other for a limited number of food sources, and the number inside the nest, “ready” to be recruited or occupied at internal tasks?

The optimal ratio between exploration and amplification is under the control of different parameters, such as the knowledge of the territory. For example *Leptothorax unifasciatus* frequently changes its nest-site [23] and chemically marks its foraging area. With newly established nest-sites, food-recruitment on unmarked territory is characterised by a high level of exploration, and on marked territory by a low level. In both cases, the number of ants at the food-source is similar. With long-established nest-sites, recruitment either on marked or unmarked territory gives rise to a low level of exploration (Aron et al; in prep.).

Marking may be seen as an external and collective memory informing a foraging ant that members of its colony have already visited this area and that the area is not too dangerous and/or possesses food resources. A freshly established society on an unmarked territory has very little information about its foraging area and the necessity for a high level of exploratory activity appears evident. If the zone is favorable, the society settles there and explores less and less (over a time-scale of several weeks). The territorial marking progressively loses its importance (similar exploration being observed on marked and unmarked territory) compared to the foragers' memory which has had time to develop.

### 3. Colony size and amplification

The loss of information that is inevitable in any communication system, ant recruitment in this case, has as a consequence that the amplification can only function if the number of participants is sufficiently high. Mass recruitment only occurs with sufficiently large colonies. We have seen how tandem recruitment reduces information loss so as to enable recruitment with smaller colonies and how asymmetrical exploitation of identical food sources also depends upon the colony size. Its role is also relevant in explaining other social activities.

This is well known in the building behaviour of termites [18, 24, 25]. The first stage in this activity

has been shown by Grassé to be the result of what appears to be disordered behaviour among termites. They transport and drop lumps of earth in a random fashion, but in doing so they impregnate the lumps with a pheromone that attracts other termites. Inevitably by chance the density of these lumps is higher at one time and place than elsewhere, attracting more termites and starting a positive feed-back loop. In this way "pillars" are formed, separated by a distance related to the range over which the pheromone spreads. However, if the density of termites is too low, building behaviour is observed, but no coherent structures develop.

### 4. A first blueprint of ant societies

The ant societies described so far have been characterized by a large number of identical foragers who exhibit a simple and "random" behaviour, with strong communication. Communication and interaction between the individuals generate collective, coherent and efficient structures which are characterized by larger scales of time, spatial dimension, ..., than the corresponding individual scale. Exploration, discovery, communication, amplification, exploitation and selection of the best resources result in social behaviour in which the "decisions" are collective rather than individual.

We shall call this type of organisation a first blueprint. The question now arises: Is this the only blueprint for insect societies?

### 5. A second blueprint: individual foraging and memory

We shall discuss here another extreme hypothetical blueprint in opposition to the first: societies with a small number of deterministic and specialized foragers, rarely communicating together. In other terms can complexity and determinism be

found at the individual rather than the collective level?

*Neoponera apicalis* [3] and *Cataglyphis bicolor* [2] are two typical examples of this second blueprint. *Neoponera apicalis* possesses two forager types. The first type is characterized by individuals permanently exploiting a well defined zone, generally far from the nest. These foragers exhibit a very deterministic behaviour, always following the same path between the nest and their foraging zone. The second type of forager is characterized by less specialized individuals having a more random behaviour, their foraging zones overlapping and being relatively close of the nest.

How would one expect such ants to be “programmed”? A more or less complex system of feed-back and communication could generate such a structure. However *N. apicalis* foragers do not communicate during food collection and it seems that this structure results essentially from an interplay between individual experience and intrasocial competition, as will be discussed below.

### 5.1. Memory during foraging

Although learning ability in social insects has been the object of numerous studies, the role of individual learning in social organization was rarely considered, despite the fact that it could be a central element in the functioning of ant societies.

Two memories related to the spatial foraging activities are known in ants. A short-term memory is described for many species. An ant that has discovered some food will return to the same neighbourhood: e.g. *Paltothyreus tarsatus* [26], *Tetramorium caespitum* [27], *Neoponera apicalis* (Fresnau et al., in prep.). With *T. caespitum*, this memory is an all-or-nothing system, i.e. if no new discovery is made, the ant does not return to this neighbourhood.

The second memory is characterized by a long time-scale (weeks, months, years). Route-fidelity to permanent food-sources in species using trunk-trails or territorial fidelity are examples of long-term memory [2, 3, 7, 28, 29].

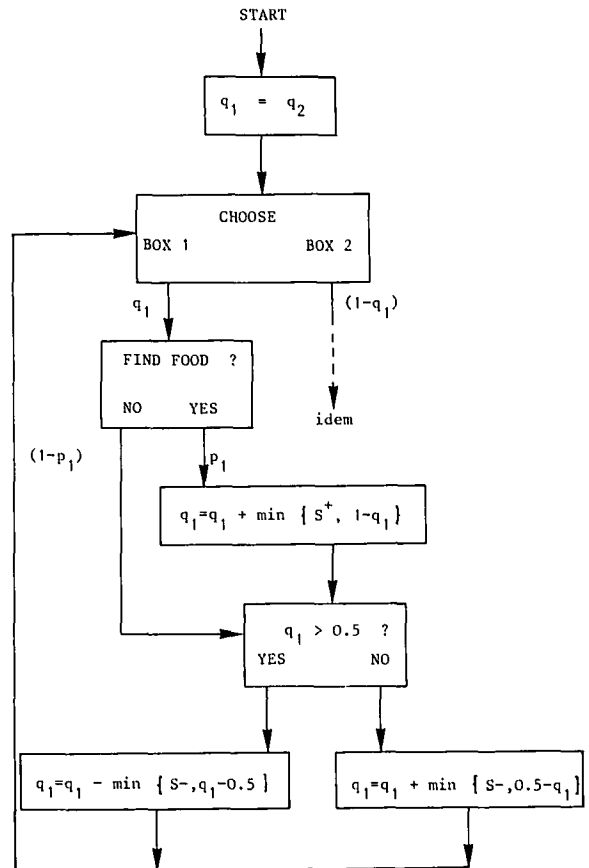


Fig. 7. Flow diagram of learning model.  $q_1$  is the probability of choosing box 1.  $p_1$  is the probability of finding food in box 1.  $S^+$  and  $S^-$  are the probability increments associated with learning and forgetting respectively.

The supposed mechanisms for the development of long-term memory could simply be successive reinforcements when the animal makes discoveries. The rate of learning, resulting from the interplay between the intrinsic capacities of learning and the rate of successful discoveries is in competition with the rate of unlearning. Like recruitment, this learning includes an amplification mechanism as, if the environment is favorable, success reinforces success. With a simple model (fig. 7), we shall see how this process could induce specialization at the individual level.

We suppose that an ant exploits an area, which is represented by two boxes. At time 0, the ant has

an equal probability of going to box 1 or to box 2. If the animal “chooses” for example box 1 and discovers a food source, its probability of returning at the next step increases by a quantity  $S^+$ . This increase is repeated with each successful trip. The animal is also characterized by a rate of forgetting. At each time step, the ant forgets, and the difference between the probability of going to box 1 or 2 decreases. Furthermore each box has a probability  $p$  ( $p_1$  and  $p_2$ ) of containing a food particle at each step, a rich box having a higher value of  $p$  than a poor box. If the rate of learning is sufficiently large with respect to the rate of forgetting, the ant becomes specialized for the exploitation of one box. The rate of learning is under the control of two factors: the quantity  $S^+$  and the richness of the box. If the two boxes have the same richness, for this game there is no advantage in being either specialized or unspecialized, but what if the two boxes are of different richness? In this case, learning would permit the ants to “select” the best box.

Intuitively, we would suspect that the faster the rate of learning the better. However, in this case the simulations show that while a large number of ants become specialized to the good box, a significant number of ants also become specialized to the poor box. The same mechanism which permits the animal to become an efficient forager, also induces a number of “sub-optimal” foragers. Thus, just as there is an optimal noise level in communication, there is optimal rate of learning. One or two discoveries by a foraging ant should not lead it to consider as rich a zone that is otherwise poor.

Now take the case in which the two-box foraging area is patrolled by  $2, 3, \dots, n$  ants of the same colony. If  $p_1 = p_2$ , it is easy to show that the “optimal” solution is to have 50% of the animals specialized for one box and the other 50% for the second box. However, the greater the number of foragers from one society, the more they are in competition with each other, the less chance they have of encountering a food source and thus the less opportunity they have of becoming specialised to one or other of the two boxes.

This picture could explain the two types of populations observed in *Neoponera apicalis*. Close to the nest, the population density is high, and the animals are not specialized. Far from the nest, the foraging density is lower and the animals have the possibility of becoming specialized. The further an ant moves from the nest the lower the density of foragers, thus the greater the probability of finding food, and the more the ant is “encouraged” to return further from the nest.

The way in which a high density of ant foragers limits the learning process may be a factor that “pushes” large colonies towards the first, non-specialized blueprint. On the other hand, it may be to the society’s advantage to keep a certain number of unspecialised foragers in reserve for unpredictable situations.

This discussion about the role of learning and communication would be incomplete if we did not take genetic determinism into account.

## 5.2. Genetic determinism versus learning

The spatial specialisation of *Neoponera* results from a learning process. To forage close to the nest or far from it, as exhibited by *Neoponera*, could however be age-dependant and programmed during the workers’s ontogenesis, though it is improbable that direction and zone fidelity could be controlled by a genetic program. It is more easy to imagine a genetic program controlling a sequence of acts to perform a task, the sequence being executed more or less randomly. E.g. to kill a prey, an ant must discover it, approach, grasp, bite and sting it at the right place. If a species always lives in the same environment and captures the same prey, a deterministic behaviour with a well-defined sequence of acts is clearly the best solution. In the case of unpredictable or very diverse environments or food-regimes, a “consultant programmer’s” first idea might be to develop a deterministic program capable of recognising every problem and of responding appropriately. However, we may easily perceive the limits of this solution, as an unpre-



dictable environment can always present situations too difficult for a finite, rigid program, giving dead-end and even disastrous results. A certain degree of randomness is necessary to provide "emergency" exits to these situations. Randomness appears to be a valid reply to unpredictability. Real plasticity is nevertheless only achieved if the program can modulate its reactions and randomness according to the situations presented and to past experience and knowledge, and predictability of the environment. The learning process may be seen as allowing an individual to become less random and more specialized.

A genetic program could control the rate of learning and forgetting and their optimal balance: with a too high rate of learning the animal could adopt too quickly a behavioural pattern which is not the most adapted to the environmental situation. Specialisation by learning is an appropriate solution for species living in environments that are very diverse but nevertheless predictable at the individual scale. However, the learning solution is not always possible. Predators of dangerous prey are generally highly specialized. As the punishment is very strong if the animal is unsuccessful, it must possess a very efficient and deterministic program, becoming inefficient for other prey.

Inversely, social life could favour specialization by learning. During their period of learning and eventually of low efficiency, the unspecialized animal receives food from nestmates. At this small cost the society acquires a plasticity which allows the development of the right specialists at the right moments. Solitary animals would be at a disadvantage during the learning period, and would rely more on genetical programming.

## 6. Choice of blueprint

We have seen how a large colony is both necessary to recruitment and limits potential learning. Small food sources cannot be efficiently exploited by the first blueprint, as there is no point in

recruiting a large number of ants to carry one load of food. The second blueprint is more adapted to small sources, and long-term memory permits a spatial specialisation of the foragers, with a higher foraging activity in the richest area. When, however, the food sources are large and unpredictable, individual exploration with recruitment is a more efficient system.

Learning and communication are different adaptations to particular situations, but are in some cases associated. This is well illustrated by the foraging behaviour of *Lasius fuliginosus* or *Formica rufa*. *L. fuliginosus* exploits food-sources which are large and unpredictable with a short "life-time" (e.g. earthworms), for which they use recruitment. They also collect honeydew from stable, long-lived aphid colonies on trees. The society builds permanent roads between the nest and the aphid colonies, and the individual ants exhibit fidelity to one particular tree along one particular road. Each spring the road system is rebuilt with great accuracy by old foragers which remember their particular road from the previous winter. Thus the same colony, year after year, exhibits the same road pattern. The aphids colonies are very large permanent food sources which are present in limited numbers. A large number of workers are thus specialized in the exploitation of a particular aphid colony. In this case individual exploration and learning as seen in *Neoponera* would clearly be inefficient, as the time needed for a large number of workers to discover and become specialized to one particular aphid colony would be very long. The permanent road therefore assures communication between specialized and unspecialized workers increasing the rate of discovery and favouring the learning process.

Bees offer another example of synergy between communication and long term memory. After a discovery the scout recruits nestmates and the recruits rapidly become specialised to the new food-source. It is also observed that there is competition between this long-term memory and recruitment: a specialised bee loses its capacity to discover new food sources and to be recruited [30].

## 7. Outlooks

Some of the points discussed in this article, are based on scattered experimental data and mathematical models and have not yet received clear experimental demonstrations. However, ants constitute a good experimental forum in which to test these points which appear in most biological and social organisations. A large diversity of life styles is observed amongst the 10–20 000 species that make up the ant family (Formicidae). This diversity appears at different levels, for example with respect to their food regime there are species which are generalist and others which are highly specialized. Some species are predators, some scavengers and others phytophagous. Some species have only solitary foragers, others hunt only collectively. Finally the colony size varies from 10 individuals to 20 millions.

Biologists are thus able to compare very different organizations, that are nevertheless built with rather similar units, an ant remaining an ant despite the obvious difference between species. From these comparisons, one may hopefully arrive at an understanding of the relations between the ants' individual characteristics, such as their learning capacity and communication, and the resulting collective organisation. In other terms, one might see how a few basic rules hidden behind this diversity may generate the many different organizations so far described.

This question is moreover not specific to social insects but is shared with many other living or even non-living systems in which numerous sub-units, having a large degree of autonomy, interact with each-other.

From this rapid survey, four key elements are seen to play a central role in the social organization: at the individual level, learning and complexity of behavioural sequences, and at the social level, communication and the number of players. At both levels, randomness is an efficient reply to environmental unpredictability. Optimal exploitation depends upon a balance between the amplification processes and the environmental

characteristics. This balance also extends to the evolutionary time-scale, the genetical program being more or less specialised, depending upon the long-term stability of an environment.

To what extent the "choice" of blueprints is dependent on the species, the environment, or the number of foragers is a major question for sociobiologists and the subject of present study.

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