Error, communication and learning in ant societies

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Abstract: When large food sources are discovered, many species recruit using different mechanisms. Numerous recruits do not reach the food source and explore the foraging area. These ants make new discoveries. The interplay between communication and exploration generates collective and efficient structures. This organisation is discussed in relation to the mechanisms of recruitment, quality and degree of aggregation of food-sources and territorial marking. This first organization, characteristic of large colonies, is compared to another foraging organisation: small societies of deterministic and specialised foragers rarely communicating together.

Keywords: Ants, foraging, recruitment, learning

Introduction

One may observe a large diversity of life styles amongst the 10-20000 species that make up the ant family, concerning the biotope inhabited, the alimentary regime, behaviour patterns, caste-system, nest-structure, and so forth. The colony size for example may vary from 10 individuals to 20 million individuals. The foraging strategy, while also highly varied, generally falls into one of the two following categories:

(i) Purely individual foraging.
(ii) Individual foraging with recruitment.

Recruitment is a collective name for the systems which enable the communication of the information concerning in this case the food resource's location. When a scout discovers a food source he returns to the nest, generally laying a chemical trail. At the nest the scout recruits, either inviting one or several ants to accompany her back to the food in the case of tandem or group recruitment (figures 1 and 2). In the case of mass recruit her fellow workers follow the trail to the food by themselves (Figure 3). The recruited ants returning to the nest reinforce the trail and recruit in their turn.

Mass recruitment allows the fastest growth of the number of ants at the source, whereas tandem recruitment is a more reliable system, group recruitment being intermediary.

Globally, the number of ants at the food source grows logistically (Verhaeghe and Deneubourg, 1983). However the above description of recruit-
The recruitment, the distance of the source, and so forth.

The following series of experiments examine some of the factors that may influence the kinetics of mass recruitment.

**Trail following**

A number of circular trails were drawn with different concentrations of trail pheromone and the length of trail followed by different individual ants was recorded, in addition to the proportion of ants crossing the trail that reacted positively to the trail (Pasteels et al., 1985).

The proportion of ants that follow a given length is an exponential function of this length (within a certain range). This implies that the probability of leaving the trail at any moment is constant, and independant of the length of trail already followed.

Some years ago, Hantgartner (1967) showed osmotropotaxy to be the basic mechanism involved in trail-following. The ant moving along a trail perceives different concentrations of the trail pheromone with her left and right antennae. If this difference, in absolute terms, is less than the threshold value, the ant continues in a straight line. If greater, she moves towards the side where the concentration is greater.

Osmotropotaxy also seems to determine whether an ant crossing a trail subsequently fol-
allows it. The difference of pheromone concentration perceived by the left and right antennae is a function of the crossing angle and the distance to the centre of the trail, the spatial distribution of the pheromone concentration being given by fickian diffusion. If the difference in concentration is less than the threshold value the ant does not react to the trail, and thus for each trail concentration there is a range of crossing angles which never induce a positive response. Experiments show that a large crossing angle (close of perpendicular) gave a low trail-following response (Pasteels et al., 1985).

This brief presentation shows some of the sources of noise that give trail-following its distinct random character. However the degree of randomness being a function of the pheromone concentration varies with the quality of the food and the number of passages along the trail (Verhaeghe, 1982; Crawford and Rissing, 1983).

The role of lost ants

During recruitment some ants are thus able to follow the trail to the source and others get lost on the way. The lost ants begin to move randomly, giving rise to a spatial distribution of ants around the trail. A species with a low level of noise presents a narrow distribution, and one with a high level of error presents a more open one.

In this paragraph we present the results of a computer simulation in which an ant society is offered a quantity of food divided into different numbers of sources. Different ants with different trail-following noise levels were compared (Figure 4). 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 thus an optimal error level which minimises the exploitation time. There is also a sub-optimal solution, and an error level above which collective exploitation is not possible (Pasteels et al., 1982; Deneubourg et al., 1983).

The role of the lost ant is further examined in a series of experiments carried out by Parro (1981). A 10\(^{-1}\) M sucrose solution food source 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 from the trail to the 10\(^{-1}\) M source, who then recruit to the 1 M source, with a higher efficiency (stronger trail-pheromone concentration), so that the number of ants grows rapidly around the 1 M source and falls off around the first, 10\(^{-1}\) M source (Figure 5). There is thus a competition between the two informations, the best one being selected via exploitation of the first source.

If two identical food sources are offered at the same time to the society, the number of ants around each source grows symmetrically until after a certain time there is an abrupt change in the kinetics and one of the sources becomes more exploited than the other. This asymmetry does not appear if small colonies are used or if the trail is manipulated so as to increase the error level, and we thus have a classical example of a bifurcation phenomenon (Nicolis and Prigogine, 1977): below
the critical values of the relevant parameters exploitation is symmetrical, above the critical value asymmetry appears, resulting from the interaction between the random and deterministic aspects of the communication involved. The use of a mathematical model shows how the changes in the error level during the course of the recruitment may give rise to symmetry breaking.

**Territorial marking and nest moving**

So far we have considered the kinetics of short-term (minutes, hours) phenomena assuming the societies to be in the same state every day. Long-term perturbations may also influence a society’s behaviour, as may be illustrated by a series of experiments carried out on *Leptothorax unifasciatus* (Aron, 1984; Aron et al., submitted).

This European ant species is characterised by its small societies and simple nest-structure, the nest-site being frequently changed. In common with many other species, *L. unifasciatus* chemically marks its foraging area.

Ants that have recently moved seemed to patrol their foraging area far more than those inhabiting a long-established nest. A recently moved society is considered to be in an excited state with regards to the quiet state characteristic of long established societies.

With newly established nest-sites, recruitment on virgin territory is characterised by a high level of exploration, and on marked territory by a low level of exploration. In both cases the number of ants at the food-source is similar. With long-established nest-sites, recruitment on marked territory gives rise to a low level of exploration, and on virgin territory to a very low or null level.

Territorial marking is a rapid process, taking from one to two weeks in the experimental set-up used here. To pass from an excited to a quiet state takes however several months. Marking provides an external and collective memory which may inform a foraging ant as to the level of activity of its society in the zone it is exploring. When the territory is virgin, the ants from stable and from recent nest-sites react in a way which accentuates the difference in their level of activity.

Information is insufficient to define the adaptive value of this behaviour. However one might propose the following interpretation. The necessity for a high level of exploratory activity in recently settled societies would appear evident, it being essential to evaluate food-resources and potential dangers. The ants mark the territory as they explore, and if it is sufficiently rewarding the society settles there, becomes progressively stable, and explores less. The poorest zones of the territory are less frequented and eventually, through lack of marking, become the equivalent of virgin territory. Few ants venture into these virgin zones, because they are unrewarding and, being unknown, potentially dangerous.

Unstable societies need to gather information and the high level of activity involved implies a high energetical cost. Stable colonies know their territory well and may exploit it at a lower cost.

**Complexity and determinism at the right-level? An ant-sized problem!**

So far in this paper the ant societies have been characterised by a large number of identical foragers who exhibit a simple and ‘random’ behaviour. The communication and interaction between these individuals generates a collective behaviour which appears coherent and efficient, and is characterised by larger scales of time, distance, etc., than the individual behaviour.

Is this the only blueprint for the ants’ foraging organisation? For example are there societies with a small number of autonomous, complex foragers, who rarely communicate or interact with other...
foragers and whose behaviour is less distinct, qualitatively speaking, from the collective foraging behaviour? In other terms can complexity and determinism be found at the individual rather than the collective level?

We may affirm that a number of ant species have a foraging behaviour that is closer to this second blueprint than to the first (Neoponera apicalis for example; Fresneau (1985)).

How would one expect such ants to be programmed? A consultant programmer's first idea might be to develop a program capable of recognizing every problem and of responding appropriately. A real environment, however, can always present situations too difficult for a finite, rigid program, with dead-end and even disastrous results. A certain degree of randomness is necessary to provide 'emergency' exits to these situations. Real plasticity is nevertheless only achieved if the program can modulate its reactions and randomness according to the situations presented and to past experience, knowledge and predictability of the environment.

The learning process may be seen as allowing an individual to become more deterministic and less random, and is always advantageous in stable and predictable environments. On the other hand, in fluctuating milieux the time-scale of the learning process must not be too short. For example one or two discoveries by a foraging ant should not lead it to consider as rich a zone that is otherwise poor. Optimal exploitation thus depends upon a subtle balance between the learning process 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 the subject of present study.

References

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