How Efficient Collective Behaviour Emerges in Societies of Unspecialized Foragers: the Example of *Tetramorium caespitum*

Jacques M. Pasteels*, Yves Roisin, Jean-Louis Deneubourg, and Simon Goss
Faculté des Sciences, Université libre de Bruxelles, 50 av. F. D. Roosevelt, 1050 Bruxelles, Belgium

Field data and laboratory experiments indicate that the foragers of T. caespitum are little specialized in their behaviour although they exploit a large diversity of resources either individually or collectively. We suggest that the colony's foraging activity is regulated by self-organization processes resulting from the interplay between stochastic events and amplificatory mechanisms. Self-organization is illustrated by the way the colony is able to select the most rewarding resources after recruitment. A mathematical model is able to simulate this flexibility, taking into account stochastic communication and non-linear trail reinforcement.

FIELD DATA

Foraging behaviour of a colony was observed on a pavement. The foraging field (about 12 m^2) was exploited from various holes scattered over the foraging surface. The number and locations of the holes varied with time. Each exit hole corresponded to a definite sector in which ants foraged individually.

The distances from these holes at which the ants started to explore rarely exceeded 1 m, and their mode was shorter than 50 cm. Marking experiments showed that short-term memory to sites of food discovery and short-term sectorial fidelity were present, but the distribution of marked ants became more homogeneous only 24 h after marking. Individual foraging varied with season according to the availability of food. Simple feed-back mechanisms could regulate the abundance and distribution of the foragers if food density and distribution influence not only short-term memory of food location, but also the probability of foraging. This mechanism deserves more experimentation. The distribution of foragers resulted also from recruitments. Distant patches of seeds were exploited by long-lasting trails. New exit holes were progressively dug on these trails and the patches were incorporated into the foraging field as new sectors exploited from the new holes by individually acting foragers.

RECRUITMENT FLEXIBILITY

Recruitments in the field were observed to a wide variety of food sources. The mechanisms allowing the ants to allocate their efforts according to food quality were investigated in the laboratory. The experimental set-up corresponded to one sector of a natural foraging territory, explored from a single exit hole. Time-lapse photography and video-recording were used to follow the recruitment dynamics and to quantify the distribution of the ants in the foraging arena. Food sources were sucrose solutions of various concentrations located at 30 or 45 cm from the exit hole.

Recruitment to a single source (1M) appeared suboptimal. Even without food exhaustion or overcrowding at the food source, a large proportion of the recruits explored the foraging arena without collecting. These ants are not considered as specialized explorers, but as lost recruits which missed the target. Experiments using artificial trails demonstrated that losing a trail is a stochastic phenomenon independent of the length of trail followed for a given concentration in trail pheromone. Trail-following behaviour improves non-linearly with trail pheromone concentration.

The value of "lost ants" appeared when 2 sources of unequal qualities were given in succession. Even when a recruitment towards a first source had reached its steady state, a richer source given later on was quickly discovered and more exploited. The distribution of the ants between the 2 sources depended on the difference of concentration between the 2 sources: the proportion of ants feeding at the poorer source was lower for greater differences in food qualities. Surprisingly, two symmetrical sources of equal quality were exploited unevenly, when given in succession or simultaneously.

SELF-ORGANIZATION DURING RECRUITMENT TO FOOD SOURCES

A mathematical model describing the recruitment to two identical sources was constructed on the following principles. Recruitment is described by the logistic-type equation, but only a fraction of the recruits reaches the source. Lost ants have a probability of finding one or the other sources or of returning to the nest. The fraction of ants reaching a source increases non-linearly as the trail is reinforced by the successful recruits.

The model and its properties will be fully described elsewhere (Deneubourg, Goss and Pasteels, submitted). The following equations describe the solution of a recruitment to two identical sources.

$$\dot{X}_1 = aX_1f_1\ (N-X-E) - bX_1 + cE$$

$$\dot{X}_2 = aX_2f_2\ (N-X-E) - bX_2 + cE$$

$$\dot{E} = a(X_1(1-f_1) + X_2(1-f_2))\ (N-X-E) - pE - 2cE$$

$$f_i = X_i\ /(g+X_i)$$

Where X_i is the number of ants at one or the other source; $X = X_1 + X_2$; f, the fraction of successful recruits; E, the number of lost ants; a, the recruitment rate; b, the departure rate; c, the probability of discovering a source by chance; p, the probability of the lost ants returning to the nest; g, a constant.

The analysis of the model's steady states indicates that when the number of participants is sufficient, the symmetrical exploitation of 2 identical sources is unstable as observed in the experiments. It further demonstrates that the stable asymmetrical exploitation is more efficient (as judged by the total number of ants feeding) than would be the unstable symmetrical exploitation. Thus collective foraging spontaneously evolves towards the most efficient pattern. What is true for this borderline situation is a fortiori true for more realistic situations when the sources are of unequal values and when trail reinforcement varies according to food quality.

Self-organization processes are probably widespread in insect societies and are an alternative or a complement to division of labour.