SELF-ORGANIZATION MECHANISMS IN ANT SOCIETIES (II): LEARNING IN FORAGING AND DIVISION OF LABOR

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Summary. Learning, like recruitment, is an amplification mechanism. Past experience conditions the probability of performing a task or returning to a part of the foraging area. In both cases, the interplay between amplification mechanisms, competition between different pieces of information and individual randomness are the factors that generate the individual behavioral patterns and the society organization. With the help of simple mathematical models, we show that this interplay is able to generate not only foraging patterns close to those observed in the field but also a certain degree of task division.

Introduction

This paper is devoted to a model of learning able to reproduce the individual foraging pattern observed in ants or in bumblebees (diffuse foraging in OSTER and WILSON's terminology, 1976) and to the analysis of learning as a mechanism of social organization.

Learning is clearly one of the most important fields of research in behavioral sciences, and mathematical models related to learning are
numerous. A lot of work has been done on learning in bees (MENZEL, 1985) and bumblebees (HEINRICH, 1979). Different forms of memory related to ant foraging have been described, for example:

- Food acceptance in relation to food quality (SUDD and SUDD, 1975)
- Forager fidelity in individual foragers (HÖLLOOBLER, 1976, 1980; WEHNER et al., 1983; WEHNER, this volume).
- Route-fidelity to permanent food-sources, characterized by a time-scale of weeks or months, in species using trunk-trails (ROSENGREN, 1971; COSENS and TOUESAINT, 1966; ROSENGREN and FORTEILUS, 1986).

The analogy between learning and recruitment is close. Like recruitment (PASTEELS et al., this volume), learning is an amplification mechanism. Task and spatial specialization are seen as autocatalytic processes, success reinforcing repetition as is well known in conditioning. In both cases, the individual behavioral patterns and the society's organization are generated by individual randomness, amplification mechanisms and task competition.

This paper is largely theoretical and somewhat speculative. Many of our hypotheses have not yet received clear experimental demonstration. Furthermore, our attitude is deliberately minimalist. The mathematical model presented takes only learning into account, and ignores all other factors, such as age or genetic differences, which could be involved in the foraging patterns' genesis. This attitude is justified on the one hand by lack of data and on the other hand in that we wish to understand the role and limits of learning as a mechanism contributing to an insect society's organization.

The model will show that, in the total absence of any communication between the workers, learning is able to generate:

- an efficient distribution of the foragers in the foraging area, as a function of different characteristics of the food distribution.
- a foraging pattern close to that of the spatial fidelity in ants or the flower constancy in bumblebees.
- a division of initially identical potential foragers into highly active and largely inactive ones.
- an age-dependent division of foragers into active and inactive ones.
Foraging and spatial fidelity in *Pheidole spicatae*

We shall take the example of *Pheidole spicatae* to illustrate our ideas. This species is characterized by a small colony size (< 100 adults). It is an individual (no food recruitment) and diurnal forager, the prey being small insects and larvae (Lachaise et al., 1986). Its strategy is close to that of *Cataglyphis bicolor* presented in this volume by Wetterer and by Schmid-Hempel. We distinguish two types of foragers (Fig. 1; FRESNEAU, 1985):

1) Close to the nest, the population density is high, and the ants forage on overlapping individual zones.

2) Far from the nest, a marked spatial fidelity may be noted. These foragers have a 'personal' zone to which they return more or less regularly over a period of one month or more. These ants are more frequently outside and capture more prey than the unspecialized foragers that hunt close to the nest.

![Fig. 1. Individual foraging zones of some foragers (labeled by a number) which exhibit high spatial fidelity. The non-specialized foragers are found much closer to the nest.](image)

How could the foragers achieve this organization, in the apparent absence of any direct communication between each other?

Different mechanisms could be involved, for example the two

<table>
<thead>
<tr>
<th>Nest</th>
<th>Without prey</th>
<th>With a whole prey</th>
<th>With a piece of prey</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>45 ± 10.1</td>
<td>31 ± 5.3</td>
<td>13 ± 1.9</td>
</tr>
<tr>
<td></td>
<td>(n = 24)</td>
<td>(n = 55)</td>
<td>(n = 24)</td>
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<tr>
<td>II</td>
<td>77 ± 24.1</td>
<td>51 ± 12.6</td>
<td>14 ± 4.0</td>
</tr>
<tr>
<td></td>
<td>(n = 16)</td>
<td>(n = 27)</td>
<td>(n = 22)</td>
</tr>
<tr>
<td>III</td>
<td>28 ± 3.2</td>
<td>16 ± 1.9</td>
<td>6 ± 1.3</td>
</tr>
<tr>
<td></td>
<td>(n = 114)</td>
<td>(n = 290)</td>
<td>(n = 31)</td>
</tr>
</tbody>
</table>

Note: Time (mean ± s.e.) spent inside the nest after a return without a prey, with a whole prey or with a piece of prey (from FRESNEAU, unpubl.)