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The Adaptive Value of Probabilistic Behavior During Food Recruitment in Ants: Experimental and Theoretical Approaches

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Communicative efficiency can be evaluated in terms of the velocity at which information is transmitted (e.g. recruitment rate), or in terms of the accuracy of communication (e.g. dispersion around the target).

Although the recruitment rates are usually considered when comparing food recruitment methods in ants (e.g. Chadab and Rettenmeyer, 1975), accuracy has been nearly completely neglected. It is well known, however, that animal behavior is probabilistic, in particular, ant communication (Wilson, 1962), and that accordingly, only a fraction of recruited ants will actually reach the food source, "lost" ants exploring the environment.

We will present here experimental evidence showing that the amount of "noise" during food recruitment communication varies considerably between species, and that "lost" ants, exploring the environment, can discover new food sources and initiate new recruitment with possible advantages for the society.

It is almost a truism to consider that when only one food source is present, the most efficient recruitment is the most accurate. However, we will demonstrate with the help of a mathematical model, that a certain amount of noise is needed in order to minimize food collection time when a multiple source situation is encountered, and when the sources show some degree of aggregation.

1. Comparison of recruitment accuracy in *Tetramorium impurum* and *Tapinoma erraticum*.

These two species are sympatric. *T. impurum* performs group recruitment : the recruiter leads a small group of recruits. However, some ants are able to follow the trail alone. *T. erraticum* uses mass recruitment: the recruitment trail suffices to guide the recruits which travel independently of the recruiter.

METHODS

Both species were exposed to the same experimental conditions. Food recruitment was initiated by offering 1M sucrose solution at 10 cm from the nest entrance after 4 days of starvation. The behavior of recruiters and recruits were videorecorded. The accuracy of recruitment was measured by the proportion of ants recruited by a first recruit which actually reached the food sources, and also by the mean length of single recruitment trail actually followed by recruiters travelling alone.

RESULTS

Clearly, a recruitment trail is a far better orientation cue for Tapinoma than for Tetramorium. In addition, mass recruitment in Tapinoma is much more accurate, even when group leading is considered together with solitary trail following in Tetramorium (table 1, Verhaeghe et al. 1980).

Table 1. - Comparison between recruitment accuracy in two ant species.

		Tetramorium impurum	Tapinoma erraticum
length (%) of single recruitment trails actually followed		17 (40)	67.7 (47)
% of recruits reaching the food source	alone	8.9 (45)	73.6 (216)
	in group	60 (10)	-
	total	18.2 (55)	73.6 (216)

Numbers in parentheses are those of ants actually observed.

2. The value of "lost" ants in a two source situation.
This was experimentally investigated by Parro (1981) for T. impurum.

METHODS

Two polyvinylchloride (5 X 20 X 30 cm) containers were connected by a bridge. The nests were placed in one container, the food in the other. Recruitment towards sucrose solutions was initiated after 8 days of starvation. Food sources were 11 cm distant from the bridge and 14 cm from each other. They were deposited either simultaneously, or with a 1 hour delay between them. Traffic was video-recorded on the bridge. The spatial distribution of ants was determined by photographs taken every 5 min during the whole experiment (up to 5 h). The ants were familiar with the experimental device, but the substrate (paper sheet) was replaced after each experiment.

RESULTS

Recruitment appeared to be only slightly accurate. Only 20 to 40% of recruits participated in the collection of food. Most of the ants lost the recruitment trail and explored the foraging area. Such very high values for "lost" ants could be partly induced by the experimental conditions, in which this territorial species recruited on an unmarked substrate.

"Lost" ants quickly discovered the second source, even when recruitment towards the first source was already well established. When the 2 sources were of equal quality, the first one discovered was exploited maximally until it was exhausted. However, the second source was colonized by the ants, and its exploitation intensified, when the first became exhausted, so that no interruption or discontinuity in food-collection rate occured.

When the second source was more concentrated than the first, the ants shifted their collecting efforts towards the most rewarding source, the latter, without however, completely abandoning the first source. The exploitation ratio of the 2 sources is function of the sugar concentration ratio of the sources. (more details in Parro 1981).

3. Optimal noise in a multiple sources situation.

Ants losing the trail are able to discover new food sources, but they do not exploit the already known food sources. What is the best balance between noise, allowing new discoveries, and accuracy, allowing immediate exploitation ? This was investigated with the help of a mathematical model in an still very idealistic situation.

MODEL

All food sources are identical, equidistant from the nest, and regularly distributed. Recruitment is initiated towards the median source, and it is assumed that recruited ants distribute themselves normally around the source. Ants hitting a source are able to initiate recruitment towards it.

Recruitment is described by a logistic equation generalized for several sources :

$$\frac{dX_i}{dt} = (a_{ii} X_i + \sum a_{ji} X_j)(N - X_1 - X_2 - \dots X_k) - bX_i$$

and when a source is exhausted by

$$\frac{dX_i}{dt} = -bX_i$$

in which $X_1, \dots X_k$ are the number of recruited ants towards the source specified by the index 1,...k, N the total number of possible recruits, and b the inverse of mean time of staying near the food source and coming back to the nest.

a_{ii} is the recruitment rate for the ants recruited to i and effectively reaching it, and a_{ji} is the recruitment rate for the ants recruited to j and erroneously going to the source i. They were calculated by :

$$a_{ji} = a \int_{r_{i-d}}^{e_{i+d}} \exp\left[-\theta^2 (r_j - r)^2\right] dr/S$$

in which S is a normalisation factor, 2d the dimension of the food sources, $r_i - r_j$ the distance between sources i and j; a is the total recruitment rate of the society (divided by N), and θ is the inverse of the standard deviation of the Gaussian distribution : the greater θ, the more accurate the recruitment.

SIMULATIONS

During the present simulations, a, b, N and d were maintained constant. The performances of recruitments for various values of θ, total food quantity available (Q), quantity of food collected by the ants (q), and number of sources (k), were evaluated by the time needed for food collection.

These simulations demonstrated that :

1) There is one value of θ, θ_{opt}, which minimizes the time of food collection in a multisource situation.

2) For the same number of food sources, θ_{opt} increases when Q increases. This implies that species living in poor environment, where food is parcelled, should be more stochastic in their recruitment.

3) When q is close to Q, the curves relating θ and time of collection show a second minimum for a lesser value of θ than θ_{opt} and a higher value of time of collection, which suggests that species could be evolutionarily "trapped" at a suboptimal level of efficiency (fig. 1).

4) The relationship between θ and time of collection depends in a complex way on the proportion of food collected to the total available (q/Q). Roughly, two different situations could occur, which could correspond to different strategies for ants. When q represents a higher proportion of Q, species should be more stochastic in their recruitment. Besides ants collecting most (above 50%) of the discovered food should possess a rather fixed θ (depending on Q, see 2.), and be able to maintain possession of the source for long period. For ants which rely on the rapidity of exploitation, but with collected food representing less than 50% of total discovered, θ could be far less critical unless the species avoids being too deterministic. This suggests that in rich environment, when most of the time only a small fraction of discovered food can be collected, recruitment strategies could be more varied depending on other biological and ecological factors that those considered here (fig.1).

5) If species could be characterized by a certain value of θ, one species will be more competitive than another under the same conditions, but less than the same in others, according to the level of food parcelling.

More details about the model and simulations will be given elsewhere (Deneubourg, Verhaeghe and Pasteels, in preparation).

DISCUSSION

Several parameters, both internal and external to the society, can affect the efficiency of food recruitment. Experimental and theoretical evidence presented here indicate that one of them is the amount of noise introduced during communication. Some level of noise during communication can be advantageous for the society by increasing the probability of discoveries, allowing the society to focus its collecting activies on the most rewarding resources, and also promotes the colonization of resources which will be fully exploited later.

The level of noise can be optimally tuned to parameters like food quantity and parcelling. Thus, species cannot be simplistically ranked along a linear evolutionary scale towards an idealistic and deterministic system of communication.

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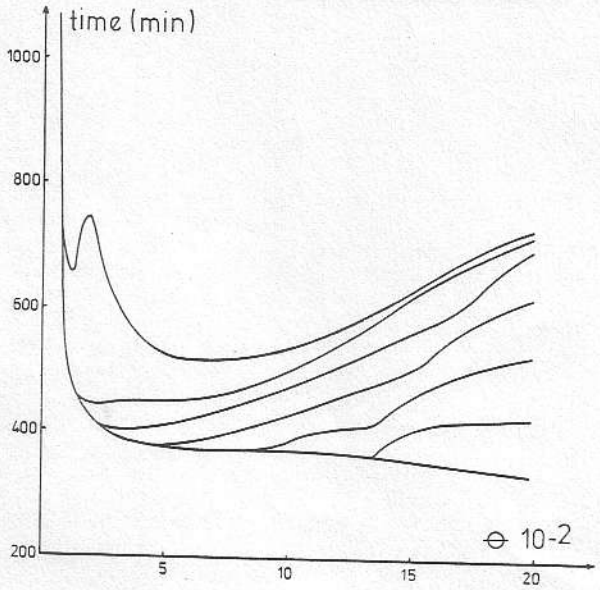

Fig. 1 - Exploitation time in function of θ when the amount of collected food (q) represents various fractions of the total available (Q). q/Q equals respectively 1, 0.9, 0.8, 0.6, 0.4, 0.2, 0.1 for curves 1 to 7. Q is maintained constant.
q = 1 ml (each ant collected 0.26 µl), N = 650, $\alpha = 10^{-3}$ min^{-1}, K = 9, $r_1 - r_g$ = 100 cm, 2d = 1.4 cm.