

Probabilistic Behaviour in Ants: A Strategy of Errors?

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Animal behaviour is probabilistic. This is exemplified by the communication behaviour of ants during food-searching. Experimental evidence demonstrates that species differ in the accuracy of their recruitment. We show here, with the help of a very simple mathematical model, that the randomness of behaviour can have an adaptative advantage for ants. The model demonstrates that the degree of randomness could be optimally “tuned” to particular ecological conditions, such as food quantity and distribution.

1. Introduction

The environment in which an ant colony lives is more or less predictable in time and space. We can compare two extreme food source situations. Tree aphid colonies are sources with a long lifetime (up to 4 or 5 months), while a dead bird is a very unpredictable source.

While exploiting the aphids, the ant colony develops stable roads from the nest to the aphids' colonies with specialized users of these different roads (Rosengren, 1971) and very few ants are scattered outside the highways. This results from the interplay between the long lifetime of the aphid colony and the amplification mechanisms inside the colony. In this situation it is beneficial to have permanent structures with a low level of error or fluctuation.

On the other hand a fluctuating environment can impede the growth of permanent structure. Moreover, long lasting structures lack the plasticity needed in a fluctuating environment and high rates of development of new rigid structures cost energy. In this situation, one possible reaction of the society is to try to eliminate external fluctuations. One way is to damp the external fluctuations with homeostatic mechanisms: the colony tries to

minimize the external fluctuations by appropriate behaviours (stock management, temperature control, . . .).

Another possible reaction to fluctuating environment is the development of temporary structure (e.g. recruitment trail) generated by a self-organization process. (Nicolis & Prigogine, 1977).

Ants, as other living systems, have developed interactions or communications, which can be more or less stochastic. In the present paper we analyse how the level of errors during communication interferes with the development and efficiency of recruitment processes.

2. Food Recruitment

The discovery of a new food source requires the mobilization of ants to insure its efficient exploitation. The mechanisms by which ant societies manage to assemble great numbers of individuals around food sources constitute the food recruitment.

The individual recruitment (the behavioural sequence which allows the recruiter to bring a given number of ants towards the food source) is broadly classified into three main categories: the tandem recruitment in which the recruiter leads only one nestmate to the food source; the group recruitment in which the recruiter lays a trail while returning from the food source to the nest and is needed to guide a group of recruits along the trail towards the food source chemically; and the mass recruitment in which the recruiter again lays a trail while returning from the food source to the nest, but the trail alone suffices to guide the ants towards the food source. In some cases, (e.g. *Tetramorium impurum*, Verhaeghe, 1982) there are intermediates between group recruitment and mass recruitment.

It has been suggested (Wilson, 1971; Maschwitz, 1975; Möglich & Hölldobler, 1975) that these three strategies represent an evolutionary series towards the best recruitment. The flow of ants between nest and food source which results from the succession of these individual acts constitute the global recruitment.

The higher the rate of reproduction of information, the higher is the rate of exploitation. However, the different recruitment techniques could also be adapted to the ants' particular ecological situations (Carroll & Janzen, 1973; Maschwitz, 1975; Hölldobler, 1978).

Until now, quantitative comparisons between recruitment performances were mainly centered on the speed of recruitment which varies considerably between species. As expected, experimental evidence demonstrates that tandem recruitment is the slowest, mass recruitment the fastest, and group recruitment intermediate (Chadab & Rettenmeyer, 1975). Very little

attention has been given to the degree of accuracy of the communication, and on its significance for the society's economy.

We will present here experimental evidence which demonstrate that the degree of accuracy in communication does (during food recruitment) indeed differ greatly from one species to another. With the help of a mathematical model, we suggest that a certain amount of noise during recruitment could play an adaptive role for the society.

3. Experimental Data on the Accuracy of Recruitment in *Tetramorium impurum* and *Tapinoma erraticum*

It is well known that animal communication is essentially probabilistic. In fact, the probabilistic element of behaviour is often included in the definition of communication (Wilson, 1971). There have been however, very few attempts to measure the level of "noise" during recruitment in ants.

In a pioneer study, Wilson (1962) measured the amount of information transmitted by the trail laid by a first recruiter of *Solenopsis invicta* (= *saevissima*), which performs mass recruitment. He found the amount of information transmitted by this technique to be rather similar to that transmitted by the wagging dance of bees (Haldane & Spurway, 1954).

Using a different approach, we shall compare the accuracy of communication in two ant species. The details of the methods used are given elsewhere (Verhaeghe, 1982). The ants were starved during four days, after which a food source (1 M sucrose solution) was presented to the ants 10 cm from the nest entrance. The percentage of ants recruited, by a single recruiter, which actually reached the food source was then determined. In this way, the accuracy of individual recruitment was measured.

Tetramorium impurum is reported as performing group recruitment, but some recruits can reach the food source by following the trail without being led by the leader (Verhaeghe, 1982). Only about 9% of the workers which followed the trail alone reached the food source (Table 1). Fewer workers followed the leader, but their success was much greater: 60% of them reached the food source. Altogether, only 18% of the recruited ants reached the food source by one way or another.

Global recruitment is not much more accurate in this species. Experiments made by Parro (1981) in somewhat similar conditions showed that during food collection only 20–30% of the recruited ants collected food. The majority of them seemed "lost" and explored the foraging area. This proportion of "lost" ants remained almost constant during the whole experiment (a few hours).

TABLE 1
Comparison between recruitment accuracy in two ant species

		<i>Tetramorium impurum</i>	<i>Tapinoma erraticum</i>
Length (%) of single recruitment trails actually followed by recruit		17 (40)	67.7 (47)
Percentage 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.

Tapinoma erraticum performs pure mass recruitment. The communication behaviour is much more accurate in these species than in *T. impurum*. With the same experimental conditions, 73% of the recruits leaving the nest reached the source by following the trail laid by a single recruit (Table 1, Champagne, 1980).

The trail of *T. erraticum* is thus a far better orientation cue than the trail of *T. impurum*. This is further illustrated by the comparison of the degree of superposition of the trail laid by a recruiter and the trajectories of the recruits (Table 1, for method see Verhaeghe, 1982). On average, only 17% of the trajectories of *T. impurum* recruits coincided with the trail, as against 67% of those of *T. erraticum* (Table 1, Champagne, 1980; Verhaeghe, Champagne & Pasteels, 1980; Verhaeghe, 1982).

4. Adaptive Significance of Probabilistic Communication

Obviously, the amount of error during food recruitment varies considerably between species, and probably within the same species according to internal and external conditions. Intuitively, several advantages can be seen in a probabilistic system of communication.

First such a system is more "resistant" to "accidents" than a deterministic system of communication. When a behavioural sequence is interrupted at some point, the goal may still be reached by more indirect means thanks to "errors".

Secondly, nuances of response can easily be introduced during communication. It is well known that ants are able to modulate the deposit of trail pheromone according to circumstances (Hantgartner, 1969; Cammaerts, 1977; Verhaeghe, 1982). This differential emission of signal will accordingly influence the probability of response and lead preferentially the ants towards the most interesting food sources. With a deterministic system,

the introduction of nuances would require a much more sophisticated communication system beyond the brain capacity of insects.

Thirdly, errors during recruitment could allow the ants to discover nearby food sources. This could be advantageous when food is parcelled and food sources aggregated (Pasteels, 1980; Pasteels, Verhaeghe & Deneubourg, 1982). Ants losing the trail can discover new food sources, but they do not contribute to the exploitation of the known food sources. This leads to the question: "What is the best a balance in various ecological situations, related, to the amount and dispersion of the food, between the noise allowing the discovery of new food sources, and the accuracy of the global recruitment, which allows a rapid exploitation of a single source?" This question is explored in the next section with the help of a mathematical model.

5. Model

To begin with, we need a valuable description of the global recruitment. The logistic equation is well adapted to this goal (de Bruyn, 1977; Maebelis, 1979; Baroni-Urbani, 1979; Verhaeghe & Deneubourg, 1984) and computer simulations are also used to analyse recruitment (Jaffe & Howse, 1980). Let X be the number of workers at the food source, the mean flow of ants arriving at the food source is:

$$J_+ = aX(N - X) \quad (1a)$$

where N is the number of ants able to participate in the recruitment (the recruits' carrying capacity), and a the recruitment rate divided by the recruits in the nest.

The flow of departure from the food source is represented by

$$J_- = -bX. \quad (1b)$$

Where b is the inverse of the mean time spent staying near the food source and coming back to the nest. When the food source is exhausted, this last term alone governs the evolution of X . The total rate of evolution of X is:

$$\dot{X} = aX(N - X) - bX \quad (\text{food not exhausted}) \quad (2a)$$

$$\dot{X} = -bX \quad (\text{food exhausted}) \quad (2b)$$

The fitting of an experiment (Verhaeghe & Deneubourg, 1984) according to these relations allowed us to extract the order of magnitude of the value of the different parameters involved in the model: $a = 32 \times 10^{-5}$ /min workers, $b = 0.016$ /min, $N = 650$, quantity transported by one ant (z) = 0.39 mm^3 (Fig. 1). Of course these values hold for one species, *T. impurum*,

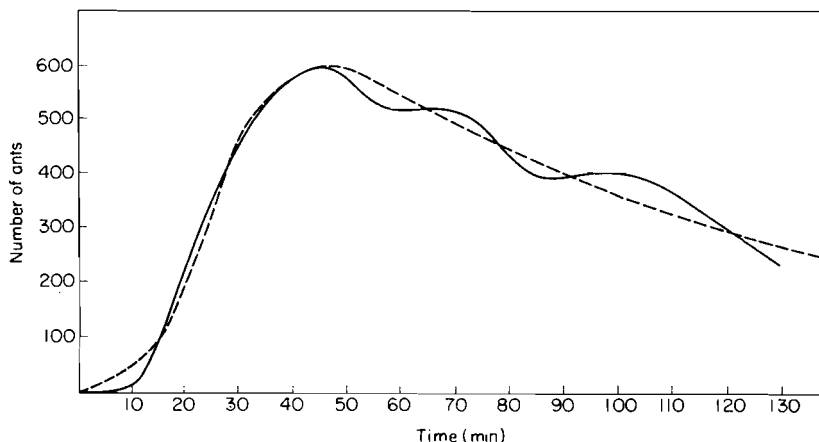


FIG. 1. Fitting of experiment, with equation (2). Value of parameters; $N = 650$, size of food source = 0.1 ml, $a = 3.2 \times 10^{-4}$, $z = 0.39 \mu\text{l}$, $b = 16 \times 10^{-3}$. — is the number of ants at the food source; --- is the fitting.

in one experimental condition. However, since our purpose is not to discuss those parameters, they will be used in all subsequent simulations. Up until now the recruitment model only describes the situations for a single food source but in the next model, several food sources are simultaneously presented to a nest.

The first food source is discovered by chance, but the future discovery of the others is a direct by-product of the noise of the previous recruitments.

The recruitments to the food sources are described by a generalized form of the previous model:

$$\dot{X}_i = \sum_{j=1}^k a_{ji} X_j \left(N - \sum_{l=1}^k X_l \right) - b X_i \quad (3a)$$

and when the food source i is exhausted:

$$\dot{X}_i = -b X_i \quad (3b)$$

where X_i is the number of ants around the food source i , a_{ii} is the recruitment rate for the ants recruited to i and effectively coming to i and a_{ji} is the recruitment rate for the ants recruited to j and erroneously going to the i . The term a_{ii} and a_{ji} are calculated according to the hypothesis that the ants going to the sources distribute themselves along a Gaussian distribution centered on the food sources.

$$a_{ji} = S^{-1} \int_{r_i-d}^{r_i+d} e^{-\theta^2(r_i-u)^2} du. \quad (4)$$

Where S is a normalization factor, $2d$ the dimension of the food source and $r_i - r_j$ the distance between the food source i and j . In this calculation, ants which do not reach a food source are considered to be lost. a is the total recruitment rate of the society and θ is inverse to the standard deviation of the Gaussian distribution. As θ increases, the noise diminishes. The more narrow the Gaussian, the more deterministic the recruitment, and the greater the proportion of the ants recruited towards one source which actually reach that source. The Gaussian distribution is a simplified representation of a combination of different events: the probability of missing the trail, and the amplitude of the subsequent random walk. This choice seems in agreement with the experiments of Parro (1981).

At time $t = 0$ a quantity of food Q distributed equally in k sources is introduced. All sources are equidistant from the nest, and this distance is kept constant (1 m). The distance between the two extreme sources is also constant and equal to 1 m. The distances between neighbouring sources are equal, but of course vary with the number of sources.

Q and K are ecological parameters, whereas N , a , b , θ are characteristic of the species. We shall discuss here the relationships between the time needed to exploit a given quantity (q) of the offered food (Q) and the parameters θ and K (number of sources).

6. Simulations

In these simulations the number of ants able to participate in the recruitment (N), the recruitment rate divided by the recruits in the nest (a) and the inverse of the mean time spent staying near the food source and coming back to the nest (b) are always constant.

1. All food offered is collected ($q = Q$) the numbers of sources (K) varies

Of course, when only one source is present the best recruitment strategy is the one which functions without mistake, and the time of collection decreases asymptotically for increasing values of θ . However when food is parcelled, there is one value of θ (θ_{opt}) which minimizes the time of exploitation (Fig. 2). Unexpectedly, the curves present two distinct minima, at least for seven or more sources. The first one, reached for a smaller value of θ (more stochastic recruitment), corresponds to a suboptimal foraging activity insofar as the time needed to collect food is concerned. Species, "falling in this hole" could be selectively "trapped" at a suboptimal level of foraging efficiency. θ_{opt} decreases when the number of sources increases, which means that species should be more stochastic when food is parcelled.

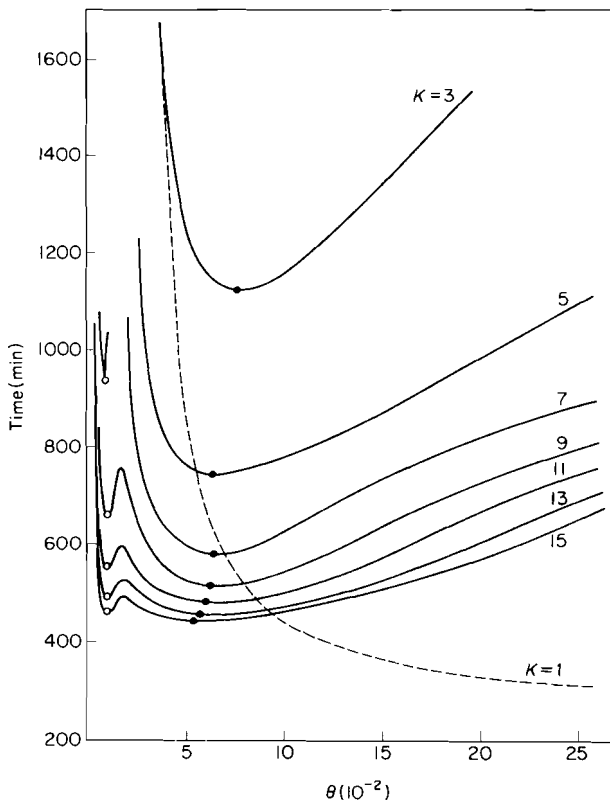


FIG. 2. Collection time for different number of food sources (K). All food offered is collected ($q = Q$). Value of parameters; $N = 650$, $Q = 1$ ml, $a = 10^{-3}$, $q = 1$ ml, $b = 16 \times 10^{-3}$, $2d = 1.4$ cm.

2. *The quantity of food collected remains constant as well as the number of sources, but the quantity offered varies (q and K constant, Q varies)*

This would represent the behaviour of a single colony in different environments as far as food quantity and dimension of sources are concerned (Fig. 3).

When Q is close to q ($q/Q = 0.9$ or more), the curves show two distinct minima as described in Fig. 2. However, when the ratio q/Q is less than 0.9, there is only one θ_{opt} . The value of θ_{opt} increases when the ratio decreases. This suggests that the recruitment should be more deterministic in an environment where food is abundant and sources large. Interestingly when the ratio q/Q is above 0.9, the best solution is reached again by more deterministic behaviour.

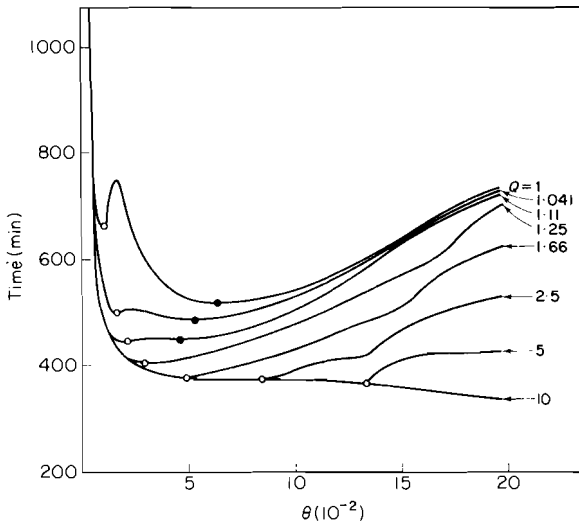


FIG. 3. Collection time for different environmental richness Q (ml). The quantity of food collected (q) remains constant as well as the number of sources (K). Value of parameters; $N = 650$, $q = 1$ ml, $a = 10^{-3}$, $K = 9$, $b = 16 \times 10^{-3}$, $2d = 1.4$ cm.

One unexpected result is that there seems to be a critical value of q/Q ($=0.5$) above which the time of exploitation increases significantly with small variations around θ_{opt} . On the contrary below this proportion, θ_{opt} increases very quickly as Q increases but with little benefit insofar as the time of collection is concerned. Values of θ smaller than θ_{opt} do not greatly affect the efficiency of food collection, but higher values have stronger effects. This suggests that when food is plentiful and sources large, the amount of noise introduced in the recruitment is less critical, unless the species avoids being too deterministic.

Since the benefit of adjusting the dispersion during recruitment to θ_{opt} becomes negligible when the proportion of collected food is less than 50% of the total, we should expect to find a larger diversity of recruitments in rich than in poor environments.

3. *The quantity offered remains constant and equally divided but the quantity collected varies (Q and K constant, q varies)*

This could represent the various behaviours of different species within the same environment (Fig. 4).

As expected, the curves show some similarity with those obtained in the preceding simulation, and only one trend will be pointed out. The "valley"

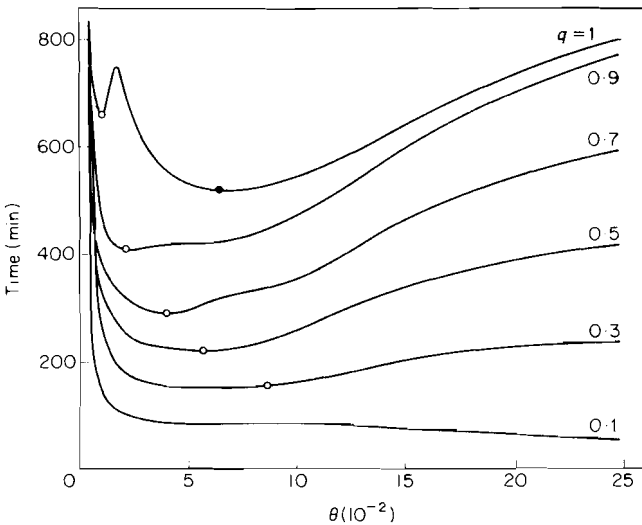


FIG. 4. Collection time for different quantities collected q (ml). The quantity offered (Q) remains constant as well as the number of sources (K). Value of parameters; $N = 650$, $Q = 1$ ml, $a = 10^{-3}$, $K = 9$, $b = 16 \times 10^{-3}$, $2d = 1.4$ cm.

of the curves is deeper when q/Q increases, and the collection time also increases rapidly. Again small variations of θ around its optimal value is more critical when the quantity of food collected is more than one half of the quantity available.

Different strategies seem possible. When there are many sources, species whose strategy is to exploit the discovered food sources to complete or nearly complete exhaustion should possess a rather small and fixed θ . Their recruitment should be rather stochastic, but the amount of "error" during recruitment should be tuned to the degree of food parcelling (Fig. 2). Moreover, they should be able to keep possession of the food sources for long periods. On the contrary, species which reckon on the rapidity of exploitation, could be much more deterministic, but much variance is allowed in the amount of noise present in their communication. Of course, for a given environment, the proportion of needed food to the total food discovered depends on the biomass of the society, i.e. size and number of ants. We should thus expect large colonies of big ants to be more stochastic in this behaviour. Interestingly, *Tetramorium impurum* and *Tapinoma erraticum* are two small- to medium-size species, living in the same environments. The most stochastic species, *T. impurum*, possesses undoubtedly

the largest colonies often more than 10 000 individuals, whereas those of *T. erraticum* rarely exceeded 2000 (Meudec, 1979).

7. Discussion

We are perfectly aware that the model is still very crude. The regular distribution of equal sources is of course idealized. Despite this, we believe that the model strongly suggests that a certain amount of noise during food recruitment can be advantageous. The differences observed in the accuracy of communication in various species could thus be interpreted as selected strategies adapted to particular social and environmental conditions, rather than as different levels of evolution towards an idealistic deterministic system of communication.

When only one source of food is exploited, the more deterministic, will be the more efficient recruitment. However, the model shows that a given amount of noise in the recruitment process is needed in order to optimize food gathering when a multiple and aggregated source situation is encountered. It is not difficult to find natural situations in which this is indeed the case, e.g. aphid colonies feeding on the same host plants or on adjoining herbaceous plants, fallen fruit on the ground and plant exudate.

The model demonstrates that the optimal level of noise depends on the amount of food discovered, the way it is parcelled and the food gathering strategy adopted by the ants: i.e. either to exploit over a period of time the sources to exhaustion or to collect as quickly as possible only part of the food available. Clearly more noise or "error" is advantageous when the food is parcelled, and when each source is less rewarding. Moreover, species exploiting food sources to exhaustion need to be more stochastic than those which reckon on the collecting of some food as fast as possible. Besides, selective pressures could be greater for the former to optimize the level of noise during recruitment. More deterministic species would be better adapted in some environments, but less in others. Thus according to their degree of accuracy, recruitment strategies cannot be ranked along a linear scale of evolution, but their efficiency is strongly dependent of environmental and social parameters.

Until now only a few ecological parameters have been investigated, such as food quantity, divided in equal parts and regularly distributed. The distances of the food sources from the nest have been arbitrarily fixed and maintained constant and equal. Clearly, other kinds of spatial distributions of the sources, as well as parameters like differential qualities of food sources, predictability of resources, aggressive competition of neighbouring societies should be investigated in the future.

Also the amount of noise is of course not the sole biological parameter involved in the efficiency of recruitment. Parameter-like recruitment rates, biomass of the society, numbers of ants and of potential recruits, were maintained constant in the present study, but they vary considerably both within and between species. These parameters together with biological characteristics like the level of specialization amongst workers (polyethism), defensive potential, exploratory and territorial behaviour, are all relevant for the adoption of one efficient recruitment strategy. The degree of interdependency of these factors needs further investigation.

An intriguing possibility is that the genesis of error could be regulated by the nature of the system of communication itself. The trail leading to a food source just at the beginning of its exploitation is of a low level of concentration. Accordingly, the number of ants losing the trail is high. With the increase of recruitment the concentration of trail grows and the number of insects losing the trail decreases. It is evident that the amount of error has a different role at the beginning than at the middle of the recruitment. Moreover, since the ants are able to modulate the quantity of trail pheromone deposited according to food quality, both the recruitment rate and the amount of noise could be modulated in this way. This should allow the ants to adapt their foraging behaviour so as to exploit preferentially the rewarding resources, following new discoveries. This possibility will be more fully examined in a further article.

Recruitment behaviour is also performed in circumstances other than food-gathering, e.g. during nest moving or territorial defence. Nest-moving probably needs a more accurate recruitment than territorial defence. Much more ecological information is needed to evaluate which selective pressures are operating for the adoption of one particular mode of recruitment in a species.

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