Pattern formation via chemical communication: collective and individual hunting strategies

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Abstract - We present a chemotaxis-diffusion model that describes collective hunting strategies using chemical communication. At the level of the individual the orientation of the animals in a scent field is described by a function that relates a chemical stimulus to a behavioural response. Two further rules are needed to describe the communication between the animals via emission of a pheromone and to characterize the interaction of the animals with prey items. The application of these rules to an ensemble of equally equipped individuals leads to coordinated hunting strategies. The hunting benefit of this strategy is compared to that of an individual strategy. This strategy is only different in that there is no communication between the animals. It is found that collective hunting is more efficient at low prey densities whereas individual strategies are more efficient at high prey densities.

Keywords: Chemical communication, aggregation phenomena, orientational mechanism, mathematical model, individual and collective hunting strategies.

Introduction

Foraging processes give us many examples of well coordinated behavioural strategies. An insect society is faced with responding to a considerable logistic problem in the correct manner; namely, how to arrange to have the right number of individuals in the right place (or the right places) at the right time. What is considered to be right may differ from one situation to another. That is, it is required that the insect colony adapts itself to different situations in a flexible manner. The primary question that arises in this context is to understand how different flexible strategies are generated at the level of the society. Does the insect colony have different strategies for situations that present themselves in different ways, or is it possible to imagine that there is a certain set of basic strategies that allow the society...
to adapt to different problems? There are good reasons to believe that a few simple rules are sufficient to generate foraging strategies that are flexible enough to permit the group of hunting animals to adapt to different environmental conditions (for an overview see Deneubourg and Goss, 1989). These approaches are characterized by being phenomenological in the sense that they are generally based on mean field equations. The example we present here is taken from a different approach in the sense that it is microscopic. This microscopic approach is complementary to the phenomenological models of the Brussels group given above and either point of view reveals some interesting properties of the biological system.

The present approach was inspired by the following idea. Is it possible to find a few basic rules that underly a large number of behavioural patterns where chemical communication plays a role? Or stated differently, can a few basic rules account for general classes of behavioural patterns. Different classes of behavioural patterns in the context of chemical communication are, for example, recruitment strategies that are based on trail following or those that are based on aggregation phenomena. Even if it will not be possible to understand all these behavioural patterns in detail with this set of fundamental rules, the observed behaviour should at least be compatible with the rules. This seems actually - within certain limits of course - to be possible. And in fact, it is not surprising at all. In this approach it was not only tested what are the possible main classes of behaviour, but it was also investigated in detail how the impact of physical constraints on the individual behaviour is reflected on the large scale structure. This results in the generation of apparently totally different behavioural strategies.

In this paper we will discuss some general results for recruitment or hunting strategies that are based on aggregation mediated by chemical communication. We will discuss quite abstract situations and compare the results to individual hunting strategies in order to see what environmental conditions (abundance of prey, size of prey, etc.) affect the yield of the harvest. We will start our discussion by outlining some general ideas underlying chemical communication and present a model that describes individual orientation in scent fields. We then apply this model to an ensemble of individuals which are equipped with these behavioural rules.

### Chemical communication and a model for orientation in olfactory landscapes

Most of the communication in insect societies (Wilson, 1971; Hölldobler and Wilson, 1990) and also in gregarious insects (Fitzgerald and Peterson, 1988) is chemically mediated. If we want to relate complex collective behaviour to individual behaviour, we have to find basic rules which govern the processes involved in chemical communication. Here by chemical communication we mean the emission of the signal, its propagation and the behavioural response. A closer inspection shows that most of the phenomena where chemical communication is used for orientation
can be reduced to following chemical trails or aggregation around pointlike sources, i.e. moving up a gradient generated by an odorous source.

What we need is thus a model for the motion in an olfactory landscape and a few rules for the pheromone emission at the level of the individual. One mechanism appears to be the main component for orientation on scent trails: osmotropotaxis (Hangartner, 1967; Leuthold, 1975). For this mechanism it is assumed that the animals detect the concentration difference between their antennae and then turn to the side of higher concentration (Fraenkel and Gunn, 1940), thus minimizing the concentration gradient between the antennae. One can translate this behaviour into a simple algorithm which is depicted in Fig. 1.

1) Perception of the pheromone concentration with the tips of the antennae and determination of the concentration difference $\Delta C = |C_l - C_r|$

2) Change of direction according to the rule:

$$\Delta \Theta = \text{sgn} \left( \frac{\Theta_{\text{max}} \Delta C}{\Delta C + \text{Ref}} \right) \Delta t$$

3) Movement of one unit step length:

$$\Delta x = (v \cos \theta) \Delta t \quad ; \quad \Delta y = (v \sin \theta) \Delta t$$

Fig. 1. - Behavioural algorithm, equations of motion and geometry of the model.

Results obtained by computer simulations such as the mean distance as a function of the trail concentration, the influence of the trail curvature are in agreement with those obtained experimentally (Calenbuhr and Deneubourg, 1989; in prep.; Calenbuhr et al., in prep.).

Aggregation phenomena

The osmotropotactic response function presented can also be used to move up the gradient if the source is pointlike, inducing motion towards the center of emission which leads to aggregation if many animals participate in the process. Not
only do such social insects as ants make extensive use of this kind of chemical communication but also groups of gregarious insects, as for example the larvae of beetles. In what follows we will show that aggregation phenomena based on chemotaxis can generate efficient hunting strategies. Imagine that one has a certain number of prey items and predators, both distributed more or less homogeneously. When a predator has found a prey item it will start to feed and after a while it might search for new prey. This scenario corresponds to an individual strategy. In a collective hunt the individual which has found a prey might "inform" conspecifics about the food finding by emitting a pheromone. The other hunters will move up the gradient and may also emit a pheromone when they have arrived at the food source. We thus will have an instability of the homogeneous distribution (given the right parameters for emission, ...) which leads to a clustered distribution of predators. After the food source has become exhausted the animals will start to search randomly until the next prey is found and the whole process is repeated. The mechanism of formation of aggregates in this case is closely related to that found in chemotaxis-diffusion systems in slime moulds, which are classical examples of pattern formation (for an overview see Segel, 1980). Here we shall not look at the formation or the form of the pattern itself, that is an ordered spatial structure, but will study a quantity that can be considered as being the result of the pattern formation process. The mechanism described leads to a series of aggregation phenomena and we will concentrate our attention on the benefit of the hunt. Since the temporal and spatial distribution of the animals is different in both cases, collective and individual strategy, we are interested in how the benefit from a hunting excursion varies as a function of the environmental conditions. These remarks concerning models of pattern formation and its relation to our model are mainly intended to avoid a misinterpretation by the reader that the presented approach would represent a kind of optimal foraging model.

There are many ways to describe and measure the efficiency of a hunting strategy, which makes the whole foraging process quite difficult to interpret. This is partly due to the many parameters that can influence the whole process. But there are also different quantities that can be measured and each way may represent a quantification of a different aspect of the foraging process. One measure we shall employ here is the total amount of units of prey captured (or eaten) per hunter. A few remarks concerning the chosen parameter values should be added before we will discuss some of the results obtained. We are interested in seeing whether there is a fundamental difference between individual and collective hunting strategies. To this end we need parameter values such that both systems display a good performance over large range of numbers of prey items, units of prey available etc.. If the prey items are so small that they have already been exhausted before other hunters can arrive at the food source a collective strategy diverts the animals more than it provides useful information. There are many more such considerations which led us to the parameters used, but we cannot go into these details here.

The ratio of the number of predators to the number of prey items will be kept (almost) constant. That means that there is always the same number of prey items
available for each predator. We investigated how the foraging benefit varies as a function of the abundance of prey items distributed homogeneously over the hunting area. We have found that an individual strategy is more efficient when the probability of finding a prey item is large. Decreasing the probability of food finding favours a collective strategy (Figs. 2,3). This is a general result valid for different ratios of prey items to hunters. The result can be easily understood qualitatively on the basis of the following argument: individual strategies retain the random distribution of the hunting animals after exhaustion of prey items whereas collective strategies favour aggregations. While in individual hunting the predators are released homogeneously after a prey item has been exhausted, in collective hunting large groups of hunters can be found in certain zones of the area and will hunt where nothing is left for hunting at high prey densities. This is also true if the distribution of prey is much more scarce. While the probability to find a prey item is the same for each predator, each member of the group will benefit from any discovery of prey, which is not the case in individual hunting.

![Graph](image)

**Fig. 2.** Number of units of prey captured per hunter after 40 min vs. number of prey items. Numbers close to the data points indicate the number of hunters. The ratio of prey items to number of hunters is 1. Although the ratio of number of prey items to number of hunter is kept constant, the probability of finding a prey item varies.

It is also interesting to see how the hunting gain varies as a function of time in both cases. While a monotonic decreasing function is obtained in individual hunting, one finds a decreasing curve that also displays maxima (for the conditions presented here only one maximum is found) in the collective case. These maxima are characteristic of recruitment processes and reflect the fact that members of the hunting group can benefit from discoveries made by others.
Fig. 3. - Number of units of prey captured per hunter after 40 min vs. number of prey items. Numbers close to the data points indicate the number of hunters. The ratio of prey items to hunters is always 1/2.

Discussion

The model presented here and the particular conditions tested correspond to rather abstract situations. It is however these abstract cases which allow us to see things much clearer, although simplified, and which permit us to draw general conclusions and make predictions. The model comprises only three basic rules of the game: the behavioural response of the individual, stop walking when a prey item has been found and emission of a pheromone as long as the food source is not exhausted. The rest of the process is determined by physico-chemical properties of the system. This set of rules is sufficient to generate a coordinated exploration of the hunting ground.

The fact that there are fundamental differences in the hunting benefit under different conditions raises interesting questions. One might suspect that these general results are also reflected in the organization of natural systems. It is worth while to investigate particular situations under the perspectives provided by the present approach. After having estimated behavioural parameters from experimental data it has been possible to simulate the experimentally observed choice between two food sources in the larvae of the beetle Rhizophagus grandis (Calenbuhr et al., in prep.).

The analysis we have started for understanding the social organization of gregarious insects, such as the larvae of certain species of beetles, attempts mainly to achieve a better comprehension of their hunting strategies in subterranean hunting territories. Natural conditions can be much more complicated than the cases treated here. Particularly important factors in many cases are the unpredictability of the
environment and physical constraints such as obstacles. It is interesting to see that there are also cases where individual strategies can be more efficient. We have tested the classical example of a hunting ground with obstacles, a maze (the habitat of the larvae of *Rhizophagus grandis*), and found important differences with the case discussed here. A more comprehensive survey of the efficiencies of collective and individual hunting strategies as a function of environmental conditions can be found elsewhere (Calenbuhr and Deneubourg, in prep.).

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**References**


