1. Introduction

Insect societies (ants, bees, termites, wasps) display an amazing number of behavioural patterns. Besides the general notions which are used to define the terminus technicus "social", that is cooperative brood caring and rearing, overlapping generations and division of labour (Wilson, 1971), there are two striking features: firstly, their organization is decentralized and secondly, the solutions found for a particular situation (problem) seem quite often to be "intelligent" and particularly efficient. These two features contrast with the seemingly erratic individual behaviour. It is already quite difficult to understand how meaningful decentralized behaviour of a group of higher animals or even humans comes about. That it works for groups which consist of such simple units as ants or termites is even harder to imagine. A model which might shed some light on how an insect society works should at least account for two things. Firstly, it should explain how (and perhaps why) erratic individual behaviour can result in coordinated actions. Secondly, one would demand an explanation for the flexibility of the overall behaviour, i.e. the capacity to adapt to unforeseen and unknown environmental constraints.

There is also the question whether the multitude of different behavioural patterns observed in the field can be traced back or even reduced to a couple of simple rules which determine the behaviour of the individuals and their communication.

From classical ethology (review: Eibl-Eibesfeldt, 1975) it is well known that a single stimulus can trigger not just one but a whole series of behavioral actions. That is, we would have a more or less deterministic behaviour based on input information. Although this principle is certainly at work in social insects we need more to understand the insect societies' performances. Indeed:

- it is quite difficult to imagine mechanisms which could account for the coordination of animals' group behaviour. Actually, there is no satisfying response within this framework;
- moreover, this approach does not seem to provide a means of generating flexible behaviour, which allows the society to adapt to different environmental constraints.
- the third problem addresses to the question how to code such a complex behaviour?

Therefore another approach has been attempted, which is characterized by putting classical ethology into a framework which considers behaviour not only as executing a program of...
predetermined actions of an isolated animal, but which puts the animal into a web of stimuli, which are generated by the animals themselves and whose overall pattern is dependent on environmental constraints. This different approach will be characterized by having simple individuals communicate (interact) with each other by emitting an odorous substance (pheromone). The individuals obey a small number of behavioural rules. Different types of behaviour will then be generated due to small variations of these rules and physical and environmental constraints, such as boundary conditions or rate of propagation of the signal and so on.

Before going into the details of this self-organization approach we should mention some of the advantages beforehand, because it will facilitate the understanding of the machinery which follows:
- since a large number of individuals will work on one problem a high degree of reliability is achieved.
- physical (for example obstacles) or environmental characteristics (abundance of prey items) will exert an influence on the motion of the individuals and on the diffusion which will result in different behavioural patterns. The behaviour and the pheromone profile form a complementary image of the physical problem.
- solving problems using such living analog computing devices does not need any symbolic representation. The system which resolves the problem is a part of the problem. Using this complementarity reduces the amount of memory drastically. It suffices to code some simple behavioral rules which automatically display a large number of collective behavioral patterns just by putting the system into an environment which, together with the system, creates a situation we would call a problem and its solution.

The major bottleneck to overcome in order to resolve the problem of bridging the gap between individual and collective behaviour lies in appreciating that complex patterns can indeed emerge in systems which consist of extremely simple subunits as is well known from many examples from the fields of physics and chemistry (Nicolis & Prigogine, 1977; Haken, 1983; Ebeling & Feistel, 1982, 1986; Murray, 1989). What appears, however, to be very important is the fact that we are not intending to just extend the ideas obtained in the field of complex dynamical systems, but to appreciate that a pattern formed in a biological system is not just "a" pattern, but that it is a structure which serves to fulfill a certain goal. Although the pattern as such has no project at all, it is part of an entity which can only be maintained if each part does its job. The pattern has a function. Without wanting to imply any teleological notions, the goal is to keep the system working (alive). Since not all patterns might serve this goal the formation of a certain pattern is interpreted by us as the solution of a certain problem.

2. Chemical communication

Most of the communication in insect societies (and also in gregarious insects (Fitzgerald & Peterson, 1980) is chemically mediated (Wilson, 1971; Hölldobler & Wilson, 1990). If we want to put down complex collective behaviour to individual behaviour, we have to find basic rules
which govern the processes involved in chemical communication, which can be defined as 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. Other factors for orientation based on memory or using astronomical marks, as the sun, coming also into play, can, however, in the cases which are considered here, be neglected.

What we need is thus a model for the motion in an olfactory landscape and a few rules for the pheromone emission on the level of the individual. Putting these two together we will then investigate the different patterns that emerge from the interactions of an ensemble of individuals as a function of the boundary conditions. An extension of these ideas and the application to other groups of animals which use chemical communication is discussed in section 7.

3. TRAIL FOLLOWING MODEL

One mechanism appears to be the main component for orientation (Hangartner, 1967; Leuthold, 1975): osmotropotaxis. 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 (Kühn, 1919; Fraenkel & 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.

![Diagram](https://via.placeholder.com/150)

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:

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

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 (Calenbuhr & Deneubourg, 1989, subm.; Calenbuhr et al., in prep.) 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 (Pasteels et al. 1986; Detrain, 1989).

4. FROM INDIVIDUAL TO COLLECTIVE BEHAVIOUR

Having at hand a model for individual behaviour as far as the response component is concerned we will investigate now what happens if we add what generates the chemical profile, i.e. rules for signal emission and propagation. Actually we will use only one simple rule for the pheromone emission, which determines the emission condition and the quantity emitted.

We will then investigate the collective behavioural patterns that emerge from having an ensemble of equally equipped individuals working together. In section 5 we will discuss trail following phenomena and what happens when the emission rate and the number of animals that emit are varied, which gives us some insight into the large number of collective recruitment strategies found in ants (Hölldobler and Wilson, 1990). In section 6 we will investigate one particular case of such a recruitment strategy and see how physical constraints, which become very important in the case of the recruitment trails of army ants and some termite species, may lead to structured traffic flow. In section 7 we will switch from trail following to aggregation phenomena and will present a result which shows that cooperative behaviour can result from simple chemically mediated interactions.

5. TEMPORAL PATTERNS AND CHEMICAL TRAILS: RECRUITMENT IN ANTS

From experimental studies it is well known that there are different strategies based on chemical trails to recruit worker ants to a food source (Hölldobler & Wilson, 1990). In the following we will present a model scenario which reveals the logic of what is found in nature. Imagine that a scout ant has found a food source and then returns to the nest to inform nestmates about the food source. Different variations on this scheme are possible dependent on the amount of pheromone emitted by the recruiter and also on the type of emission, i.e. emission into the air or on the ground. The quantity and the mode of emission, and the number of potential recruiters are the only parameters which are necessary to account for these variations:

- An invited nestmate may follow the pheromone plume emitted by the scout which returns to the food source. Stronger emission will invite more ants to follow the leader to the food source. The recruited ants may become leaders on their own and invite even more ants to leave the nest after successfully homing from the food source (group-recruitment).

If all information is conveyed by the trail, such that the differences between recruiters and recruits become blurred one speaks of trail recruitment.

What is important for the understanding of the different recruitment strategies is that they do not need to be entirely different types of behaviour but only quantitative variations of a basic scheme. It can be shown that different recruitment strategies can be reproduced by just changing the amount of pheromone emitted and its physical characteristics (Calenbuhr et al, in prep.). The switch from group- to trail-recruitment can also be
understood in this framework. The resulting strategy is no more than a consequence of the physico-chemical environment, the actual state of the food source and the way the pheromone is emitted (species dependent). This is not in contradiction with more complex communication found in natural systems and which would produce more variations on this basic scheme.

How the scout finds its way back to the nest does not matter in our case. Also, the trail is not necessary for other ants to return to the nest, but it helps to find the food source and by conveying information about the degree of exploitation of the food source, is a means of regulating recruitment activity.

6. SELF-ORGANIZED TRAFFIC FLOW IN ARMY ANTS AND TERMITES

In most of the species, the traffic on the trail is not structured: ants going from the nest towards the food source frequently collide with homing ants. The spatial capacity of the trail is not saturated. However, there are species like army ants and termites which have been observed to form large trails which are followed by thousands of individuals and extend easily over 100 m. These trails display sometimes multi-lane traffic where the inner lanes carry the nest-bound traffic and the outer lanes carry the outward traffic. Moreover the flanks of the trail are guarded by large soldiers protecting the busy traffic (Schneirla, 1940; Jander & Daumer, 1974; Topoff, 1980).

The basic idea to model this phenomenon is that as there are many ants following the trail collisions are inevitable and the individuals have to perform dodge-maneuvers. As soon as a critical traffic density is reached, one might suspect a transition phenomena sets in, which reduces the collisions drastically. If this scenario were correct the mere physical constraint that there cannot be more than one animal at one place should already be sufficient.

Computer simulations have shown that the problem is not so simple but needs something more to be resolved. Actually, it turned out that the pattern might be an example of self-assembly. This being achieved by permanent emission of a pheromone by each worker which follow the signal of the animal moving ahead. (Wilson suggested this hypothesis in other words in 1971). Simulations have shown that this emission is in fact a stabilizing effect, that has to be added in order to maintain the lane structure of the traffic flow.

Two or more separate chemical trails are formed in that way and are kept at distance by collisions. Although this self-assembly improves the situation a lot, destabilizing ruptures of the chains are still possible, which can be reduced changing adsorption/evaporation properties of the ground.

No complex rules are needed. It is just the emission of the pheromone, moving up a gradient and the physical constraint of having no more than one individual at one place, which becomes only important at high traffic densities, which can account for some of the properties of the spatial pattern.

Structured traffic flow which became quite popular in transportation sciences (Prigogine & Herman, 1971) in the sixties has actually been invented by social insects a long time ago. Whereas human engineering still tends to the development of centrally organized systems
army ants and termites provide examples which show that under certain circumstances, which become ever more likely in today's metropolitan areas, self-structuring of traffic flow becomes possible.

Fig. 2: The picture on the left (redrawn from Jander & Daumer, 1974) shows structured traffic flow as observed in the termite species *Lacessititermes lacessitus*; the two photographs on the right were obtained by a computer simulation based on the rules discussed in the text. Above: starting configuration. Below: photograph taken after 150s, each individual has walked along a line of animals which extends over 6m.

7. COLLECTIVE HUNTING AND PROBLEM SOLVING

The osmotropotactic response function presented can also be used to move up the gradient if the source is pointlike, inducing motion and aggregation towards the center of emission. Not only do 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 foodsource. We thus will have an instability (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.

There are many ways to describe and measure the efficiency of a hunting strategy. One measure we shall employ here is the time needed to harvest a given area, which
corresponds also to the energy consumed. The ratio of the number of predators to prey items will be kept 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 more or less 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 (fig. 3). This can be easily understood qualitatively on the basis of the following argument: individual strategies retain the homogeneous distribution of the hunting animals after exhaustion of prey items. Collective strategies favour aggregations. While in individual hunting the predators are released homogeneously after a prey item has been exhausted, large groups of hunters can be found in certain zones of the area and will hunt where there is nothing left for hunting at high prey densities using a collective strategy. The same is 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 for individual hunting (Calenbuhr & Deneubourg, in prep.).

Since our model is based on inducing consecutive instabilities of a chemotaxis-diffusion system it can be expected to be a model for wider applications. 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.).

![Diagram showing time needed to harvest a hunting ground as a function of the number of prey items.](image)

**Fig. 3:** Plot of the time needed to harvest completely a hunting ground as a function of the number of prey items;

8. DISCUSSION

One should not be so naive to try to reduce the whole variety of ant or termite behaviour to the emission of a pheromone, the response to this pheromone and its physico-chemical
properties. This would not only be an oversimplification but it would be false. Yet, what is actually shown by the approach presented is that there is not always a need for complexity on the level of the individuals. An ensemble of very simple units, "Braitenberg-like automata" (Braitenberg, 1984) is able to "imitate" the behavioural patterns of real living systems. What this approach is good for hence, is showing how the coordination of decentralized operating and interacting individuals comes about and how flexibility in behaviour is achieved, which answers the two key questions posed at the beginning.

Within this framework one or a few simple rules unfold a large class of possible solutions into which the system relaxes.

Chemotaxis-diffusion systems are often found in nature and are the sources of pattern formation e.g. in social bacteria and slime moulds (review: Segel, 1980). Besides the problem of how patterns arise we now ask another question, namely what is the purpose of such patterns - which leads us to our last point of the discussion: problem solving. The function of a behavioural pattern is very much like the function of an organ. It should do its job within the framework of the whole. If the job to do requires being clever then one would should employ something smart. It does not matter whether the system is aware of what it is actually doing.

In general, we translate a problem into a symbolic representation which is accessible to mathematical analysis. For social insects nature has invented another way, based on complementarity. A property of the problem is translated into a mirror image via the emission of the pheromone, whose profile reflects the topology of the problem, the state of the food source, etc.. Besides this a system is needed which is capable of using this mirror image. This part is done by the insects' behavioral response. What is needed on the level of the individual is not more than the storing capacity for this simple behavioural rule and the emission. The complementarity lies in having a system which generates a mirror image of the problem which in turn permits the system to relax into a solution...

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