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Collective Patterns and Decision-Making*

In recent years, the study of group behaviour has been dominated by two questions, namely "What is the evolutionary process by which social life has developed?" (e. g. Wilson 1975, Barash 1977), and "Is behaviour optimal?" (e.g. Krebs & Davies 1984). Preoccupied with these ideas, sociobiology has more or less forgotten to ask *how* groups or societies forage, move, defend themselves, and generally do what they do. As a result, while the adaptive value (*why*) of belonging to a group is well documented (anti-predator, reproduction, etc; e. g. Morse 1980, Broom 1981), we only poorly understand the mechanisms (*how*) by which these groups are formed and modified as a function of their activity. While there are detailed descriptions of collective behaviour, on the one hand, and equally detailed descriptions of individual behaviour on the other, the causal links between the two and their often surprising difference in complexity are usually neglected.

The key to bridging these gaps lies in remembering that at each moment the members of an animal group decide, act and interact, both amongst themselves and with the environment, permanently changing the state of the group. Just as sociobiology, with its population genetics and games theory, shows the importance of dynamics and individual interactions in the evolution of social behaviour, we propose the analysis of these interactions as the straightest path to understanding the short term collective behaviour of animal groups.

The most widely-observed social interaction concerns allelomimesis in its many forms (roughly speaking, do what my neighbour is doing; see e. g. Sudd 1963, Scott 1972, Altmann 1985). For example, one bird takes off, those near it also take off, and very quickly the whole flock has taken off. Recruitment in social insects is another classical example, in which one forager discovers an important food source, recruits inactive foragers in the nest to go to it, which in turn recruit still more foragers. Allelomimesis is by definition autocatalytic, in that if I do as others, then others do as I,

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and we all shall end up doing the same thing. Another term for this is positive feed-back, and we shall use the three terms rather indiscriminantly. In the context of this article, they all refer to the idea that the probability of an individual adopting a particular behaviour or state is an increasing function of the number of individuals already exhibiting that behaviour or state. Most often allelomimesis is considered as little more than a mechanism for aggregation, cooperation and reciprocal altruism (e. g. Milinski 1987) or synchronisation. We would like to emphasize three of its less intuitive properties or consequences:

- Allelomimesis is important in structuring a group's activities.
- Even very simple allelomimetic behaviour can be the source of complex and often surprising group behaviour.
- Different group behaviour can be based on identical allelomimetic behaviour.

Such parsimonious ideas strongly contrast with the traditional biological approach, in which individual complexity is necessarily at the root of collective complexity, and in which the observation of a different collective behaviour automatically elicits the search for a different individual behaviour.

To show these properties — better known in physical and chemical systems as self-organisation (Nicolis & Prigogine 1977) — as clearly as possible, we deliberately minimise both individual behavioural complexity and long-term differences between the members of a group, whether due to age, experience, or any other factor. In our wish to concentrate on the mechanisms behind collective behaviour, we shall more or less ignore its fitness or benefit, either collective or individual.

While we illustrate our ideas mainly with examples of social insect foraging behaviour, they apply to a wide range of animal species' group behaviour. Mathematical models play an essential role in linking the individual and the collective behavioural levels. Quantitative individual observations define the model's kinetics. Its dynamics and stationary states correspond to the collective pattern or decision observed (and can also be used to calculate a benefit), and are compared with experimental results to test the model's validity.

Patterns and decision-making via trail pheromone in social insects

Of the different animal groups, social insects are those in which these properties are the most easily and clearly shown. To varying degrees, their societies are composed of a large number of individuals, characterised by the simplicity of their behavioural repertoire, their limited individuality

and capacity for learning, and the inherent randomness of their behaviour (this last characteristic is by no means limited to social insects). On the other hand, communication between individuals, notably by pheromone, is usually highly developed.

In spite of this individual simplicity, and perhaps, as we shall see, because of it, the twenty thousand or so social insect species exhibit a bewildering panoply of social behaviour, fully illustrating the contrast between their individual and collective levels of complexity (e. g. Wilson 1971). Furthermore, we can experiment on these societies in a way impossible in any other kind of collective decision-making organisation. Unlike molecules or cells, workers are easily visible, and we can manipulate insect societies and place them in experimentally controllable situations with relative ease.

An important benefit of sociality is that it provides an opportunity for the exchange of information, and foragers of most social insects can communicate the location of a food source or a favourable foraging zone to their nest-mates by one means or another. We shall consider the means used by the majority of ant and termite species (and some bees): trail pheromone.

The same autocatalytic scenario may be observed whenever trail pheromone is used. The direction chosen by a forager that passes a given point laying pheromone will influence the direction chosen by the next ant that passes, which also adds pheromone in the direction chosen. In this way, one specific direction is rapidly and collectively selected out of a number of initially equivalent possibilities. Repeated along a series of points, this process is the means by which the foragers form a well-defined trail between, for example, the nest and the source or foraging zone. We shall now examine some of the widely different patterns and decisions generated by this one autocatalytic mechanism.

Army ant swarm patterns:

(Raignier & Van Boven 1955, Schneirla 1971, Franks 1989). Army ants live in colonies of up to 20,000,000 individuals, roughly 1 cm long and practically blind. Their group behaviour is anything but simple. Every day, a colony will form a swarm raiding system made up of 200,000 foragers, covering 100 X 10 m, catching some 30,000 prey items which are all transported to the nest, and they do this in highly structured and species characteristic patterns, in the total absence of any central organisation (Fig. 1).

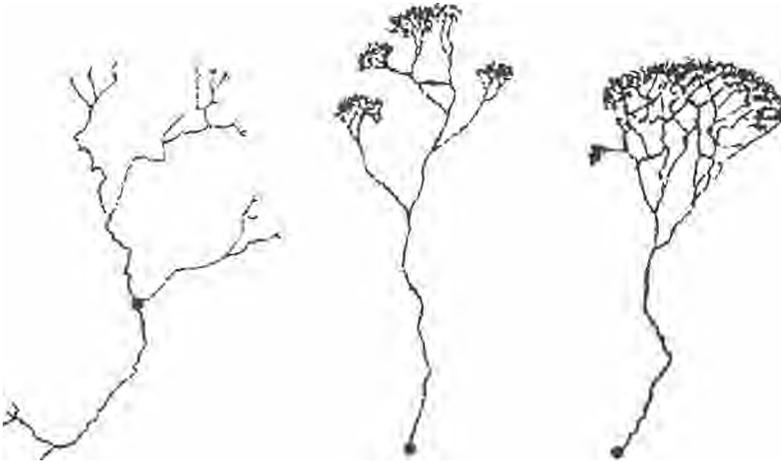


Figure 1 Foraging patterns of three army ant species (redrawn from Rettenmeyer 1963 and Burton & Franks 1985). A, *Eciton hamatum*; B, *E. rapax*; C, *E. hurchelli*.

The traditional approach to these different swarm patterns is to assume that each is optimal for the prey these species hunt, and corresponds to complex, species-specific individual behaviour. For example, *Eciton burchelli* has a more dispersed swarm and feeds more on scattered arthropods than *E. hamatum*, which feeds more on insect colonies and has a more concentrated pattern, *E. rapax* being intermediary in diet and pattern. However, Monte Carlo simulations of one simple trail laying/following behaviour can generate different characteristic swarm patterns (Deneubourg et al. 1989). With a homogeneous, low-density food distribution, the simulation generates a front and a central trail (Fig. 2A), very like those of the Argentine ant *Iridomyrmex humilis*' exploratory swarms (Deneubourg et al. 1990). With a higher food density, the central trail branches repeatedly, forming a river delta pattern very like that of *Eciton burchelli* (Figs 2B and 1C). With a heterogeneous food distribution, the delta splits into a number of more or less concentrated sub-deltas, forming a pattern intermediate between that of *E. hamatum* and that of *E. rapax* (Figs 2C and 1A, B).

While the individual ants in the simulations have exactly the same qualitative and quantitative behaviour, the different spatial distributions of the foragers returning with food (via the different food distributions) interact with the flow of ants heading away from the nest to produce the qualitatively different patterns.

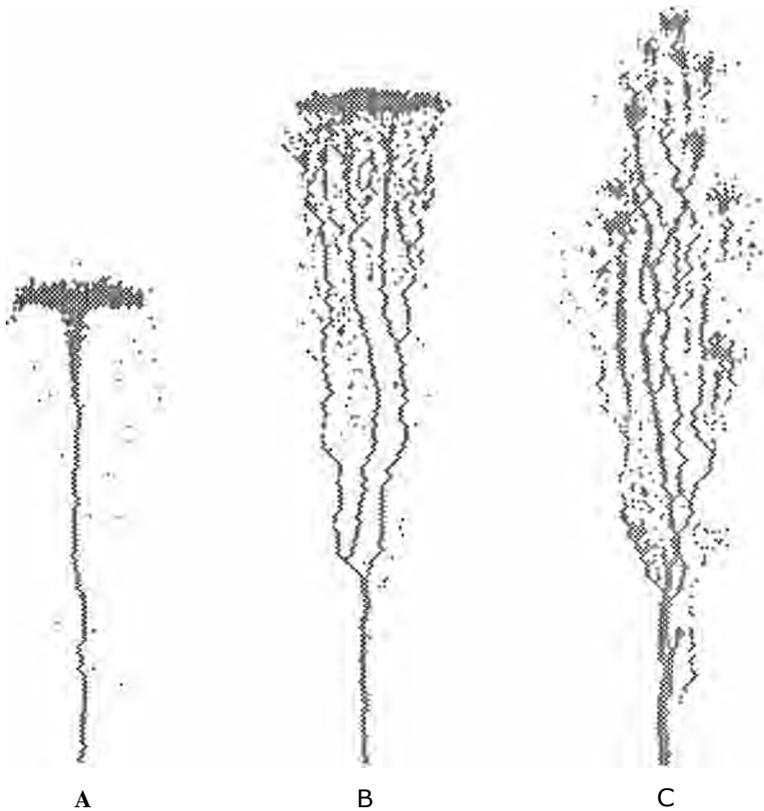


Figure 2 — Three distinct foraging patterns developed by Monte Carlo simulations of the same model with three different food distributions (reproduced from Deneubourg et al. 1989). Ten ants leave the nest per step. Ants advance into the foraging area. If they find food they return to the nest. At each point, the probability of moving per time step $= 0.5 + 0.5 \tanh [(L + R)/100 - 1]$, where L and R are the quantities of pheromone ahead left and right. Those that move choose between ahead left and ahead right, with the probability of choosing ahead left $= (5 + L)/(5 + L)^2 + (5 + R)^2$. A maximum of 20 ants are allowed at each point. Having moved, the advancing ants lay 1 pheromone unit at the point chosen (with a saturation level of 300 units), and returning ants lay 10 pheromone units (with a saturation level of 1 000 units); 1/30th of the pheromone at each point evaporates per time step. A, each point has a 1/10 probability of containing 1 food item; B, each point has a 1/2 probability of containing 1 food item; C, each point has a 1/100 probability of containing 400 food items.

The simplicity and autocatalytic nature of their trail laying/following is further illustrated by the occurrence of circular mills. One can sometimes observe in the field (or easily provoke in the laboratory) a group of army ants turning around and around a circular obstacle. The more they turn the more they lay trail around the obstacle, only stopping when they are totally exhausted. Removing the obstacle makes no difference once the circular trail has been formed (Fig. 3B), and one can justifiably describe the army ant foraging system as the blind leading the blind. (Note that army ant foragers lay trail pheromone both when returning to the bivouac with food and more or less continually as they move outwards from the nest.)

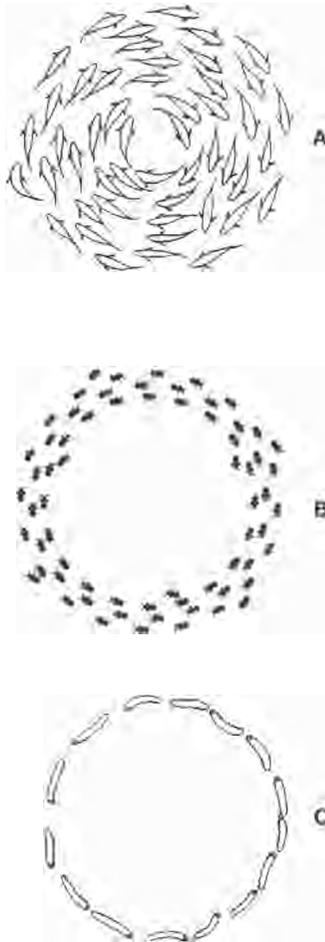


Figure 3 — Three circular mills generated by the same process in three widely different species, namely fish (A, redrawn from Parr 1927), army ants (B, redrawn from Schneirla 1971) and gregarious caterpillars (C, based on Fabre 1879). The circular mill based on *Eciton* illustrates how chemical signals dominate their movement. The workers are dropped into a small tray containing a large circular object. They start to move round the object, laying trail pheromone as they go. This causes them to move faster and faster as the trail gets stronger. The object is then removed, but the ants continue to turn until exhausted.

Messor pergandei's rotating foraging trail pattern:

Bernstein (1975) and Rissing & Wheeler (1976) described a spatial oscillation in *Messor pergandei*. A concentrated foraging column develops in a sector of the foraging area and rotates like the hand of a clock around the nest with a period of 1—3 weeks and with a variable degree of irregularity. These columns change direction more slowly in years or regions when food is abundant. This complex behaviour can be modelled with the same autocatalytic scenario as above (the foragers laying pheromone only when returning with food) without needing to invoke spatial memory, complicated systems of coordination or any change of individual behaviour with food density (Goss & Deneubourg in press).

Briefly, the ant foragers choose a foraging sector as a function of the pheromone concentration associated with each sector. The choice is autocatalytic, as foragers that find food in a sector add to its pheromone. As a sector's food runs out, the trail is less reinforced and starts to diminish in strength. The foragers start to explore the two adjacent sectors, and in the same way concentrate on one of them. When that sector runs out of food, one of the two adjacent sectors is empty, having been exploited just before, and the other is full. The trail to this latter sector is thus more reinforced than the first. The colony thereafter spontaneously switches from sector to adjacent sector, and the column may rotate indefinitely (Fig. 4).

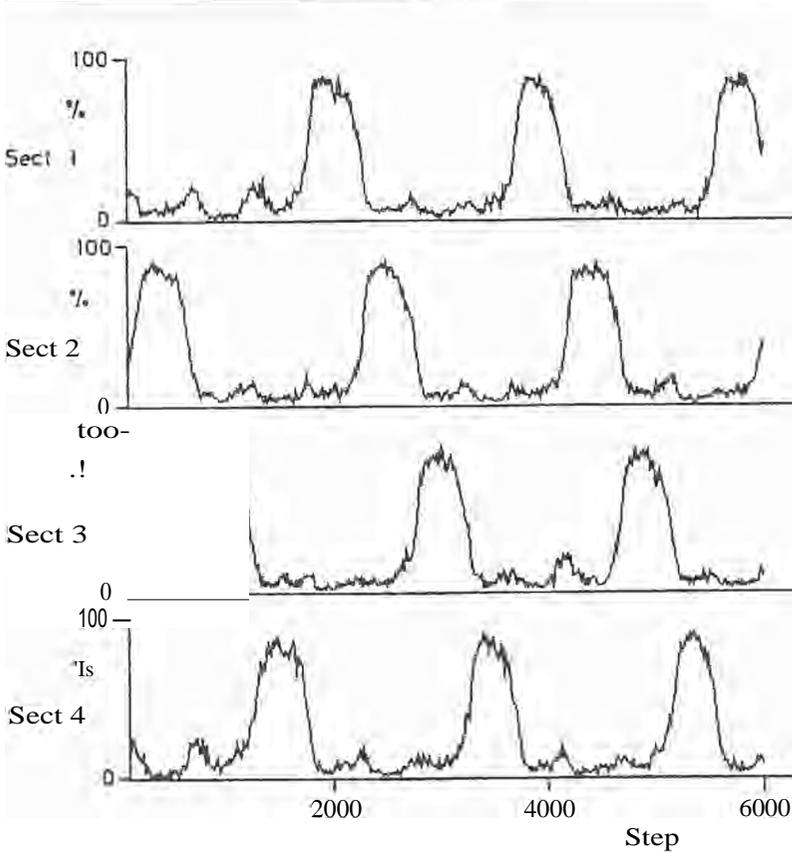


Figure 4 — Monte Carlo simulation showing the percentage of foragers in each of four sectors of a circular foraging area as a function of time (reproduced from Goss & Deneubourg 1989). The foragers clearly form a trail that starts in sector 2 and rotates clockwise to sectors 3, 4, 1, 2, 3, etc., with a regular period. Each sector contains initially 2000 seeds; 2 seeds arrive and 1/1000th of the total number disappear per unit time in each sector. A trail leads to each sector, characterised by C pheromone units, of which 1/30th evaporate per unit time; 100 foragers leave the nest per unit time. A fraction, $f = (20 + C)^2 / E(20 + C)^2$, choose sector i . Of these, 1/20th diffuse into each of the two adjacent sectors. The number of ants that find seeds in a sector = $0.1 F_i S_i / (1000 + S_i)$, where F_i and S_i are the corresponding numbers of foragers and seeds. At the end of each step, all the foragers return to the nest. Those that have found a seed add one pheromone unit to the trail leading to the corresponding sector. Those that find no seeds return without marking.

With increasing food abundance, the model passes from random foraging to the formation of a trail that rotates about the nest. The greater the abundance the more slowly the trail rotates until it finally becomes fixed on one sector (a trunk trail), thus agreeing with the experimental observations. As with the army ant swarms, the same simple behaviour generates different complex patterns under different conditions. That *M. pergandei* develops rotating trails, while another harvester ant species forms trunk trails, (e. g. *Pheidole militica*: Hölldobler 1974) and another forages randomly (e. g. *Pogonomyrmex maricopa*: Hölldobler 1974; *P. californicus*, even though this species can form recruitment trails: S. W. Rissing pers. comm.) need not necessarily correspond to a behaviour that is species specific, but could, at least in part, simply be due to different ecological conditions and/or food preferences.

Collective decisions:

The army ant swarm patterns and the *M. pergandei* clock pattern are spectacular examples of a more general problem concerning the spatial organisation of a group of foragers. The use of trail pheromone however is not only a system adapted to the exploitation of a patchy environment or of prey needing cooperative exploitation, but is also the touchstone of a collective decision-making system.

When new sources are discovered simultaneously, recruitments are started to them. Responding to the food sources' different quality, the foragers lay more or less pheromone when returning to the nest. The recruitments to them proceed at different rates, and they compete for inactive foragers, who are waiting in the nest to be recruited. This competition can generate complex social decisions well beyond the capacity of an individual.

Experiments combined with modelling have shown that trail-laying ants can use their trail recruitment to choose the richest food source (Passteels et al. 1987, Beckers et al. 1990). For example, *Lasius niger* foragers, when offered simultaneously a 0.1 M and a 1 M sucrose solution, concentrate their activity on the 1 M source (Fig. 5A). When offered two identical 1 M sources simultaneously, they concentrate on one of them rather than exploiting both equally (Fig. 5B). However, they can become prisoners of their trail system in the sense that once one trail is well-established, a new trail is unable to compete with it and develop, even if it leads to a richer source. When offered just a 0.1 M source, *L. niger* foragers establish a trail to it and exploit it. If you then add a richer, 1 M source, they discover it but are incapable of switching their activity to it (Fig. 5C). This illustrates quite clearly that optimal foraging theory is not always the most appropriate model for understanding collective, autocatalytic behaviour.

Seeley (1985) analyses a similar collective decision-making process in honeybees that allows the hive to select the best of two sugar sources.

Ants that lay trail pheromone more or less continuously, such as army ants and *Iridomyrmex humilis*, can select the shortest route to a source (Goss et al. 1989), again via the competition between two rival recruitments. If you place a bridge that has a short and a long branch between an *I. humilis* nest and a food source, the interplay between those going to the food and those returning gives an initial advantage to the shorter branch. The autocatalytic trail system amplifies this initial difference, leading to the selection of the shortest branch of the bridge (Fig. 6). Again, they can be prisoners of their own history, and do not always choose the optimal solution. If you at first place a bridge with just one branch, the ants establish a trail on it. If you then add a second and shorter branch, they are incapable of switching to it.

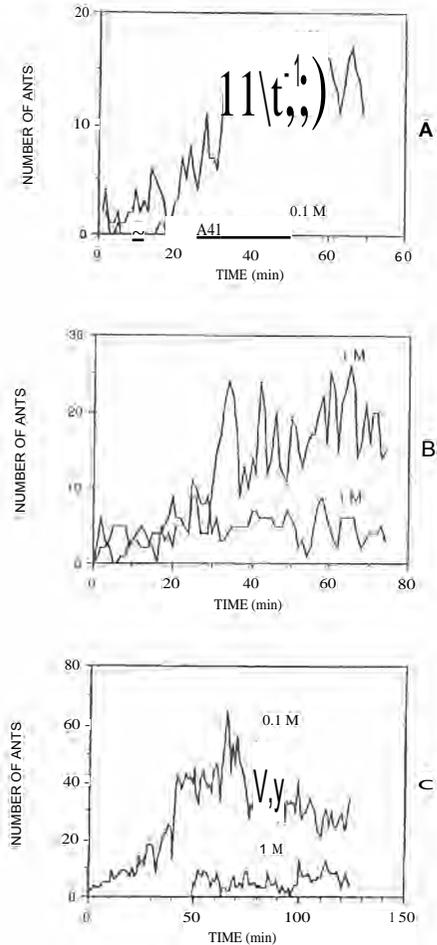


Figure 5 — Three examples of collective decision-making via food recruitment in ants, as shown by the time evolution of the number of foragers around two sucrose sources presented to a colony in a 0.8 m^2 arena (reproduced from Beckers et al. 1990). A, faced with a choice between two simultaneously presented sucrose sources of different quality, 1 M vs 0.1 M, the *Lasius niger* colonies always concentrate their activity on the richer source. B, faced with a choice between two 1 M sucrose sources, the *L. niger* colonies always concentrate their activity on one of them. C, presented with a 0.1 M sucrose source, the *L. niger* colony starts to exploit it; if you then introduce a 1 M sucrose source, they remain faithful to the first discovered, albeit weaker source, even though they have discovered the richer source.

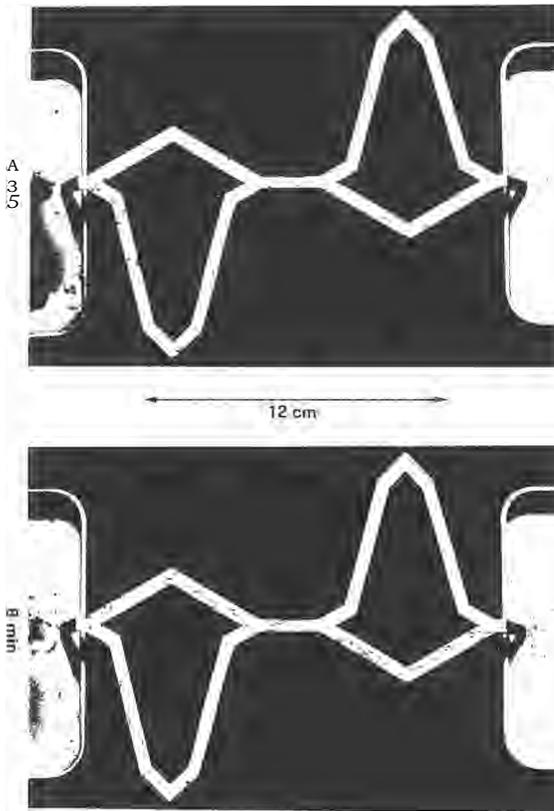


Figure 6— A colony of *Iridomyrmex humilis* selecting the short branches on a bridge between the nest and the foraging area (photos taken 4 and 8 min after the bridge was placed). (Reproduced from Goss et al. 1989).

It should be stressed that the choices described above are not the result of individual foragers comparing the quality of the two food sources, the lengths of two bridges, nor even the result of inactive recruits in the nest comparing the signals from different recruiters. Via the autocatalytic amplifying mechanism, exactly the same trail-laying and trail-following behaviour can generate different patterns and decisions if there is:

- different past activity;
- different environmental conditions.

Chemical communication organises widely different animal societies

The use of chemical signals to maintain group cohesion and guide group movement is by no means limited to social insects, and it is remarkable how widely different species have developed similar systems that generate similar, if not exactly the same spatial patterns and decisions, underlining the generality of the organisational principles we present.

For example, social bacteria use chemical trails to form army-ant-like "swarms" (reviews in Reichenbach 1986, Shapiro 1988; models in Pfister 1989, Stevens 1989). The gregarious caterpillars *Malacosoma neustria* also use trails in a manner similar to army ants, enabling them both to diffuse information about richer foraging zones (more trail is laid to better food sources) and to find the same collective nest site at the end of a day's activity (Fitzgerald & Peterson 1988). Circular mills, similar to those observed in army ants, can be seen in the caterpillar of the European processionary moth *Thaumetopoeia pityocampa* (Fabre 1879) and also in the mud-snail *Nassarius obsoletus* (Crisp 1969), generated by a combination of chemical, tactile and perhaps visual cues.

Other intertidal molluscs use trails to help each other find protected rest sites (Focardi et al. 1985). Many different larvae, such as *Dendroctonus micans* (Grégoire 1988), use pheromone to recruit to favourable food sources. As a consequence, *D. micans* forms different group structures under different conditions, or even under the same conditions, with the same individual behaviour (Deneubourg et al. 1990).

Finally, Le Masne (1952) reviews an astonishing range of chemically and tactilely coordinated group behaviour in insects and other invertebrates, such as the rhythmically synchronised feeding in *Trichiocampus viminalis* larvae (which leave regular parallel perforations in leaves), or the massive group migrations of certain Nonctuidae larvae or army worms.

Visually-mediated collective patterns and decisions in widely different animal societies

The organisational properties of allelomimesis are by no means limited to groups using chemical communication, as in the examples described so

far. Visual communication is more widespread and can in the same way generate the same or similar patterns and decisions in animal groups such as swarms of locusts, schools of fish, flocks of birds, troops of antelopes, etc. All may take different forms in different situations (resting, feeding, moving, predator-avoiding, ...) (review in Wilson 1975) in a manner that appears highly coordinated but with no leaders. All may function with the same logic of simple individual behaviour, amplified and structured by autocatalytic communication.

Spatial patterns:

For example, in a number of fish species, the same school can move in an amoeba-like fashion, in a circular mill (Fig. 3A, C, as army ants, processionary caterpillars and mud-snails), in a rectilinear form, form defensive pods, or split in different manners to avoid predators or feed on different prey (e. g. Parr 1927; Breder 1959, 1976). Many of these forms can be generated by a single mathematical model which defines the movements of an individual as a function of the velocities, positions and orientations of its neighbours (Sakai 1973, Suzuki & Sakai 1973, Huth & Wissel 1989). Thus allelomimesis with identical individuals can structure the school. It could also be behind the observation that many fish, such as surgeonfish (Barlow 1975) and killifish (Fraser 1973), form schools under some conditions, but not under others, without having to invoke factors like genetically different populations.

Similarly, many mammal species such as musk-oxen (Teuer 1965) or sheep and cows live in herds that take different forms under different conditions, such as the presence of predators, or during different forms of activities such as resting, ruminating and grazing. Elephants, bison and quail form defensive circles, and predators often adopt complex attacking patterns to cope with defensive formations. As with fish schools, Jarman & Jarman (1979) propose that the tendency to take the same speed and direction is the major force that allows ungulate herds to be a stable and structured organisation. Focardi & Toso (1987) have modelled this.

Hoffman et al. (1981) describe large mixed flocks of seabirds that form foraging patterns very like those of army ants, via a recruitment mechanism. Double-crested cormorants form coordinated fishing flocks whose form depends on their size (Bartholomew 1942), and Rand (1954) gives a number of different species that form complex collective foraging patterns. It will be a challenge to show to what extent simplicity and allelomimesis could be behind this multitude of group forms.

Collective decisions:

The information centres described in relation to communal roosting or

colonial nesting bird species (Ward & Zahavi 1973) show a strong analogy with social insect colonies. Members of a roost, for example, are thought to be capable of recognising when other members of the colony return from a successful foraging flight and to choose their next flight direction accordingly, this being the equivalent of trail recruitment. Similar complex decisional or spatial patterns have been observed, and can be understood by similar and even identical analyses of the individual kinetics. For example, weaver birds have been shown to switch from a poorer food source to a richer one (De Groot 1980), and pigeons may concentrate on one source, neglecting nearby identical ones (Lefebvre 1983). Again, these are more than just simple aggregation mechanisms.

Another classic example concerns the dances used by honeybees to recruit workers to make a collective selection of the best site to move their nest to (Lindauer 1961, Seeley 1985). Again, non-linear positive feed-back is important, as only one nest must be chosen out of a number of alternatives.

Collective Construction

We have illustrated our article with examples taken from two highly visible collection behaviours, foraging and grouping. However, we would not like to finish without mentioning collective construction. Roads, tunnels, nests, warrens, dams, collective inhabitations, ... Who are the animal architects? In other words, do the principles described above also apply to this aspect of social activity?

At first sight these complicated structures appear highly deterministic, and again it is not surprising that the "plans" have been thought to be explicitly contained in the individual's genetic code. Grassé's (1939, 1959) classic study of the way termites build complex and regular nest structures (completed by Deneubourg 1977, Bruinsma & Leuthold 1978) shows that this is not necessarily the case, and that a large number of pheromone-mediated autocatalytic interactions between random builders (I tend to lay mud bricks where others have laid mud bricks) can lead to the formation of regular and complex physical structures in the complete absence of any planning, either centralised or in the heads of each individual. A similar process has been shown to be behind the construction of bee nests (Darchen 1959, Belic et al. 1986).

Discussion

In our wish to be clear in showing how a consideration of social dynamics can promote the understanding of group behaviour, we have inevitably made some rather provocative simplifications, not least of which being our treatment of individuals as simple identical "molecules". The degree

of individual complexity found in animal groups is of course extremely variable, not only when comparing very different species such as termites and primates, but also when comparing more closely related ones. While self-organisation can and does appear with complex individuals just as with simple individuals, it is evident that it is not the only mechanism active, and that individual complexity or division of labour can also be the source of collective complexity.

The question raised by the variability in individual complexity may be stated in the following terms: At what level does a society's complexity appear, that is to say does it lie within individuals or between individuals? What part of social behaviour must be explicitly coded into the individuals's behaviour, and what part is determined by the interactions between individuals? This problem is not only fundamental to the relationship between an individual and the society, but also underlies the relationship between an organism and its organs, an organ and its cells, and between a cell and its macro-molecules. If we have deliberately stressed here the role of collective complexity in group behaviour, it is because we both wished to show up its multiple and powerful possibilities and because it has hitherto been neglected (with the notable exceptions of Grassé 1939, 1959; Darchen 1959; Lindauer 1961, Wilson 1962; Breder 1976; Seeley 1985).

When feed-back is discussed in animal groups, it is nearly always negative feed-back that is considered and its role is limited to that of a regulatory mechanism, in which fluctuations are damped and equilibrium is the goal, and again social insects provide many examples. For example, Wilson & Hölldobler (1988) review a number of situations in which ants, with only local information, are capable of regulating which type of food the foragers are encouraged to bring back, or the number of individuals of different castes produced. Positive feed-back is only rarely considered.

Generally speaking, the role of positive feed-back is reduced to that of a mechanism that not surprisingly produces exponential growth and spatial/temporal coordination. For example, it allows groups to exploit *en masse* random discoveries (e. g. Sudd 1963, Deneubourg et al. 1983, Towne & Gould 1988), or to form clusters, but nothing more (e. g. Scott 1972, Altmann 1985). In this article we have stressed the fact that competing positive feed-backs very rapidly amplify external or internal fluctuations. The examples we have given show how the resulting patterns and decisions are surprisingly complex and "creative".

Such self-organising societies have a number of properties that compare favourably with a more deterministic organisation, such as sexual division of labour, social hierarchy, caste-regulation (Oster & Wilson 1978), or age-related ethology. Firstly, they can be based on simple individuals, requiring only simple programming and autocatalytic communication.

Large numbers of individuals can thereby be coordinated into collective structures. Moreover, these structures can interact with the environment, allowing different collective behaviour to appear from the same individual behaviour under different conditions. In this way they combine the advantages of simplicity, reliability and adaptability with a considerable economy of genetical coding. Only the limited number of simple rules describing the individual behaviour and interactions need be explicitly coded. It is not necessary to foresee every situation as complex and flexible collective structures are automatically generated from these simple rules.

Because of these advantages, such self-organising algorithms are also destined to play a more active role in what is the major characteristic of our industrial society, namely the use of machines to perform useful tasks. Specifically, the principles governing self-organisation in animal societies can be used in the design of fail-safe distributed control systems for robot teams, and are already being applied to the management of distributed data networks (Gallagher 1977, Merlin & Segall 1979).

In the light of the ideas presented here and the wide range of species to which we have seen they apply, simple causes should perhaps be considered more systematically when seeking to explain complex collective behaviour. It is our belief that any species adopting allelomimetic-type behaviour, for whatever reason, will "unwittingly" and automatically provide itself with a capacity for collective decision-making and pattern formation, and general structuring that far exceeds that of its isolated individuals. Along with the better-documented reproductive and defensive benefits, this is surely one of the major reasons why sociality has flourished independently and many times across all the major animal orders.

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