HOW DO ANTS AND SOCIAL CATERPILLARS COLLECTIVELY MAKE DECISIONS?

1   Introduction

In social insects, collective decisions occur when a colony is faced with several opportunities, for example food sources of different qualities. Numerous studies have shown that the colony focuses its activity on one particular option (e.g richer food source, even though no individual is aware of all the alternatives. This raises the interesting question of how colonies make collective decisions. However, the study of decision-making in social insects has been dominated by questions of why insect colonies make the decisions they do, for instance "what is the evolutionary process by which collective decision-making has arisen?" (Wilson 1975; Barash 1977), and "is the decision reached the optimal one?"(e.g Krebs and Davis 1993). Preoccupied by these ideas, sociobiology has more or less forgotten to ask about the mechanisms used by insect colonies to reach these decisions. As a result, the adaptive value of collective decisions is well documented (e.g. anti-predator defence, foraging success, etc), but it is only recently that the study of mechanisms underlying collective decision has become a subject of interest (see Camazine *et al.* 2001).

There exist detailed descriptions of collective decisions by insect colonies (for example see, ants: Davidson 1978; Warburg 2000; review in Hölldobler and Wilson 1990; caterpillars: review in Fitzgerald 1995), on the one hand, and equally detailed descriptions of individual decisions on the other (for example see, ants: Sudd 1987; review in Hölldobler and Wilson 1990; caterpillars: review in Schoonhoven 1987, caterpillar foraging Stamp and Casey 1993), but the causal link between the two has not received much attention. In particular, the surprising difference in complexity between the decisions made by individual insects and those made by colonies is often ignored (excepted for some recent studies, review Detrain *et al.* 1999). Bridging this gap requires the realization that collective decision-making emerges out of the interactions between individuals and between individuals and their environment.

The most widespread social interaction between individuals leading to collective decision-making is allelomimesis (roughly speaking, do what my neighbour is doing; see e.g. Sudd 1963; Altman 1985; Deneubourg and Goss

1989). Allelomimesis, by definition, leads to amplification, or the snowball effect: i.e. I imitate others, others imitate me, and we all end up doing the same thing. Amplification refers 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. This phenomenon is an essential component of many collective decision observed in social insect, e.g. aggregation of individuals in one site (Deneubourg *et al.* 1990; Saffre *et al.* 1999; Depickère *et al.* 2004), collective defence against a predator(Franks & Partridge 1994; Millor *et al.* 1999), recruitment to a single food source (Pasteels *et al.* 1987; Seeley *et al.* 1991; Fitzgerald 1995) or to a new nest site(Camazine *et al.* 1999; Visscher and Camazine 1999; Pratt *et al.* 2002) among several possibilities, etc. In all these phenomena collective decision emerge because an individual behaviour is amplified by the action of many other individuals. For example, during food recruitment, an ant that has discovered a profitable food source leaves a pheromone trail leading to the source. Other ants leaving the nest amplify this trail by depositing additional pheromone.

This amplification process means that slight differences in the tendency of individual animals to display certain behaviours can lead to very different results at the collective level (Dussutour *et al.* 2005; Camazine *et al.* 2001). This may have important evolutionary consequences when these differences are expressed between species: for example, two species of wasp that exhibit slight differences in the way they put down building materials will end up building nests very different in size and shape and in adaptive value (Theraulaz *et al.* 1999), for instance in terms of thermoregulatory or anti-predator properties. Nest characteristics, like individual wasp characteristics, are subject to natural selection, and therefore selection pressures acting on the result of collective behaviour (i.e. the nest) drive the evolution of individual behaviour (i.e. the rules followed in putting down building materials) (Dawkins 1999).

In this paper, we emphasize that complex collective decisions in social insects do not require complex individual behaviour or complex social organization. First we will demonstrate that simple behaviours such as trail laying and trail following can be the source of sophisticated collective decision-making when an insect colony is faced with two food sources of different quality. Second, we will show that insects with different degrees of sociality (caterpillars and ants) can reach an identical collective decision under the same conditions. These parsimonious hypotheses contrast with the traditional biological approach, in which individual complexity is necessarily at the root of collective complexity.

This paper revisits previously published experiments conducted with ants and caterpillars, in order to make comparisons between these two groups as well as between species within each group that differ in their mode of foraging and recruitment.

2   Methods

2.1   Ants:

Ants are eusocial insects, that is, they exhibit sophisticated social organization including division of labor, overlapping generations, cooperative brood care, reproductive caste specialization (only queen reproduce).

Investigators of foraging in ants have characterized a diversity of recruitment strategies, including tandem running, group recruitment and mass recruitment are among the most prominent strategies described (Fig. 1). From an evolutionary perspective, tandem running appears to represent the most primitive recruitment strategy (Hölldobler and Wilson 1990; Liefke *et al.* 2001).

During tandem running, a scout that has discovered a food source leads a single nestmate back to the food find (Möglich *et al.* 1974; Möglich 1979; Liefke *et al.* 2001). The nestmate keeps close antennal contact with the scout and only one nestmate is recruited per trip.

Group recruitment differs from tandem running in that multiple nestmates follow a scout on each trip (Szlep-Fessel *et al.* 1970; Hölldobler 1971). Scouts lead groups, not only by direct bodily contact, but also indirectly by laying chemical trails that nestmates are able to follow. Because scouts can lead multiple nestmates per trip, group recruitment is much more efficient than tandem running at aggregating large numbers of nestmates at a food site. Tandem running and group recruitment are often preceded by the scout performing an invitation display inside the nest. Invitation behavior may be accomplished by antennation, by the presentation of food samples, by agitated displays by the recruiter, or by secretion of chemicals that alert nestmates to the presence of a chemical trail that leads to the food find.

But the most "evolutionary advanced" system used by ants involve mass communication, in which the pheromone itself is the prime, if not the sole, signal. The number of ants recruited is related to the amount of pheromones secreted. In mass recruitment, a scout discovers a food source and returns to the nest, laying a chemical trail. At the nest, other foragers detect the trail and follow it to the source (e.g. Hölldobler and Wilson 1990). Ants arriving at the

source load food and return to the nest reinforcing the trail. Unsuccessful trail-followers explore the foraging ground before either returning to the nest or finding the food source. As the trail is reinforced, more ants are recruited and fewer recruits lose the trail: trail laying and following is hence an allelomimetic amplification process (e.g. Pasteels *et al.* 1987). The pheromone is adequate to both stimulate and orient trail following; therefore, direct physical interaction between individuals is not required.
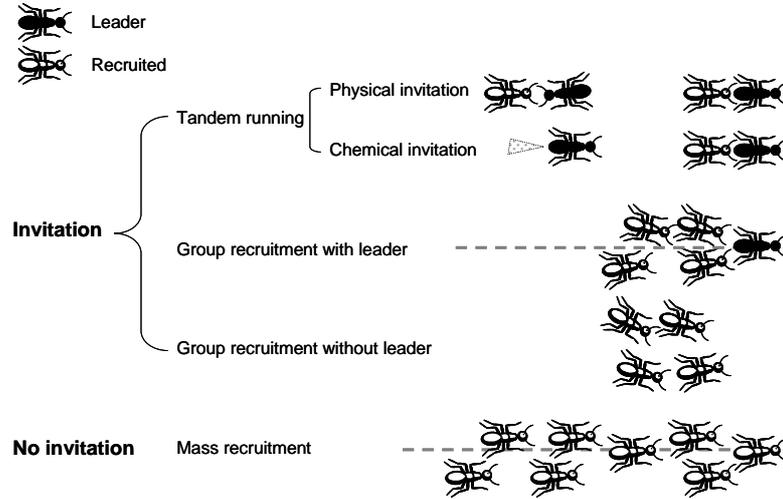

Fig 1: Foraging pattern in ants: tandem running, group recruitment and mass recruitment (from Passera 1984)

In this paper we have chosen a species which use group recruitment : *Myrmica sabuleti* and a species which use mass recruitemnt: *Lasius niger.*

M. sabuleti is an European species living mainly in dry grasslands and on south slopes (Gaspar 1971). The mean size of their colonies is about 1000 workers and a few queens (Brian, 1972). Foragers individually collect small prey items, but use group recruitment to collectively exploit sugar solutions or large prey (Cammaerts and Cammaerts, 1980; de Biseau and Pasteels 1994; de Biseau *et al*. 1997).

L. niger or "black garden ant" is a common Palaearctic species (Gaspar 1971) The mean size of their colonies is about 10 000 workers and a one queen. The ants feed mainly on aphid honeydew and use mass recruitment through chemical trails to exploit collectively abundant food sources (Pontin 1958; Flatt and Weisser 2000).

2.2   Caterpillars:

Unlike eusocial insects such as ants, caterpillars only form colonies during part of their life cycle. Colonies are less integrated and less cooperative. However, different caterpillar species do show varying degrees of sociality. These can be classified by foraging behavior, as was done above with ants. Caterpillar foraging strategies can be broadly classified as either patch-restricted, nomadic (e.g. the forest tent caterpillar, *Malacosoma disstria*) or central-place foragers (e.g. the Eastern tent caterpillar, *Malacosoma americanum*) (Fitzgerald 1995, Fig. 2).

In patch restricted foragers, colonies of caterpillars typically confine their feeding activity to the leaves found within a single continuous patch of leaves. The colony's foraging arena is often enveloped in silk, and the caterpillars feed and rest within the envelope. Trail markers play little or no role, enabling the caterpillars to enjoy the independence of movement.

In contrast to patch restricted foragers, nomadic foragers wander widely in search of feeding and resting sites. The behavior of colony members is more closely inter-dependent than in patch restricted foragers, and periods of activity and rest are typically synchronized among all member of the group. The integrity of the colony is maintained by trail pheromones. In the forest tent caterpillar, each individual lays down a chemical trail by pressing the tip of its abdomen against the substrate as it advances along a branch, much in the manner of ants (Fitzgerald and Costa 1986). During the foray, the caterpillars travel en masse and feed simultaneously at the same site. After feeding to repletion, the caterpillars set off in search of a suitable temporary resting site or bivouac. The fed colony remains together because the caterpillars mark branches with recruitment pheromone as they move away from the food find. Caterpillars reassemble at the new resting site to digest their meal (Fitzgerald and Costa 1986).

Central place foraging is the least common mode of foraging found among social caterpillars. Central place foragers establish permanent resting sites from which they launch intermittent forays in search of food. The nest, like those of ants, serves as a communication center where hungry caterpillars are alerted to the discovery of food. Central place foragers, like nomadic foragers, lay and follow pheromone trails. However, in central place foragers, colonies do not discover food sources en masse, but instead send out scouts that return to the nest to recruit colony mates. Like ants, recruited caterpillars reinforce the pheromone trails they follow leading to allelomimetic amplification.
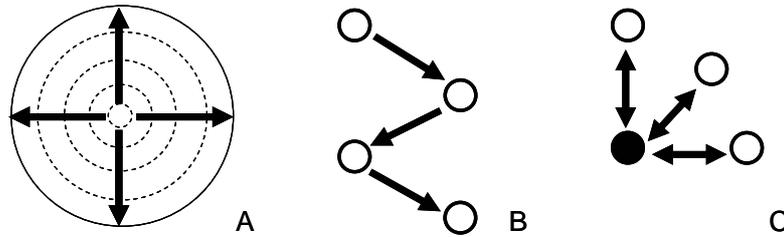
Fig 2: Patch restricted, nomadic and central-place foraging patterns of social caterpillars. Arrows show how the larvae move (A) within patches, (B) between patches, and (C) between the resting site (solid) and feeding sites (from Fitzgerald and Peterson 1988)

In this paper we have chosen a specie which use nomadic foraging pattern: *Malacosoma disstria,* and a specie which use central-place foraging pattern: *Malacosoma americanum.*

The nomadic forest tent caterpillar *M. disstria* and the central place foraging Eastern tent caterpillar *M. americanum* are common pest of several species of deciduous trees in Canada. All are colonial during the larval stage. Colonies typically consist of several hundred siblings that emerge from a common egg mass. The forest tent caterpillar is the only species of tent caterpillar that does not spin silk tents. They spin silk threads for pathways that are marked with pheromone to and from their feeding sites on the trees, and they also spin silken mats as bivouacs. By contrast, Eastern tent caterpillars construct a silk tent in the branch of their host tree soon after hatching. The larvae launch forays from the structure in search of food (Fitzgerald 1980, Casey *et al.* 1988, Fitzgerald *et al.* 1988). Between bouts of feeding, the caterpillars rest and digest in or on the shelter.

2.3   Experimental set-up and protocol:

In each experiment, a group of either ants or caterpillars starved for a few days was given access to a bridge leading to two food sources. The food consisted in a sucrose solution for ants and in leaves for caterpillars.

The experiments were performed with two kinds of bridges (Fig. 3):

- A Y-shaped bridge with two branches of equal length, which give access to two food sources of equal quality.

- A Y-shaped bridge with two branches of equal length, which give access to two food sources of different quality.

More than fifteen replicates were observed in each case. In all experiments, the traffic on the bridge was filmed. Data were collected both at the collective and individual level.
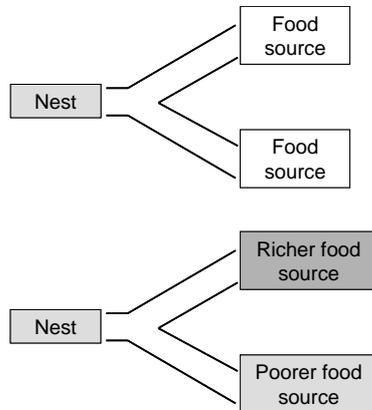
Fig 3: Experimental set-ups used in the experiments.

2.4 Experimental investigation:

The first step in the study of collective behaviour is to characterize the group level pattern in detail, to obtain a clear picture of the basic phenomenon to be explained (Fig. 4). Then we look inside the group to identify its subunits and observe their interactions.

The approach just described is likely to yield strong suggestions about how the group works. However, testing the accuracy and completeness of ones understanding requires a further step, the formulation of a rigorous model that embodies the mechanisms underlying group dynamics and that can predict group behaviour under novel conditions. Here a bottom-up approach is taken to model building, using empirical findings rather than intuition to shape the model.

The principal aim of modelling is to check whether the processes and individual behaviour identified through experiments do produce the actual patterns observed in groups. Simple qualitative reasoning often fails to predict the properties of systems, such as animal groups characterized by

multiple interacting subunits and amplification processes. Mathematical equations and computer algorithms, on the other hand, enable prediction of the properties of complex systems and provide a means of evaluating a model of a group's internal machinery.
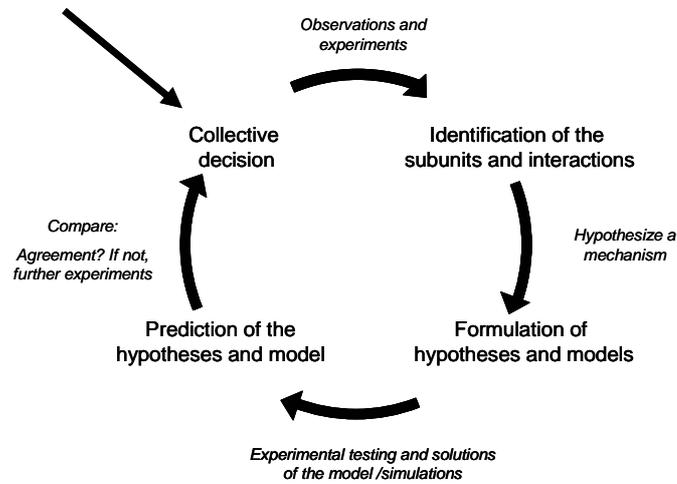

Observations and experiments

Collective decision

Identification of the subunits and interactions

Compare:

Agreement? If not, further experiments

Hypothesize a mechanism

Prediction of the hypotheses and model

Formulation of hypotheses and models

Experimental testing and solutions of the model /simulations

Fig 4: Integrated experimental and modelling approach used in the study of how collective decisions emerge (from Camazine *et al.* 2001).

Data collected at the Collective level

Characterizing the collective level pattern involved measuring the traffic on the bridge. Counting began as soon as the first insect discovered the bridge and climbed on it. The flow of insects leaving the nest and that leaving the food source was measured.

There are two possible outcomes for these experiments: either the traffic is distributed symmetrically on the two arms of the bridge, or most of the individuals select one branch and the traffic is asymmetric.

Data collected at the individual level Individual level

The foragers were observed on the bridge using a video camera to measure the extent of trail laying behavior as the individuals returned from the source. Tent caterpillars deposit pheromone trails by lowering and brushing the last abdominal segment against the substrate. Ants curve their

abdomen vertically to the ground, stop walking and back up to deposit pheromone.

A marking trip was defined as a passage on the bridge during which an individual made at least one mark. The frequency of trail-laying was defined as the proportion of trips that included marking, and the intensity of trail-laying was defined as the number of marks laid per marking trip.

Modelling

Models build using this data are not presented here (for more details see e.g. Beckers *et al.* 1993)

3   Results

Table 1 summarizes the decisions made by ant and caterpillar colonies presented with either two identical or two different food sources.

When a colony was offered two identical sources at the same time, after a short period of equal exploitation, a bifurcation is observed and one of the sources becomes much more exploited than the other. This result is true for all four species studied. At the beginning of the experiment, the two sources are equally exploited. Rapidly however, random small initial differences in the concentration of trail pheromone between the two branches of the bridge are amplified, because the caterpillars and the ants chose stronger trails over weaker trails. In consequence, the recruited insects select the branch with the higher concentration and reinforce it. Finally, one of the trails dominates and the other one disappears.

This amplification phenomenon is reinforced in social caterpillars by the fact that an individual is able to detect the fresh trail of a single colony-mate when it overlays older trails from multiple caterpillars. Moreover, the nomadic caterpillars *M disstria* use direct physical contacts with preceding caterpillars as well as trails in choosing a direction (Colasurdo and Despland 2005).

In the case of two food sources of different quality, most frequently, the insects showed a clear preference for the richer source.

At the individual level, we observed modulation of trail-laying according to the quality of the source. Foraging ants exploiting the richest source were found to deposit trail marks more frequently than those exploiting the poorer source. Fitzgerald and Webster (1993) observed the same phenomenon in

foraging *M americanum* caterpillars. This study suggests that caterpillars may also vary the amount of a chemical component they apply in accordance to the quality of the food. Nevertheless, the authors are not clear whether the caterpillars modulate trail strength by applying more or less pressure as they drag the tips of their abdomens over the substrate, or whether they actively control the rate at which the pheromone is secreted as has been demonstrated with ants. In *M disstria* we have no evidence for such modulation; however our preliminary results suggest that foragers of *M disstria* seem to modulate the time they spend feeding at the source according to the quality of the source. In *M. disstria* and other social caterpillars, we know that mechanical cues have been associated with the trail following abilities of many social caterpillars (see for example Fitzgerald 2003; Colasurdo and Despland 2005) but it is not clear yet if the modulation of such contacts varies with food quality.

In addition to modulating deposition of the trail pheromone, the foragers of *Myrmica sabuleti* varied the intensity of their invitation displays according to food quality (Cammaerts and Cammaerts 1980). In the group recruitment strategy used by these ants, increasing the intensity of the invitation display increases the number of colony-mates recruited on a single foraging trip.

The small differences in trail-laying and invitation displays described above are amplified due to the allelomimetic nature of the recruitment. Mathematical modeling has demonstrated that this amplification process is sufficient to lead to selection of the richest source, without appealing to complex individual behavior such as comparison of the two food sources (Taylor 1977, 1978).

Food variables	Species (reference)	Origin of collective decision	Amplification mechanims	Collective decision
Food quality: *Equal*	NOMADIC CATERPILLARS: *M disstria* (Fitzgerald and Costa 1986, Colasurdo and Despland 2005, Dussutour and Despland in prep).	Random fluctuation	Preference for the stronger trail. Preference for fresh trail. Follow the lead caterpillar.	Collective choice of one of the two sources.
	CENTRAL- PLACE CATERPILLARS: *M americanum* (Fitzgerald 1995).	Random fluctuation	Preference for the stronger trail. Preference for fresh trail.	Collective choice of one of the two sources.
	MASS RECRUITMENT ANTS: *Lasius niger* (Beckers and al 1993, 1992).	Random fluctuation	Preference for the stronger trail.	Collective choice of one of the two sources.
	GROUP RECRUITMENT ANTS : *Myrmica sabuletti* (Cammaerts and Cammaerts 1980, de Biseau *et al* 1991).	Random fluctuation	Preference for the stronger trail.	Collective choice of one of the two sources.
Food quality: *Different*	NOMADIC CATERPILLARS: *M disstria* (Fitzgerald and Costa 1986, Colasurdo and Despland 2005, Dussutour and Despland in prep).	Modulation of the time spend at the source according to food quality	Preference for the stronger trail. Preference for fresh trail. Follow the lead caterpillar. Stay longer at the rich food source.	Not clear, seem to choose the richer food source.
	CENTRAL- PLACE CATERPILLARS: *M americanum* (Fitzgerald 1995).	Modulation of trail laying according to food quality	Higher percentage of individuals lay trail to rich food source. Higher intensity of individual chemical marking to rich food source. Preference for the stronger trail. Preference for fresh trail.	Collective choice of the richer food source.
	MASS RECRUITMENT ANTS: *Lasius niger* (Beckers and al 1993, 1992).	Modulation of trail laying according to food quality	Higher percentage of individuals lay trail to rich food source. Higher intensity of individual chemical marking to rich food source. Preference for the stronger trail.	Collective choice of the richer food source.
	GROUP RECRUITMENT ANTS : *Myrmica sabuletti* (Cammaerts and Cammaerts 1980, de Biseau *et al* 1991).	Modulation of trail laying according to food quality Modulation of invitation displays according to food quality	Higher percentage of individuals lay trail to rich food source. Higher intensity of individual chemical marking to rich food source. Preference for the stronger trail. Higher percentage of inviting individuals to rich food source.	Collective choice of the richer food source.

Table 1: Collective decisions are related to the recruitment behavior of individuals. Collective decisions, their origins and the amplification mechanisms are summarized.

4   Discussion

In this paper we compare the mechanisms by which ant and caterpillar colonies reach collective decisions between two competing food sources.

Recruitment dynamics is shown to closely depend on the proportion of insects laying a trail or inviting colony-mates in the nest, and on the intensities of invitation behavior or chemical trail marking performed by recruiting individuals. Amplification then leads to asymmetrical foraging between the two sources and ultimately to choice of a single source. In the case of two equal sources, random fluctuations in recruitment behavior lead one of the two trails to become slightly stronger than the other, and to therefore be followed more accurately. As recruits become recruiters in their turn, amplification and positive feedback generate a snowball effect and one of the trails is abandoned. In the case of two sources of different quality, the selection of the richest source occurs via the same amplification process, but in this case initial differences in trail strength are not random, but instead arise because foragers modulate their behavior in accordance to food quality. Although the exact cues involved differ between species (e.g. trail strength *vs* mechanical stimulation *vs* invitation displays) the fundamental mechanisms involved are the same.

The elegance of this foraging system is that the collective decision to exploit the better food source arises automatically from the trail following behavior, without the need for a leader with a synoptic overall view of the situation and knowledge of all available options. Indeed, no individual insect visits both food sources, compares them, and decides which is the best. The studies presented in this paper show that the intensity of individual recruitment behavior increases as a function of the quality perceived by the forager (Detrain *et al.* 1999). Though this recruitment decision rule seems trivial, it is sufficient for colonies to select valuable food sources and hence appears to be an efficient mechanism for a group to make good decisions in complex environments.

These mechanistic explanation of collective foraging decisions contrast with a more functional approach, such as that developed in similar experimental context by Taylor (1977, 1978), in which the colony is somehow supposed to maximise some metric of performance. Without excluding the possible existence of more sophisticated mechanisms based on a more complex individual behaviour, our results emphasize the fact that

adaptive foraging strategies can emerge out of simple individual behavioural rules and through the iterative amplificatory process of trail-laying and trail following. Any parameters which can influence the perceived quality of a food source (e.g. distance from the nest, level of traffic congestion) can also influence the decision-making process at the collective level via this simple recruitment process (Beckers *et al.* 1992, Dussutour *et al.* 2004, Dussutour *et al.* submitted). However, these parameters do not need to be specifically measured or coded by individual foragers. Ants and caterpillars, like other group-living animals (Camazine *et al.* 2001; Conradt and Roper, 2005), appear to have developed a simple but effective means of making decisions. By interacting with each other and with the environment, insects, despite their limited behavioural repertoire and local individual perception, are able to make complex decisions adaptively.

The degree of individual complexity found in animals is of course extremely variable, as are forms of social organization and the mechanisms used by individuals to communicate with other group members. Nevertheless the results presented here show that in four model systems representing very distantly related groups (one highly social and one less social) and different foraging systems, collective decision emerge from individual interactions in a very similar fashion and consistently lead to an adaptive solution i.e. the selection of the richest source. The question raised by the variability in individual complexity may therefore 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' behaviour, and what part emerges out of by the interaction between individuals? This problem is not only fundamental to the relationship between individual and the society, but also underlies the relationship between a organism and its organs, an organ and its cells, and between a cell and its macro-molecules.

The findings presented here suggest that simple explanations should perhaps be considered first when seeking to explain complex collective decision-making. The mechanisms we describe in this paper are ubiquitous and generic, and can be shown to operate in a wide range of systems, from collections of molecules to animal groups (Camazine *et al.*, 2001) to human societies. For example, in an emergency a panicking crowd use only one of several available exits (Helbing *et al.* 2000). Indeed, any system exhibiting allelomimetic behaviour automatically acquires a capacity for collective decision-making. In biological systems, collective decision-making can be a significant adaptive advantage, since information from multiple individuals can be integrated to find an optimal solution. 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 groups.

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