

Collective decision and foraging patterns in ants and honeybees

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Abstract

Ants and honeybees are useful biological models for studying collective decision making in group-living animals. In terms of foraging, information about food sources are gathered by individual scouts and shared with nestmates through recruiting signals, which may be adaptively tuned depending on food profitability. In addition, negative feedbacks (e.g. food depletion) counter the amplifying effect of recruiting signals, so that the number of recruits is adjusted to the level of food availability and food demand. While the general scenario of recruitment is similar for ants and honeybees, it is achieved through quite different communication channels. A mainly tactile signal (i.e. the waggle dance) drives honeybee recruitment to flower patches, whereas a chemical signal (i.e. the trail pheromone) shapes collective foraging in ants.

In this review, we begin by considering the chemical nature of recruitment in ants and how it is intimately related to their mode of locomotion. Whereas ants walk on the ground,

honeybees use the air, setting several constraints which prevent the use of odour trails and steering a unique mode of symbolic communication in which an updated 'flying map' is provided to each nestmate.

Secondly, we emphasize on the higher level of non-linearity associated with chemical signals compared to tactile signals (i.e. the ants' trail as compared to the honeybee dance). We argue that such a difference deeply influences the dynamics of information transfer, as well as the foraging patterns displayed by ant nests or by hives. In ants, the use of chemical trails makes the collective choice of only one food resource more likely and impedes the reallocation of ants when food profitability changes. Conversely, a hive should dispatch foragers more evenly among food resources and should more readily shift towards more profitable flower patches. In this study, we infer that the level of non-linearity of one species' interactions is in accordance with its foraging ecology - as well as to its need for flexibility or cooperation in food exploitation.

Thirdly, we show that both insect societies have to make a trade-off between a high accuracy of communication - increasing foraging efficiency-, and a low accuracy - allowing for new food discoveries. Recruitment accuracy is tuned by varying the amount of emitted trail pheromone in ants and by varying the precision of directional information coded in the waggle runs in bees. The coupling of randomness in communication with competition between recruitment signals appears to be a powerful strategy to optimize foraging success. Finally, we demonstrate that dances and chemical trails lead to quite different spatial patterns. Foraging routes of the hive appear as a juxtaposition of straightaways (beelines), the directions of which follow changes in the spatial distribution of flower patches. In addition, ant trails organize themselves into a network, of which the final pattern is influenced by group size, history of food discoveries, or by any factor preventing or facilitating the journey of foragers towards food sites.

Throughout this review, we support the ideas that 1°) adaptive choices may emerge without the need for any leaders, from the coupling between simple positive and negative feedback; 2°) that major differences in collective patterns may arise from seemingly small differences in the properties of recruiting signals and 3°) that new insights into the evolution of communication and cooperation in group-living animals may arise from comparing decision making processes in insect societies.

1. Introduction

Organisms inhabit a heterogeneous world in which resources are distributed patchily, vary in size or quality over time, and trigger the interest of several competing species. In addition, the physical properties of the environment -such as the air wind-flow for flying species or the substrate granularity for walking ones- determine the energetic costs, as well as the time investment associated with the searching and the exploitation of food resources. Hence, during its entire life, each individual forager has to choose between a range of alternatives: it has to decide not only which food type to exploit, but also which part of its home-range to explore, which foraging risk to face or which path to follow. Decision making is even more complex for animals living in social systems (Krause and Ruxton, 2002). Indeed, the decision of each individual is closely related to the behaviour of the other group members. Such social influence on individual decision making is essential to group-living animals, for which cooperation plays a key role by enhancing fitness. It is a prerequisite for the emergence of coordinated behaviour; for example the reaching of a consensus about moving in a common direction, or the collective choice of exploiting a single food patch. Situations in which group members choose between two or more mutually exclusive actions with the specific aim of reaching a consensus are usually termed as 'collective decision-making' (Deneubourg and Goss, 1989; Conradt and Roper, 2005; Couzin et al, 2005; Sumpter, 2006; Dyer et al, 2008, ...). Examples of collective decisions were demonstrated in several different taxa and contexts such as the choice of a common feeding place in birds (see e.g. Perusse and Lefebvre, 1985) or the choice of a common moving direction in fish schools (e.g. Couzin et al, 2005) and in mammal troops (e.g. Kummer, 1968; Boinski and Garber, 2000). Put in a historical perspective, the study of collective decision making find its roots in political sciences and several theories have been built since Condorcet's formulation (1785) of the voting paradox. These theories have shown how individual preferences may lead to quite different social choices depending on the underlying voting procedures (Gaertner, 2001). Even though political sciences and life sciences may seek to answer similar questions - and often share the same vocabulary (List, 2004) - when they talk about decision-making, collective choices made by animals are, however, governed by procedures that are very different from voting procedures in humans.

Ants and honeybees are useful biological models for studying collective decision-making processes in group-living animals. Insect societies containing up to several thousands of individuals nevertheless succeed in behaving in a coordinated way. Both the ant nest and the beehive display striking examples of collective responses in a variety of contexts such as foraging (see references further in the text), nest moving (Franks et al, 2002; Seeley and Visscher 2004; Seeley et al, 2006; Pratt et al, 2002; Pratt and Sumpter 2006) or territorial defense (Lumsden and Hölldobler, 1983; Millor et al, 1999). In most – although not all- cases, the best food patch, the best nesting site or the safest place is selected. Amazingly, hundreds of nestmates, each with their own agenda, their own past experience as well as their own behavioural profile, are able to coordinate their efforts to behave in a highly cohesive way.. Beehives or ant nests then appear as integrated social structures that gather a vast array of information, acquired by its members and that compare the relative value of each resource with respect to actual colony needs. These societies then “wisely” deploy their workers over their home range area. Moreover, collective decisions give birth to social-built structures that are characterized by relatively larger spatio-temporal scales than the corresponding ones observed at the individual level (Camazine et al, 2001). Indeed, while one ant individual can only forage over a few square meters at most, the trail network of the whole colony can

extend over several acres. Likewise, while one forager, due to physiological limitations (e.g. water loss), can stay outside the nest for at most a couple of hours, the colony taken as a whole can forage over food patches for relatively longer time scales –i.e. for several days or weeks.

In the last decade, life scientists have had to face one exciting challenge which was to explain how collective decisions may arise in societies made up of thousands of individuals. Since collective behaviour may lead to a high level of cohesion, one can get the impression that “social patterns” are obeying some complicated hidden blueprints or a centralized strategy imposed by one or a few leaders. This is not the case. Instead, for many social activities, the coordinated behaviour of an insect colony relies on a multitude of local decisions made by individual workers. Collective structures are the dynamic by-products of interactions between colony members, and result from a decentralized decision-making process (see for example Seeley 1995; Theraulaz and Spitz, 1997; Camazine et al, 2001; Detrain and Deneubourg, 2006; Sumpter, 2006). Any individual that makes a decision based on its local perception of the environment may contribute to the final foraging decision of the whole colony. Since each individual may influence the colony’s response and its fitness, such an individual has to constantly monitor the environment for cues and signals that indicate whether it should change its occupation, intensify its participation in current tasks and /or transfer the acquired information to nestmates. In a foraging context, the information the individual perceives about food profitability helps each worker to decide not just how, where and when to exploit a food patch, but also whether or not to recruit nestmates.

In this review, we shall compare how collective decisions emerge in hives and in ant nests by relating the properties of recruiting signals with the foraging strategies displayed by these two insect societies. We shall first briefly describe the main positive and negative feedbacks that self-regulate the activities of foragers in accordance with environmental constraints and opportunities. Even though honeybees and ants share a similar scenario of recruitment, we shall recall that they differ greatly in the nature of their recruiting signals as well as in the ways information about food patches is conveyed to nestmates. In honeybees, tactile signals (i.e. the waggle dances) rule many aspects of recruitment to flower patches whereas chemical communication (i.e. recruitment trails) is the backbone of collective foraging in ants. We will emphasize the intimate link that relates the mode of locomotion of one species (i.e. walking or flying) to the media “chosen” to communicate information about food resources. In particular, we shall see that the distinct properties of chemical and tactile signals matches the environmental constraints faced either by ant individuals walking on the ground or by honeybees flying through the air.

One goal of this paper is also to advocate that the use of either chemical or tactile signals in recruitment has set constraints on communication and may account for the different foraging patterns displayed by ant nests or by hives. Therefore, in the second part of this review, we shall compare how ants and honeybees make collective choices between identical sources, code information about food characteristics and select the most profitable resources. In particular, we shall argue that differences in the collective patterns displayed by ant nests or hives depend on the level of non-linearity of their recruitment process, or, in other words, on the amplifying potential of their communication (what is the amplifying potential?). In addition, we shall examine how randomness may lead to a diversity and a flexibility of foraging patterns, instead of simply cutting down the efficiency of food exploitation.

Throughout this review, collective patterns displayed by hives and ant nests will be placed in a behavioural ecology perspective: we will try to connect together the properties of recruiting signals, environmental constraints, as well as the efficiency of the foraging strategies displayed by these insect societies. Finally, by referring to other group-living arthropods, we

will address generic issues about the processing of information, about its dissemination among conspecifics and about the emergence of cooperative behaviour.

2. Building up collective foraging behaviour through feedbacks

The ways individuals process information about current food opportunities or foraging risks and communicate with each other are crucial to the foraging success of insect societies (Seeley, 1994, 1995; Detrain *et al*, 1999; Sendova-Franks and Franks, 1999; Camazine *et al*, 2001; Franks *et al*, 2002). Insect societies have to communicate not only how far and in which direction food is located - but they also have to decide how many foragers should be engaged in food exploitation. A large part of information can be exchanged through direct interaction between nestmates, such as antennal contacts or chemical emission of pheromones. In addition, workers can get information through animal-induced changes within a shared environment. Indeed, any individual that modifies its environment -and hence that of nestmates - indirectly influences the further behaviour of other group members. For instance, when an individual impoverishes an area by regularly feeding on it, it decreases the foraging success rate of conspecifics and hence influences their further foraging decisions. This may lead namely to spatial specialization and related division of labour (Deneubourg *et al*, 1987; Beshers and Fewell, 2001; D'Ettore, 2007; Ravary *et al*, 2007).

Interactions between nestmates or between nestmates and their environment can be classified into two main categories: positive and negative feedback. A positive feedback is an interaction that increases or amplifies the response to an initial stimulus. One of the best-known examples of positive feedback is the emission of recruiting signals by foragers having discovered a new food source. This signal is emitted either incidentally or actively by successful scouts: it will mobilize and attract additional nestmates to the food site that, after feeding, will in turn reinforce and amplify the recruiting signal (Hölldobler and Wilson, 1990; Seeley, 1995). Without an antagonizing mechanism, however, the process may become uncontrollable. Negative feedback, such as food exhaustion or over-crowding of food sites, act to counter or "dampen" amplifying effects that would otherwise lead to an excessive mobilization of foragers. Such mechanisms act as stabilizing force and play a regulatory role by adjusting the number of recruited foragers to the number and size of food items. Insect societies may thus be seen as a network of coupled feedbacks. Their ecological success depends on the subtle interplay between positive and negative feedback loops that focus the colony foraging effort onto profitable sites, lead to the emergence of optimal patterns and open the way to cooperation in food exploitation and defence (see e.g. for honeybees Seeley, 1995; Seeley *et al*, 1991, 2000; for ants, Hölldobler and Wilson, 1990).

2.1. RECRUITMENT: THE QUINTESSENCE OF POSITIVE FEEDBACKS

Many examples have been described and a vast body of literature has been devoted to the recruitment phenomenon, notably in social insects. Recruitment can be passive and the by-product of a spying behaviour. For instance, the feeding activity of an animal can be perceived by conspecifics that will join it at the food source. Such passive recruitments have been reported for a variety of animal species and are associated with complex cost and benefit trade-offs, since conflicts between individuals often occur to get access to food sources (Thomas and Valone, 1989; Valone and Templeton, 2002; Danchin *et al*, 2004). Social insects

are one of the rare examples in which the recruitment of nestmates is a truly active process. The successful scout decides to emit specific signals that attract and guide workers to the food. Hence, every time a forager returns to the nest, it brings home not only food but also information about the characteristics of the exploited resources that it shares by means of recruitment signals. These signals provide a positive feedback that attracts nestmates, concentrates the foraging force around one food source, and contributes to a social consensus about when, where and how to forage (Camazine et al, 2001).

Although both ants and honeybees prove to be highly successful in coordinating their foraging activity and in making adaptive choices about where to forage, recruitment is achieved by using quite different communication channels.

In the case of ants, recruitment signals are essentially chemical ones. In some ant species, the recruiter leads one recruit (tandem recruitment) or a small group of recruits (group recruitment) from the nest to the newly discovered food source. The cohesion of the tandem or of the group is maintained by mechanical contacts between the leader's gaster and the follower's antennae and/or by short-range chemical signals emitted by the leader (Möglich et al, 1974; Verhaeghe, 1982; Hölldobler and Wilson 1990; de Biseau et al, 1994; Liefke et al, 2001; Franks and Richardson, 2006; Richardson et al, 2007). However, the most widespread recruitment procedure in ants is through the laying of a chemical trail (figure 1A) (Wilson, 1962 a,b; Traniello and Robson, 1995; Beckers et al. 1989). In this latter case, the odour trail laid by the successful scout on its way back to the nest triggers the exit of nestmates and guides them to the food source. Recruits having found and fed at the food source reinforce the trail in turn when coming back to the nest. By doing so, successful foragers draw out of the nest an increasing number of nestmates and provide them with an efficient guiding trail. In the case of honeybees, several hundred foragers bring in information about food sources and maintain a strong flow of information about food opportunities to the hive. The honeybees have a unique way of recruiting nest mates to food sources; the famous waggle dance (Figure 1B)(von Frisch, 1967). Waggle dances, which consist of a series of waggle runs each followed by a semi-circular return, convey information about the direction and distance of the foraged site visited by the dancing bee. The angular deviation of waggle runs from the vertical corresponds to the angle of the food source relative to the current sun azimuth. The distance between the nest and the feeding site is encoded in the duration of the waggle run. Dances are thus a sophisticated means for honeybees to translate into a coded language the food location (for a review see Dyer and Seeley, 1991, Dyer 2002; Seeley 1995). The information encoded in this symbolic language is then read by unoccupied foragers to fly off and locate the foraging site. In addition to distance and direction information, bees that follow dances learn the odour of the food and then search for that scent in the field (Gould 1976, Sherman and Visscher 2002).

2.2. THE WAY YOU MOVE RULES THE WAY YOU RECRUIT

One may easily conceive that the way an animal guides recruits to food sources is constrained by the way it moves. Walking on the ground or flying through the air has presumably imposed strong constraints on the type of recruitment signals used by ants and honeybees.

Quite obviously, the way that ant scouts recruit nestmates is intimately related to their ability to lay signposts while walking between the nest and the food source. Successful foragers that return to the nest can easily bend their gaster downwards and hence can exert a step-by-step control on the amount of recruitment signals laid over the substrate. The chemical trail that is progressively built and reinforced by those successful foragers is then followed by ants as an invisible highway on the ground connecting the ant nest to the food place. In this case,

information about the location of food, such as its spatial coordinates, is not explicitly coded by the trail or by any other signals emitted by recruiters inside the nest. In other words, recruits that exit the nest and start following the trail, have no idea where the food is located or at which distance from the nest. Foragers track the trail at a local scale through osmotropotaxis by moving their antennae over the substrate until they reach the food source (Hantgartner 1967, 1969; Detrain et al. 1988; Hölldobler and Wilson, 1990; Calenbuhr and Deneubourg 1992; Calenbuhr et al, 1992). The recruitment trail is thus like an Ariane thread that guides foragers to a food source and provides them with step-by-step directional information. The use of a trail is not limited to ants, since other walking social insects such as termites rely on this mode of communication as well. Indeed, trail pheromones elicit recruitment and orientation for termite species in which workers forage outside the nest or move from one nesting site to another. (Kaib et al. 1982; Traniello 1982; Heidecker and Leuthold, 1984; Traniello and Leuthold 2000; Pasteels & Bordereau 1998, Reinhard & Kaib 1995, 2001).

In addition to its guiding role, the following of a trail also gives an opportunity for foragers to come across many nestmates. During these head-on encounters on foraging trails, ant workers perceive several cues informing them not only about the partner's identity but also about the type of food being exploited or about the profitability of one foraging patch (i.e. through the percentage of laden foragers) (Lebreton & Fourcassié 2004; Roces 1990; Roces & Nunez 1993; Howard et al. 1996). For instance, the mere contact of recruits with food residues over the recruiter's body informs them about the food characteristics prior to their arrival at the feeding site and activates a food searching pattern leading to an increase in patch finding (Lebreton & Fourcassié 2004). Conversely, flying insects such as honeybees cannot exchange information about food sources along their foraging journey: they have to estimate food characteristics within the hive – namely through the perception of floral odours- before flying out to the flower patch (Seeley 1995).

While the laying of chemical marks over the ground is a reliable way for walking insects to guide nestmates, it is far less convenient for flying animals such as bees. Actually, the use of chemical trails by flying insects is limited to a few species of social stingless bees, which show a range of behaviour; from odour marking of the food alone to full trail-marking between the nest and the food source (Nieh et al 2003). In these melipone species (Lindauer and Kerr 1958, 1960; Michener 1974; Jarau et al 2003, 2004; Schmidt et al, 2006 a, b; Schorkopf et al. 2007), scent marking bees rub their proboscis over the substrate, start laying labial gland secretions and land regularly to deposit marks over twigs and leaves on their way back to the nest. The recruiting bee then triggers the exit of nestmates, which are guided by the scent trail towards the food source. The shorter foraging distances, as well as the larger sizes of stingless bee colonies compared to those of honeybees, have presumably facilitated the use of such chemical trails (Lindauer and Kerr, 1958; Beckers et al, 1989; Jarau et al, 2003, 2004; Schmidt et al, 2006a). Conversely, for honeybees, flying over long distances has set several constraints that impede the use of odour trails. First, chemical marking of the substrate requires frequent landings and take offs, which may become highly costly in time and energy for the bee scout over long distances. In addition, aerial trails emitted by a flying scout would be too labile and subject to wind or air turbulence to be an accurate and reliable orientation cue for recruits over long distances. These flight-related constraints have prevented the building and/or the efficient following of chemical trails by honeybees. By developing their unique mode of communication about food resources through dances, honeybees have freed themselves from flight-related constraints on information transfer. The spatial information encoded within the dance allows recruits to be immediately informed about the way to go near the food (Riley et al, 2005), while the floral odour inside the nest

(Farina et al, 2005; Sherman and Visscher, 2002; Diaz et al, 2007) allows recruits to pinpoint the resource in the final stages of their flight when they approach the flower patch. Instead of being progressively built up through successive trail reinforcements (as in ants), information about the location of flower patches is “summarized” inside the hive by the honeybee dancers. While ant recruits walk along the trail without knowing their final destination, dance followers know the direction and the distance of flower patches before departing from the hive. In the hive, wagging runs along the comb provide an updated and accurate ‘flying map’ to nestmates, who can respond immediately with a direct flight to the specified patch.

2.3. REGULATION AND NEGATIVE FEEDBACKS

The ecological success of social insects depends not only on their ability to recruit nestmates but also to adjust the number of recruits to the available resources. To achieve such regulation of the worker force, positive feedback such as recruitment signals have to be coupled with negative feedbacks. The latter are often by-products of the foraging activity, such as crowding effects, food exhaustion or filling of nest reserves (figure 1A, 1B; Dussutour et al, 2004; de Vries and Biesmeijer 1998, 2002; Schmidt et al, 2006b). As a result, the growth of the population of foragers at a food source can usually be defined by a logistic curve, which increases exponentially until negative feedbacks create a plateau. These negative feedbacks include the limited number of potential recruits within the nest or limited access to the food source (Figure 1C).

In ant populations, food exhaustion or overcrowding is known to suppress or weaken recruitment (Fig. 1A). This adaptive response is based on a simple rule evidenced by Wilson (1962 a,b): a recruited ant having no more access to food goes back to the nest without laying a trail. As the trail is no longer reinforced, the pheromone evaporates and recruitment comes to an end (Wilson, 1962 a, b). Such an “all-or-nothing” response of foragers to food access is explained by a more generic rule of thumb: the “desired volume” rule. A forager having found a food droplet will lay a trail only when it is able to ingest a desired volume of its own that acts as a threshold value (Mailleux et al 2000, 2003a). The use of such a criterion by ants is not restricted to a single source but can be generalised to multiple food sources, such as in the case of aphid honeydew droplets. This behavioural rule is then a powerful and economical means for the society to adjust the number of potential food-carriers to the global quantity of available honeydew (Mailleux et al 2003b). When an aphid colony is overexploited, aphid-tending ants can no longer succeed in ingesting their desired volume, they therefore no longer reinforce the trail and recruitment slows down due to pheromone decay. Such negative feedback allows a constant readjustment of the foraging force to the current productivity of aphid colonies. At any time, information about the food volume still available is conveyed to the society by the number of trail-laying ants –i.e. individuals having reached their desired volume. In some species, a volatile, no-entry pheromone may also aid in trail choice during active foraging by closing off unrewarding paths at the bifurcations of the trail network (Stickland et al, 1999; Robinson et al 2005). The coupling between such negative feedback and amplifying recruitment signals may lead to dynamics that are more complicated than simple sigmoidal ones (fig 1C), such as oscillations in the number of feeding foragers (Verhaeghe and Deneubourg, 1983) or periodic activity patterns (Rissing and Wheeler, 1976; Franks and Fletcher, 1983; Goss and Deneubourg, 1989). In addition, any environmental constraint that alters the dynamics of trail recruitment can contribute to the regulation of foraging without any explicit coding of information by the worker individuals (Dussutour et al, 2006). For instance, if an ant colony is given the choice between two paths at low densities, it will forage over one trail but, in crowded conditions, both branches will be equally followed. Indeed, high rates of collisions between ants leaving the nest and those

returning with food force some of them to take the second pathway. This negative feedback- the collision rate- guarantees that an optimal rate of food return is maintained (Dussutour et al, 2004) and also generates a temporal organization of foragers' traffic (Dussutour et al, 2005b). Negative feedbacks may also occur within the ant nest (Fig. 1A). For example, when faced with different food sources (e.g. proteins vs. sugars), workers will selectively forage the food type that best meets the colony requirements. In this case, we suspect that the propensity of inner nest workers to accept trophallaxis or to respond to recruiting stimuli gives a cue to the recruiter about the actual colony food demand, as well as about the filling of nest reserves (Howard and Tschinkel, 1981; Sorensen et al. 1985; Cassill and Tschinkel 1999a,b; Cassill, 2003). Any difficulty experienced by a recruiter to unload its crop content may then testify from a decreased interest for such a resource and may lead to its progressive neglect by foragers.

Regarding honeybees, the mechanisms that regulate recruitment to flower patches exhibit strong similarities with those of ants (fig 1B). Several negative feedback loops may dampen the recruiting response triggered by dancing foragers. One should notice that, unlike in ants, most of the negative feedbacks discovered so far, take place inside the hive. Indeed, a bee that returns to the nest with a load of nectar has to find a receiver bee before recruiting and going back to the flower patch. The search time experienced by this forager, before being relieved of its cropload, depends on the number of bees that are simultaneously free and is also highly correlated with receiver motivation to accept such a food resource (Seeley and Tovey 1994). Short latencies before being unloaded increase the probability of a forager carrying out a large number of waggle dances. Conversely, long latencies result in foragers queuing up to be unloaded and performing fewer wagging runs or none at all. In some cases, the unloaded bee may start a tremble dance, which fosters additional bees to function as receiver bees (Seeley 1992). Even though tremble dancing may somewhat prolong food retrieval, foraging progressively slows down, as no more receiver workers are available within the hive (Seeley et al. 1996). The decision of a bee scout to recruit nestmates is thus based on a simple cue -the unloading time- which acts as a feedback mechanism to reduce the recruitment effort towards resources that are of decreasing interest for the hive. This decision rule is a reliable way to assess the demand-offer balance for a given resource: it integrates information about the number of empty cells free for food storing in the comb, the food demand of larvae, as well as the number of nestmates available for food processing in the hive. Other feedback loops may also occur outside of the hive and take place at the flower patch itself. Because the patch size is limited, some bees may have to fly around and wait for a place at the source to become free or the bees return empty (de Vries and Biesmeijer 1998, 2002). Chemical cues may be also used by bees to slow down the foraging recruitment, such as the marking of a deteriorated source by a repellent pheromone, avoiding further visits by foragers (Giurfa 1993).

In insect societies, the amplifying effects of recruitment are thus counteracted by negative feedbacks of which the importance increases as food sources become depleted, overcrowded or of lesser interest for the colony. Even though hives and ant nests display a similar logic in the regulation of foraging, the nature of feedback loops involved are quite different. As discussed in the following sections of this review, the different ways foragers are recruited lead, at the collective level, to quite different collective choices and foraging patterns that are non-intuitive and hard to predict.

3. The way you recruit rules the way you make collective choices

In natural conditions, ant colonies or hives may be faced with several food sources and then have to make efficient collective choices between these alternatives. Many parameters are likely to influence such collective choices: food characteristics may differ, competitors and predators may interfere with the colony activity, temperature and other climatic conditions may influence the energetic/time costs associated with foraging. Each colony has therefore to allocate foragers to food patches in a way that ideally maximizes energy input and minimizes foraging costs. Here we will review simple situations that show how the competition between recruitments to several food sources may lead to collective responses that are adaptive for the whole society. We will first refer to laboratory experiments made on ants. Although these experiments may appear somewhat artificial, they help to identify, at the individual level, the simple recruitment rules that underlie the diverse and sometimes unexpected foraging patterns displayed by the ant colonies. Moreover, they allow us to build models and to test their predictions. Such models can be extended and adapted to the recruitment logic of honeybees (Camazine and Sneyd 1991; Seeley et al, 1991; de Vries and Biesmeijer 1998, 2002). They are also convenient tools for comparing the impact of recruitment properties on the collective decisions made by ants or by honeybees and for discussing to which extent emergent patterns are presumably adapted to the foraging ecology of these social insects.

3.1 COLLECTIVE CHOICES AND TRAILS : EXPERIMENTAL EVIDENCE IN ANTS

The choice between identical resources is an unusual situation in natural conditions and seems of poor interest from an ecological point of view. However, binary choice experiments between identical sources can be very useful to highlight how seemingly small differences in the communication process may act upon collective decisions. When two identical sources are available, the most intuitive pattern would be the equipartition of foragers among the two resources. Indeed, an allocation of foragers that is strictly proportional to the availabilities of resources -i.e. an ideal free distribution of foragers between sources (Giraldeau and Caraco, 2000)- seems the best way for one species to maximize its fitness by reducing the costs of competition between conspecifics. However, quite unexpectedly, an equipartition of foragers is scarcely observed in the majority of trail-laying ant species. After a short period of equal exploitation, a bifurcation is observed, meaning that one source is selected and more strongly exploited than the other even though the two food sources are identical (Figures 2A, 3A). This is not the result of any asymmetry of the experimental set up since the side of the chosen source may change over successive tests (Pasteels et al. 1987; Beckers et al, 1990; Sumpter and Beekman, 2003). Similarly, when the colony has the choice between two paths of the same length, most of the ants will end up travelling and sharing only one foraging route (Deneubourg et al, 1990; Beckers et al, 1992b; Dussutour et al, 2004). The process of colony-level choice between equivalent branches or between identical food sources is thought to start by chance with an imbalance in the pheromone amount between the two branches that is large enough to trigger a positive feedback loop. The disproportional numbers of workers choosing and laying pheromone on the more travelled branch means that the ants' stream to one source/path out competes the stream to the other source/path. (Goss et al 1989).

3.2. A MODEL OF FOOD SELECTION INVOLVING CHEMICAL TRAILS

The bifurcation process – i.e. the selection of one food source among several identical ones- can be predicted by a behavioural model of food recruitment that relates the behaviour of recruiting individuals to the foraging choice emerging at the society level (Deneubourg and

Goss, 1989; Beckers et al., 1992a, 1993; Nicolis and Deneubourg, 1999; for a review see e.g. Detrain et al., 1999; Sumpter and Beekman, 2003; Sumpter and Pratt, 2003). This model, built upon empirical findings, describes how the amount of trail pheromone, and hence the traffic of ants over each trail, will change over time. In this model, an ant leaves the nest, chooses a path, reaches one of the two food source, ingests food and promptly returns to the nest laying a trail pheromone. Each ant has to take two decisions: 1°) to leave the nest or not and 2°) to choose one of the trails leading to equidistant food sources of identical quality (i.e. a bridge with two equal branches in a binary choice experiment). For each ant, the probability of leaving the nest increases with the total amount of trail pheromone at the nest entrance. Over time, the increasing rate of nest departure coupled with trail reinforcement by successful foragers contributes to the sigmoidal growth of the recruits' population. Here we will neglect time variations in nest exits since they do not affect the general dynamics of collective choices (Camazine et al, 2001).

An ant having left the nest has to choose one of the two paths: the probability for an ant of choosing one path i depends on a general choice function $A_i/(\sum A_i)$ in which A_i is the attractiveness -i.e. the amount of trail pheromone- of the trail i leading to the source i (Figure 4). We can quantify the ant's decision at the choice point by equation (1) in which the orientation toward one source and/or towards one trail compared to the others depends on the values of the pheromone concentration c_i on each trail i (Deneubourg and Goss, 1989).

$$P_i = \frac{A_i}{\sum_{l=1}^s A_l} = \frac{(k + c_i)^n}{\sum_{l=1}^s (k + c_l)^n} \quad i = 1, 2, \dots, s. \quad (1)$$

$s=2$ in the case of a binary choice between two food sources.

- n determines the steepness –i.e. the level of non-linearity- of the recruitment response. A high value of n means that ants are highly sensitive to changes in the intensity of recruiting signals: even a slightly higher amount of pheromone over one branch will markedly increase the probability of ants to choose this branch
- k corresponds to the intrinsic degree of attraction of an unmarked branch of the bridge. For high k values, high differences in trail concentration between branches are needed to get a non-random choice of one path.

On its return journey from a food source, each ant lays a quantity of pheromone q_i . In the case of identical food sources ($q_1 = \dots = q_s = q$), each ant deposits the same amount of pheromone on its homeward journey and the pheromone concentration over one trail is directly proportional to the flow of foragers (ϕ) over this trail. At each time unit, a quantity $q\phi P_i$ of pheromone is added to the trail i while νc_i is the decay of the trail pheromone amount. The trail is thus assumed to evaporate at a rate proportional to its concentration with ν being the inverse of the mean trail lifetime. The following system of s differential equations describes the rate of change in pheromone concentration on trails.

$$\frac{dC_i}{dt} = q\phi P_i - \nu C_i \quad i = 1, \dots, s \quad (2)$$

Monte-Carlo simulations based on these equations and on parameter values obtained experimentally for *Lasius niger* species give the time evolution of the ants' population over each branch. Initially, both sources are exploited equally but a break suddenly occurs, after which one source becomes more exploited than the other. One food source is selected and exploited by more than 60% of foragers in nearly all cases (in around 90% of the simulations) (Fig. 5A). As for laboratory experiments (Fig.2A), the asymmetrical exploitation of identical food sources arises as one trail becomes slightly stronger than the other, resulting in it being more often followed and further reinforced by trail-laying foragers in a positive feedback cycle. Due to the non-linearity ($n > 1$) of the ant response to the recruitment trail, the selection of one food site arises through the amplification of what are initially slight differences in the relative concentration of trails. However, one can never say which trail will dominate or which source will be chosen since this selection is based on random events.

We can use the model to assess the role of each parameter in the final selection of one food source. This reveals that collective responses can be even more complex and sophisticated. One can find out that an asymmetry of the food exploitation is more marked and more quickly reached when the foragers' flow or the colony size is large, as expected from any phenomena based on amplifying processes (Figs 3A, 5A). Below a certain number of ants or interactions, the exploitation pattern may be symmetrical whereas, above this value, a collective choice is very likely to emerge with most of the foragers being ultimately focused on one or only a subset of available resources (Nicolis and Deneubourg, 1999). Likewise, when the individual trail laying behaviour is more intense, or when the rate of pheromone decay is lower, a random fluctuation in the trail amount over one path is likely to be amplified and to quickly lead towards an unequal exploitation of food sources. To observe these phenomena experimentally, one may vary the "foragers' flow" parameter by comparing colonies of different sizes or one can increase the intensity of the trail laid by the ants (q) by increasing the quality of food sources (e.g. the sugar concentration). However, the influence of pheromone evaporation rate on the ants' collective pattern is more difficult to investigate experimentally since it is determined by a multitude of parameters such as the ground temperature or the perceptive physiology of the ants. In this latter case, the model has a strong heuristic potential by allowing "numerical experiments" to be performed that would be difficult or even impossible to carry out in the laboratory.

3.3. COLLECTIVE CHOICES AND DANCES: A MODEL FOR HONEYBEES

Like ant colonies, the hive has to make a collective decision about which flower patches to exploit and how many foragers should be allocated to available resources. Under natural circumstances, the concurrent availability of several food sources is probably common as plants may undergo synchronized blooming. The model developed for trail-laying ants can be transposed to food recruitment in honeybees (Camazine and Sneyd, 1991; Seeley et al, 1991). The number of dancing bees is analogous to the trail concentration and determines the attractiveness A_i of one foraging site over another. In honeybees, the probability of a recruit going to an advertised site is proportional to the number of waggle runs performed by the bees recruiting for that site (Camazine and Sneyd, 1991; Seeley et al, 1991). In addition, foragers dancing on the comb are able to attract with a vibratory signal dance-followers that are too far to perceive tactile signals (Tautz et al, 2001). Following the observations made by Judd (1995), although the average number of bees simultaneously orienting to a dancer can be as high as five or six, at most only one or two bees are simultaneously receiving the dance information. Camazine and Sneyd (1991) have implemented this observation in their model in such a way that at most one bee at a time can follow the dance and extract information from

it. Hence, for honey bees, the attractiveness of a food source A_i or in other words the number of bees recruited towards food source i is directly proportional to $(D_i d_i)^n$, where D_i is the number of bees in a dancing state. However, since these bees may stop for a while between successive dances, D_i is multiplied by the relative amount of time (d_i) during which recruiting bees actually dance. When the two food sources are of identical quality, d_1 is equal to d_2 .

The probability for one honeybee to forage on flower patch i is then given by equation 3:

$$P_i = \frac{A_i}{\sum_{l=1}^s A_l} = \frac{(k + d_i D_i)^n}{\sum_{l=1}^s (k + d_l D_l)^n} \quad i = 1, 2; \dots s. \quad (3)$$

The parameter n accounts for the non-linearity of the response and reflects the sensitivity of recruits to the relative occurrence of a dance i associated to food source i . A value of $n > 1$ would mean that a recruit would be more likely to forage at a given flower patch when there are several dancers coding for this source. However, in the case of honeybees, as predicted by Camazine and Sneyd (1991) and demonstrated experimentally by Seeley *et al* (1991), bees do not sample dancers in an effort to compare the relative profitability of food sources. In other words, a bee recruit is influenced only by a single dancing recruiter at any one moment. Since there is no synergetic effect of concurrent dances, the n value in equation (3) should be equal to 1. In other words, the attractiveness A_i of one foraging site i over the others should be directly proportional to the occurrence of dances $D_i d_i$. Hence, even though the number of dances is analogous to the trail concentration, the honeybee recruitment differs from that of ants in its level of non-linearity ($n=2$ for trail laying ants, $n= 1$ for dancing bees). This difference has only a slight impact on the probability of one individual choosing a path or a food source (Fig.4) but it is responsible for the very different properties of collective patterns displayed by honeybees and by ants. Indeed, the model predicts that the hive will select one source only occasionally and that the most frequent response of honeybee foragers will be their even distribution between identical food sources (figs 3B, 5B). Furthermore, unlike the ants, which more frequently select one source when the number of foragers increases (Fig. 5A), the honeybees show an even distribution of foragers whatever the hive size (Fig. 5B). This prediction finds some support in the fact that small hives foraged at approximately the same number of patches as large colonies (Beekman *et al* 2004). As the hive size increases, the model also predicts that the foragers will be even more equally allocated among food sites and that the presence rate of bees at one of the two food sources will shift from a flat to a monomodal distribution with a peak at 50% (Fig. 5B). Hence, an increase in colony size has unexpected opposite effects for hives than for ant nests: larger forager flows should enhance the collective selection of one food source by ants whereas it should draw the honeybees towards a more equal exploitation of resources (Figs 3A, 3B). In the field, no symmetry breaking between identical sources has yet been reported for honeybees and further experimental evidence is still needed to confirm the model's predictions of an even distribution of bee foragers between flower patches. Nevertheless, one should be aware that the selection of one food source by honeybees may occur due to some "hidden" amplifying behavioural traits associated with recruitment. For instance, once a recruiter enters the hive, it stimulates forager mates to return to a known feeding place not only by dances but also by nectar transfers which reactivate experienced foragers. This may act as a snowball effect since

those experienced bees follow a significantly lower number of waggle-runs and are more easily reactivated to perform nectar collection (Gil and Farina 2002). Another source of non-linearity could be the memorization of food location as well as the learning of flying routes that facilitate the orientation of bees and shorten their foraging journeys. These phenomena are translated, from a mathematical point of view, by an increase of the parameter n value and may lead to symmetry breakings as predicted by de Vries and Biesmeijer (2002).

In insect societies, collective decisions arise as a result of the competition between different sources of information that are amplified by recruitment signals. Through its trail-laying, an ant colony with a large forager population will select and focus its effort on one resource even if all available sources are of identical quality. Alternatively, an ant colony may exploit all sources equally if the colony itself is small or if the number of sources is very large (Nicolis and Deneubourg, 1999). Such switching in the foraging pattern, which is not predicted by the honeybee model, matches the features of food resources exploited by ants. Unlike bees that wander among short-lived flower patches, several mass recruiting ant species feed on honeydew and forage on rather stable food sources such as aphid colonies. By focusing the foraging force on a limited number of food sites, ant colonies can protect and monopolize these resources through cooperative defence against competitors or predators. Such an “owner strategy” can be efficiently implemented only by large sized ant nests since the costly loss of workers may be fatal to small incipient nests (Franks and Partridge 1993, see also Mailleux et al. 2003a).

By contrast, a hive presented with an array of identical sources will scarcely focus its activity on a single flower patch. It seems more advantageous for a honeybee colony to distribute thousands of workers among multiple flower patches rather than to be crowded at a single food source or to monopolize a flower patch of highly fluctuating profitability.

Hence, the different ways through which ants and honeybees allocate foragers between identical resources are not primarily due to differences in the sensory or physiological capacities of the individuals. Instead, they appear as by-products of the properties of their recruiting signals (chemical trail versus dances) that shape decision-making operating at the collective level.

4. Choosing the best food resource.

The ant colony as well as the hive provides striking examples on how rather simple individual behaviour and decision rules can lead to different but equally efficient patterns of food exploitation. The previous section has considered the case study in which identical sources were simultaneously offered to a colony. However, the availability of food resources most often vary in space and time, while their profitability differs according to several parameters such as food quality, distance, safety and so on. Since individuals have only a local and partial knowledge of their environment, one may wonder how insect societies adjust their foraging effort in order to preferentially exploit the most profitable resources.

In both honeybees and ants, foragers are adequately allocated to the best food sites without any of the participants having a broad knowledge of all food opportunities. An ant or a honeybee scout does not compare nor keep track of information from multiple foraging sites: its knowledge of the array of food sources is limited to its particular food site of which it makes its own assessment by using functional cues (honeybees: Seeley et al 1991, Seeley 1995, Dyer 2002, Stingless bees: Biesmeijer and Ermers 1999, Schmidt et al 2006a; ants: Hölldobler and Wilson 1990, Detrain et al 1999, Detrain and Deneubourg 2002). Based on this individual estimate of food profitability, the scout will decide how strongly to advertise

the source by either laying a trail or by dancing in the hive. The best food source is then selected by the whole colony - not by centralized decision-making- but simply by competition between recruitment signals differing in their intensity and/or duration. While a tuning of recruitment allows both ants and honeybees to make adaptive choices, these insect societies are expected to somewhat differ in the robustness of their collective decisions. Indeed, while the removal of a dancing bee would be like losing part of the information about food opportunities, the removal of one ant would hardly affect recruitment since foragers “interact” mainly with the trail itself and thus are kept informed about food quality and food location. The strength of amplification processes – i.e. the recruitment rates towards different food sources- depend on two main categories of parameters (Detrain and Deneubourg, 2002, 2006). The first category of parameters consists of any modulation of the recruiting signals that may enhance the mobilisation of inactive nestmates towards a food source. For example, an individual scout bee may lengthen the dance duration or an ant may lay a higher amount of trail in relation to its own estimate of food profitability. The second set of factors involves various environmental features 1°) that may influence the duration of a foraging cycle such as the impact of temperature on walking/flying speed of foragers or 2°) that may alter the trail lifetime such as the absorbency of the substrate (Detrain and Deneubourg 2002; Detrain et al. 2001; Jeanson et al, 2003). Likewise, a longer path toward a feeding site (Goss et al, 1989) or a longer food distance from the nest (Detrain et al, 1999) may reduce the rate of trail reinforcement and lead to a remote food source losing out in its competition with other resources. In these latter cases, one food source or one path can be selected without any modulation of the recruiting signal by the individuals. Here, we shall consider only the first set of factors that act upon recruitment dynamics by reviewing how an ant or a honeybee actually fine tunes its communication in order to select the best food sources.

4.1. FOOD SELECTION AND TUNING OF TRAIL PHEROMONE BY ANTS

In the case of trail-laying ants, if a rich source (1 M sucrose solution) is discovered at the same time as a poor one (0.1 M sucrose solution) , the food source with the highest sugar content is selected and exploited by most of the foragers (fig. 6A). There is no evidence of any qualitative change in the chemical content of recruitment trails laid by ant scouts depending on food quality. Information about food quality is “coded” only through quantitative changes in the trail intensity: more frequent trail spots will be laid by recruiting ants to more concentrated sugary liquid sources (see e.g. Hantgartner 1969, Wilson and Hölldobler, 1990; Detrain et al, 1999). Experimental data show that this trail modulation as a function of food quality is rather weak. For instance, in *Lasius niger*, the ratio between the average number of trail marks laid towards a 1 M versus a 0.1 M sugar solution is of 1.5 only (Beckers 1992a,1993). Then, as predicted by equation 1, at the trail bifurcation point, the likelihood for one individual to choose the more concentrated trail is only slightly higher than towards the less marked trail path (3-4 % higher for the first steps of recruitment). The slight impact of differences in signal intensities on the choice of ant individuals (Figure 4) contrasts with the clear-cut collective choices that ultimately emerge at the colony level (Figure 6A). Indeed, based on numerical simulations, there is always a higher percentage of foragers that orient themselves towards the sweetest source, this rich food source drawing more than 80% of ants in nearly all cases. Hence, due to the non-linearity of the response to chemical trails, even a slight modulation of the recruiting signal drives the whole colony to a nearly unanimous choice of the most profitable food source.

Beside food quality, foragers can also convey information about food size. The decision of each scout to lay a trail is ruled by simple criteria such as the ability to ingest a wanted volume of liquid food (Mailleux et al, 2000, 2003b). The prey resistance to traction is another

criterion used by foragers to estimate prey size: for small preys, foragers lay only a weak trail whereas, for a prey item too large to be individually retrieved, ants dash back to the nest laying a more continuous chemical trail and trigger an intense food recruitment (Detrain and Deneubourg, 1997; de Biseau and Pasteels, 1994). Such decision criteria are highly functional as they incidentally take into account multiple information such as the food size, the food weight or the current number of ants cooperating in food retrieval (Detrain et al 1999; Detrain and Deneubourg, 2002). They act as individual thresholds above which a scout decides to recruit nestmates so that, at the colony level, a higher percentage of trail-laying foragers will occur towards large food sources.

Hence, due to the autocatalytic nature of chemical recruiting signals, ants have a high potential to draw most of the foraging force towards the most profitable food source (Beckers et al 1990, 1993, Sumpter and Beekman 2003, Portha et al. 2004). Even slight changes in the trail-laying behaviour of a few foragers can boost the reinforcement of one foraging path by the following ants and can ultimately lead to the exploitation of the most profitable food by the whole colony.

4.2. FOOD SELECTION AND TUNING OF RECRUITMENT DANCES BY HONEYBEES

As for trail-laying ants, the recruitment activity within the hive is adjusted to both increasing and decreasing food profitability: honeybees will allocate more recruits to resources that are of higher pay-off for the colony. If food profitability is gauged as low by one forager, it will abandon the resource, whereas if its estimate is high, the forager may decide to recruit nestmates and to tune the intensity of recruiting signals according to food profitability (see e.g. von Frisch 1967; Seeley and Towne 1992; Seeley 1994, 1995; Seeley et al 2000; De Marco and Farina 2001, Afik et al 2008). Mainly quantitative instead of qualitative changes in the recruitment signals occur. Indeed, the strength of dances inside the hive intensifies with the profitability of the flower patch. The number of waggle dances (D_i) as well as their relative duration (d_i) can then be viewed as indicators of the overall value of nectar sources; such as the distance of the flower patch or the sweetness of nectar. A higher occurrence of dances coding for a rich resource (D_i d_i) slightly increases the likelihood for one bee to be recruited towards this source (Fig. 4). This tuning of dances results in a cascade of positive feedback at the colony level so that, at the stationary state, more than 60% of foragers' flow will be focused on the sweetest flower patch in around 80% of cases (Fig 6B). For the remaining cases, the collective choice of the most profitable food source is however less clear-cut than for the ants, since 20 to 40% of the honeybees go on exploiting the poorer source. These predictions have been supported by experiments showing that the hive is actually able to focus its foraging effort on the food source with the highest sugar concentration –i.e. with the highest energetic reward (von Frisch 1967; Seeley 1995; Dyer 2002).

4.3 REDIRECTING COLLECTIVE CHOICE IN A CHANGING ENVIRONMENT

Ants and honeybees share the same potential to select the best food source when several resources are discovered simultaneously (Fig.6). However, hives and ant nests differ greatly in their ability to redirect their choice depending on the temporal sequence of food discoveries.

In the case of ants, if a rich source (1M sugar solution) is discovered *after* recruitment is well underway to a first discovered but poorer source (0.1 M), then the poor source will remain the most exploited while the rich one will be neglected (Figs 2B, 7). Theoretical simulations predict that the poor source will keep on attracting the majority of foragers in all cases (Fig. 8A). The difficulty of ant colonies to redirect their foraging activity towards more profitable sources has been experimentally confirmed in several mass-recruiting species (Beckers et al, 1990; Traniello and Robson 1995). Like the ants, scent-marking stingless bees may be “trapped” in the exploitation of the firstly discovered food source (Schmidt et al, 2006a). When stingless bees experience an increase of sugar concentration over time, the newcomers at the richer source never outnumber the number of bees that have already exploited the poor source and reinforced the scent trail (Biesmeier and Ermers, 1999). The difficulty of both ants and stingless bees to redirect foraging towards more profitable food sources could be due to the chemical nature of their communication. Indeed, chemical recruiting signals elicit responses which are strongly non-linear and highly sensitive to slight differences in signal intensities. The new trail to the richer source will never succeed in overcoming the ongoing recruitment to the first discovered food source despite its lower profitability. Likewise, the selection rate of a food source will correlate with the number of workers already exploiting this food and this is likely to increasingly reinforce the scent trail (Pasteels et al, 1987; Goss et al, 1989; Sumpter and Beekman 2003; Sumpter and Pratt 2003).

Conversely, in the case of honeybees, the hive is expected to be able to select the most profitable nectar source, even if poorer food sources have been discovered previously. If among two nectar sources, the sugar concentration of one is suddenly increased, the number of foragers exploiting the other source decreases, as experimentally shown by Seeley et al (1991). As predicted by theoretical simulations, the delayed introduction of a sweeter source induces a reorientation of the honeybee foraging at the expense of the firstly discovered source (Figs 7, 8B). Over time, the sweetest food source will attract more foragers, will reach the same level of exploitation as the first food source and ultimately will become preferentially foraged by honeybees. In the majority of cases, 60% to 80% of bee foragers will end up redirecting and focusing their activity towards the rich food source (Fig.8B). The high flexibility of honeybee foraging patterns is due to the proportional relation linking the occurrence/duration of dances to the number of recruited foragers. Provided inactive workers are still available within the hive and ready to engage themselves into foraging, they can be recruited towards a richer flower patch by dancers coding for this new target. The reorientation towards more profitable resources may be facilitated by the phenomenon of cross-inhibition between forager groups (described by Seeley 1995). Indeed, upon entering the hive, bees loaded with nectar of lesser value experience longer search times for nectar receivers, which decrease the rate of dances coding for this poor source.

Being flexible and able to easily shift to a more rewarding food patch provides obvious benefits to the insect society in terms of optimal exploitation of environmental resources. One may question why ants differ from bees in displaying such poor flexibility in their foraging patterns. The answer depends in part upon whether there is a selective advantage in being aggregated to concentrate the colony's efforts on a single site or whether it is better to distribute colony work force more widely. While the amount of flower nectar collected by the hive results from the simple summation of foraging journeys by crop-loaded bees, the food amount retrieved to the ant nest is more variable. Indeed, it closely depends on the ability of workers to cooperate in the killing of prey or to collectively retrieve large food items. Besides, while cooperative defence in bees is restrained to the hive surroundings (Guzmannova and Page 1994, Hunt et al, 2003; Millor et al, 1999), ants benefit from

cooperative defence of food sites and their aggressiveness toward aliens increases with the number of surrounding nestmates (see e.g. Sakata and Katayama, 2001; Pontin, 1961; Levings and Traniello, 1981; Czechowski 1984; Lumsden and Hölldobler, 1983). The concentration of foraging effort on a few patches gives an edge to the ant colony when it has to face competitors, while limiting the defensive investment of food sources with the highest rates of return. Moreover, within a large group of cooperating ant workers, specialized castes and task partitioning become possible, which may contribute to increasing the global foraging efficiency (Detrain and Pasteels, 1991; Ratnieks and Anderson, 1999; Anderson et al, 2002). As regards honeybees, due to the specificities of dance recruitment, scouts having discovered more profitable flower patches can easily redirect the hive activity towards these new resources. The flexibility of the dance recruitment, coupled to an intense exploration, allows the hive to maintain a long-term foraging success even when flowering patches are ephemeral and variable in richness. Dance-language recruitment is presumably well-adapted to the “boom or bust” economy experienced by the hive (Seeley and Visscher, 1985; Sherman and Visscher 2002).

All these examples have questioned whether and how insect societies make collective decisions in order to exploit the most profitable food sites. There are striking similarities in the mechanisms allowing ants and honeybees to reach such a collective decision: no individual visits all food sources, none compares them nor decides which one is the best. Instead, accurate collective decisions arise from the competition between positive feedback loops and from the tuning –even if slight- of recruiting signals towards the various food alternatives. The different pools of foragers “compete” to recruit more of their comrades towards each food location. However, the amplifying potential of recruitment strongly differs between ants and honeybees with a higher level of non-linearity associated to trail pheromone signals than to dances. Such a difference has a deep impact on the properties of patterns emerging at the collective level. The high non-linearity of chemical trails will make the occurrence of bifurcation more likely – i.e. collective choice of one food source-when identical food sources are offered simultaneously. On the other hand, the non-linearity of the ant response to chemical recruitment will impede the reallocation of foragers when food profitability changes.

5. Randomness and foraging: adaptive tuning of error in ants and honeybees.

In the previous chapters, the recruitment process was described in an idealized way so that every recruited worker succeeds in reaching the food target. However, for a long time, biologists have been puzzled by the following paradox: impressive structures and consensus emerge at the society level, while individuals show a random, highly variable and – in some cases- not very efficient behaviour (see e.g. Grassé stimergy theory (1959) about the building behaviour of termites). The duality between the stochasticity of individual behaviour and the determinism of the colony response is not peculiar to insect societies, but occurs in other biological and non-biological systems (Nicolis and Prigogine, 1977). To solve this paradox, many researchers have argued that social insect behaviour is less erratic than it appears or have considered randomness as an unavoidable side effect of animal behaviour. Insect societies are expected to afford more easily such a variance because of the large number of interacting workers (Oster and Wilson, 1978). If one ant fails, another will succeed: some inefficiency due to randomness in individual behaviour is compensated by a reliability of the whole system that will ultimately reach the goal. However, stochastic events should not be

reduced to side-effects since they may have more creative and adaptive consequences for the fitness of one species (Deneubourg et al., 1983). At first sight, the most accurate system of communication may seem the best one. This is certainly the case when only one food source is present and located at the same place for a while. Natural environments, however, are more complex, with several sources that may fluctuate or be simultaneously available to the ants. The “lost” recruits that wander around the foraged sites may then discover new food sources of higher profitability. Hence, when multiple food sites are available, there is an optimal error level which minimizes the time needed for discovering food sources and which maximizes foraging efficiency.

One may question how an insect society finds the optimal strategy between a high accuracy of communication allowing immediate food exploitation and a low accuracy allowing new food discoveries. In ants, randomness is intimately related to the ability of foragers to orient and to follow a chemical trail. Recruits that leave the nest may lose the trail and never reach the food source. Hangartner (1967, 1969) showed that orientation along a trail is mainly due to osmotropotaxis, meaning that the ant perceives different concentrations in trail pheromone between its left and right antennae. For a given concentration in trail pheromone, the number of ants that are still present on the trail decreases exponentially as a function of the length of trail already followed (Pasteels et al., 1986; Detrain et al 1988; Calenbuhr and Deneubourg 1992, Calenbuhr et al 1992). Besides, the mean length of trail followed by ants increases with trail concentration and the ants’ orientation may become impaired above a certain trail amount. Since the amount of trail pheromone determines the width of its active space, it determines the probability of foragers to stay within the pheromonal tunnel during their sinuous walk and to reach the food source. Hence, an ant colony can easily modulate the accuracy of recruitment, by varying the quantity of trail pheromone deposited. If the food source is of high quality, a strong trail and its large active space will make its loss less likely by foragers and will guide nearly all recruits to the feeding site. If the food source is of poor quality, a weak trail may result into more frequent exits from the active space, may lead to a more diffuse spatial distribution of workers and may promote an extensive search for new food sources over the foraging area (Deneubourg et al. 1983; Edelstein-Keshet et al 1995). Similarly, at the beginning of recruitment, when the trail amount is still weak, the fraction of ants losing the trail is high and new food sources are likely to be discovered. The error level decreases as recruitment proceeds due to trail reinforcement by new recruits. The coupling of randomness in trail following behaviour with a competition between recruitment trails appears as a powerful strategy for optimizing foraging success.

An adaptive tuning of error has also been suggested to interpret variations in the accuracy of honeybee dances (Towne and Gould, 1988). Indeed, information about food locations differs in its level of accuracy as a function of the distance from the nest. At short distances (a few decametres), the dance is circular and contains no directional information. When food sources are remote, i.e. hundreds of meters from the hive, a bee recruiter is potentially able to code spatial information with a high level of accuracy through the direction of waggle runs. However, one curious feature of bee dancers is that their consecutive waggle runs may be produced with some directional scatter. Indeed, a bee dancing for a less remote food source will perform relatively less precise waggle runs so that recruits will be distributed across several flower patches instead of being focused where the communicating bee has been foraging (Weidenmuller and Seeley 1999) The high energetic costs associated with flight may have favoured a higher accuracy of communication about more remote food location. It is, however, suggested that imprecision in dance communication is caused primarily by physical constraints such as the ability of dancers to turn around quickly enough when the advertised site is nearby (Beekman et al, 2005; see also Tanner and Visscher 2006). The accuracy of directional information to food sources also changes according to the size of the

resource. When the target of recruitment is a large flower patch, the dances show a lower directional accuracy and a higher angular divergence of consecutive waggle runs than in dances coding for a more definite spot in space such as a nestbox. This tuning of the dances' information content, which spreads recruits over a certain area, can be viewed as an adaptation to the typical spatial configuration of the recruitment targets (Weidenmuller and Seeley 1999).

The modulation of the amount of trail pheromone laid by ants, as well as the fine tuning of the angular divergences of bee dances, can be viewed as both striking adaptations and as trade-offs between an efficient exploitation of food and new food discoveries around the nest.

6. Spatial patterns

6.1 BEE LINES AND TRAIL NETWORKS

In both ants and honeybees, the spatial distribution of foraging routes follows that of food resources: routes leading to highly rewarding food patches will be preferentially foraged while routes leading to poor or exhausted resources will be neglected. There are however several major differences in the spatial foraging patterns displayed by ant colonies or hives. As a whole, the pattern of foraging routes displayed by the hive appears as a juxtaposition of straightaways (beelines) between the nest and the food sources (fig 9B). These beelines effectively translate information encoded in the waggle dance. Even though some local deviations may occur due to the imprecision of the communication or to physical obstacles, newly recruited bees fly directly from the hive to the vicinity of a food source. Then, in the final stages of their flight, recruits proceed to search for the exact location of the flowers, their flight may become sinuous and their spatial information may be completed by odour and visual cues that help in the localization of exploited flowers (Tautz and Sandeman 2003; Riley et al, 2005; Arenas et al, 2007). This searching behaviour close to the flower patch accounts for the fact that the arrival of recruits at the source is often later than would be expected for a direct flight between the hive and the food source.

A major feature of honeybee lines is that the trajectory of each forager is purely individual. Before leaving the hive, each recruit has received, through the recruitment dance, the whole information needed to locate a flower patch. Each recruit exiting the hive then takes a flying route of its own. Ideally, this route should connect the hive entrance to the food patch in the straightest way possible in order to minimize the energy expenditure associated with flight. Hence, the spatial foraging pattern of the hive can be seen as a bundle of hundreds of bee lines that radiate out of the hive entrance and that are more concentrated in the angular zones leading to exploited flower patches. The spatial distribution of beelines is thus expected to be highly flexible: it should reflect changes in the direction coded in waggle runs and should closely follow changes in the spatial distribution of flower patches (Figure 9B).

In ants, the spatial configuration of the foraging trails is quite different from that of beelines. Instead of being the mere juxtaposition of individual routes, trails often organize themselves into a network. Depending on the species, ants try to minimize the travelling time (Dussutour et al, 2006) and/or the energy costs (Denny et al, 2001) so that the final pattern of the trail network is deeply influenced by a set of spatial factors as well as by the history of the foraging activity (e.g. food discoveries, level of area marking,...) (Traniello et al, 1991; Fourcassié et al, 2003). For example, if a new food source becomes available close to a source that is already foraged by ants, scouts will be more likely to discover it, they will lay a trail and, through path integration, they will follow a rather straight trajectory towards the nest. On their homeward journey, scouts may cross a well-established trail leading to another exploited

food patch and may then decide to join the main stream of workers going back to the nest. Over time, successive visits of the foragers to the new food source will lead to the emergence of a new lateral trail branched onto the main foraging trail (Hölldobler and Wilson, 1970, 1990; Hölldobler and Möglich, 1980; Quinet and Pasteels, 1991; Watmough and Edelstein Keshet, 1995; Quinet et al, 1997; Detrain et al. 1990) (Figure 9A). In the simple case of two close food sources, two straight independent trails leading to each food source scarcely coexist and most often merge into a common trail. As a result, the foraging activity becomes more concentrated on fewer paths as one travels from the food sites towards the nest entrance. The geometry of trail bifurcations within this network provides polarity information to foragers joining a trail who can adaptively reorientate themselves if they initially walk in the wrong direction (Jackson et al, 2004). At the individual level, a tree-shaped trail network may lengthen the distance travelled by one forager since its trajectory somewhat deviates from a straight line directly connecting the food source to the nest. However, at the society level, the building of a tree-shaped trail network certainly decreases hugely the total trail length in comparison to a “star graphs” network with one direct trail going to each food source. Several benefits are associated with tree topologies: by reducing total network length, they facilitate the maintenance of foraging pathways (i.e. by actively cleaning or building construction around them; Howard 2001) as well as their defence against competitors or predators. The diversity of trail networks reported for ant species is a by-product of the interactions between trail-laying ants and any environmental parameters that may impede the access to food sources or that may influence the probability of connecting two trails, such as the spatio-temporal availability of food resources (Deneubourg et al, 1989; Franks et al, 1991; Lopez et al., 1994). For instance, two trails are more likely to merge into a common trunk trail when the two sources are persistent, close to each other and/or remote from the nest. The higher sensitivity of the trail network to group-size effects is another major difference between ants and honeybees. In honeybees, an increase in the foraging effort will simply lead to an increase in the number of concurrent beelines. Conversely, in trail-laying ants, an increase in the number of workers may lead to qualitative changes in the spatial patterns of foraging routes. For instance, there is a shift from a diffuse foraging pattern to a tree-like trail network as the number of interacting foragers increases. (Detrain et al, 1991; Nicolis and Deneubourg 1999). Such dependence on colony size is the typical signature of a self-organized process of pattern formation.

6.2. SELECTION OF THE SHORTEST PATH

For walking ants that encounter large obstacles (stones, crevices, etc) compared to their tiny size, recruitment trails not only prevent them from losing their way but also allow them to select the shortest route towards the feeding site. While the choice of one path is random over a bridge with two equal branches, most of the foragers follow the shortest path of a bridge with branches of unequal length (Goss et al, 1989; Vittori et al, 2006). This adaptive selection of the shortest path occurs even though individual ants have no knowledge of relative path lengths as well as no memory of the routes they have previously taken. For ants that lay a trail in both directions (from the nest to the food source and reciprocally), this selection is simply due to the shorter trip duration and hence to the increased rate of trail reinforcement over the short path. For some ant species that lay a trail only during their homeward trip and that move quickly (Beckers et al, 1992b), the selection of the short path is also due to the U-turns made by workers that double back on a trail, return to the common branch point and then follow the second branch. Since when an ant is back-tracking after its U-turn it does not lay down trail pheromone, the higher frequency of U-turns along the long path ultimately leads to a lower amount of pheromone over the long branch. The adaptive selection of the shortest path thus

arises “automatically” at the colony level from differences in the recruitment dynamics depending on branch length. This results from the synergistic effect of a shorter duration of foraging trips and of a lower frequency of U-turns on the rate of trail reinforcement. It is difficult to find the counterpart for the honeybees. Firstly, the spatial information provided by the orientation of waggle dances is, by essence, the shortest flying route connecting the hive to the flower patch, since it results from a quite efficient path integration of the foraging journey by the recruiter (Collet and Collet, 2004, 2006; Collett et al, 2006). Nevertheless, in the presence of obstacles, short-cuts and shorter-lasting foraging journeys may be achieved on an individual basis by honeybee foragers that are more experienced about how to reach the flower patch.

7. Conclusions

7.1. WHAT ABOUT OTHER GROUP-LIVING ARTHROPODS?

Collective decision making can be as accurate and effective as decisions made by solitary animals - even those that are famous for their well-developed capacities for information processing such as vertebrates (Krebs and Davies, 1984). The strength of collective decision making is that adaptive choices may arise automatically without the need for any leaders, which would have a synoptic view of all environmental opportunities. Consensus decisions can be reached even when the individuals do not know how the information they possess compares with that of conspecifics. Many examples of collective decision-making have been reported in the literature not only for ants or honeybees (Hölldobler and Wilson, 1990; Seeley, 1995; Theraulaz and Spitz, 1997; Bonabeau *et al*, 1999; Camazine *et al*, 2001) but also for other group-living organisms including bacteria, which may achieve quorum sensing and behave collectively (Miller and Bassler, 2001; Ben Jacob et al, 2004). Likewise, complex patterns have been reported in fungal networks (Bebber *et al*, 2007) and slime-moulds (Shirakawa and Gunji, 2007). In this respect, group-living arthropods display amazing collective patterns and coordinate their efforts efficiently even though their social organization is less complex than that of social insects (Costa, 2006; Fitzgerald, 1995; Fitzgerald and Costa, 1999; Deneubourg et al, 2002). The choice of a common shelter or the cooperative exploitation of one resource by several individuals is then guided not only by cues related to the quality of these resources but also by recruiting and/or arresting signals emitted by conspecifics. Hundred of examples of aggregative behaviour which rely on pheromones have been reported for species living in very different ecological situations (e.g. *Triatoma* kissing bugs (Lorenzo and Lazzari 1996); cockroaches (Said et al, 2005; Miller and Koehler, 2000); *Drosophila* fruit flies (Takahashi 2006); lobsters (Horner et al, 2006; for a review see Wertheim et al, 2005)). The active recruitment of conspecifics toward a common place can also be mechanically-mediated as has been shown for the gregarious larvae of herbivorous insects such as treehoppers, which use vibrations to orient themselves and to eventually move from low- to high-quality sites (Cocroft, 2005).

Although collective patterns of aggregation are widely reported in arthropods, there are surprisingly few experiments investigating how collective choices emerge among group members and how they are influenced by the ways conspecifics interact with each others. The use of silk impregnated with pheromone is one of the most studied long-range interactions in gregarious arthropods. Social caterpillars (Fitzgerald, 1995) and mites (Yano, 2008) may lay silk threads that attract conspecifics in a manner similar to ant trails. The tuning of the amount of pheromone released over the silk enables caterpillars to collectively select richer leaf

patches as well as to reach a consensus about a common resting site at the end of a day's activity (Fitzgerald and Peterson 1988, Fitzgerald, 1995; Ruf *et al.*, 2001). Moreover, like ants or stingless bees, forest tent caterpillars, *Malacosoma disstria*, show a lack of flexibility in their collective decision making. Indeed, when faced with a nutritionally balanced and a less profitable, unbalanced source placed at opposite ends of a bridge, the colony of caterpillars as a whole randomly discovers one of the two resources, goes on following the recruitment silk threads and becomes trapped for at least one day in the exploitation of the first discovered resource - independently of its quality. (Dussutour *et al*, 2007).

Group-living spiders provide another striking example of collective decision-making. The strong correlation between the amount of exploratory webs and the localization of the spiders' population suggests that conspecifics' draglines are used as a recruitment means for colony formation. Actually, groups of *Anelosimus studiosus* spiders can follow individuals sequentially released at a common spot only when draglines are left in place on the substrate (Furey 1998). The silk network orients the movement of individual spiders: it acts as a recruiting structure and, due to the pattern of draglines' attachment, it may lead in a binary choice setup to the collective selection of only one aggregation site (Saffre *et al*, 1999, Jeanson *et al*, 2004b).

The emergence of collective patterns does not necessarily imply the emission of recruiting signals but may also be triggered by short-range physical contact. For instance, the aggregation of cockroaches under a common shelter is due to their perception of contacts with conspecifics, in which the individual probability of moving decreases with the number of neighbours resting under a shelter (Amé *et al*, 2004, 2006; Jeanson *et al*, 2005; Halloy *et al*, 2007). Other spatial patterns (other than binary choices) may be seen as by-products of collective choices in which the group members choose between two or more mutually exclusive actions. For instance, in groups of locusts of increasing density, a rapid transition occurs from a disordered movement of individuals within the group to a highly aligned collective motion. This transition may be explained by mechanisms and decision rules similar to those described previously (Buhl *et al*, 2006).

7.2. NON-LINEARITY OF INFORMATION FLOW: THE KEY-STONE OF COLLECTIVE DECISION-MAKING

The ways individuals interact with each other and give birth to collective responses vary depending on the concerned species and may involve chemical signals, physical contacts or both types of stimuli (Camazine and Sneyd, 1991; Seeley *et al* 1991; Visscher and Camazine, 1999a,b; Visscher, 2007). Insect societies such as the hive or the ant nest are real life models that offer a unique opportunity to investigate 1°) how collective structures emerge in complex biological systems made up of numerous individuals and 2°) how collective behaviour may be shaped by the properties of one species' form of communication. Due to the specificities of chemical trails versus dances, ant nests and hives differ in the amplifying potential of their recruiting process. Likewise, in group-living arthropods, a difference in the level of non-linearity of one individual's response to recruiting stimuli may have major consequences on the collective patterns displayed by the whole group. Usually, chemical signals are characterized by a pheromone decay rate and a receiver response curve that are both highly non-linear. Such a non-linearity of information flow - as found in ants' chemical trails- favours the focusing of the group at one or a few sites but restrains the flexibility of the group to shift to more profitable resources. Hence, a non-linearity of receivers' response is expected to be found in species that benefit from cooperation in the exploitation or in the defence of resources, as well as in species exploiting resources which are rather stable in time

and space. Conversely, tactile signals such as the honeybee dances are expected to show less non-linear properties than chemical ones since the rates of contacts should be proportional to the number of interacting individuals. The individual response to contact rates may nevertheless be non-linear as found in the case of nest-moving recruitment (Pratt et al, 2002; Seeley and Visscher, 2003; Pratt and Sumpter, 2006; Jeanson et al, 2004a) or in the case of aggregation patterns in ants (Gordon et al, 1993; Nicolis et al, 2005; Depickère et al, 2004;) and cockroaches (Amé et al, 2004, 2006; Jeanson et al, 2005). Whatever the type of between-nestmate interactions, a low level of non-linearity favours an even distribution of individuals among identical resources. It also allows a closer fitting between the number of animals allocated to one resource and its relative profitability (as predicted by an ideal free distribution). Finally, it facilitates a higher flexibility of the group decisions when environmental resources are changing. This should benefit to species that 1° exploit resources of which the availability is highly variable in time and space, 2° that do not need to monopolize resources against competitors and 3° that do not need to cooperatively defend food sites because individuals are well protected against predators (e.g. by defensive secretions or effective weapons such as for honeybees).

The evolution of communication in gregarious insects has been presumably steered by whether, for a particular colony sizes and habitat, a recruitment increases food collection, favours the monopolization of resources or prevents attacks by predators. Then, the payoff of one type of recruitment should vary depending on the foraging ecology of the species. In particular, recruitment mechanisms with a higher level of non-linearity seem well-adapted to species that benefit from cooperation and collective selection of a subset of resources at the expense of a lower flexibility to changing environmental conditions. In this respect, being able to shift between signals differing in their level of non-linearity may be advantageous for one species. For example, within the same recruitment process, some ant species may change their way to communicate with each other: scouts that have discovered a new source first perform group recruitment to activate nestmates and thereafter shift towards mass recruitment by chemical trails. Group recruitment (like tandem recruitment or honeybee dances) is characterized by a low level of non-linearity: the number of recruited foragers is grossly proportional to the number of successful scouts since the group of recruits has to be physically guided by a recruiting leader until they reach the food source (e.g. *Tetramorium* ant species, Verhaeghe, 1982; de Biseau et al, 1994; see also Hölldobler and Wilson, 1990). Over the course of food exploitation, mass recruitment and non-linear properties of chemical trail recruitment become prevailing with most of the foragers being concentrated on a few food sources (Pasteels et al, 1987). This double recruitment process confers a higher flexibility for the ant nest. Indeed, any patrolling ant which has missed the first food source and that discovers a more profitable one, can behave as a leader: it guides groups of recruits towards this new resource, counteracts the attractiveness of the chemical trail leading to the first exploited target and – as observed for honeybees – facilitates the shift of the foraging activity towards richer food sources (Beckers et al, 1990).

A higher complexity of communication is an additional means for a group-living species to improve the flexibility as well as the diversity of its collective patterns. In the case of foraging, recruitment signals are often a blend of molecules with different life-times, operating at different stages of food exploitation. Another example is the synergistic effect of recruitment trail and home range marking, the latter being ant density dependent (Devigne and Detrain, 2006; Devigne et al, 2004): this means that workers are recruited to areas as a function of their frequentation level and hence their potential interest as foraging sites. Foraging efficiency can also be improved if repellent pheromones are used to mark unrewarding areas (Giurfa, 1993; Stickland et al, 1999; Robinson et al, 2005). A challenge for

future research will be to investigate to what extent the level of non-linearity of one species' interactions matches its need for cooperative behaviour or for flexibility to adapt to environmental changes.

7.3. WHAT ABOUT INDIVIDUALITIES AND THEIR IMPACT ON COLLECTIVE DECISION-MAKING?

Whatever their levels of sociality, group-living species share the following common property: the potential for amplifying, at the group level, individual traits or individual preferences. For instance, when ants are given the choice on a diamond-shaped bridge between a branch with or without a wall, about 65 % of the foragers will prefer to follow the walled branch in the absence of a recruitment trail. But, as recruitment proceeds, this propensity of ants will increase and will lead up to 85% of the foragers to choose the walled path (Dussutour et al, 2005a). This demonstrates that non-linearity in between-nestmate interactions may enhance even slight preferences of the individuals and lead to much more clear-cut choices by the group as a whole. Likewise, a synergy may exist between individual memory or fidelity to an area or to a given resource and the amplifying potential of recruitment; so that the specialization of a small number of recruiters will focus most of the colony in this particular sector or onto this food source. Amplifying phenomena that underlie most collective decisions are thus powerful means by which slight changes in physiological preferences (e.g. thermopreferendum values), changes in behavioural traits (e.g. thigmotaxis) or changes in individual knowledge of the environment can have deep consequences on the way a species will live as a group, will shelter exclusively in a peculiar resting site, will travel over a determined foraging path and will focus its foraging effort on a given resource. One may erroneously think about collective decision making and about idiosyncrasy as being opposite concepts (Deneubourg et al, 1999). In fact, individual memory and individual experience do not necessarily prevent the reaching of a consensus but instead make the patterns that will emerge at the colony level more complex and diverse (Couzin et al, 2005). When "conflicts" exist between the preferences of different individuals, there are multiple possible outcomes. One is the splitting of the group with individuals possibly losing the benefits associated with being part of a large group (Krause and Ruxton 2002) but with the group enlarging its occupation range of the environment. Second is the reaching of a consensus with a small proportion of informed individuals acting as leaders and guiding a group primarily composed of naïve individuals towards a target location. Research should now focus on how individualities may be enhanced at the group level by positive feedbacks and give birth to a multiplicity of collective patterns increasing the fitness of one species. As a corollary, one should question how species that benefit from maintaining group cohesion have evolved mechanisms resolving potential conflicts between different individual preferences. Part of the answer could be found in the ratio of recruiters (or informed individuals) versus naïve ones, as well as in the level of non-linearity of their communication. Answers to these questions will ultimately provide new insights into the evolution of communication and cooperation in group-living animals.

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