Chapter 13
Communicative and Cognitive Underpinnings of Animal Group Movement

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Abstract The topic of collective animal behaviour has seen a surge of interest in recent years, with the diversity of organisms under study ranging from bacteria to humans in crowds. A large part of this research has been devoted to the identification of the mechanisms underlying decision making in the context of collective movement. In this chapter, we provide an overview of different processes that have been invoked to explain group coordination. Using baboons as a model, we illustrate the importance of signalling behaviour and behaviour-reading to achieve group movement, and we discuss the cognitive processes associated with collective action. We conclude by evaluating the differences in human collective action compared to collective action in other animals, with particular regard for the intentional structure of human communication.

13.1 Introduction

It is the wee hours of an African morning. The air is still cool and the birds have just begun to sing. Up in their sleeping trees by the Gambia River, a group of Guinea baboons is showing the first signs of activity. While some animals are still stretching their limbs, the dry leaves of the palm trees rustle as others begin the descent from the trees to linger in the area. Some animals huddle, others bask in the first sun rays. Eventually, as if on command, the entire group walks off in one direction to begin their daily travel routine.

What are the rules underlying this apparently coordinated behaviour? Do different animals take different roles in initiating the descent from the sleeping trees or the onset of travel? How does a group of baboons reach a decision about when to leave and where to go? Which signals – if any – do these animals exchange when they

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behave collectively? And what are the cognitive underpinnings underlying group movement? These are the questions that we will address in the present chapter.

The topic of collective animal behaviour has received increasing attention in recent years, with the diversity of organisms under study ranging from bacteria to humans. The movement patterns of ants, honey bees, and locusts, as well as of fish schools and bird flocks, have become the topic of experimental studies as well as mathematical modelling (reviewed in Sumpter 2009). The central question in collective animal behaviour concerns the process of how individual 'decision making' gives rise to collective behaviour. Collective behaviour encompasses all instances where aggregations of subjects engage in one type of activity. Coordinated behaviour, or group coordination, refers to a subset of these instances where some form of regulation of group activity appears to be needed to achieve collective action. 'Group decision making' is frequently used to describe the process that eventually leads to coordinated action. However, it should be made clear that such 'group decisions' are based on the behaviour of individuals. 'Group decision making' is of interest because individual decisions strongly depend on the behaviour of others and are thus not independent of each other, resulting in specific dynamics of certain behaviours at the group level.

The fact that individual subjects make specific decisions points to one of the major factors, namely, the question of whether individual interests overlap or diverge. Further, it raises the questions of in which way the behaviour of others may influence individual decisions and how subjects integrate environmental and behavioural information to make their choices. In the following sections, we will focus on the mechanisms that have been invoked to explain collective behaviour, with particular regard for potential conflicts of interest, the flow of information, and the cognitive processes (see Chap. 15 for an additional discussion on collective primate behaviour). Conflict of interest refers to the fact that individuals have to pit the costs associated with a given decision against the benefits of group living. Before we turn to the decision-making processes in more detail, we briefly review the advantages of group living. We will then illustrate some of the processes outlined beforehand with a review of studies on baboons (*Papio* spp.), whose coordination of group travel has been studied in some detail. We conclude with a discussion of the differences and similarities in animal and human group coordination.

13.2 Living in Groups

Many species form aggregations or groups, and the vast majority of primates, including humans, live in groups. Whenever the advantages of group living for individuals outweigh the costs incurred by the disadvantages, such as increased transmission of pathogens or competition with group mates for food or mating partners, group living should be selected (see Chap. 2; Krause and Ruxton 2002). Once group living has evolved, animals are often faced with the need to choose, collectively, between mutually exclusive actions.

The benefits of group living have been explored in a large range of species, and a thorough review of the respective literature is far beyond the scope of this chapter. Here we will just list the main benefits that may have facilitated the evolution of group living. However, the various advantages do not apply to all species in the same way, and data to test hypotheses regarding the specific benefits are difficult to obtain, in particular for large and long-lived vertebrates such as non-human primates (Krause and Ruxton 2002).

Reducing the risk of predation is believed to be one of the major driving forces of group living in most species (Alexander 1974; Anderson 1986; van Schaik 1983). In addition, group living allows animals to defend their home range or feeding grounds cooperatively: A group can drive other animals out of its home range or away from a food resource, and larger groups can outcompete smaller ones (van Schaik 1983; Wrangham 1980). Group hunting is an important strategy in a number of large carnivores such as wild dogs, lions, and hyenas (Bertram 1978). Although non-human primates are not carnivores, group hunting also occurs in the primate order, albeit rarely. Only some populations of chimpanzees, *Pan troglodytes,* are known to hunt in groups (e.g. Boesch 1994). Finally, behavioural thermoregulation may favour group living, as huddling together to conserve energy and share body heat during cold periods can be an advantage. This applies mainly to small-bodied species and appears to be relevant only for a small number of primate species (Hanya et al. 2007; Ostner 2002).

In order to take advantage of the benefits of group living, animals face the challenge to stay together, coordinate group movement, and synchronise their behaviour within a group. These processes may pose additional costs on group-living animals that are related to decision making. Decision making about the direction of the morning departure from a sleeping site in hamadryas or chacma baboons, for example, can take up to 1 h (Stolba 1979; Stückle and Zinner 2008).

13.3 Concepts in Group Coordination

13.3.1 A Terminological Conundrum

Research topics that transcend disciplines require a careful clarification of terminology. Depending on the discipline, 'decision making' may refer to the outcome of a statistical process, such as the firing of neurons (Beck et al. 2008). In the behavioural sciences, 'decision making' is used to describe situations in which subjects can adopt one of two (or more) alternative behaviours. In human research in particular, 'decision making' is frequently associated with reasoning, that is, a mental simulation of the outcomes of different scenarios, such as the next move in a chess game (Koechlin and Hyafil 2007). Moreover, decision making in humans is typically linked to intentionality (e.g. Sutter 2007). For the time being, we will be agnostic with regard to the underlying cognitive processes and simply use the term

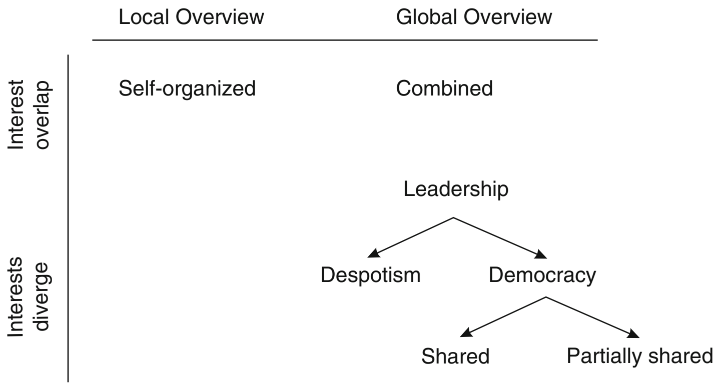

Fig. 13.1 Conceptions of the processes underlying group decision making. Two of the major determinants are the distribution of information (local vs. global overview) and the distribution of interests (overlapping vs. divergent). Within this framework, more detailed characterisations are possible. Note also that local and global processes may interact

'decision making' broadly, reserving the discussion of the cognitive requirements for the final section of this chapter.

In terms of the processes giving rise to collective action, there are unfortunately a number of different, partly overlapping, and not fully compatible concepts. To make matters worse, the terms are not always used consistently. In addition, a number of terms are adopted that describe highly complex human social institutions (see Conradt and List 2009 for an overview of terms used in the natural and social sciences, respectively). In some cases, such a transfer of terms appears to have larger metaphorical than explanatory power.

There are two major axes explaining the dynamics of decision making in animal or human groups or aggregations: One dimension is whether the behaviour is organised at the local level, where subjects simply pay attention to what their neighbours are doing, or whether global information is also factored in. The second dimension is whether or not the individual constituents of the group have overlapping or diverging interests (see Fig. 13.1). These processes are embedded in the respective physiological and ecological conditions, which may pose specific constraints (Conradt and List 2009).

13.3.2 *From Rule-Governed Behaviour to Complex Processing of Information*

Many people may know the example of starlings when they perform their spectacular acrobatic swarm flights on their way to their autumn sleeping sites. In fact, such seemingly complex group behaviours can be generated by rules that govern the behaviour locally, without any information at the individual level about the global movement pattern. These processes have been described as ‘self-organisation’ (Camazine et al. 2001). In principle, the behaviour of swarms can be generated by modelling individuals as self-propelled particles linked to their neighbours through attraction, repulsion, and alignment. Directed behaviour of large groups, as well as the formation of more complex behaviours such as the confusion of predators, can be explained by these simple rules (Gregoire et al. 2003).

The issue becomes more complex when individuals possess both local knowledge about the behaviours of those around them as well as global knowledge about some aspect of the environment. When both types of information are not in agreement, subjects need to make decisions. Take, for instance, a situation at the airport where a crowd is exiting the arrival hall through one of two doors, although the second door is also clearly marked with the word ‘Exit’. You may be inclined to factor in that global information and leave through the second door, or you may be influenced by other people’s behaviour and walk with the crowd, possibly musing that some of them must know that the other door is locked. In such cases, conflicts of interest may occur and individuals have to consider the costs (checking if the door is locked requires the risk of wasted time and energy) and benefits (less inhibited exiting) of choosing one alternative over another.

It is important to note that a subject’s probability of exhibiting a given behaviour can take the form of a sharply non-linear function of the number of other individuals already performing this behaviour. This phenomenon has been described as *quorum response* (Sumpter 2006). One form of quorom responses, namely quorum sensing has also been invoked to explain the collective action of bacteria. For instance, individual bacteria are able to detect the number and strain identity of other bacteria around them and vary their behaviour (e.g. biofilm production) accordingly (Nadell et al. 2008). In bacteria, quorum sensing is based on the secretion and detection of autoinducer molecules. The concentration of these molecules gives some indication of the cell density in that particular area. Once concentrations of these molecules have reached a certain threshold, it affects the behaviour of quorum-sensing cells. Quorum sensing has been linked to a number of processes in bacteria, including sporulation and bioluminescence (Miller and Bassler 2001), and it constitutes one of the simplest means of achieving collective action in social organisms.

A more complex example where quorum sensing and decision making both play a role is the emigration of an insect society from an old nest to a new one. First of all, this requires the assessment of different sites, a comparison between them, and an eventual choice of the new nest site (Pratt et al. 2002). Once a suitable new nest site has been found, the entire colony needs to be moved there. Several studies have shown that honey bee (*Apis mellifera*) and ant colonies are able to achieve this goal without any central control. Furthermore, these cases constitute intriguing examples for studying the link between behavioural rules and the flow of information between individual members. The ant *Leptothorax albipennis*, for instance, achieves the selection of a new site on the basis of a process in which several individuals function as scouts. Once a scout has identified a suitable site, it returns home. The initiation of recruitment behaviour is inversely proportional to the quality of the site, thus providing some indirect information about site quality (Pratt et al. 2002). The recruitment occurs in the form of so-called tandem runs. Once a certain number of animals are found at the new site (quorum sensing), tandem runs are abandoned in favour of transport runs in which passive members are carried to the new site. In sum, a combination of relatively simple rules is sufficient to achieve such a complex collective action as the move of a colony to a new nest site.

13.3.3 Overlapping and Diverging Interests

When interests overlap, collective behaviour may arise through ‘combined’ decision making (Conradt and Roper 2005). In a combined decision, there is no conflict of interest and external stimuli direct individual decisions in the same direction. An example is provided by a herd of thirsty animals walking to the nearest water source. When interests diverge, subjects need to reach ‘consensus’ decisions. Such scenarios raise the question of whether specific individuals exert a disproportionate influence on the outcome of behaviour, for instance, because of their social role in the group or because of an uneven distribution of information. In such cases, animals can be characterised as leaders and followers (King et al. 2009). Two principal forms of leadership have been proposed (1) *personal leadership* (*despotism*), where a single individual uses its high-dominance status or experience to lead the group, resulting in an unshared decision; (2) *distributed leadership* (*democracy*), where either all group members reach an equally shared decision, or a subgroup of individuals reaches a partially shared decision (Conradt and Roper 2005; Leca et al. 2003). In cases of divergent interests, decision making also requires some form of interaction among the involved individuals, whereas a combined decision can be achieved without any such interaction. Hence, consensus decisions are also described as *aggregate* or *collective* decisions, whereas combined decisions are described as *interactive* decisions (Conradt & List 2009).

One of the most famous examples for despotism is found in mountain gorillas, where the silverback male directs the group by heading in his preferred direction (Watts 2000). In this example, the apparently coordinated behaviour is based on the fact that other group members have no choice but to follow the leader if group cohesion is to be maintained. Similar processes have also been observed in mongooses (Rasa 1983) and wolves (Mech 1970). Shared decisions are generally thought to be more profitable for group members than accepting unshared decisions made by a single leader (Conradt and Roper 2007), because on average there is a greater overlap of interest. Distributed leadership has been observed in such diverse species as honey bees (Seeley and Buhrman 2001), coatis (Gompper 1996), and red deer (Conradt and Roper 2003). Note that in relation to group movements, leadership often refers to individuals initiating movements or changes in direction that are followed by the rest of the group (e.g. Leca et al. 2003; Trillmich et al. 2004). These animals are not necessarily the decisive subjects when it comes to agreeing on a certain direction (see ahead). In a recent study, Conradt and colleagues showed that the assertiveness with which animals opt for one option over another depends on the cost of splitting, compared to the benefits of going to the leader's preferred target. The assertiveness, in turn, can be thought of as a function of meeting an individual's need. Animals that are highly motivated to direct the travel to a water source because they are thirsty may have a disproportionate effect on the group's eventual travel direction than less needy individuals (Conradt et al. 2009). Conradt and Roper explored the conditions under which unshared decisions are – in evolutionary terms – more successful than shared ones. Using a combination of self-organising systems and game theory, they revealed that shared as well as unshared decision types can evolve without invoking global knowledge in the individual members of a group. They found that unshared decisions are favoured when conflicts are high compared to grouping benefits due to the inherent expediency and simplicity of unshared decisions (Conradt and Roper 2009).

13.3.4 Information Transmission

As we have seen earlier, the transmission of information among individuals can be an important determinant of collective action. Information can be transmitted through communication, that is, the usage of signals that are emitted by a sender and received and processed by one or many recipients (McGregor and Peake 2000; Skyrms 2009). Signals are defined as structures or behaviours that predominantly serve information transmission, having little survival value otherwise. In contrast to signals, cues are considered to reflect more directly the physiological or morphological state of an individual. Thus, cues encompass all sorts of features or behaviours that may influence a specific animal's actions (Maynard Smith and Harper 2003). Note that not all authors use these terms consistently (e.g. Hauser 1996), but it is generally agreed that signals evolve from cues, which in turn are a subset of an animal's behavioural features.

Importantly, from the recipient's point of view, signals are not necessarily more informative than cues or the simple behaviour of another subject. In other words, if one animal watches another animal move in a certain direction, there is no doubt that the animal is doing just that – moving in a certain direction. In contrast, signals typically predict imminent behaviour, but not fully reliably. Nevertheless, signalling is important because it constitutes a means of information transfer that is generally less costly than the proposed action itself, and, depending on the circumstances, the use of signals may be the only way of transmitting information. The signalling systems involved in collective action may take a variety of forms, including the secretion of chemicals in bacteria that lead to quorum sensing, as well as the waggle dance of bees or the usage of vocal signals.

Animals gather information about others' locations not only by attending to their signals, but also by generally attending to their activities. Among socially living animals, knowledge about food or water sources is frequently transmitted socially without invoking explicit instruction. Research during the last two decades has identified different social learning mechanisms that encompass a range of different forms with varying degrees of cognitive complexity. The common denominator is that the behaviour of one subject facilitates or influences the behaviour of another subject. Of particular importance in the current context are social facilitation, stimulus enhancement, and local enhancement (see Fischer 2008 for a full review). Social facilitation is invoked when an individual's learning is affected by the activity of another animal. Animals typically pay a lot of attention to what others, particularly their group mates, are doing. This may lead to stimulus enhancement, such as an increase in the salience of stimuli others are paying attention to, as well as local enhancement, such as when the subject learns something about a specific situation simply because it is near an individual who does something particular. Social facilitation may lead to quorum responses, with a non-linear spread of specific behaviours, and it may even influence the dynamics of information transmission in a given group.

13.4 Baboons as Models to Study Animal Group Coordination

13.4.1 Social Organisation and Decision Making

The initiation of group movements and the coordination of travel have been studied extensively in baboons. Baboons range all over sub-Saharan Africa and the Arabian Peninsula. They inhabit a large range of different habitats and exhibit very different social systems. Hamadryas baboons, for instance, live in a multi-layered society that consists of small one-male units (OMU) of one male with a few females. Several OMUs may form a clan, which forage together and which are believed to be connected by close kin relationships among the male leaders of the respective OMUs. Several such clans form a band, which shares a common home range and can include more than 100 individuals. Bands are seen as the ecological units of the hamadryas society, whereas OMUs are seen as reproductive units. Individuals rarely change from one band to another. Several bands may aggregate at certain rare sleeping cliffs where they spend the night and form troops of up to several hundred individuals.

Typically, members of a band leave their sleeping cliff together at the same time and in the same direction. Each morning before leaving the sleeping site, a significant amount of time is devoted to agreeing on a joint direction of travel. Hans Kummer, who pioneered the study of group movement initiation, distinguished between initiative individuals (I) and decision-making individuals (D-ID-System). The initiative and decision-making individuals are males, mainly older ones, with leaders of OMUs having apparently the greatest influence in the decision-making process (Kummer 1968). Kummer concluded that 'leading' individuals do not need to determine group movement from the vanguard position since it was also possible to 'lead the troop from the back' (Kummer 1968; Stolba 1979). Thus, hamadryas baboons provide an example of partially shared leadership (Kummer 1968; Leca et al. 2003).

Geladas (*Theropithecus gelada*), close relatives of baboons, live in a superficially similar social organisation as hamadryas baboons. However, here the dominant female of the OMU fulfils a pivotal role in maintaining coordination between the male and his other females. Progressions are usually initiated by lactating females, but decisions whether to follow or not are shared by the dominant female and the male. Females monitor the behaviour of the male but try at the same time to stay in proximity to their preferred social partners (Dunbar 1983).

In contrast to hamadryas baboons and geladas, savannah baboons typically live in female-bonded multi-male–multi-female societies. Savannah baboons encompass the traditionally recognised morphotypes of chacma, yellow, and olive baboons. Because of the importance of females in these groups, it became of interest to elucidate their role in initiating group movements. In a study in South Africa, Stückle and Zinner (2008) examined whether a group would reveal evidence for distributed leadership that included females. Before taking off for their daily march, these baboons rested below their sleeping trees. After some time, one animal (the so-called initiator) moved away from the rest of the group. In such instances, others either followed (successful attempt) or stayed behind (unsuccessful attempt). The minimum number of consenting adult individuals that normally guaranteed that the entire group would depart was five. Therefore, six adult individuals (initiator and five followers) seem to be sufficient to pull the entire group of 39 into the pursued direction, making the initiative successful. If not enough animals followed, the initiator normally moved back to the group until a second attempt was made, either by the first initiator or by another animal. Approximately 75% of all adult animals successfully initiated a collective move, with 67% of initiations being made by males. The relative success of an initiation was equally distributed among adult group members, with almost two thirds of the initiatives being successful. If a successful initiation of a collective move is regarded as equivalent to leadership, then these baboons show a system of distributed leadership. However, although the probability of being successful was similar for males and females when initiating a move, males had more influence on the morning departure process by initiating more start attempts, thereby making appreciably more successful initiations. Among males, there was a trend for higher-ranking (more dominant) individuals to make a higher total number of initiation attempts as well as a higher number of successful attempts than lower-ranking ones. A similar trend was not obvious in females, most likely because a possible effect of dominance was masked by a confounding effect of females' reproductive state. High-ranking females were the ones with dependent offspring, which most likely forced them to stay in the centre of the group or in close vicinity of a male protector instead of taking the lead when leaving the sleeping site (Stückle and Zinner 2008).

In contrast, King and colleagues (King et al. 2008) reported that in another chacma baboon population, the decision-making process was despotic and not distributed. In this study, an artificial clumped food source was offered in the home range of a baboon group. The baboons had to decide whether to visit the feeding site or to go elsewhere to forage. When visiting, the dominant male obtained the largest share of the resource, while others received less or nothing at all. Nevertheless, the group's foraging decisions were consistently made by the dominant male. Subordinate group members followed the leader in the interest of staying together despite considerable consensus costs (no food) to these subordinate members. King and colleagues interpreted the behaviour of the subordinates by the value of their social bonds with the dominant male. These baboons seem to face a dilemma: either to maintain close proximity to the dominant male by following him to his preferred feeding site even though they do not benefit from the food, or to leave the dominant male and forage on their own, thus jeopardising their social relationship with the dominant male (King et al. 2008).

13.4.2 Signalling Behaviour: Non-vocal Signals

As in hamadryas baboons and other primate species, particular behaviours or postures may be used to communicate during the decision-making process. Hamadryas males seem to communicate intensively during the decision-making process and 'negotiate' the direction of travel (Kummer 1968; Stolba 1979). Males present each other in a particular way, called *notifying*. Notifying can be a complete behavioural sequence entailing the approach of one male to within arm's reach of another, turning the body, presenting the hindquarter, and looking back to the first male, who can then touch the penis of the presenting male. The mildest form of this behaviour is just a short glance of one male to a second, followed by an abrupt turn of his head. Notifying is normally accompanied by vocalisations of both males. When proposing a certain direction, males may walk in a particular manner in the preferred direction or they may stand on outstretched arms and legs, as stiff as a sawhorse, and will then advance in the direction of the body axis. A male can also vote against a proposed direction by sitting down and abruptly lowering his head on the chest without moving within the next 2 min. Possible equivalent behavioural patterns in chacma baboons also include the presence or absence of a 'back glance' when the initiator is looking back to the rest of the troop while walking away, 'pauses' of the initiator during locomotion, and 'walking speed' of the initiator – either trotting or walking fast away from the troop. Such behaviours have been interpreted as intentional signals to recruit group members (Meunier et al. 2008). This view is also in line with the classical ethological concept that these signals have evolved from intentional movements, which are viewed as expressions of the motivation to move.

13.4.3 Signalling Behaviour: Vocal Signals

Vocal signals play an important role in baboon group movements. It has been assumed that calls indicate the motivational state of the sender and provide some information about the sender's propensity to take a certain action. Moreover, such signals can facilitate emotional contagion, thus raising the probability of collective action such as a group departure. Baboons emit soft tonal calls, called grunts, to facilitate social interactions with others or when they are travelling. Moreover, animals utter grunts when they are moving through high grass, but also when the group is about to initiate a group movement either in the morning or after the group has taken a rest during the day. A pilot study on a Namibian population of baboons indicated that an increase in the call rate reflects an increased probability that the group will start moving (Fig. 13.2). Although this system deserves further detailed study, it suggests that each animal's calling can be viewed as the expression of its motivation to get going. Once a certain number of animals are grunting at the same time, this predicts that others are willing to follow if the first animal sets itself in motion. This system would also lend itself to experimental testing, as the grunt rate could be experimentally augmented. Similarly to baboons, vervet monkeys utter so-called move into open grunts (MIO) when they sit near trees and before entering the open grassland (Cheney and Seyfarth 1982), while Barbary macaques emit soft tonal calls termed 'girneys' when they initiate group movements (Fischer and Hammerschmidt 2002).

In the context of group travel, baboons also frequently emit so-called barks. These barks have a tonal structure (Fischer et al. 2001, 2002) and are emitted when subjects have lost contact with specific individuals – for instance, their offspring – or with the rest of the group. Typically, several animals can be heard calling at the same time, giving rise to the notion that these animals may in fact 'answer' each other's calls. Cheney and colleagues set out to test this assumption in a group of baboons in the Okavango delta in Botswana (Cheney and Seyfarth 1996). They followed the adult females of the group for 2.5 h after the departure from the sleeping site and noted for each call the identity of the caller, the context, and the

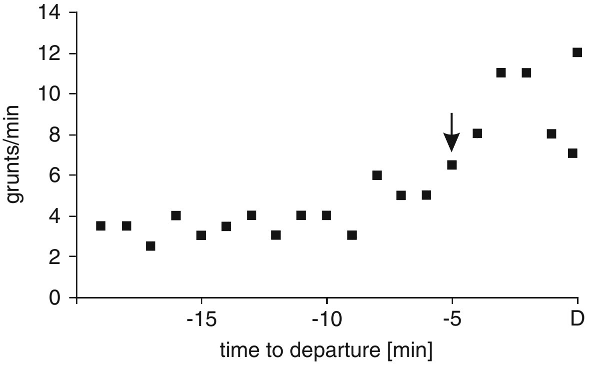

Fig. 13.2 Baboon grunts as cues to imminent group departure. Average grunt rate per individual and minute recorded at the sleeping site of baboons at Tsaobis (Namibia) before departure (D). The *arrow* indicates a significant increase in call rate (determined by means of a change-point analysis) about 5 min prior to the first animal leaving. (Data were kindly made available by Kristine Meise, Christina Keller, and Guy Cowlishaw)

relative location of the animal compared to the rest of the group (front, middle, or rear). For more than 1,600 calls, the observers were able to ascertain the identity of the caller and her location. More than 80% of calls were given by individuals in the rear third of the group. A sequential analysis revealed that these calls typically occurred in a clumped fashion, with one signaller emitting several calls in succession, and several animals calling at the same time. In fact, 92% of calls occurred within 5 min of another call, either following another subject's call, or because the animal was emitting a series of calls in a bout. A more detailed inspection revealed that calling was primarily driven by the caller's risk of becoming 'lost' (hence, these calls have also been termed 'lost calls'). To examine this finding systematically, Cheney and colleagues initiated a set of playback experiments where they played back the clear barks of females to close female relatives, and then checked whether they would 'answer' their kin. In 7 of 36 trials, the subject indeed responded to the playback with a vocal response within 5 min. However, as in the previous observational study, these females were themselves lagging behind the group, suggesting that the immediate context and the risk of getting lost drive the calling behaviour, and not the intention to inform other group members about one's own location (Cheney and Seyfarth 1996).

Contact-calling may be influenced by the visibility (or lack thereof) and, hence, the visual control of the other group members' locations. Accordingly, one would predict that animals call more frequently when visibility is poor. Indeed, in Botswana, clear calls occurred more frequently in woodland habitat than on open flood plains, or when the group gathered near their sleeping trees (Cheney and Seyfarth 1996). Similarly, the rate of grunts given by olive baboons studied in Uganda varied with the habitat type: Baboons uttered grunts at a significantly higher rate in forest than in open habitat. In a population of olive baboons in Nigeria, in contrast, the grunt rate did not vary with the habitat quality and the visibility conditions. However, in both cases, the calls were significantly longer in the forest compared to the open habitat (Ey et al. 2009). Moreover, the rate of loud calls in Nigeria did not differ in relationship to the habitat. This suggests that calling rates are not simply determined by visibility. Moreover, this observation raises the question of whether the differential call rate in Botswana could be indirectly mediated by the fact that in this group, animals lose contact with others less frequently in open habitats, while the much smaller group in Nigeria is generally more cohesive.

13.5 Cognition and Collective Behaviour

Humans like to think of themselves as being highly cognitive creatures who deliberately consider different outcomes of specific actions before making a decision. Frequently, humans believe that they are approaching an optimum when doing so. Yet, they often rely on simple heuristics (Gigerenzer 2001). Morgan pointed out that, 'In no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development' (Morgan 1903, p. 59). This is meant to also apply to the human animal. Therefore, considering coordinated behaviour in putatively more simple organisms is useful in identifying how minimal sets of rules can give rise to collective action without the need to invoke cognitively demanding operations. For instance, a number of studies have shown how simple local processes govern the movement patterns of human crowds (e.g. Dyer et al. 2008).

At the same time, it is also of interest to clarify how cognitively elaborate group decision-making processes in animals can be. One important issue here is the question of whether the usage of signals (or other forms of behaviour) can be considered as intentional. In the domain of animal communication and cognition, researchers frequently invoke the definition of Dennett (1971). Dennett described different stages of intentionality, where zero-order intentionality would apply to simple expressions of emotion or fixed action patterns given in response to sign stimuli. First-order intentionality describes communicative acts employed in order to alter the behaviour of the recipient. This does not necessarily imply that the signaller is conscious of her own behaviour or mental state (Bruner 1981) in the sense that the sender is aware that she does have such an intention. To identify (first-order) intentionality, Tomasello and Call (1997) proposed, as a diagnostic, the observation that animals may have different means to achieve a specific goal. Second-order intentionality would apply to cases where the sender intends to alter the knowledge state of the other but not necessarily his or her immediate behaviour. For second-order intentionality to apply, the sender must know that the receiver's mental state can be different from his own mental state. So far, there is no convincing evidence for second- (or higher-) order intentional communication in animals (Seyfarth and Cheney 2003). Thus, most of the studies ask whether primates use signals with the intention to alter their group mates' behaviour.

For our specific purposes, Dennett's scheme is powerful because it clearly distinguishes between the intent to alter the mental state vs. the behaviour of another subject. This research falls under the umbrella of so-called Theory of Mind research, a field that investigates the attribution of beliefs, desires, and knowledge to others. The term was introduced by Premack and Woodruff (1978) in a paper entitled 'Does the Chimpanzee have a Theory of Mind?' To date, there is some evidence that non-human primates indeed understand something about the link between seeing and knowing (Hare et al. 2000; Kaminski et al. 2008; Tomasello and Call 2006; also see Cheney and Seyfarth 1990), but they appear to lack a full-blown attribution of mental states. Thus, it seems fairly safe to conclude that non-human primates use signals with the possible intention to alter the movement patterns of others (see Hesler and Fischer 2007), but they do not call with the intention to provide others with the information that they are about to leave (Fischer 2008; Seyfarth and Cheney 2003). Accordingly, Couzin (2009) suggested that the field of animal collective action may profit from studying the properties of neural assemblies and the information flow in such systems instead of invoking higher-level cognitive processes.

The differences in mental state attribution have important implications for the conceptualisation of collective action and mechanisms underlying decision making. According to Bratman (1992), shared collective action refers to situations where (human) subjects have a concept that a given activity is shared, and that each subject intends that the group performs the collective action by coordinating ‘subplans that mesh’ (Bratman 1992). For instance, each member in a team of surgeons in an operating room will assume that all the other members have the same goal, namely, to successfully perform the operation, and also assume that the others are aware of the communality of that goal (see Chap. 5). Along these lines, Tomasello pointed out that human communication is grounded in fundamentally cooperative and shared intentions (Tomasello 2008). In contrast, no such cognitive assumptions are made in the animal domain.

13.6 Conclusion

Animal models are valuable for investigating the mechanisms that lead to collective action without invoking attribution of mental states. As we have seen, simpler models are useful to understand the minimal requirements to achieve a certain type of collective behaviour and at the same time identify the differential needed to achieve a more complex form of coordination, especially in the identification of the mechanisms underlying decision making in the context of collective movement. Thus, bird flocks are useful to understand the behaviour of human crowds, while bacteria help to illuminate the selective pressures that play a role in the evolution of sociality in general. However, animal models are often less useful for gaining insights into the psychological, cognitive processes at work when humans engage in shared collective behaviour.

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