



Decision-making processes: The case of collective movements

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ABSTRACT

Besides focusing on the adaptive significance of collective movements, it is crucial to study the mechanisms and dynamics of decision-making processes at the individual level underlying the higher-scale collective movements. It is now commonly admitted that collective decisions emerge from interactions between individuals, but how individual decisions are taken, i.e. how far they are modulated by the behaviour of other group members, is an under-investigated question. Classically, collective movements are viewed as the outcome of one individual's initiation (the leader) for departure, by which all or some of the other group members abide. Individuals assuming leadership have often been considered to hold a specific social status. This hierarchical or centralized control model has been challenged by recent theoretical and experimental findings, suggesting that leadership can be more distributed. Moreover, self-organized processes can account for collective movements in many different species, even in those that are characterized by high cognitive complexity. In this review, we point out that decision-making for moving collectively can be reached by a combination of different rules, i.e. individualized (based on inter-individual differences in physiology, energetic state, social status, etc.) and self-organized (based on simple response) ones for any species, context and group size.

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1. Introduction

Collective movements of insects, fish, birds or herds of ungulates are among the most compelling social manifestations in the biological world. Moving together is a necessary part of group living in itself, the adaptive consequences of which have classically attracted considerable attention (Boinski and Garber, 2000). However, how collective movements unfold raises several issues, among them: what is the motivation to move and is it shared among group members, when to go (time of departure), who initiates movements, where to go (direction) and how individuals choose a common direction.

Collective movements are ubiquitous in gregarious invertebrate and vertebrate species including humans. Definitions of spontaneous collective movement, however, are rare or inexistent. How can we distinguish them from a mere collection of individuals moving independently? Independent individual decisions to depart should lead moving individuals to behave in the same way as solitary ones, keeping aside the physical constraints that the presence of surrounding conspecifics impose on them. Random trajectories could not account for regular patterns and emergent properties

assigned to collective movements on a large scale such as shape, density of individuals and polarity of orientation. Collective movement could therefore be defined as **a group of animals that decide to depart/move quite synchronously, move together in the same direction (which implies the animals have a choice between different alternatives) and maintain cohesion until the group stops moving or starts a new activity, all resulting in a change of location. It implies non-independent individual decisions to move and relies on information transfer between group members mediated by behavioural cues or signals, and social responses whose dynamics may be modulated by the ongoing collective movement itself. The environmental physical template (photoperiod, wind, trail or stream) does influence the trajectory of groups, but cannot be the main factor responsible for such movement and collective properties.**

How coordination is achieved and how spatial patterns emerge from individual movements has often been the source of putative explanations, inspiring theoretical models (Czirok et al., 1996; Grégoire et al., 2003; Grégoire and Chate, 2004; Giardina, 2008). It is only recently that the combination of experimental biology and mathematical modelling has allowed a better understanding of group-level properties (Camazine et al., 2001; Parrish and Edelstein-Keshet, 1999). Although external factors or templates may influence the way animals move, they cannot alone account for the emergence of collective output. Collective patterns or prop-

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erties at the group-level arise as a consequence of local interactions between individuals, without centralized control, a common pre-determined goal to be reached or reference to a global pattern at the individual level (Bazazi et al., 2008; van de Koppel et al., 2008). Self-organization seems to be a parsimonious way to explain the complexity of animal societies (Deneubourg and Goss, 1989; Camazine et al., 2001; Detrain and Deneubourg, 2006). Collective movements imply more or less simultaneous changes in location of group members. Whether they involve short or long distances, movements need to be initiated. In social insects, it is commonly accepted that some individuals possessing information about their environment are responsible for the recruitment of non-informed fellows. The recruitment may involve specific signals produced by the scouts or conspecific leading or transport. The choice of a new home or of a food source eventually involves a rapid collective choice. How the multitude of individuals takes a decision (consensus or quorum-based) is most often still hypothetical (Seeley and Visscher, 2004). In parallel, biological understanding of collective movements in vertebrates has often been focused around the social status of the few individuals initiating the move, i.e. the leaders. The debate around leadership has fruitfully issued renewed questions concerning the pre-departure periods and how the so-called collective decision emerges (Biro et al., 2006; Harcourt et al., 2009; King et al., 2009). The ongoing movement of a multitude of individuals has inspired physicists to propose heuristic models to account for the coordination of movements and global and structural features of groups (Giardina, 2008). The debate is not to determine whether macroscopic properties can be derived from microscopic rules, but which behavioural rules are indeed at work, challenging biologists in their enterprise to identify them. For instance, which information do individuals really consider in their decision-making (Ballerini et al., 2008b)? Does the collective response that often fits a quorum-like pattern involve the same kind of mechanism at the individual level? Does the quorum-like response involve negotiation, vote or consensus decision within the groups (Sumpter and Pratt, 2009)? These concepts are metaphors for how animals behave and which sensory and cognitive mechanisms underlie their decisions. They have to be defined clearly in order to test their relevancy. They should also inspire research to test alternative hypotheses to account for individual decisions and resulting behaviours.

Theoretical approaches have shown that the same simple interaction rules at a local scale may account for the fact that high-order multiple stable modes of collective behaviour can co-exist for the same set of parameters (Nicolis and Prigogine, 1977; Camazine et al., 2001; Sumpter, 2009). However, distinct underlying individual mechanisms may also lead to similar spatial patterns (Camazine et al., 2001; Couzin et al., 2002; Couzin, 2008). Self-organization is often studied in species living in large groups. The rationale is that collective properties associated with socio-spatial patterns are observed at scales beyond the individual scale. It is now commonly accepted to consider that any individual in a large group will only interact with and extract information from a few neighbours. However, in many cases, individuals that compose large aggregation are also often found in smaller groups. Whether small group characteristics and their dynamics emerge from the same local interaction rules as those involved in large groups is a central question (Giardina, 2008). Often, collective decisions are density-dependent or reported to result from individual responses triggered above a stimulation threshold (Weidenmüller, 2004; Visscher and Seeley, 2007). Thus, in order to be able to generalize rules of decision, we need to establish whether or not self-organized principles apply to species living in small groups. Besides, many studies have considered all individuals in groups as equivalent. Collective decision-making may then result from simple interaction rules between interchangeable individuals (Amé et al., 2006). However,

individuals of the same species and dwelling in the same groups may differ in a number of behavioural traits, either temporarily or more persistently (Weidenmüller, 2004; Michelena et al., 2010), sometimes as a result of social interactions (Jeanson et al., 2005). Within groups, social interactions may also be exchanged among only a subset of group members. Thus, a group decision to move may emerge from very general simple rules shared by all the group members, but potentially from individuals responding to different thresholds of stimulation or to the kind of partners.

Decision-making implies several different issues for the animals: whether moving at all or staying in the same place, when to go (time of departure) and where to go (direction), moving cohesively or in another direction. Joining is an important part of the decision process and has been neglected until recently. Cohesion during movement can only be maintained if the group members decide either to follow each other or to stop at the same time. Another central question is how individual animals decide exactly when and where to stop movement.

Detailed biological observations are necessary in order to pinpoint relevant individual behavioural rules and quantify the dynamics of decision-making processes for movement. The key question is: how does each group member come to a decision, and how far is this decision modulated by the behaviour of other group members? Indeed, individuals might differ in their characteristics (age, sex, dominance status), internal state (level of satiety, reproductive status) or sensitivity to external stimuli. Groups may thus be composed of individuals differently motivated to move. Moreover, species differ in their cognitive capabilities and communicative abilities, and show various degrees of complexity in their social worlds. This paper will consider from a comparative perspective how individual motivation, knowledge and social relationships can influence collective decisions. We will finally discuss whether these mechanisms might help to reach accurate and efficient decisions on an adaptive level.

In collective movements, group members have to choose between either moving or staying, and, in cases of concurrent alternatives, have to decide on either one direction or another. Different behavioural processes could influence the decision, depending on their time of occurrence. In this review, we consider the whole process encompassing decision-making before and during the collective movement. The decision-making precedes the departure of the initiator(s), continues with the collective movement and elicits the stopping of all moving animals.

2. The pre-departure period

When reviewing the literature, one might notice that the events preceding the effective departure of a group are often ignored, though not neutral. The collective mood of the group before departure might influence (passively or not) the next group movement in terms of the number of participants or joining speed. The collective mood concerns the arousal state of group members (Ramseyer et al., 2009b; see also Ward and Zahavi, 1973 for a definition of the “mood of the roost”); it reflects the readiness of the group to move. This group state can be measured by general group activity or vigilance, for example, or by the spatial dispersion and orientation of individuals. A more clustered group is a factor that increases the subsequent number of followers in species as different as white-faced capuchins (*Cebus capucinus*) (Leca et al., 2003), rhesus macaques (*Macaca mulatta*) (Sueur and Petit, 2008a), sheep (*Ovis aries*) (Ramseyer et al., 2009a) and geese (*Anser domesticus*) (Ramseyer et al., 2009b). If the stationary period in a new resting or foraging zone is short, a start attempt would be more likely to fail than after a long stationary period, as found in white-faced capuchins (Leca et al., 2003). Indeed, a minimal amount of time

spent on one activity would increase the chance that a majority of group members would be willing to move to change activity or zone (Gautrais, this issue). Similarly, a minimal staying time might allow a compromise between low- and high-motivated individuals to move.

Some individuals can also display behaviour that indicates their motivation to move, either facing a direction, moving away or using specific postures. Prins (1996) described cows (African buffalo, *Syncerus caffer*) urinating and defecating more and more often before a collective movement. They also adopted a particular stance after having shuffled around, seemed to gaze in one direction and kept their heads higher than the normal resting position (Prins, 1996). In sheep and cattle (*Bos taurus*), a phase of preparation with an increase of group activity and vigilance before departure that increases the number of participants has been described (Ramseyer et al., 2009a,c). Mech (1970) described a complex process before departure in grey wolves (*Canis lupus*) where any high-motivated animal, but more frequently the alpha male, gets up after a resting period and awakes all the pack members successively and afterwards a group ceremony occurs. Similarly, golden jackals (*Canis aureus*) and Cape hunting dogs (*Lycaon pictus*) display group greetings before moving that have sometimes been qualified as “social rallies” (Holekamp et al., 2000). Domestic geese increase their rate of wing flaps and vocalizations as well as group vigilance and orientation in the minutes preceding a departure (Ramseyer et al., 2009b). In their pre-flight sequences, swans (*Cygnus sp.*) speed up their rate of head bobbing as the time of take-off approaches (Black, 1988). Canada geese (*Branta canadensis*) also increase their activity one hour or more before take-off, especially head-tossing and low guttural vocalizations (Raveling, 1969). The participation of the gander in this phase shortens the time before take-off. Collective movements occur after communal scent marking in dwarf mongooses (*Helogale undulata rufula*) (Holekamp et al., 2000). Mountain gorillas (*Gorilla gorilla beringei*) express their readiness to move with grunts (Stewart and Harcourt, 1994) or double-syllabled close calls at the end of a nap (Watts, 2000) while Verreaux’s sifakas (*Propithecus verreauxi*) emit grumbling vocalizations in the few minutes preceding a group movement (Trillmich et al., 2004). Chacma baboons (*Papio ursinus*) at some point produce grunt calls before their morning departure (Stueckle and Zinner, 2008). The piping of scout bees was found to prime swarms of honeybees (*Apis mellifera*) for take-off (Visscher and Seeley, 2007). Concomitantly, and more and more often, the same bees produce a buzz-run that disperses and activates still-resting bees (Rittschhof and Seeley, 2008). These buzz-runners contact other bees by pushing, still buzzing their wings (Rittschhof and Seeley, 2008), and this is reminiscent of the waking-up behaviour of wolves before a group ceremony (Mech, 1970). In African elephants (*Loxodonta africana*), this process is more individualized, with one family member moving to the periphery, standing facing away from the rest and giving a “let’s go” rumble while lifting a leg and thus repetitively until other group members join it, and the group moves off in unison (Poole et al., 1988). In Przewalski horses (*Equus ferus przewalskii*), this pre-departure period involves “primers” that signal their motivation to move in one direction by taking peripheral positions. This phase lasts longer when animals are confronted with many ecological alternatives, meaning that the horses need more time to resolve motivational conflicts about the direction in which to move (Bourjade et al., 2009). In macaques (*Macaca sp.*), notifying individuals display back glances and intention movements to signal their motivations to go (Sueur and Petit, 2008a), as hamadryas baboon males (*Papio hamadryas hamadryas*) do before their morning departures (Kummer, 1968) and apparently diademed sifakas (*Propithecus diadema edwardsi*) and red-fronted lemurs (*Eulemur fulvus rufus*) males, which indicate different directions before another individual sets off in one

of these directions (Erhart and Overdorff, 1999). In yellow baboons (*Papio cynocephalus*), direction appears to be indicated by females climbing into a raised position and orienting their bodies and gazing in a particular direction while also monitoring group activities. The directions and apparent endpoints or goals indicated by these females are frequently taken by the troop (Norton, 1986).

In the many examples described above, pre-departure behaviours occurring during the stationary period have been reported, eliciting a collective movement or increasing its number of participants (Raveling, 1969; Sueur and Petit, 2008a; Ramseyer et al., 2009a,b,c) but not systematically (Black, 1988; Stueckle and Zinner, 2008). In such a priming phase, the underlying mechanism might be of a mimetic kind with more and more animals notifying (see point 5 for the definition of mimetism) after having seen their congeners displaying cues or signals, as suggested by data on Canada geese reported by Raveling (1969). Moreover, the number of such “primers” (Bourjade et al., 2009) or “notifying individuals” (Sueur and Petit, 2008a) might be decisive: when reaching a certain value (either an absolute number or a proportion), it could represent a quorum at the individual level triggering the subsequent movement. These pre-departure phenomena might facilitate successful joining after the departure of any initiator. That might explain why, in some species, the identity of the initiator does not really matter (brown lemurs (*Eulemur fulvus*), Jacobs et al., 2008; geese, Ramseyer et al., 2009b; sheep, Ramseyer et al., 2009a; Tonkean macaques (*Macaca tonkeana*), Sueur and Petit, 2008a) since the group would have already decided to leave (Kummer, 1968; Prins, 1996; Visscher and Seeley, 2007). Without such pre-departure behaviours, one can speculate that the next initiation would be delayed or that the joining process might break down or take more time to be completed. Nonetheless, no data are available to confirm this assumption. Such postures, vocalizations or glances illustrate that the decision-making process may start well before the departure of a single individual and that the pre-departure period is worth studying. However, it is important to note that not all collective movements are preceded by noticeable pre-departure behaviour (Dyer et al., 2008; Sueur and Petit, 2008a; Pillot et al., 2010). It would be interesting to compare cases of departure preceded by pre-departure behaviours with those without, especially concerning the direction choice. As shown in horses, the final goal might be the main constraint on the decision-making process and counterweigh the lack of pre-departure behaviours (Bourjade et al., 2009). Such influence of the travelling destination on decision-making has already been suggested in cattle (*Bos indicus*) (Reinhardt, 1983).

A special and scarce phenomenon that can happen during this pre-departure period must be mentioned. The two frequently cited examples concern buffalos and hamadryas baboons and their supposed voting behaviours. In these cases, animals are reported to behave more intentionally than in the above instances by showing a specific direction or placing themselves in a specific position. For Prins (1996), the orientation of the standing cows showed two remarkable features: first, the consensus in directionality was often high and, secondly, the resulting confidence region of the mean compass bearing nearly always overlapped with the compass bearing of the area where they were going to graze that night. Kummer (1968) described the obvious and repeated behaviour of hamadryas baboon males, followed by their unit, who presented their hindquarters to other males, thus showing the direction they favoured. The troop finally went in the direction favoured by the male who recruited most of the other males. In Tonkean macaques, the final direction chosen among two by two different semi-free-ranging groups was the more advertised one, in terms of the number of “notifying” individuals and/or “notifying behaviours” (Sueur and Petit, in press). “Notifying behaviours” may also indicate a kind of voting process (Conradt and Roper, 2003, 2005). Accord-

ing to the Oxford English Dictionary, a vote is defined as a formal indication of a choice between two or more candidates or courses of action (Sueur and Petit, *in press*), which corresponds quite well to the above descriptions.

3. The status of the initiator

3.1. The misleading concept of leadership

Collective movements are often considered to be the outcome of one individual's departure followed by all the other group members. The leader of movements is presumed to hold a specific social status, i.e. social leadership. Indeed, dominant individuals were classically considered as leading the group exclusively or more often than other group members in several taxa (for instance: dwarf mongooses, Holekamp et al., 2000; grey wolves, Mech, 1970; green woodhoopoes (*Phoeniculus purpureus*), Radford, 2004; horses (*Equus ferus caballus*), Feist and McCullough, 1976; mountain gorillas, Schaller, 1963; Watts, 2000). Similarly, females are reported to lead the group (horses, Welsh, 1975; brown and black lemurs (*Eulemur macaco*), Kappeler, 2000; leaf monkeys (*Presbytis johnii*), Stanford, 1990; white-handed gibbons (*Hylobates lar*), Barelli et al., 2008). As mentioned by Lamprecht (1991), there is no leader without followers. Similarly, Krause et al. (2000) consider as a leader an initiator of a new direction which is readily followed by other group members (see King, this issue for further discussion on this concept). Considering social status does indeed tell nothing about what causes individuals to be more or less successful in triggering a collective movement (Couzin and Krause, 2003). Dominant animals may be apparently more successful than non-dominant ones simply because they perform more departure attempts. The social leadership concept could also lead researchers to think that all departure attempts or initiations are successful, disregarding the (many) cases where they fail or when not all the group members follow. Initiators of movement, even when dominant, do not explicitly exert any kind of herding prior to departure. Keeping the above in mind, it would be worth studying what precedes the departure of the leader, and the joining process of group members. The pre-departure period might be crucial for the initiator's behaviour itself and the collective movement. Personal or consistent leadership where a single individual takes the decision by initiating every collective movement appears to be relatively scarce in nature or limited to a specific context (Lusseau and Conradt, 2009; Bourjade and Sueur, this issue; reviewed in fish by Krause et al., 2000). In one of the rare cases of personal leadership described in the literature, the dominant male in mountain gorillas (Schaller, 1963), departures appear to be not so much limited to this single animal since Stewart and Harcourt (1994) reported that the dominant male's departure was preceded by grunts emitted by group members. The concept of social leadership also tends to be irrelevant in the many cases where individual decisions are not made independently of conspecifics' decisions.

Leca et al. (2003) contrasted the concept of personal leadership with that of distributed leadership. Distributed leadership can be defined from repeated observed events of group movements. Indeed, the identity of the movement initiator may differ from one instance to another (event after event, day after day, Allee et al., 1947), but on the scale of a moving event, one lone animal initiates a movement. Some authors (Conradt and Roper, 2005; Sueur and Petit, 2008a) have considered this distributed leadership to be the equivalent of a shared consensus where many or all group members participate in decision-making. Leadership may then be a temporary role (see Peterson et al., 2002; Couzin et al., 2005; Reeb's contribution, this issue, for details of leadership bouts). Moreover, in this case, other group members can influence the joining of fol-

lowers (see the pre-departure period). Thus, when considering the initiation of collective movements over time, we see that the decision is distributed among many group members in many species. This kind of pattern has been observed in invertebrate species (e.g. honeybees, Seeley and Buhrman, 1999) and vertebrate species (birds, Allee et al., 1947; Radford, 2004; Ramseyer et al., 2009a; ungulates, Prins, 1996; Conradt and Roper, 2003; Dumont et al., 2005; Bourjade et al., 2009; Pillot et al., 2010; primates, Stolba, 1979; Boinski, 1993; Leca et al., 2003; Trillmich et al., 2004; Barelli et al., 2008; Jacobs et al., 2008; Sueur and Petit, 2008a).

3.2. In a biological context, is it relevant to use the term "leadership"?

Commonly, the word "leader" in the behaviour literature often refers to a single actor who decides for others and leads them by being in front. Note that the first moving animal is not systematically the front animal in progressing groups though qualified together as the leader. In addition to the fact that this term may preclude searching for any information about what makes other group members follow this individual, it also strongly suggests that a leader is always followed when moving (Lamprecht, 1992; see also Dyer et al., 2008). However, initiators fail to be followed and give up when not joined (Raveling, 1969; Byrne et al., 1990; Boinski, 1993; Stueckle and Zinner, 2008; Sueur and Petit, 2008a; Petit et al., 2009; Ramseyer et al., 2009a,b,c; Gautrais, this issue). Non-initiating individuals greatly influence the joining of group members and the outcome of an initiation as described in macaques (Sueur and Petit, 2008a) and chacma baboons (Byrne et al., 1990). Individuals may play a key role in the joining process thanks to their hierarchical status (rhesus macaques and baboons) or the strength of their social network (Tonkean macaques). In this context, it would be more relevant and less misleading to use "initiator" instead of "leader". Indeed, this term avoids the confusion between initiation and the probability of being followed, and any prediction about the next events, i.e. tautology.

3.3. Initiator identity and propensity for initiation

When individuals are equivalent, the probability of being a recurrent initiator of movement may be random. However, some individuals may perform departure attempts more often than other group members (Leblond and Reeb, 2006), although they may not necessarily be more successful in triggering a collective movement. The identity and state of the initiators may determine the group movement that emerges (Fischhoff et al., 2007; Krause et al., 2000). Behavioural properties, reversible in time, of an individual may temporarily bias its probability of being a recurrent initiator (Gueron et al., 1996; Couzin et al., 2002; see Krause et al., 2000 for a review of leadership in fish). This does suggest that individuals might have different thresholds regarding the internal or external stimuli above which they start moving (Messe and Ewbank, 1973 in Syme, 1981), explaining higher initiation rates when compared with individuals endowed with a higher threshold (Scott, 1956). Differences in threshold can be linked to rank, age, sex, body size, reproductive state, satiation level, temperament or experience (Michelena et al., 2010). Furthermore, rates of initiation might vary according to the behavioural context (foraging or social) (Krause and Ruxton, 2002).

In some species, adults predominantly initiate group movements (chacma baboons, Rowell, 1969; rhesus macaques, Sueur and Petit, 2008a; bar-headed geese (*Anser indicus*), Lamprecht, 1992; Canada geese, Raveling, 1969) whereas, in others, initiation may be shared between adults and juveniles (coatis (*Nasua narica*), Holekamp et al., 2000; brown lemurs, Jacobs et al., 2008; Tonkean macaques, Sueur and Petit, 2008a; white-handed gibbons, Barelli et

al., 2008). Although subadult and younger group members overtly participate in travel coordination among a diverse set of species, full adults are most active and their decisions predominate (Boinski, 2000). This lower propensity of juveniles to initiate a move could be related to predation pressure (Rhine and Westlund, 1981) and/or lack of experience (Raveling, 1969).

In grey wolves, imbricated variables (i.e. hierarchical status, sex and reproductive state) together explain initiation rates with the dominant animals that are the breeders leading travels more frequently than subordinate ones and breeder females more than non-breeder ones (Peterson et al., 2002). However, the predominance of dominant breeders initiating travels in smaller groups is relaxed in large packs of wild wolves (Peterson et al., 2002). The alpha male is reported to be the consistent first mover in group movements of mountain gorillas (Schaller, 1963; Watts, 2000) and dominant green woodhoopoes are more likely than subordinates to instigate movement to a new foraging site (Radford, 2004). Since they are in the group for longer than subordinate individuals, the dominant individuals may have the greatest knowledge of the territory and its most profitable areas. However, in this latter case, social status and reproductive state again overlap since dominant animals are also the breeders. This is also the case for dwarf mongoose pack movements that are initiated by the dominant breeding female (Holekamp et al., 2000). However, in the case of moving toward a neighbouring group, there is no more difference between high- and low-ranking individuals in green woodhoopoes (Radford, 2004).

Depending on the species, individuals of one sex may play a prominent role in leading. Females are reported to lead group movements proportionately more than males in some primate species (white-handed gibbons, Barelli et al., 2008; capped leaf monkeys, Boinski, 2000; diademed sifakas and red-fronted lemurs, Erhart and Overdorff, 1999; ringtailed lemur (*Lemur catta*), brown and black lemurs, Kappeler, 2000; Verreaux's sifakas, Trillmich et al., 2004; spider monkeys (*Ateles geoffroyi*), Milton, 2000), horses (Welsh, 1975; Berger, 1977), lions (*Panthera leo*) (Schaller, 1972) and hyenas (*Crocuta crocuta*) (Holekamp et al., 2000). Conversely, there is usually an adult male in the lead in chacma baboons (*Papio anubis*) (Rowell, 1969), savannah baboons (*Papio cynocephalus*) (Rhine and Westlund, 1981), brown capuchins (*Cebus apella*) (Boinski, 2000) and canids (Mech, 1970; Holekamp et al., 2000; Peterson et al., 2002) or during morning departures in chacma and hamadryas baboons (Kummer, 1968; Stueckle and Zinner, 2008). Finally, in new-world monkeys where females differ in their colour vision, it has been assumed that at least one trichromatic female will lead the group to fruiting trees (Smith et al., 2003). However, in moustached tamarins (*Saguinus mystax*), trichromatic females do not lead the progression more frequently than other individuals, whereas saddleback tamarin (*S. fuscicollis*) males preferentially initiate group movements (Smith et al., 2003).

It can be assumed that the motivation of individuals initiating movement is frequently physiologically based. Lactating females generally initiate progressions more than non-lactating females in plain zebras (*Equus burchellii*) (Fischhoff et al., 2007) and geladas (*Theropithecus gelada*) (Dunbar, 1983) whereas less frequently than pregnant or cycling females in chacma baboons (Stueckle and Zinner, 2008). Conversely, female squirrel monkeys (*Saimiri sciurus*) no longer participate in leading groups soon after giving birth (Boinski, 2000) and the sexual differences in initiation rates no longer exist for cycling females in white-handed gibbons (Barelli et al., 2008). A higher probability to move might depend on physiological condition, such as a low level of energy reserves (Krause et al., 2000; Rands et al., 2003, 2008, this issue; Holekamp et al., 2000, concerning dwarf mongooses). Physiological needs vary over time and animals may be forced to move to find the resources (food, water, refuge) required to fulfil their needs. The animals with the

greatest needs will be more likely to initiate group movements toward areas offering the needed resources, as exemplified by lactating females zebra (Fischhoff et al., 2007). As a consequence, the tendency to initiate a move varies seasonally, as in bar-headed geese where females lead significantly more than males in the pre-incubation and laying periods and less in other periods (Lamprecht, 1992).

When crossing dangerous roads, chimpanzee males (*Pan troglodytes*) move ahead and are described as less fearful (Hockings et al., 2006). Similarly, in fish, since predators tend to attack individuals at the front (Bumann et al., 1997), the individuals that initiate shoal movements are supposed to be bold (Leblond and Reeb, 2006). Such temperament effects on leadership may be further enhanced if individuals tend to interact more strongly with those ahead, so-called "frontal bias" (Huth and Wissel, 1992), which has found support from empirical work on fish shoals (Bumann and Krause, 1993). This may be a result of having a blind area to the rear in which fish cannot detect others, or individuals having evolved to bias their movement decisions more heavily to those ahead of themselves in moving groups. However, influence of starvation was found in roach (*Rutilus rutilus*) with food-deprived animals occupying front positions more often (Krause et al., 1998). Similarly, when testing golden shiners (*Notemigonus crysoleucas*) of similar size and experience, Leblond and Reeb (2006) suggested that hunger is likely to explain why some subjects consistently/frequently occupy the front position, although leading and boldness are not correlated. On the contrary, Harcourt et al. (2009) showed that bolder sticklebacks (*Gasterosteus aculeatus*) display greater initiative and are less responsive to their partners, whereas shyer individuals display less initiative but follow their partners more faithfully, favouring high leadership tendencies in the bolder partner among a pair. Likewise, shy sheep remain close to congeners when grazing whereas bold sheep graze at greater distances (Sibbald et al., 2009). In the same line, Conradt et al. (2009) suggested that individuals that are more socially indifferent than others instigate group movements. Ramseyer et al. (2009b) found that more reactive geese more often hold front positions during movement. Similarly, the more active and exploratory member of a pair of zebra finches (*Taenopygia guttata*) first arrives at a food source (Beauchamp, 2000). Kurvers et al. (2009) suggested that leadership in barnacle geese (*Branta leucopsis*) is closely related to some specific aspects of personality and that the movement patterns of a group might be shaped by the combination of personality types present in the group, as demonstrated by Harcourt et al. (2009).

3.4. What causes an initiator to be successfully followed?

Initiators may greatly vary regarding their success in being followed by group members. As stressed before, success may be influenced by the pre-departure period. However, what makes an initiator successful in triggering a collective movement is an important question. Generally, a successful start attempt is measured in terms of the number of followers. Is the number of followers the correct measure? Obviously, this number is directly dependent on the group or subgroup size (Jacobs, this issue). Therefore, in some cases, the number of potential followers around the initiator or, better, those able to witness its departure requires inspection. Nevertheless, the success of a start attempt is an arbitrary variable: some authors consider that an initiation is successful when at least one animal is following (Trillmich et al., 2004), whereas for some three followers are required (Leca et al., 2003) or more than 50% of the group (Erhart and Overdorff, 1999). In this context, we believe that a great number of followers, if not all the group members, are nevertheless a good indicator of group cohesion. As a consequence the exact number of participants is recommended to evaluate the influence of the initiator's behaviour and status.

Two initiators in similar contexts may differ in their number of followers, but their success may also vary from one day to another. Factors like the position within the group, behaviour or inherent attributes of the initiator as well as group disposition may explain the inter-individual or temporal differences in success.

The social status as related to the hierarchical or affiliative relationships with other group members sometimes influences the decision of joining of these latter (see point 5.2). It is noteworthy that the frequency of initiations does not predict the success of recruitment in white-faced capuchins (Leca et al., 2003), Tonkean macaques (Sueur and Petit, 2008a) and brown lemurs (Jacobs et al., 2008).

Females initiate group movements more frequently than males in some species of lemurs (Erhart and Overdorff, 1999), but no more difference between sexes is found when considering failed start attempts. Still in lemurs, Verreaux's sifakas females entrain more animals and over longer distances than males (Trillmich et al., 2004) while the opposite is found in chacma baboons (Stueckle and Zinner, 2008) and Canada geese (Raveling, 1969). Immature individuals fail to be followed in Canada geese (Raveling, 1969) and give up after having flown a short distance. Similarly, in bar-headed geese, when juveniles move while emitting a leaving call whereas parents do the same in another direction, the young run back to follow their parents (Black, 1988).

The position within groups before departure potentially affects the joining of group members. White-faced capuchins and rhesus macaques are more followed when departing from a central position (Leca et al., 2003; Sueur and Petit, 2008a). Departing from a central position perhaps prevents disrupting the communication and some group members missing a departure. However, such centrality does not provide any further advantage in dispersed or large groups. Thus, the result of an initiation seems to be related to the degree of cohesion of a group prior to departure, as found in white-faced capuchins (Leca et al., 2003). Also, the number of participants in the next move is positively related to the number of neighbours in close proximity to the initiator in several species, certainly thanks to local interactions (Ramseyer et al., 2009a,b,c). In addition to the spatial position, behaviours such as signalling departure and recruitment attempts influence the level of joining. This was described for initiators starting from the periphery of the group and thus not directly visible to the resting group members (Boinski, 1993). Radford (2004) suggested that vocalizing when leaving a group allows initiators to advertise their departure and attract the attention of other group members within a forest, i.e. a habitat that impairs visual communication. By contrast, subordinates proceed more frequently alone and silently than dominants when leaving a group, probably because being alone for a while would be advantageous for food access (Radford, 2004). Initiators signalling their departure by vocalizations (squirrel monkeys, Boinski, 1993; white-faced capuchins, Leca et al., 2003; green woodhoopoes, Radford, 2004), glances (macaques, Sueur and Petit, 2008a, 2009; white-faced capuchins, Leca et al., 2003), pauses (macaques, Sueur and Petit, 2008a, 2009), movements of different parts of the body (Ramseyer et al., 2009a,b) or speed (white-faced capuchins, Leca et al., 2003; macaques, Sueur and Petit, 2008a, 2009) are more followed than individuals that start without any display. As Black (1988) suggested, a bird with a non-attentive mate needs more time and more signals to stimulate its mate to a joint take-off.

However, in some species these displays did not really change the issue of a start attempt (Melhman, 1996; Trillmich et al., 2004; Stueckle and Zinner, 2008). Indeed, the behaviours produced before departure, assimilated to communication, may solely reflect the internal motivation of the initiator to move, a willingness to be followed or may intentionally be produced to recruit followers because of reluctance to go alone. Such intentionality of behaviours

can be guessed by the waiting time of initiators when not followed by a sufficient number of group members (Meunier et al., 2008; Ramseyer et al., 2009a,b,c) or by their preferred partners (Sueur and Petit, 2008a; Sueur et al., 2009) as well as by the giving-up propensity of initiators when not followed (geese, Ramseyer et al., 2009b; green woodhoopoes, Radford, 2004; hyenas, Holekamp et al., 2000; sheep, Ramseyer et al., 2009a; cattle, Ramseyer et al., 2009c; horses, Berger, 1977; chacma baboons, Byrne et al., 1990; macaques, Sueur and Petit, 2009; squirrel monkeys, Boinski, 1993; tamarins, Menzel and Beck, 2000; white-faced capuchins, Petit et al., 2009). Moreover, this is confirmed by the fact that initiators are often involved in pre-departure periods by displaying intention movements and so expressing their motivation in geese (Raveling, 1969; Black, 1988; Ramseyer et al., 2009a), sheep (Ramseyer et al., 2009b), cattle (Ramseyer et al., 2009c), horses (Bourjade et al., 2009) and macaques (Sueur and Petit, 2008a).

In some species, dominance status is positively related to an increasing probability of being followed when departing (rhesus macaques, Sueur and Petit, 2008a; green woodhoopoes, Radford, 2004; Canada geese, Raveling, 1969) whilst, in other species, the affiliative relationships become critical in the joining process (Tonkean macaques, Sueur and Petit, 2008b; Sueur et al., 2009; brown lemurs, Jacobs, personal communication). It has been proposed that social style and type of consensus might covary, with a greater influence of dominant individuals in decision-making in despotic species, and a more shared process in egalitarian species (Leca et al., 2003; Sueur and Petit, 2008a; see also Beauchamp, 2000). Dominant females that are known to lead packs of dwarf mongoose emit a "moving out" call before moving and only high-ranking callers are followed by other pack members (Holekamp et al., 2000). In some cases, the high status of the initiators allows them to move without displaying any signal since the whole group monitors the behaviour of these dominant individuals (rhesus macaques, Sueur and Petit, 2008a,b; brown capuchins, Boinski, 2000; social carnivores, Holekamp et al., 2000).

The time of initiation is a factor influencing the outcome of the initiation. In white-faced capuchins, if the period that covers the time elapsed between the arrival of the last joiner of a previous collective movement and a new start attempt of an individual is too short, the new start attempt will fail (Leca et al., 2003; Petit et al., 2009). Some animals still try to move during this refractory period while others never start during this time. One putative explanation to account for this discrepancy is that some individuals could be cognitively able to evaluate the stay time of the group or its mood in terms of vigilance and/or activity, as buzz-runners in bees do when travelling into the nest to feel how ready other bees are to fly (Rittschof and Seeley, 2008). As a consequence, an individual might refrain from initiating a movement during the refractory period. We have little information on the perception of time in animals, but some observations clearly suggest that dogs, pigeons and rats can time the intervals between two food deliveries, for example (Roberts, 2002). Animals are sensitive to time: they can learn to go to a particular place for food at a particular time of day (Reebs, 2000) and they can learn to time short intervals precisely upon the presentation of an external stimulus (Roberts, 2002). Alternatively, the initiator may be efficient in perceiving other group member behaviours (intention movements or activity changes) and thus decide to move or not accordingly. Visual processes such as those used in facial recognition (Kendrick et al., 1995; Dufour et al., 2006), following gaze direction (Tomasello et al., 1998; Kaminski et al., 2005) and facial expression (van Hooff, 1972) allow mammals to perceive fine details. We can assume that complex visual cues are processed and integrated by the initiator to achieve the accurate perception of the dispositions of other individuals (Barton, 2000). Differential efficiency in initiating a movement would emerge if some individuals prove to be more accurate than others in such

an evaluation of time or of others' behaviours, and in turn make different decisions. Similarly, Aubé and Shield (2004) found that initiators possess global knowledge of their environment, unlike other agents.

3.5. Do individuals benefit from initiating movement?

Erhart and Overdorff (1999) proposed that leading individuals benefit from greater control over the timing, distance and direction of the move as well as preferential access to resources (Barelli et al., 2008), an advantage over other group members during other daily interactions (King et al., 2008; Petit et al., 2009) and finally positive fitness consequences (Beauchamp, 2000).

By initiating and coordinating group movements, individuals, especially the females, may be able to manipulate their daily foraging efficiency and nutritional intake, and, thus, possibly impact on their long-term reproductive success (Boinski, 1991). In zebras, the lactation state was a key determinant of the initiator's role within a harem. By initiating harem movements, lactating females bring their harems to water before other harems and thus gain priority to water, which proves to be advantageous when water resources are restricted (Fischhoff et al., 2007).

4. Communication and information

Gregarious animals are known to be able to use information conveyed by their conspecifics in various aspects of their life, like group coordination during movement. Indeed, decision-making may be mediated by conspecifics' behaviour. In Bechtein's bats (*Myotis bechteinii*), individuals consider both their own information and the behaviour of others when deciding where to roost (Kerth et al., 2006). This information can be produced inadvertently, i.e. cues, or intentionally, i.e. signals (Maynard-Smith and Harper, 2003; Danchin et al., 2004; Searcy and Nowicki, 2005). Information produced during pre-departure periods, by the time of departure and also during the travel may be decisive for the fate of collective movement.

Departure attempts prove to be more successful when initiators employ looking back and trills in white-faced capuchins (Leca et al., 2003). Whether these behaviours represent true signals is unresolved because collective movements in this species also occur without trills and looking back before departure. We reported above that movements, postures, calls and glances increase before departure in several species. A change in frequency of behaviours before departing may not represent a sort of recruitment. They may reflect a higher level of arousal or muscular tonus (Trillmich et al., 2004). They can also allow animals to monitor their conspecifics (hyenas, Holekamp et al., 2000; white-faced capuchins, Meunier et al., 2008; macaques, Sueur and Petit, 2009). Indeed, sheep are reported to modify their behaviour when not followed by group members. Ramseyer et al. (2009a), although disregarding that these preliminary behaviours may represent signals, suggest however that sheep may intentionally emit these behaviours in order to recruit conspecifics (Prins, 1996). Alternatively, repeated attempts of sheep that are not followed soon may reflect a conflict of motivation, or anxiety associated with moving away from conspecifics, stopping when group members join the initiator. Fish, birds and mammals may move collectively without seemingly displaying preliminary, intentional or initiation behaviours prior to departure (Radford, 2004; Pillot et al., 2010). The question arises as to whether initiators' behaviour when departing or already moving may influence the decision-making of potential followers. In addition, in a moving group, cohesion requires that group members take into account the behaviour of neighbours, but which information and how many individuals are taken into account in decision-

making is still a puzzling issue. Conflicting data are reported about the influence of departure speed. Stueckle and Zinner (2008) found no significant effect of initiator speed on the success of initiation attempts in chacma baboons. The speed of departure contributes to the success of collective moves in white-faced capuchins: initiators are more successful in being followed when departing slowly (Leca et al., 2003). By contrast Tonkean macaque initiators are more successful in recruiting followers when the speed is high (Sueur and Petit, 2008a). More recently Pillot et al. (2010) found that trained sheep initiating a movement toward a target they were trained to approach move more rapidly than when moving between two grazing bouts. The greater the speed of the initiator may be a cue explaining that they are followed systematically (Sueur and Petit, 2009). Speed in itself is not a signal; however, its variation could be assessed and used by group members to decide whether to move or not. The conflicting results between species may be due to the fact that different types of movements are considered. It may be assumed that the decision to follow for the same animal may differ when a group member moves between two feeding bouts and when fleeing a predator.

Recent models show that directed group movements can result from leadership by a small number of goal-oriented individuals (Beekman et al., 2006; Couzin et al., 2005). Two categories of individuals may compose groups: those possessing valuable information about their environment and those unaware of this information (Reebs, 2000). We need to distinguish the cases of informed animals moving without signalling from individuals providing signals before or while moving. Are informed individuals more decisive or influential on collective decision-making? Informed individuals may transmit the information via direct or indirect recruitment. The study of mechanisms implied in the recruitment of conspecifics before emigration reveals the complexity of communication involved in bees, for example (Seeley et al., 2006; Vischher, 2007). Signals are required to draw other informed scout bees to a consensus for a new home, but also to activate non-informed bees (Rittschof and Seeley, 2008). However, cues may be used in insect societies. For instance, the frequency of interactions between *Temnothorax albipennis* scouts in new nests is a key mechanism modulating the speed of transition between the tandem run of active ants and the transport of inactive ants. When the rate of interaction increases, the transition is shorter (Pratt, 2005).

Conradt and Roper (2005) suggested that consensus is reached in large groups through self-organisation whereas in small groups through direct communication. It is now commonly admitted that interactions underpinning higher-scale properties at the level of the group in many species are local. Radakov (in Couzin and Krause, 2003) suggested that fish schools might interact through the propagation of relatively local information among group members. Collective behaviour needs no leader or global information, but may rely on the rapid propagation of local information about the motion of the nearest neighbours. Recent experiments have shown that interactions among small sets of individuals even in species that dwell in large colonies exhibit the basic ingredient of collective activities. Indeed, Pratt (2005) showed that a small population of scouts or, better, that the rate of interactions among a small number of *Temnothorax albipennis* scouts is decisive to catalyse the emigration of a colony toward a new nest. Meunier et al. (2008) also demonstrated that the transition between two functional areas in primates involves a rapid transition within small groups of white-faced capuchin monkeys.

Tracking the collective properties of biological systems is largely inspired by statistical physics (Ballerini et al., 2008b; Cavagna et al., 2008a,b; Giardina, 2008). The search for collective properties focused researchers' efforts on large biological systems or high-density populations. However, individuals of fusion–fission species that sometimes aggregate in large groups may also occur in

smaller groups (Sueur et al., 2010). Collective behaviours are partly defined as resulting from and emergent from a multitude of local interactions between individuals. In most cases, the distances of interactions are inferred because, except for a few cases, we have no access to them. Also, when groups gather in a large number of animals, the animals themselves constitute a physical barrier that impedes or hampers distant group members from interacting at least visually (Couzin, 2008). In this case interactions are obviously restricted to only the nearest neighbours although which information and which surrounding animals are taken into account are a matter of challenge (see Ballerini et al., 2008b for a discussion and Gautrais, this issue). Some fusion–fission species in fish, birds and mammals that occur in multitudes also live in smaller groups (Couzin and Laidre, 2009). Individuals possess senses such as vision or hearing that enable them to see all the conspecifics when the group size is small or moderate. Indeed, in these species, individuals are not obligated to participate in group living and they may be free to join or leave conspecific groups. One major question is whether the study of small groups is relevant in the scope of collective behaviour (Giardina, 2008, this issue). For example, do individuals behave in the same way when moving in small groups and in large ones? How the behaviour of individuals is modulated by group size and whether we can predict the collective properties of large groups by studying the behaviour of individuals in small groups are challenging key questions in biology. Local communication implies short distances and is mostly invoked for large groups. In small groups, individuals may have the opportunity to monitor all the activities of their neighbours. However, do individuals really collect information about all the group members in small groups, or do they only consider a few neighbours, as seen in large groups? In the latter case, are local interactions sufficient to account for group coordination? Furthermore, both types of communication can co-exist: for instance, in a troop of baboons composed of different units or subgroups, local communication occurs within subgroups while global communication underlies coordination between subgroups (for the entire troop). Acoustic communication has been evidenced in sparse individuals belonging to the same groups (McComb et al., 2000), facilitating group coordination (Braun et al., 2005). Another concern is that too much information could alter the efficiency of communication and raises the issue of which information to use or when to use it. In large and cohesive groups, mimetism via local interactions and closed neighbours will underlie the joining. Large and small groups may differ in the number of neighbours as well as in the quantity of information needed to reach a decision. A mere consequence is that the proportion of neighbours taken into account might be higher in small groups than in large groups, but very little literature has explored this point.

5. Mechanisms of joining movement

Two main mechanisms are often proposed to account for joining mechanisms: local rules that imply mimetic processes or internal and environmental constraints on individuals' choices. However, the processes involved in joining do not fit one or the other assumption only.

5.1. Local interactions and mimetism

Local interactions refer to information extracted about members' activity at a short range, i.e. on a scale much smaller than that of the group where interactions operate (Camazine et al., 2001; Detrain and Deneubourg, 2006; Couzin, 2008). The information may trigger or induce a non-linear increase in the probability of performing a behaviour already performed by group members through allelomimetism.

Collective movements are on a par with other collective activities performed by animals. The studies of cohesion in moving groups, which requires the coordination of multiple individual movements, have attracted much attention. Theoretical models inspired by self-propelled particle physics have proposed that simple rules of interaction, such as alignment, attraction at long range and avoidance at short distance, were able to reproduce different stable states/phases of moving groups and the transition between them (reviewed in Giardina, 2008). The empirical validation of these types of models is an acute issue, because it requires collecting data on large groups. Even more crucially, we need to measure interaction rules of individuals and ascertain which information/neighbours decision-making is based on. Large groups, to remain cohesive, must reach a collective or communal decision without any centralized control, involving agents that have access only to partial and local information (Couzin, 2008). The interactions of individuals between only a limited number of neighbours may however lead to a far higher number of individuals taking the same decision. The complex patterns observed (e.g. succession of departure, associations between individuals at the departure of a collective movement) are frequently explained using simple mimetic rules supposedly adopted by the multitude of agents (Couzin et al., 2005), more rarely taking into account social relationships (see below). Scott (1956) argued that group activities in canids are coordinated by allomimetic behaviour that is defined by a tendency to do what other animals in a group are doing via some degree of mutual stimulation. Mimetic behaviour where animals act like their congeners is well known in animal societies and implies positive behavioural feedback (Deneubourg and Goss, 1989; Sumpter, 2006; Petit et al., 2009). It allows the amplification of a decision taken by a few individuals, as exemplified by white-faced capuchins, where the collective choice of a direction in a binary choice artificially induced depends on mimetism (Meunier et al., 2008). A similar process has been qualified as social facilitation or response facilitation elsewhere (Byrne, 1994) but corresponds to the same mechanism. Using simple and local rules, some authors successfully explained using empirical data how biological systems may experience transition between different states. Buhl et al. (2006), using a modification of a Viscek model, simulate successfully the degree of alignment and the time spent aligned by marching locusts as a function of density. Thanks to 3-D reconstruction, Cavagna et al. (2008b) showed that large flocks of starlings manoeuvre in rather layer-like structures. An anisotropy was found in the distribution of the nearest neighbours, occurring more on the side of flying birds (Ballerini et al., 2008a). The major thesis is however that birds would interact with a fixed number of birds, independently of distance and therefore of density, rather than on neighbours depending on their distance (Ballerini et al., 2008b). Moreover, mimetism is likely to be ubiquitous in joining as demonstrated by empirical studies and models that proved its relevance to explaining group movements (insects, fish, birds, primates, etc.), but it is in itself unlikely to be sufficient to account for the collective moving of the whole group (see giving up and quorum).

5.2. Influence of social relationships

Almost all models of collective behaviour hypothesize that individuals are similar and thus involve the same interaction rules. Whether this assumption holds in all cases is questionable. Many species are capable of inter-individual recognition and/or display stable relationships among group members. However, few studies have tackled the joining decision as a function of social relationships or the structure of a social network (Sueur et al., 2009, 2010). Patterns of interactions relate to the degree of nepo-

tism that characterizes each species and constrains the daily interactions of these groups (Thierry, 2004). In rhesus macaques, offspring preferentially followed their mothers during movements whereas Tonkean macaques had the same probability of joining any other group member, except peripheral males who moved together (Sueur and Petit, 2008b). Meunier et al. (2008) showed how subordinate individuals avoid joining a movement for social reasons, choosing an opposite direction in an experimental setting. In addition, when investigating how an individual decides to join a movement, mimetism depends on social relationships. This selective mimetism has been found in brown lemurs (Jacobs, personal communication) and Tonkean macaques (Sueur et al., 2009), where individuals join a movement when their preferred partners have already moved. Such a pattern has been revealed by a modelling approach. Rhesus macaque initiators are reported to wait and recruit kin-related group members whereas Tonkean macaques eventually move if followed by affiliated partners (Sueur and Petit, 2009). The decision to move is conditioned by the network of social relationships and the decision of close partners when joining group mates (Camazine et al., 2001). Similarly, male Merino sheep have been reported to be more prone to mimic each other than females, leading to a higher synchrony of activity among males than among females (Michelena et al., 2006; Gautrais et al., 2007). In addition, the position and associations of group members during progression are influenced by affiliative relationships (Sueur and Petit, 2008b). Geese linked by close bonds are clustered during group movements (Ramseyer et al., 2009d). Selective mimetism probably exists in other species characterized by long-term social relationships and should be investigated deeply. Moreover, these findings advocate incorporating the fact that the responsiveness of individuals differs according to the identity of group members in some species in models of decision-making. However, considering that individual rules may differ according to social releasers does not preclude collective decisions obeying self-organized properties.

5.3. Order during progression

More studies were dedicated to order in groups' progression. No specific order during flight was reported in Canada geese (Raveling, 1969) but this random organization is scarcely reported in the literature. As proposed in the protection theory (see Sueur and Petit, 2008b), environmental constraints like predation pressure should lead powerful animals to walk at the more exposed front and the most vulnerable ones in the centre. In several species, organization often depends on age–sex classes. Buffalo display a repeatable structure caused mainly by adult bulls concentrating in the (sub-)front and (sub-)rear of the herd and a small concentration of them at the centre of the herd (Prins, 1989). Mothers and offspring are usually found travelling together in groups of ungulates (Tyler, 1972; Prins, 1989; Reinhardt, 1983) or primates (Altmann, 1979; Sueur and Petit, 2008b). Male baboons are often reported to walk at the front or back positions of progressions, the other group members occupying a more central position (Rhine and Westlund, 1981). Actually, such an arrangement may be partly due to the tendency of other group members to avoid the extreme locations of the progression by competing for the safest positions in a group as Hamilton (1971) proposed in the selfish herd effect. In some species, such a pattern does not imply a specific and consistent position for each group member (Altmann, 1979) whereas it is the opposite in other species (Rhine, 1975; Prins, 1989; Barelli et al., 2008). In a same age and sex group, geese held preferential positions during movements, with three of the most reactive being more often in the three

first positions than in any other position (Ramseyer et al., 2009d). Dumont et al. (2005) found that one heifer in a group of two-year-old animals occupied the first rank position in almost 50% of cases of movements between feeding areas or toward water points. Two animals were more often at the back. However, the leadership changed in other types of movement. There is a significant fidelity to the location within the herd by adult cows except when changes in reproductive status are involved (Prins, 1989). A fixed position within the herd can lead to differential access to high-quality food. Cycling females occupy the first positions in group movements of white-handed gibbons and arrive first at food sources while primary males walk in the last positions after the juveniles (Barelli et al., 2008). Buffalos located at the sub-front of a herd, such as high-ranking adult bulls, have the highest food intake and so a high condition (Prins, 1989). As a consequence, good or poor locations can be distinguished with regard to food intake (King et al., 2009). Pregnant cows improve their rank location, being in the best location relative to their original location at the lactation peak before moving back to their original location at the end of lactation (Prins, 1989). Adult bulls, after losing their prime condition and high rank, are found at the rear of the herd. Dominant adult males are found at the front in several primate species (Rhine, 1975; Rhine and Westlund, 1981; Waser, 1985; Boinski et al., 2000; Sueur and Petit, 2008b) while subordinate adult males more often occupied rear positions (Rhine, 1975; Rhine and Westlund, 1981; Waser, 1985). Squires and Daws (1975) documented that order in a progressing sheep flock is related to dominance, with dominant males being consistently found at the head. In grey-cheeked mangabeys (*Cercocebus albigena*), adult females are usually distributed rather randomly in progressions whereas independent juveniles are overrepresented in the centre (Waser, 1985). Similarly, cub and subadult lions walk in the middle of a travel progression (Holekamp et al., 2000). In yellow baboons, small juveniles are more centrally located than large juveniles and large juvenile males are more towards the front than large juvenile females (Rhine et al., 1991). This changing pattern reflects the position that individuals of each sex will occupy when reaching adulthood (Rhine et al., 1991). Dominant adult males are probably found more often than subordinate ones at the front because they also tend to be physically prime males, who are more confident and less cautious than older animals, and perhaps less hesitant about striking out for feeding and watering places (Rhine and Westlund, 1981; Hockings et al., 2006). Indeed, the senior male usually brings up the rear in cattle (Reinhardt, 1983) and, apparently, old or injured individuals are found at the end of the progressions in grey-cheeked mangabeys (Waser, 1985). The less nervous stallions were observed leading the group to drinking areas in horses (Berger, 1977). However, even if the members of a herd of cattle hold a specific position with consistency, the travelling order does not depend on dominance in cows (Reinhardt, 1983). As reported above, similar orders are reported whatever the considered taxa. Such a result suggests that environmental conditions could not solely explain this recurrent organization of individuals as the studied species live in very different conditions and environments. Thus, internal constraints, like boldness, age, knowledge or individual motivation might be good candidates to explain the emergence of such a configuration. This implies that the position within a progression is not the result of an intentional tactic to occupy the best place even if some positions allow some benefits.

The order and individual associations that are observed in collective movements are probably a consequence of internal constraints like individual motivations, physiological state, communication and social relationships (Sueur et al., 2009). Such simple rules can explain the observed regularity without referring to external constraints.

5.4. Does the decision-making depend on quorum rules?

Mimetic behaviour is not sufficient to explain non-linear responses. Individuals may be sensitive and respond to a change of behaviour of one group member, e.g. a departure but independently of neighbours' decision-making. Positive feedback effects are required to explain how the probability of mimetism, e.g. following already departed group members, increases non-linearly or in a step-like function (Sumpter, 2006; Petit et al., 2009). Recent research has established that quorum responses, in which an animal's probability of committing to a particular option increases sharply when a threshold number of other individuals have committed to it, are an important mechanism in the decision-making of ants, honey bees, cockroaches, fish and even humans (Pratt and Sumpter, 2006; Sumpter and Pratt, 2009). According to Conradt and Roper (2003), a quorum is a minimum number of group members that have to take or favour a particular action in order for the whole group to adopt this action. The threshold increases with group size, and thus so, too, does the accuracy of the decision (Sumpter et al., 2008, see below). However, if a non-linear response is observed at the level of the population or sub-population, experimental evidence that individuals follow the same rule is scarce. A group decision in bees and ants depends on a few informed individuals or scouts. Two hypotheses have been proposed to account for how bee scouts abide by one unique nest choice (Seeley and Visscher, 2004). First, a group decision would result from a consensus sensing, with bees moving to the new nest when all the bees performing waggle dances indicate one site, a kind of vote according to Conradt and Roper (2005). Second, take-off toward the new nest would follow a quorum sensing, the scouts noting when one site is being notified by a sufficiently large number of scouts. It was concluded that bees conform better to the quorum sensing hypothesis. Quorum sensing implies that bees do not depart until a threshold of 10–15 bees is reached. Pratt et al. (2002) also concluded that the transition between a tandem run and transport of inactive workers occurs in ants *Leptothorax albigipennis* when the number of ants in the new nest comprises between 9 and 17 ants. The transition from a tandem run to transport in ants and the time needed for the colony to emigrate depends on the size of the sub-population and encounter rates between nest mates in the nest, a higher quorum being required in larger nests (Pratt, 2005). More recently Petit et al. (2009) summarized a series of studies conducted with monkeys and proposed a model accounting for the collective departure of white-faced capuchin monkeys. In this species, individual animals make departure attempts. Movement success involves two key events: the probability of an initiator giving up and the probability of mimicking the movement of already departed animals. The collective movement has a high probability of occurring when a quorum of at least 4 monkeys move in the same direction. Initiators are highly dependent on followers' behaviour: the probability of remaining still after a backward glance if there are fewer than three followers is high. Above this threshold the probability abruptly drops. Following probability increases non-linearly with the number of departed animals (Petit et al., 2009). The combination of these two processes results in a U-shaped distribution of the number of monkeys moving together. In the same way, in the case of the recruitment of specific group members, macaques finally moved when joined by three preferred partners (Sueur and Petit, 2009).

In a recent experiment, three-spined sticklebacks *Gasterosteus aculeatus* were exposed to a situation of conflict by being confronted with identical or dissimilar numbers of replica fishes moving in two directions (Ward et al., 2008). The results show that when the number of replicas moving in each direction is equal, all the tested fishes choose to follow one replica most of the time. When the number of replicas differs, fishes collectively choose to follow the larger replica groups. The experimental data show that

only an excess of one replica is sufficient to obtain a majority of experiments with a consensus decision. This outcome became more clear-cut when the difference between the replica group size is ≥ 2 . However, whether sticklebacks use an absolute number or a relative number of replicas as quorum sensing remains unsolved.

Studies concluding quorum-based individual responses however do not provide unambiguous data. It may also be arguable whether a quorum-based response at the collective level relies exclusively on an individual-based quorum response, or whether individuals following a quorum lead to a quorum-based collective response.

6. Rationality, accuracy and efficiency of the collective decision

A collective decision would allow not only cohesion but also a rapid and accurate collective choice (Sumpter and Pratt, 2009). Groups are more likely to adopt the best choices when relying on collective decision-making than when conforming to the choice of a single individual (who can entrain a whole group in a false direction if possessing wrong information). This does not prevent groups from making a wrong choice or lacking flexibility. Ants *Lasius niger* can become prisoners of a collective choice in the sense that, once a first trail toward a food source has been established, a new trail is unlikely to compete with the first one and develop, even if leading to a richer source (Deneubourg and Goss, 1989). Nevertheless, a collective decision would usually be more accurate since it is based on the knowledge of many individuals (cf. Conradt and Roper, 2005). Biro et al. (2006) demonstrated that pairs of pigeons were better when homing than individuals navigating alone. Ward et al. (2008) found that the superiority of the collective decision in three-spined sticklebacks confronted with binary choices would however require more than eight individuals, indicating that accuracy depends on group size. During the pre-departure period, the decision speed would be higher due to the readiness of the group and the display of individual motivations (for direction and time of movement) for alternatives. Whenever a decision depended on a quorum rule, the decision speed also increased because a small number of individuals might tip up the decisional process. Fish are considered highly effective in integrating information without a direct comparison of the available options (Sumpter et al., 2008). However, integrating speed and accuracy may be conflictual. Accuracy probably depends on the number of individuals involved in the decision-making process. In the case of a single individual deciding for the whole group, even if the decision process is fast, the risk of the whole group making the wrong choice is high. On the contrary, when many individuals are involved in the decision-making process, they slow it down. However, the resulting final choice is the average of individual knowledge and choices and will probably be the most correct and adaptive (Conradt and Roper, 2005), for example, horses engaged in a long decision-making process when facing challenging choices about which direction to move in (Bourjade and Sueur, this issue). However, does high speed also allow accuracy? In some cases, deciding rapidly could be adaptive, especially in inter-group encounters or in the presence of predators (Ward et al., 2008). However, Franks et al. (2009) stated that, in cases of emergency, a rapid decision may be less accurate.

7. Conclusion

Most of the literature on collective movements over last years focused on a minimalist point of view, proposing models strongly influenced by statistic physic. The motive relies on proposing the simplest rules of interactions among individuals that allows the emergence of some universal collective patterns. On the other

side, biologists recently dedicated themselves to understand collective decision-making, forwarding several parallels with human decision-making. Fish, birds and mammals would obey despotic decision, consensus, decide upon voting decision or respond following quorum sensing. Most of these hypotheses remain to be tested, requiring quantifying detailed individual responses implied in collective moving. We defend the idea that a collective movement corresponds to a temporal sequence that firstly involves individual decision-making during the pre-departure period and initiation (signalled or not) and secondly consecutive mimetic behaviour (with or without selectivity) that corresponds to the following during the ongoing movement. In this review, we pointed out that decision-making for moving collectively can be reached by a combination of different rules, i.e. individualized (based on inter-individual differences in their physiology, energetic state, social status, etc.) and self-organized (based on simple response) ones (Camazine et al., 2001; Detrain and Deneubourg, 2006; Meunier et al., 2008; Petit et al., 2009; Sueur et al., 2009). One of the ways to switch from individualized mechanisms to self-organized ones might be that individuals follow a quorum rule. As proposed by Sueur et al. (2009), the first followers may join the movement according to a combination of selective responsiveness to movement induced by group members and self-organized mechanisms. Affiliative relationships explain selective mimetism, and once a quorum of followers is reached, the movement tips over with the joining of the last group members according to an anonymous mimetic process (Sueur et al., 2009).

One can assume that, in the period preceding departure, there is a pre-selection of one of the possible alternatives and that, in the second phase, it is the selection of the best alternative that is implemented, in most cases by amplification. Thus, inasmuch as collective decision may allow optimal choice, it derives from self-organized mechanisms.

According to Conrardt and Roper (2005, 2009), consensus could result from either an unshared or a shared decision. In a shared decision, part of (partially shared) or all of the members (equally shared) of a group would participate in the consensus. In an unshared decision, one individual would decide and the others abide by its decision (Conrardt and Roper, 2005). However, in most cases, following is not the result of coercion. Thus all followers participate in the process and, as a result, share the decision. In this context, following is the simplest outcome of an individual decision. Animals may choose to stay or follow, or choose between alternative destinations. So, even in the cases where a single animal could be observed initiating all movements, other group members may indeed influence or intervene in the collective decision. As a consequence, the accuracy of the decision could vary since decisions taken collectively are often more accurate, because they efficiently utilize the diverse information possessed by group members (Conrardt and Roper, 2005; Franks et al., 2002). Moreover, a shared motivation limits the conflicts of interest and allows the decision to be reached more rapidly at the selection step, i.e. before departure.

The same intricate combination of selective responsiveness with individualized and non-linear anonymous responses acting together could also be applied in the context of predation or the case of urgency. In some cases, a few individuals are informed of a danger and by their anti-predator response will give information to their congeners thanks to local communication, provoking collective escape (Giardina, 2008). Such situations do not imply different scenarios from the one proposed above. This is the balance between anonymous responses and more individualized ones submitted to self-organized mechanisms that differs in emergency contexts with the former contributing more to the whole process.

Moreover, the rules described above would still hold whatever the group size and its stability over time (see Kerth, this issue).

In large groups, collective movements will involve less individualized mechanisms and more self-organized ones, contrary to small groups or species with developed cognitive skills and/or social relationships in which the converse arrangement will be found (more individualized and less self-organized mechanisms). Indeed, despite an apparent similarity between individuals in species living in large groups, some bold fish are for instance more prone to initiate movement than shy fish, which often become followers (Harcourt et al., 2009). Likewise, in ants, where inter-individual differences are often underestimated, nutrient status and knowledge are parameters explaining why some individuals lead group movements more often (Robinson et al., 2009). Moreover, contrarily to what is often proposed, anonymous processes have been recently demonstrated in primates (Meunier et al., 2008; Petit et al., 2009; Sueur et al., 2009).

Thus, our postulate is that the same scenario probably underpins nearly all cases of collective movements but the balance between anonymous and individualized responses in the global decision-making process will differ according to the environmental context, group size, the degree of sociality of the considered species and its cognitive capacities. It is now necessary to undertake studies focusing on inter-individual differences in species living in large groups as well as research investigating mimetic processes in species living in small groups or with great inter-individual variability. This would allow us to go beyond the traditional reported dichotomy between small and large groups and their supposed different behavioural rules, in order to elucidate entirely the complexity of these fascinating collective phenomena and make true advances in the domain.

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