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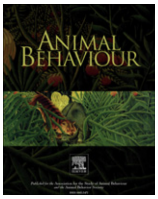

Selective mimetism at departure in collective movements of *Macaca tonkeana*: an experimental and theoretical approach

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In primates, authors have reported the specific organization of individuals during collective movements. Some authors have suggested that intentional mechanisms underlie this particular organization because primates have high cognitive abilities that can allow them to use this kind of behaviour. However, mechanisms underlying the emergence of complex systems are not necessarily complex and can be based on local rules. We investigated the joining processes observed during collective movements in one semifree-ranging group of Tonkean macaques, using an individualized agent-based model. The complex patterns observed, such as departure latencies, associations and order of individuals at departure of a collective movement, could be explained using a rule based on affiliative relationships. The decision an individual took to join the movement depended on the departure of its strongly affiliated individuals. Thus even in primates, complex collective behaviour may emerge from interactions between individuals following local behavioural rules.

Living in groups reduces predation risk (Wrangham 1980) while increasing foraging efficiency (Alexander 1974; Giraldeau & Caraco 2000). However, this strategy requires group members to be cohesive and thus synchronize their activities (Krause & Ruxton 2002; Conradt & Roper 2005). In many species, different activities cannot be carried out in the same area. Animals often have a place to rest: a cliff for some primates or birds (Kummer 1968; Danchin et al. 1998), a burrow for many social carnivores or rodents (Fox 1972; Rasa 1986), a collective nest for social insects (Camazine et al. 2001). However, individuals have to move collectively to another spot to forage or to drink (Kummer 1968; Boinski & Garber 2000; Fischhoff et al. 2007).

In primates, authors have reported a specific organization of individuals during collective movements (Rhine & Westlund 1981; Waser 1985; Rhine & Tilson 1987; Hockings et al. 2006). For instance, dominant individuals may occupy a specific position in the group movement, to obtain prior access to food or to decrease the predation risk (Whitten 1983; Waser 1985; Janson 1990; Hall & Fedigan 1997; Boinski et al. 2000). Intentional mechanisms might underlie this specific organization, thanks to the high cognitive abilities of primates as discussed in Hemelrijk (2002) and Tomasello & Call (1997). In fact, Boinski & Campbell (1995) have suggested that white-faced capuchins, *Cebus capucinus*, show coercive behaviour to manipulate intentionally the decisions of other group members, thus demonstrating a 'Machiavellian intelligence' (Whiten & Byrne 1997). However, other complex systems exist and mechanisms underlying their emergence are not necessarily complex (Camazine et al. 2001). For instance, the complexity of nests in social insects is not run by a central authority requiring sophisticated cognitive abilities but emerges from simple and local rules between the insects themselves and between the insects and their environment (Deneubourg & Goss 1989; Bonabeau et al. 1997; Camazine et al. 2001). Using these simple rules, authors have explained how large groups such as fishes in shoals or birds in flocks coordinate their movements (Camazine et al. 2001; Couzin & Krause 2003; Biro et al. 2006), fireflies synchronize their flashings (Strotgatz & Stewart 1993; Ramirez-Avila et al. 2003) and locusts coordinate their marching (Buhl et al. 2006). Self-organization seems to be a parsimonious way to explain the complexity of

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animal societies (Deneubourg & Goss 1989; Camazine et al. 2001; Detrain & Deneubourg 2006).

Recent studies have demonstrated that such self-organized processes can also exist in small groups with highly structured relationships. For example, 'mimetic synchronization' exists in Merino sheep, *Ovis aries* (Gautrais et al. 2007), where the probability that an individual will carry out an activity increases with the number of other group members already displaying this activity. Similarly, in semifree-ranging white-faced capuchin monkeys, the choice of a direction seems to depend on 'anonymous mimetism' (Camazine et al. 2001) when collective movements involving binary choice are artificially induced (Meunier et al. 2006). These self-organized processes exist even through capuchins are known to use recruitment behaviours to initiate a movement (Leca et al. 2003) or to occupy specific spatial positions within the group (Janson 1990; Hall & Fedigan 1997). From these contrasted findings, it is therefore crucial to investigate whether the organization of individuals during a movement may be explained by local rules.

In this study, we assessed how individuals join a collective movement in a semifree-ranging group of Tonkean macaques. Tonkean macaques use recruitment signals and preliminary behaviours to coordinate their movements (Sueur & Petit 2008a). Moreover, the organization of group members at departure seems to be relatively stable and specific, and affiliative relationships seem to influence this pattern (Sueur & Petit 2008b). Nevertheless, these previous quantitative analyses only allowed us to highlight some correlations between variables, and it remains unknown why or how an individual decides to join a movement. Only modelling would allow an assessment of which mechanism underlies the individual decision.

With a modelling approach, two alternative options are possible: one can (1) predict some behaviour or (2) explain it (Bryson et al. 2007; Sellers et al. 2007; Epstein 2008). By using an agent-based model, we can recapture all variables of observed collective movements and then compare the observed with the simulated phenomena. This kind of analysis was not possible using traditional approaches (Couzin et al. 2005; Meunier et al. 2006; Bryson et al. 2007; Sellers et al. 2007; Epstein 2008). We aimed to assess whether the decision to move responded to simple rules based on the number and the identities of individuals already moving (Pratt et al. 2005; Sellers et al. 2007). We do not claim that collective movement would be only self-organized processes. As reported above, Tonkean macaques seemed to use intentional behaviours during collective movements (Sueur & Petit 2008a). Furthermore, self-organized processes as well as more complex behaviours such as intentional ones can underlie the same phenomenon (Camazine et al. 2001; Hemelrijk 2002; Detrain & Deneubourg 2006; Meunier et al. 2006). Nevertheless, we expected that the joining processes (i.e. the probability that an individual joined a movement) would be based on simple and local rules (Deneubourg & Goss 1989; Camazine et al. 2001) rather than on a calculation of the best strategic position to occupy during movement (Whitten 1983; Waser 1985; Janson 1990; Hall & Fedigan 1997; Boinski et al. 2000). Scientists have long considered rationality to be the best explanation of how an individual behaves faced with its conspecifics (Sumpter 2006). Nevertheless, we have to give priority to the more parsimonious explanation among different hypotheses (principle of Occam's razor). In this context, self-organization is a simpler explanation than intentional behaviours implying high cognitive abilities (Detrain & Deneubourg 2006) and could lead to well-adapted choices (Sumpter & Pratt 2009).

Comparing the experimental data on collective group movements to an individualized agent-based model (i.e. characteristics and relationships of each studied Tonkean macaque were implemented in the model), we tested four hypotheses: (1) Individuals are independent (null hypothesis). (2) Individuals join a movement according to the number of individuals having already joined whatever their identity (anonymous mimetism) as found in capuchin monkeys (Meunier et al. 2006) or in merino sheep (Gautrais et al. 2007). (3) Individuals only join a movement when their relatives are already involved in it (mimetism according to kinship). Indeed, several authors have reported that kinship influences a range of social behaviours in primates (Gouzoules & Gouzoules 1987; Mateo 2003; Chapais & Berman 2004). (4) Individuals join a movement if their preferred partners (i.e. kin and nonkin individuals) have already moved (mimetism according to affiliation). Indeed, affiliative relationships seem to influence certain behaviours such as social information transmission (Coussi-Korbel & Fragaszy 1995; Voelkl & Noë 2008), alliances (Chapais et al. 1991; Chapais & St-Pierre 1996) or grooming (Thierry et al. 1990). In the last two hypotheses, individuals will base their decision to join a movement on the identities of the individuals that have already moved. In fact, in Tonkean macaques, we expected that an individual's decision to move would depend on mimetic processes modulated by social relationships between group members, especially affiliative ones.

METHODS

Subjects and Environment

The group of Tonkean macaques under investigation was bred in the Centre of Primatology at the University of Strasbourg, in seminatural conditions. All group members were born in captivity. The study group was composed of five matrilines (see Supplementary material for details). At the time of the study (November 2005 to March 2006), it consisted of 10 individuals: one adult male (10 years old), five adult females (10, 9, 7, 6 and 5 years old), one subadult male (3 years old) and three juveniles (2, 1 and 1 year old). The composition of the group was comparable to that of several wild and stable groups (Whitten et al. 1987; Supriatna et al. 1992) that were composed of a small number of individuals (6–14) and with only one or two males (Pombo et al. 2004; Riley 2005, 2007). The study group lived in a park (0.5 ha), which included trees, bushes and grassy areas. Individuals had an inside shelter, where commercial pellets and water were provided ad libitum. Fruit and vegetables were distributed once a week, outside of observation hours. Group members used the parkland in a heterogeneous way and moved collectively (see Observed and simulated distributions of number of joiners in the Results) between areas devoted to specific activities. The mean distance of a collective movement was 33.7 ± 1.42 m. The park range was thus large enough to study collective movements as shown in several previous studies on several species with various group sizes (from 10 to 22 individuals; Leca et al. 2003; Meunier et al. 2006; Gautrais et al. 2007; Jacobs et al. 2008; Sueur & Petit 2008a, b).

Definitions

The beginning of a collective movement was defined by the first departure of an individual who walked more than 10 m in less than 40 s. This criterion was the same as the one used by Leca et al. (2003), Jacobs et al. (2008) and Sueur & Petit (2008a, b) and it allowed us to discriminate first departures (i.e. initiations) from other movements such as foraging movements or intention movements used in the preliminary period (Sueur & Petit 2008a). The departure of the first individual to depart over a distance of more than 10 m was an obvious signal for other group members (Leca et al. 2003; Jacobs et al. 2008; Sueur & Petit 2008a, b).