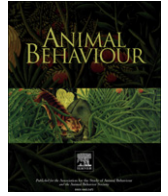


Contents lists available at [ScienceDirect](http://www.sciencedirect.com)

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

C. Sueur^{a,b}, O. Petit^{a,b,*}, J.L. Deneubourg^{b,1}^a *Ethologie des Primates, Département d'Ecologie, Physiologie et Ethologie, Institut Pluridisciplinaire Hubert Curien*^b *Service d'Ecologie Sociale, Université libre de Bruxelles*

ARTICLE INFO

Article history:

Received 14 January 2009

Initial acceptance 13 March 2009

Final acceptance 19 July 2009

Available online xxx

MS. number: 09-00032R

Keywords:

affiliation
agent-based model
consensus
decision making
kinship
Macaca tonkeana
primates
self-organization
Tonkean macaque

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.

© 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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

* Correspondence: O. Petit, Ethologie des Primates, Département d'Ecologie, Physiologie et Ethologie, Institut Pluridisciplinaire Hubert Curien, 23, rue Becquerel, 67000 Strasbourg, France.

E-mail address: odile.petit@c.strasbourg.fr (O. Petit).

¹ J. L. Deneubourg is at Service d'Ecologie Sociale, Université libre de Bruxelles, CP 231, Campus Plaine, Boulevard du Triomphe, 1050 Brussels, Belgium.

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 matriline (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).

A 'joiner' was defined as any individual walking for more than 5 m in a direction that formed an angle of less than 45° with the direction of the first individual to depart. We considered a collective movement as finished when no individual joined the movement within 5 min of the departure of the first individual or the last individual to join (Sueur & Petit 2008a, b).

Observation Procedure

The group was observed and filmed 4 h per day between 1000 and 1600 hours. Each collective movement was recorded onto videotape. When the first departing individual was joined by at least one other individual, a collective movement was observed using the all-occurrence sampling method (Altmann 1974). Participants (first departing individual and joiners) were observed one by one using video scoring. Only movements not associated with conflict or sexual consort, and for which all group members were present at the start (≤ 10 m from the point where the first departing individual started, Sueur & Petit 2008a, b), were considered. We observed a total of 146 collective movements but only 111 collective movements fitted our criteria and were analysed below.

Data Scoring and Calculation

We scored the number of joiners for each collective movement. Then, we calculated the frequency of collective movements for each number of joiners. We scored the identity and the departure latency of the first departing individual (ΔT_{01}) and of every joiner ($\Delta T_{j-1,j}$). We calculated the rank of each individual, regardless of its identity, during the joining process. The rank of the first departing individual was rank 1, the rank of the first joiner was rank 2, and the rank of the j th joiner was rank $j + 1$. We calculated the departure latency of the first departing individual ΔT_{01} by scoring the time elapsed between the end of the previous collective movement and the departure of this individual. This latency corresponded to the duration for which this individual was stationary, that is, carrying out an activity other than moving. We then scored the departure latency of each joiner, that is, the departure latency of the joiner j , $\Delta T_{j-1,j}$ corresponding to the time elapsed between the departure of the joiner $j - 1$ (i.e. the previous departing individual, first departing individual included) and the departure of the joiner j . Since we never observed an individual joining the movement at the same time as another, two individuals never had the same rank. According to the equation of each model version, the joining of the joiner j was not solely influenced by the identity of the joiner $j - 1$ but by all already moving agents. This formulation ($j, j - 1$) was only a way to calculate the departure latencies between ranks and the order and associations of individuals during the joining.

Affiliative Relationships

The affiliative relationships correspond to preferential association between certain group members (nonkin-related and kin-related). Using instantaneous sampling every 5 min (Altmann 1974) outside a moving context, we quantified affiliative relationships by the number of scans where individuals were observed in body contact. We only kept scans in which all group members were observed. In total 111 scans were collected. For subsequent analyses, we used the 'ratio of contacts'; this was the number of scans for which two individuals were in contact per the total number of scans (see Supplementary material for details). The distribution of affiliative relationships was not homogeneous with some individuals seen together more often than others (chi-square of

homogeneity: $\chi^2_{33} = 67.9$, $P = 0.0003$). Kinship and affiliative relationships were not significantly correlated (matrices correlation, Dietz R test: $r = 0.07$, $N = 10$, $P = 0.357$).

The Model

Definitions of indices and coefficients can be found in Table 1. The coding details of the different versions of the model can be found in the Supplementary material.

Parameters

As the distribution of the first departure latencies corresponded to an exponential distribution (see Preliminary analyses in the Results), the departure probability of the first individual ψ_{01} was the log gradient of this exponential distribution, that is, the inverse of the mean departure latency of the first departing individual (Amé et al. 2006; Meunier et al. 2006; Gautrais et al. 2007):

$$\psi_{01} = \sum_{i=1}^n \lambda_i \quad (1a)$$

Given that $\psi_{01} = 0.0007$ per s and $n = N = 10$, the probability per individual of departing first is $\lambda_i = 0.00007$ per s.

Individuals may have the same mean departure latency while their frequency of departing first (i.e. departure probability) may differ. Based on this result, the mean latencies to depart first (ΔT_{01}) were equal whatever the individual, even though the individual probabilities to depart first may be different:

$$\Delta T_{01} = \frac{1}{\psi_{01}} \quad (1b)$$

Thus, individual differences in first departure probabilities were taken into account in the model (see Supplementary material for details).

In a mimetic process where the departure probability is proportional to the number of individuals already moving, the

Table 1
Definitions of parameters used in this study

Parameter	Definition
a_i	Number of non-kin related moving agents for individual i
C	Mimetic coefficient
ΔT_{01}	Departure latency of the first departing individual, i.e. time elapsed between the end of the previous collective movement and the departure of this individual
$\Delta T_{j-1,j}$	Departure latency of a joiner j , i.e. time elapsed between the departure of the joiner $j - 1$ (first departing individual included) and the departure of the joiner j
j	Number of individuals participating in the movement
λ_i	Departure probability of individual i
k_i	Number of kin-related moving agents for individual i
$M(k,i)$	Ratio of contacts between the moving individual k and the resting individual i
ψ_{01}	First departure probability, probability of starting a movement, equal to the sum of λ (departure probability of each individual)
ψ_i	Probability per unit time of an individual i becoming a joiner (corresponding to the kinship hypothesis and the affiliation hypothesis where the identities of individuals are taken into account)
ψ_j	Probability per unit time that one of the n resting agents became the j th joiner (corresponding to the independent hypothesis and the anonymous mimetic hypothesis where the identities of individuals are not taken into account)
n	Number of resting individuals
N	Number of individuals in the group

probability per unit time that one of the n resting agents became the j th joiner was:

$$\psi_j = (\lambda + C(j-1))n \quad (2a)$$

where C was the mimetic coefficient per individual.

The departure latency of the joiner j was:

$$\Delta T_{j-1j} = \frac{1}{(\lambda + C(j-1))(n - (j-1))} \quad (2b)$$

or

$$\begin{aligned} \frac{1}{\Delta T_{j-1j}} &= (\lambda + C(j-1))(n - (j-1)) \\ &= (\lambda - C)(n+1) + j(2C + Cn - \lambda) - Cj^2 \end{aligned} \quad (2c)$$

As the distribution of the inverse of departure latencies of joiners fitted a parabolic curve (see Preliminary analyses in the Results), the equation of the departure probabilities was:

$$\frac{1}{\Delta T_{j-1j}} = -0.0131 + 0.0237j - 0.0021j^2 \quad (2d)$$

with $\lambda = 0.00007$ per s , $n = N = 10$ and C approximately equal to 0.001–0.002 (see Supplementary material for details of the calculation of C).

The number of individuals, individual identities, network of kinship and affiliative relationships of the observed group were included in the model. Thus, the number of agents N was fixed to 10. We set the values of kinship at 0 for nonrelated individuals and at 1 for related individuals, whereas the values of affiliative relationships were the ratios of contacts for each dyad, which varied from 0 (individuals never in contact) to 1 (always in contact). We chose to consider the kinship as binary because several studies have reported the influence of kinship (basically kin or nonkin) on many social behaviours, whatever the degree of relatedness (see Gouzoules & Gouzoules 1987; Chapais & Berman 2004). At the start of a simulation, all agents (N) were in an area called the resting area and had to move to another area, the foraging area. We implemented the departure probability λ_i of each agent. The departure probability of the first departing individual, the only individual that would not be influenced by the other group members to move, was the same for the four versions of the model. Given that (1) the distribution of affiliative relationships was not homogeneous, (2) the affiliation differed from an anonymous system, (3) affiliative relationships were not correlated with kinship relationships (see *Affiliative relationships* for details), we can consider the three models (anonymous, kinship and affiliation) as distinct with no overlap of joining mechanisms. Owing to the scale of the area covered by the observed group (see *Methods*), we assumed in the model that all agents were aware of the state (resting or moving) of all other agents at any time. This condition was necessary to assess whether individuals had global or local information about the joining process.

Independence hypothesis

The first hypothesis assumed that individuals were independent: the departure probability of an individual was not influenced by the departure of the other group members. As a consequence, the individual departure probability remained constant (independent of the rank).

Under this hypothesis, the probability that one of the n resting agents (e.g. individual i) became a joiner j per unit time was λ_i . According to equations (1a) and (1b), the departure latency of the joiner j was the inverse of the sum of the λ_i of the n resting agents:

$$\Delta T_{j-1j} = \frac{1}{\sum_{l=1}^n \lambda_l} \quad (3)$$

In our case, the probabilities were identical with $\lambda_1 = \dots = \lambda_N = \lambda$

Anonymous mimetic hypothesis

The second hypothesis specified that individuals will be influenced by the departure of their conspecifics, thanks to a mimetic process. To test this hypothesis, we added a mimetic coefficient C in the above version of the model (independent hypothesis). The probability per unit time that one of the n resting agents became the joiner j under the anonymous mimetic hypothesis was obtained from equation (2a) and its departure latency from equation (2b). In this version of the model and according to equation (2a), a resting agent had the same probability of joining the already moving agents whatever their identities. Thus, whatever their identity, all moving agents had the same probability of being joined by resting agents.

Kinship hypothesis

The third version of the model tested the influence of kinship relationships. In this case, the departure probability of an individual was only influenced by the number of its relatives participating in a movement.

The identity and kin relationships of each individual were included in this version of the model. In contrast to the previous versions, the probability per unit time that one of the n resting agents became the joiner j differed between agents with respect to their kin relationships with the already moving agents.

The probability of an individual i of becoming a joiner j under the kinship hypothesis was:

$$\psi_i = \lambda + C(k_i \times 1 + a_i \times 0) = \lambda + Ck_i \quad (4)$$

where k_i is the number of kin-related moving agents for individual i and a_i is the number of nonkin-related moving agents for individual i . In this version of the model and according to equation (4), the more a resting agent had kin-related moving agents, the greater was its probability of joining them. Thus, the more a moving agent had kin-related resting agents, the greater was its probability of being joined.

Affiliation hypothesis

In this hypothesis, we tested the influence of the affiliative relationships between group members on the decision to join.

This version of the model took into account the individual identities and the affiliation of each dyad. Each observed affiliation relationship (measured by the number of scans where individuals were observed in body contact, see *Affiliative relationships*) of the study group was implemented in the model allowing us to consider affiliation differences between dyads. The probability per unit time that one of the n resting agents became a joiner j differed between the resting agents with respect to their affiliative relationships with the already moving agents.

The probability of an individual i becoming a joiner j under the affiliation hypothesis was:

$$\psi_i = \lambda + C \sum_{k=1}^N M(k, i) \quad (5)$$

where $M(k, i)$ was the ratio of contacts between the moving individual k and the resting individual i which accounted for their affiliative relationship (see above for how ratio of contacts was measured).

In this version of the model and according to equation (5), the more a resting agent had strongly affiliated moving agents, the

greater was its probability of joining. Thus, the more a moving agent had strongly affiliated resting agents, the greater was its probability of being joined.

Simulation

We implemented the different versions of the model, corresponding to each hypothesis, in Netlogo 3.1.4 (Wilensky 1999; Bryson et al. 2007). At each time step (1 s) in the model, a number between 0 and 1 was randomly attributed to each resting agent (i.e. at the resting area); when this number was higher than the theoretical departure probability of each agent, the individual left the resting area for the foraging area; if this number was smaller than the theoretical departure probability, the agent did not move. The identity, the rank and the departure latency of each agent participating in a movement (first departing individual or joiner) were scored for each simulated collective movement.

To be consistent with the experimental situation, we stopped a simulation when no agent joined within 300 s of the departure of the first departing individual or the last joiner (see Definitions). As with the observed collective movements, from zero to nine agents can join a first departing individual in the simulated collective movements. We set the number of simulations to 1000 for each hypothesis and each set of tested parameters.

Statistical Analysis

The observed distribution of the number of joiners and those obtained from the simulations (under the four hypotheses) were compared using Spearman rank correlation tests. Observed and simulated means and variances of departure latencies were compared using Kolmogorov–Smirnov tests. We used a Dietz R test to correlate matrices of observed and simulated frequencies of direct joining (i.e. when individual A was the joiner j and B the joiner $j + 1$ or when individual B was the joiner j and A the joiner $j + 1$). We set the number of permutations to 10 000 for matrices correlations. Permutations of the rows and columns of one of the two matrices were automatically generated and, for each permutation, statistical values were calculated. This method provided more accurate and stable P values (Hemelrijk 1990; de Vries et al. 1993; Whitehead 1997). We used Spearman rank correlation tests to compare the observed and simulated orders of individuals at departure.

The significance level was set at 0.05. All tests were two tailed. We carried out tests using SPSS 10.0 (SPSS Inc., Chicago, IL, U.S.A.) and SocProg 2.3 for the correlations of matrices (Whitehead 1997; Whitehead 2007; Sueur & Petit 2008b).

RESULTS

Preliminary Analyses

Analysis of the observed departure latencies

We compared the different observed departure latencies for the group. A Kruskal–Wallis test showed that the distribution of the interindividual departure latencies was not consistent ($H_9 = 197.8$, $P < 0.00001$; Fig. 1). A Dunn's multiple comparisons test revealed that the departure latencies of the first departing individual were 20-fold higher than the departure latencies of all other (nine) joiners ($P < 0.00001$) suggesting a mimetic process.

Departure of the first departing individual

There was no difference in the observed departure latencies between the different first departing individuals ($H_9 = 10.65$, $P = 0.300$). The distribution of the departure latencies of the first departing individual, whatever its identity, fitted with a theoretical

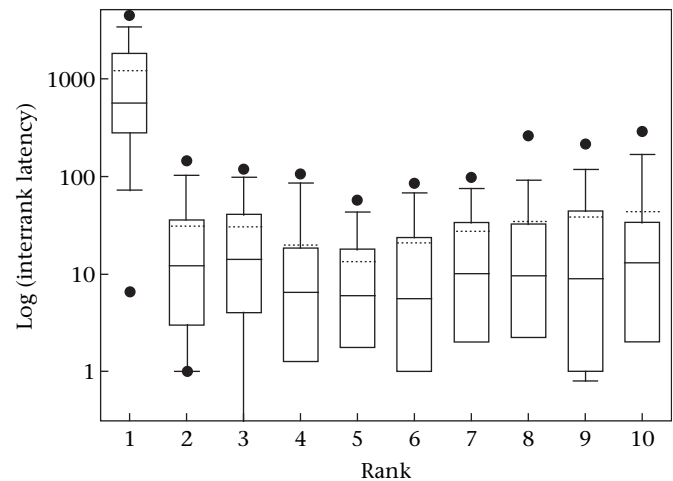


Figure 1. Distribution of the interrank latency per rank (logarithmic scale). Rank 1 corresponds to the first departing individual; rank 2 to the first joiner, etc. Solid lines in boxes represent the median (middle line) and percentiles (25–75% for lower and upper lines, respectively; 5–95) for error bars. Circles represent the extreme values. The dashed line represents the mean value.

exponential distribution (curve estimation: $F_{1,110} = 5619$, $R^2 = 0.98$, $P < 0.00001$, see Fig. S1 in the supplementary material). The log gradient of this exponential distribution was the inverse of the mean departure latency of the first departing individual and corresponded to the departure probability of the first individual ψ_{01} (equation 1a; Amé et al. 2006; Meunier et al. 2006; Gautrais et al. 2007).

Nevertheless, neither sex (Mann–Whitney, U test: $U = 9.5$, $N_{\text{male}} = 4$, $N_{\text{female}} = 6$, $P = 0.593$; $\text{mean}_{\text{male}} = 10.7 \pm 4.8$, $\text{mean}_{\text{female}} = 16.8 \pm 5.8$) nor age (Spearman rank correlation: $r_S = 0.43$, $N = 10$, $P = 0.245$) nor dominance (Spearman rank correlation: $r_S = -0.51$, $N = 10$, $P = 0.160$) influenced the probability of departing first in this study group as found in another Tonkean macaque group (Sueur & Petit 2008a).

The joiners' departure and the mimetic process

For each rank, we compared the distribution of the departure latencies of the joiner to a theoretical exponential distribution and to a linear distribution. If the distribution fitted an exponential one, then the departure probabilities of joiners would be constant per unit time. If it fitted a linear one, then the departure probabilities of joiners would depend on time. The observed distributions for all ranks best fitted an exponential distribution (curve estimations: $F_{1,110} > 1645$, $R^2 > 0.85$, $P < 0.00001$, see Fig. S2–10 in the supplementary material). Consequently, the departure probabilities of joiners were constant per unit time.

The inverse of the departure latency (equal to the departure probability) was a parabolic function of j (equation 2c; Dussutour et al. 2008) as shown by a Spearman rank correlation test ($r = 0.86$, $n = N = 10$, $P = 0.002$).

Observed and Simulated Distributions of Number of Joiners

First, we analysed the observed distribution of the number of collective movements according to the number of joiners. This distribution was not homogeneous (chi-square test: $\chi^2_9 = 206$, $P < 0.00001$) and was bimodal. There were more collective movements with no joiner (16.2%) and with all joiners (48.6%) than collective movements with one to eight joiners ($4.4 \pm 1.1\%$; Fig. 2). This bimodality was the signature of an 'all or nothing' process:

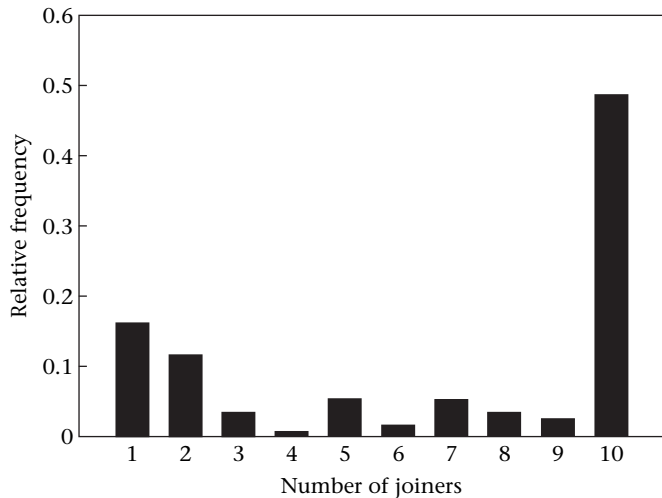


Figure 2. Observed distribution of the number of collective movements according to the number of joiners.

either no collective movement occurred or the entire group moved (Meunier et al. 2006; Gautrais et al. 2007).

We then compared the four simulated distributions of the number of joiners to the observed one. We never observed bimodality for the independent hypothesis. The distribution was unimodal with a maximum at no joiners and the percentage of collective movements where all individuals moved was 0% (see Fig. S11 in the supplementary material). For the other three hypotheses we conducted simulations with different mimetic coefficients C (from 0.0005 to 0.002), since the calculated value of the mimetic coefficient was approximated (equation 2d). For the anonymous mimetic hypothesis, we observed bimodal distributions that correlated with the observed distribution (with $0.0005 \leq C \leq 0.0009$; Spearman rank correlation tests: $r_s \geq 0.58$, $N = 10$, $P \leq 0.032$; Fig. 3a), with the highest correlation for $C = 0.0007$ (Spearman rank correlation test: $r_s = 0.72$, $N = 10$, $P = 0.016$; Fig. 3a). The percentage of collective movements where all individuals moved was 64.6% (compared to 48.6% for the observed collective movements). In contrast, we never obtained bimodality for the kinship hypothesis. All simulated distributions were unimodal with a maximum at zero or one joiner. As a result, the simulated distributions of the number of joiners did not correlate with the observed distribution (Spearman rank correlation test: $r_s \leq 0.14$, $N = 10$, $P \geq 0.790$; Fig. 3b) and the percentage of

collective movements where all individuals moved was 0%. Concerning the affiliation hypothesis, we observed bimodal distributions with a correlation with the observed distribution only for $C = 0.0009$ (Spearman rank correlation test: $r_s = 0.62$, $N = 10$, $P = 0.044$; Fig. 3c). The percentage of collective movements where all individuals moved was 67.2%.

Observed and Simulated Distributions of Mean Departure Latencies

Since the first departing individual latency was the same for all versions of the model, only joiners' mean departure latencies were of concern in this comparison. Kolmogorov–Smirnov tests revealed that the simulated distributions of the mean departure latencies of the independent hypothesis and the kinship hypothesis (whatever the value of the mimetic coefficient) differed from the observed distribution ($Z \geq 2.05$, $N = 5$, $P \leq 0.0001$; Fig. 4; see the supplementary material for figures with error bars; Figs S12–S15). Conversely, distributions of the mean departure latencies of the anonymous mimetic and affiliation hypotheses did not differ from the observed distribution (with $0.0009 \leq C \leq 0.002$, $Z \leq 0.94$, $N = 10$, $P \geq 0.301$; Fig. 4). Because of these results, in the next analyses we focused only on the anonymous mimetic and affiliation hypotheses.

Observed and Simulated Distributions of Variances of Departure Latencies

The distribution of variances of departure latencies may reflect the signature of the influence of social relationships. According to equation (2a), the probability of joining under the anonymous mimetic hypothesis did not depend on identities and social relationships. Thus, the variances were only influenced by λ and C . Conversely, the probability of joining under the affiliation hypothesis was influenced by the identities and the social relationships; thus the variances were influenced as well by λ , C and by the sum of $M(k,i)$ (see equation 5). As a result, the variances of the departure latencies of the affiliation hypothesis would be wider than for the anonymous mimetic hypothesis. Kolmogorov–Smirnov tests showed that the simulated distribution of variances of departure latencies under the anonymous mimetic hypothesis differed from the observed distribution whatever the value of C ($Z \geq 1.41$, $N = 10$, $P \leq 0.033$; Fig. 5), whereas the simulated distribution under the affiliation hypothesis did not differ from the observed distribution (with $0.0008 \leq C \leq 0.002$, $Z \leq 1.342$, $N = 10$, $P = 0.055$; Fig. 5).

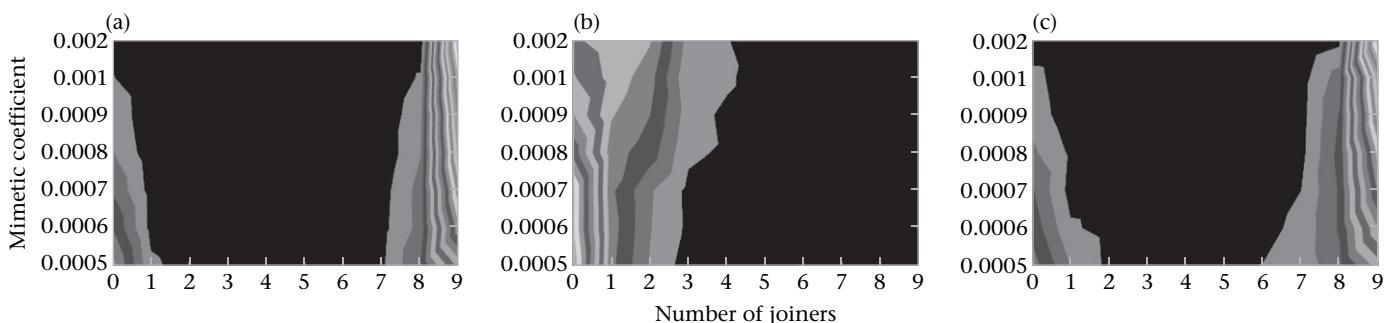


Figure 3. Simulated distribution of the frequencies of collective movements according to the number of joiners under (a) the anonymous mimetic hypothesis, (b) the kinship hypothesis and (c) the affiliation hypothesis. The frequency is expressed as a percentage (5% per unit). For each version of the model, the most represented values were from 0 to 5% for approximately two to seven joiners (in black). The distribution of the frequencies under the kinship hypothesis was unimodal with a maximum for zero or one joiners. The distributions of the frequencies under the anonymous mimetic hypothesis and the affiliation hypothesis were bimodal.

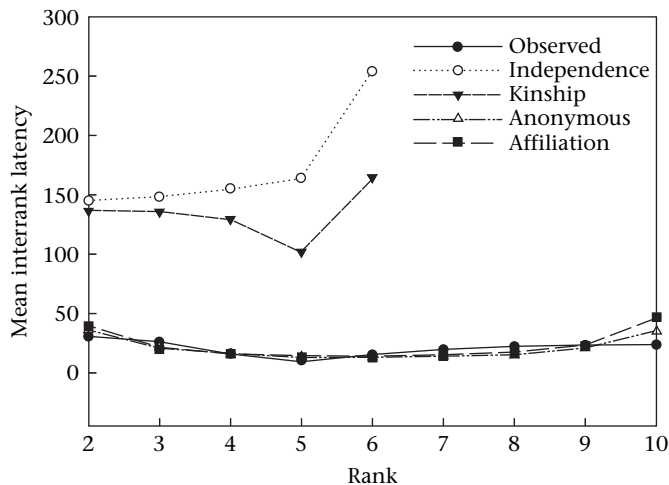


Figure 4. Mean departure latency of joiners for the observed distribution and the simulated distributions of the model under the different hypotheses. The first departing individual (rank 1) is not indicated. Under the independent hypothesis and the kinship hypothesis, no collective movement with more than five joiners occurred because of the criterion of 300 s. The mimetic coefficient equalled 0.001 for the anonymous, kinship and affiliation hypotheses.

Observed and Simulated Organizations of Group Members

The probabilities that two individuals directly joined each other in the observed and simulated collective movements under the anonymous mimetic hypothesis were not correlated (Dietz R test: $R = 0.06$, $N = 10$, $P = 0.319$). Conversely, these probabilities were significantly correlated under the affiliation hypothesis (Dietz R test: $R = 0.31$, $N = 10$, $P = 0.002$). These results meant that affiliative relationships allowed us to predict the associations of group members at departure of a collective movement.

For each first departing individual, we compared the observed orders of the nine joiners at departure to the simulated ones obtained under the two hypotheses using Spearman rank correlation tests. Under the anonymous mimetic hypothesis, the simulated orders were never correlated with the observed ones, ($r_s \leq 0.55$, $N = 9$, $P \geq 0.124$). Under the affiliation hypothesis, the simulated

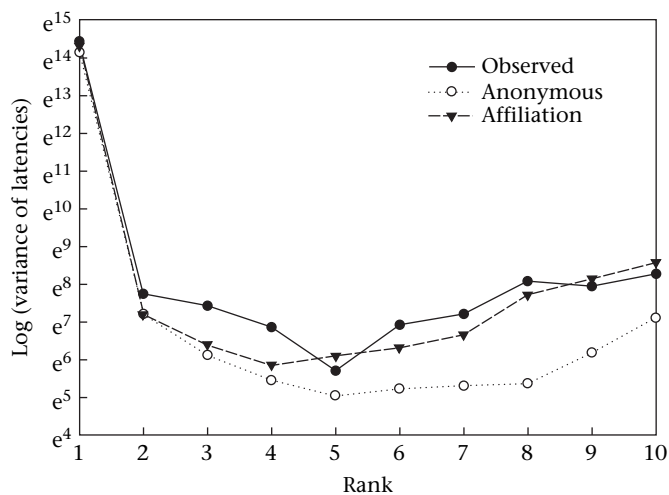


Figure 5. Variance of departure latencies per rank (logarithmic scale) for observed data and for the anonymous and affiliation hypotheses. The mimetic coefficient equalled 0.001.

orders were correlated with the observed ones for four of the 10 first departing individuals ($r_s \geq 0.64$, $N = 9$, $P \leq 0.044$).

DISCUSSION

In this study, we showed that a simple rule based on social relationships can explain the dynamics and organization of collective movements. We showed that individuals did not behave independently when deciding to move but considered the network of social relationships when joining groupmates (Camazaine et al. 2001). These findings recall social facilitation (Tolman 1964; Zajonc 1965) or response facilitation (Byrne 1994), in which an individual performing a specific act increases the probability that an observer will also perform this act. Similarly, mimetism underlies collective movements in different species (Detrain et al. 1999; Camazine et al. 2001; Couzin & Krause 2003; Jeanson et al. 2005; Sumpter 2006; Gautrais et al. 2007). In primates, a study on artificially induced collective movements reported that an anonymous mimetism process seemed to explain the joining process in capuchin monkeys (Meunier et al. 2006). Capuchins based their decision on the number of individuals already moving, regardless of their identities. Such an underlying anonymous process probably exists because a 'shot signal' (a whistle) induced these collective movements; this pattern was compared to a situation of predation risk in which it is more important to flee than to take care of social partners. Conversely, in spontaneous collective movements, as we studied here, animals can choose between either resting or moving and therefore may actually consider their social relationships before deciding. The selective mimetism we found differed from Meunier et al.'s findings (2006) since the only hypothesis explaining all patterns we observed was the affiliation one. The departure probability of an individual did not depend simply on the number of joiners, but also on the social relationships it possessed with these individuals. A similar influence of relationship was found in Merino sheep, with males more frequently imitating other males than females (Michelena et al. 2006; Gautrais et al. 2007). We did not exclude from our study the possibility that the joining process may be a mix of different underlying mechanisms. For instance, the first joiners may join the movement according to their affiliative relationships while the last joiners may join according to an anonymous mimetic process. As our results showed, the distribution of mean departure latencies also looked like an anonymous mimetism but only the affiliation model can explain all the patterns we studied. Affiliation influence was the more accurate explanation for the joining process in the study group of Tonkean macaques.

The bimodality of the observed distribution of the number of joiners was recreated under both anonymous mimetic and affiliation hypotheses and suggests a high cohesion of the group. When an individual 'decided' to move, either it was joined by all group members or it was not joined at all, leading to an 'all or nothing' phenomenon. For these hypotheses, we obtained slightly inferior mimetic coefficient values than the estimated ones. This might be because of some simplifications through modelling or other variables. For example, Sueur & Petit (2008a) reported that in Tonkean macaques, when a first departing individual was not joined, it gave up and generally went back to the group. This behaviour might modulate the distribution of the number of joiners and reinforce its bimodality. Within the 300 s criterion, in seven cases (6.3%), the first departing individual went back when it was not joined or was joined by one individual. Because of this small number of 'giving-ups', we ignored this parameter in our model.

In many species, affiliative relationships may be constrained by kinship and dominance (Drews 1993), but may occur between nonkin individuals (Hill 1990; Matsumura 1993; Perry 1998). Many

authors have suggested that kinship is one of the most important factors influencing behaviour and group stability (Hamilton 1964; Gouzoules & Gouzoules 1987; Mateo 2003; Chapais & Berman 2004). However, Chapais and collaborators (Chapais et al. 1991; Chapais & St-Pierre 1996) showed that nonkin relationships were crucial in alliances and contributed to the stability of matrilineal dominance in Japanese macaques, *Macaca fuscata*. Moreover, proximity and/or contact between individuals seems to be a good predictor of social information transmission (Coussi-Korbel & Fragazy 1995; Voelkl & Noë 2008), as we found for the dynamics and organization of collective movements in Tonkean macaques. Affiliative relationships seem to be a key characteristic of the cohesion and the stability of groups (Wey et al. 2008), whereas groups split if cohesion mechanisms are only based on kinship, as the kinship hypothesis showed in the present study. The Tonkean macaque society is well known for its mixing of different matrilineal during social interactions. In this species, strong affiliative bonds do not solely depend on kinship (Thierry 2004, 2007). Thus, it is not surprising that an individual decided to join a movement when its highly affiliated partners had departed and not only because the first individual had departed. In this context, the key individuals or determinants (Byrne et al. 1990; Sueur & Petit 2008a) seemed to be mostly the strongly affiliated individuals. These results may help to clarify the still controversial definition of leadership. We can wonder, who is the leader? The first departing individual or these key individuals of the joining process?

In Tonkean macaques, the departure of a collective movement was highly structured with specific patterns of order, timing and subgroups of individuals. This stable organization may be explained by our rule of joining, based on affiliation and mimetism. This explanation corresponds to the definition of a self-organized process: complex collective behaviour may emerge from interactions between individuals following simple behavioural rules based on local information (Bonabeau et al. 1997; Detrain & Deneubourg 2006; Sumpter 2006). In the same way, Hemelrijk (2000, 2002) explained some aspects of social and spatial behaviours of macaques, using an agent-based model that did not implement their developed cognitive abilities (Hemelrijk 2002). Nevertheless, some authors (Conradt & Roper 2005; Stueckle & Zinner 2008) have opposed consensus (more complex negotiation) and combined decisions (self-organized processes). We showed that both processes can underlie group movements; Tonkean macaques displayed negotiation and recruitment behaviours (Sueur & Petit 2008a) as well as self-organized behaviour such as selective mimetism (present study). We did not exclude the possibility that other factors could affect the joining probability such as intrinsic factors or recruitment behaviours. We did not need to implement these factors in our model, however, to explain the joining process accurately. We are aware that this model has only been tested in a single group. However, the methodology used here could be applied to other social species to demonstrate the importance of such rules in collective decision making, regardless of their cognitive complexity.

Acknowledgments

We are grateful to J. Dubosq for the video analyses, P. Uhlrich for technical assistance and R. Knowles for language editing. This work was supported by the European Doctoral College of Strasbourg Universities, the French Research Ministry (EGIDE) and the French Foreign Ministry (Lavoisier Excellence Scholarship). J.L.D. is research associate from the Belgian National Funds for Scientific Research. Thanks are extended to F. Amblard, A. Banos, J. Lyons and J. Steiner for discussions and help with the model.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi: 10.1016/j.anbehav.2009.07.029.

References

- Alexander, R. D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics*, **5**, 326–383, doi:10.1146/annurev.es.05.110174.001545.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–265.
- Amé, J. M., Halloy, J., Rivault, C., Detrain, C. & Deneubourg, J. L. 2006. Collegial decision making based on social amplification leads to optimal group formation. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 5835–5840, doi:10.1073/pnas.0507877103.
- Biro, D., Sumpter, D. J. T., Meade, J. & Guilford, T. 2006. From compromise to leadership in pigeon homing. *Current Biology*, **16**, 2123–2128, doi:10.1016/j.cub.2006.08.087.
- Boinski, S. & Campbell, A. F. 1995. Use of trill vocalisations to coordinate troop movement among white-faced capuchins: a second field test. *Behaviour*, **132**, 875–901.
- Boinski, S. & Garber, P. A. 2000. *On the Move*. Chicago: University of Chicago Press.
- Boinski, S., Treves, A. & Chapman, C. A. 2000. A critical evaluation of the influence of predators on primates: effects on group travel. In: *On the Move* (Ed. by S. Boinski & P. A. Garber), pp. 43–72. Chicago: University of Chicago Press.
- Bonabeau, E., Theraulaz, G., Deneubourg, J. L., Aron, S. & Camazine, S. 1997. Selforganization in social insects. *Trends in Ecology & Evolution*, **12**, 188–192, doi:10.1016/S0169-5347(97)01048-3.
- Bryson, J. J., Yasushi, A. & Lehmann, H. 2007. Agent-based modelling as a scientific methodology: a case study analyzing primate social behaviour. *Philosophical Transactions of the Royal Society*, **362**, 1686–1698, doi:10.1098/rstb.2007.2061.
- Buhl, J., Sumpter, D. J. T., Couzin, I. D., Hale, J. J., Despland, E., Millor, E. R. & Simpson, S. J. 2006. From disorder to order in marching locusts. *Science*, **312**, 1402–1406, doi:10.1126/science.1125142.
- Byrne, R. W. 1994. The evolution of intelligence. In: *Behaviour and Ecology* (Ed. by P. J. B. Slater & T. R. Halliday), pp. 223–265. Cambridge: Cambridge University Press.
- Byrne, R. W., Whiten, A. & Henzi, S. P. 1990. Social relationships of mountain baboons: leadership and affiliation in a non-female-bonded monkey. *American Journal of Primatology*, **20**, 313–329, doi:10.1002/ajp.1350200409.
- Camazine, S., Deneubourg, J. L., Franks, N. R., Sneyd, J., Theraulaz, G. & Bonabeau, E. 2001. *Self-Organization in Biological Systems*. Princeton, New Jersey: Princeton University Press.
- Chapais, B. & Berman, C. M. 2004. *Kinship and Behaviour in Primates*. Oxford: Oxford University Press.
- Chapais, B. & St-Pierre, C. E. 1996. Kinship bonds are not necessary for maintaining matrilineal rank in captive Japanese macaques. *International Journal of Primatology*, **18**, 375–385, doi:10.1023/A:1026334400201.
- Chapais, B., Girard, M. & Primi, G. 1991. Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour*, **41**, 481–491.
- Conradt, L. & Roper, T. J. 2005. Consensus decision making in animals. *Trends in Ecology & Evolution*, **20**, 449–456, doi:10.1016/j.tree.2005.05.008.
- Coussi-Korbel, S. & Fragazy, D. M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, **50**, 1441–1453.
- Couzin, I. D. & Krause, J. 2003. Self-organization and collective behaviours in vertebrates. *Advances in the Study of Animal Behavior*, **32**, 1–75.
- Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513–516.
- Danchin, E., Boulinier, T. & Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology*, **79**, 2415–2428, doi:10.2307/1768.
- Deneubourg, J. L. & Goss, S. 1989. Collective patterns and decision-making. *Ethology Ecology and Evolution*, **1**, 295–311.
- Detrain, C. & Deneubourg, J. L. 2006. Self-organized structures in a superorganism: do ants 'behave' like molecules? *Physical Life Review*, **3**, 162–187, doi:10.1016/j.jprel.2006.07.001.
- Detrain, C., Deneubourg, J. L. & Pasteels, J. 1999. *Information Processing in Social Insects*. Basel: Birkhäuser-Verlag.
- Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour*, **125**, 283–313.
- Dussutour, A., Nicolis, S. C., Despland, E. & Simpson, S. J. 2008. Individual differences influence collective behaviour in social caterpillars. *Animal Behaviour*, **76**, 5–16, doi:10.1016/j.anbehav.2007.12.009.
- Epstein, J. M. 2008. Why model? *Journal of Artificial Societies and Social Simulation*, **11**, 12.
- Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M. J. & Rubenstein, D. I. 2007. Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour*, **73**, 825–831, doi:10.1016/j.anbehav.2006.10.012.

- Fox, M. W. 1972. *Behavior of Wolves, Dogs and Related Canids*. New York: Harper & Row.
- Gautrais, J., Michelena, P., Sibbald, A., Bon, R. & Deneubourg, J. L. 2007. Allelomimetic synchronization in Merino sheep. *Animal Behaviour*, **74**, 1443–1454, doi:10.1016/j.anbehav.2007.02.020.
- Giraldeau, L. A. & Caraco, T. 2000. *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Gouzoules, S. & Gouzoules, H. 1987. Kinship. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 299–305. Chicago: University of Chicago Press.
- Hall, C. L. & Fedigan, L. M. 1997. Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour*, **53**, 1069–1082, doi:10.1006/anbe.1996.0392.
- Hamilton, W. D. 1964. The genetical evolution of social behavior. *Journal of Theoretical Biology*, **7**, 1–52.
- Hemelrijk, C. K. 1990. A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at a group level. *Journal of Theoretical Biology*, **143**, 405–420.
- Hemelrijk, C. K. 2000. Towards the integration of social dominance and spatial structure. *Animal Behaviour*, **59**, 1035–1048, doi:10.1006/anbe.2000.1400.
- Hemelrijk, C. K. 2002. Understanding social behaviour with the help of complexity science (Invited Article). *Ethology*, **108**, 655–671, doi:10.1046/j.1439-0310.2002.00812.x.
- Hill, D. A. 1990. Social relationships between adult male and female rhesus macaques. 2. Nonsexual behaviour. *Primates*, **31**, 33–50.
- Hockings, K. J., Anderson, J. R. & Matsuzawa, T. 2006. Road crossing in chimpanzees: a risky business. *Current Biology*, **16**, 668–670, doi:10.1016/j.cub.2006.08.019.
- Jacobs, A., Maumy, M. & Petit, O. 2008. The influence of social organisation on leadership in brown lemurs (*Eulemur fulvus fulvus*) in a controlled environment. *Behavioural Processes*, **79**, 111–113.
- Janson, C. H. 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **40**, 910–921, doi:10.1016/S00033472(05)80993-5.
- Jeanson, R., Rivault, C., Deneubourg, J. L., Blanco, S., Fournier, R., Jost, C. & Theraulaz, G. 2005. Self-organized aggregation in cockroaches. *Animal Behaviour*, **69**, 169–180, doi:10.1016/j.anbehav.2004.02.009.
- Krause, J. & Ruxton, G. D. 2002. *Living in Groups*. Oxford: Oxford University Press.
- Kummer, H. 1968. *Social Organization of Hamadryas Baboons*. Chicago: University of Chicago Press.
- Leca, J. B., Gunst, N., Thierry, B. & Petit, O. 2003. Distributed leadership in semi-free-ranging white-faced capuchin monkeys. *Animal Behaviour*, **66**, 1045–1052, doi:10.1006/anbe.2003.2276.
- Mateo, J. M. 2003. Kin recognition in ground squirrels and other rodents. *Journal of Mammalogy*, **84**, 1163–1181.
- Matsumura, S. 1993. Intergroup affiliative interactions and intergroup transfers of young male Japanese macaques (*Macaca fuscata*). *Primates*, **34**, 1–10.
- Meunier, H., Leca, J. B., Deneubourg, J. L. & Petit, O. 2006. Group movement decisions in capuchin monkeys: the utility of an experimental study and a mathematical model to explore the relationship between individual and collective behaviours. *Behaviour*, **143**, 1511–1527, doi:10.1163/156853906779366982.
- Michelena, P., Noël, S., Gautrais, J., Gerard, J. F., Deneubourg, J. L. & Bon, R. 2006. Sexual dimorphism, activity budget and synchrony in sheep group. *Oecologia*, **148**, 170–180, doi:10.1007/s00442-005-0347-2.
- Perry, S. 1998. Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour*, **135**, 139–172.
- Pombo, A., Waltert, M., Mansjoer, S. S., Mardiatuti, A. & Muhlenberg, M. 2004. Home range, diet and behaviour of the Tonkean macaque (*Macaca tonkeana*) in Lore Lindu National Park, Sulawesi. In: *Land Use, Nature Conservation and the Stability of Rainforest Margins in Southeast Asia* (Ed. by G. Gerold, M. Fremerey & E. Guhardja), pp. 313–325. Berlin: Springer.
- Pratt, S. C., Sumpter, D. J. T., Mallon, E. B. & Franks, N. R. 2005. An agent-based model of collective nest choice by the ant *Temnothorax albigipennis*. *Animal Behaviour*, **70**, 1023–1036, doi:10.1016/j.anbehav.2005.01.022.
- Ramirez-Avila, G. M., Guisset, J. L. & Deneubourg, J. L. 2003. Synchronization in light-controlled oscillators. *Physica*, **182**, 254–273, doi:10.1016/S0167-2789(03)00135-0.
- Rasa, O. A. E. 1986. *Mongoose Watch: a Family Observed*. New York: Anchor Press.
- Rhine, R. J. & Tilson, R. 1987. Reactions to fear as a proximate factor in the socio-spatial organization of baboons progressions. *American Journal of Primatology*, **13**, 119–128.
- Rhine, R. J. & Westlund, B. J. 1981. Adult male positioning in baboon progressions: order and chaos revisited. *Folia Primatologica*, **35**, 77–116.
- Riley, E. P. 2005. The loud call of the Sulawesi Tonkean macaque, *Macaca tonkeana*. *Tropical Biodiversity*, **8**, 199–209.
- Riley, E. P. 2007. Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *International Journal of Primatology*, **28**, 107–133.
- Sellers, W. I., Hill, R. A. & Logan, B. S. 2007. Simulating baboon foraging using agent-based modeling. *Philosophical Transactions of the Royal Society B*, **362**, 1699–1710, doi:10.1098/rstb.2007.2064.
- Strotgatz, S. H. & Stewart, I. 1993. Coupled oscillators and biological synchronization. *Scientific American*, **269**, 102–109.
- Stueckle, S. & Zinner, D. 2008. To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, **75**, 1995–2004.
- Sueur, C. & Petit, O. 2008a. Shared or unshared consensus decision in macaques. *Behavioural Processes*, **78**, 84–92, doi:10.1016/j.beproc.2008.01.004.
- Sueur, C. & Petit, O. 2008b. Organization of group members at departure of joint movements is driven by social structure in macaques. *International Journal of Primatology*, **29**, 1085–1098, doi:10.1007/s10764-008-9262-9.
- Sumpter, D. J. T. 2006. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B*, **361**, 5–22, doi:10.1098/rstb.2005.1733.
- Sumpter, D. J. T. & Pratt, S. C. 2009. Quorum responses and consensus decision-making. *Philosophical Transactions of the Royal Society B*, **364**, 743–753, doi:10.1098/RSTB.2008.0204.
- Supriatna, J., Froehlich, J. W., Erwin, J. M. & Southwick, C. H. 1992. Population habitat and conservation status of *M. maurus*, *M. tonkeana* and their putative hybrids. *Tropical Biodiversity*, **1**, 31–48.
- Thierry, B. 2004. Social epigenesis. In: *Macaque Societies: A Model for the Study of Social Organization* (Ed. by B. Thierry, M. Singh & W. Kaumanns), pp. 267–284. Cambridge: Cambridge University Press.
- Thierry, B. 2007. Unity in diversity: lessons from macaque societies. *Evolutionary Anthropology*, **16**, 224–238.
- Thierry, B., Gauthier, C. & Peignot, P. 1990. Social grooming in Tonkean macaques. *International Journal of Primatology*, **11**, 357–375.
- Tolman, C. W. 1964. Social facilitation of feeding behaviour in the domestic chick. *Animal Behaviour*, **12**, 245–251.
- Tomasello, M. & Call, J. 1997. *Primate Cognition*. New York: Oxford University Press.
- Voelkl, B. & Noë, R. 2008. The influence of social structure on the propagation of social information in artificial primate groups: a graph-based simulation approach. *Journal of Theoretical Biology*, **252**, 77–86, doi:10.1016/j.jtbi.2008.02.002.
- de Vries, H., Netto, W. J. & Hanegraaf, P. L. H. 1993. Matman: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour*, **125**, 157–175.
- Waser, P. M. 1985. Spatial structure in mangabey groups. *International Journal of Primatology*, **6**, 569–579.
- Wey, T., Blumstein, D. T., Weiwei, S. & Jordan, F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour*, **75**, 333–344, doi:10.1016/j.anbehav.2007.06.020.
- Whitehead, H. 1997. Analysing animal social structure. *Animal Behaviour*, **53**, 1053–1067, doi:10.1016/0197-2456(92)90017-T.
- Whitehead, H. 2007. Programs for Analyzing Social Structure. <http://myweb.dal.ca/hwhiteh/MANUAL.htm>.
- Whitten, P. 1983. Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology*, **5**, 139–159.
- Whiten, A. & Byrne, R. W. 1997. *Machiavellian Intelligence II: Extensions and Evaluations*. Cambridge: Cambridge University Press.
- Whitten, A. J., Mustafa, M. & Henderson, G. S. 1987. *The Ecology of Sulawesi*. Yogyakarta: Gadjah Mada University Press.
- Wilensky, U. 1999. *NetLogo*. Evanston, Illinois: Center for Connected Learning and Computer-Based Modeling, Northwestern University. <http://ccl.northwestern.edu/netlogo>.
- Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. *Behaviour*, **75**, 262–300.
- Zajonc, R. B. 1965. Social facilitation. *Science*, **149**, 269–274.