

Short-term group fission processes in macaques: a social networking approach

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SUMMARY

Living in groups necessarily involves a certain amount of within-group competition for food. Group members may have different motivations, implying the reaching of a consensus to stay cohesive. In some cases individuals fail to reach a common decision and the group splits; this can be temporary, as seen in fission–fusion dynamics, or even irreversible. Most studies on fission–fusion dynamics published to date have focused on the influence of environmental constraints on sub-grouping patterns, but little is known about how social relationships affect individual choices for sub-groups. In this study, we used an agent-based model to understand the mechanisms underlying group fission in two semi-free-ranging groups of macaques: one group of Tonkean macaques (*Macaca tonkeana*) and one of rhesus macaques (*M. mulatta*). The results showed that sub-grouping patterns were mainly influenced by affiliative relationships. Moreover, the species-specific social style appeared to affect the probability of choosing a particular sub-group. In the tolerant Tonkean macaques, mechanisms underlying sub-grouping patterns resembled anonymous mimetism, while in the nepotistic rhesus macaques, kinship influenced the mechanisms underlying group fissions. As previous studies have shown, fission–fusion society may be a way to avoid social conflicts induced either by food or by social competition.

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Key words: decision making, consensus, sub-group, kinship, affiliation, agent-based model.

INTRODUCTION

In social animals, the way individuals interact with their conspecifics can depend on ecological factors. Predation pressure and food searching efficiency seem to favour the aggregation of animals (Krause and Ruxton, 2002). A social group is usually defined as an entity of individuals interacting more together than with other individuals of the same species and evolving in the same home range (Kummer, 1971). Living in groups does, however, involve within-group competition for food (West-Eberhard, 1979). Group members have to make trade-offs and reach a consensus before moving collectively from one area to another chosen area (Conradt and Roper, 2005; Sueur and Petit, 2008a). Nevertheless, when group size increases or when intrinsic differences between group members become too large, individuals may fail to reach a consensus. This failure may lead to the group splitting: a first sub-group decides to move in one direction while a second one decides either to stay in the current area or to move in another direction (Kerth et al., 2006; Ramos-Fernandez et al., 2006). This splitting can be observed in all social species from insects to primates. Individuals could be confronted with different options. This can be on a short-term scale, for example for the choice of different sleeping sites [bats, *Myotis bechsteinii* (Kerth et al., 2006)] or different foraging sites [ants and bees (Camazine et al., 2001; Dussutour et al., 2009); cockroaches, *Blattella germanica* (Jeanson and Deneubourg, 2006); caterpillars, *Menduca disstira* (Dussutour et al., 2008); buffaloes, *Syncerus caffer* (Prins, 1996); primates, *Papio hamadryas* (Kummer, 1968)]. The choice of different directions to avoid predation is another example [fish, *Gasterosteus aculeatus* (Ward et al., 2008)]. On a long-term scale (irreversible fission), we can quote the choice of new nest sites [bees, *Apis mellifera* (Seeley and Visscher, 2003; Seeley and

Visscher, 2004); ants, *Leptothorax albipennis* (Pratt et al., 2002), *Messor barbarus* (Jeanson et al., 2004)] and choices taken in order to avoid within-group competition [primates, *Papio ursinus* (Henzi et al., 1997), *Macaca maurus* (Okamoto and Matsumura, 2001)]. Group splitting is observed whatever the species, with the possibility that a general mechanism underlies these phenomena (Sueur et al., 2009; Sumpter, 2009). This fission can be irreversible or temporary. Fission–fusion societies (Kummer, 1971) or fission–fusion dynamics (Aureli et al., 2008) – where fissions are temporary – characterise many mammalian species [*Pan troglodytes* (Lehmann and Boesch, 2004); *Crocota crocuta* (Holekamp et al., 1997); *Leo panthera* (Packer et al., 1990); *Loxodonta africana* (Wittemyer et al., 2005); *Tursiops* sp. (Lusseau et al., 2006); *M. bechsteinii* (Kerth et al., 2006)]. Aureli and colleagues (Aureli et al., 2008) suggested that animal groups may show a continuum from systems with higher group cohesion stability, ‘lower-FF’, to systems characterised by a higher degree of fission–fusion dynamics, ‘higher-FF’, according to their ecological environment or social structure. The group structure can fluctuate over short temporal and/or spatial scales from one to several sub-groups (Altmann, S. A., 1974; Lehmann and Boesch, 2004; Packer et al., 1990). Most studies on fission–fusion dynamics have focused on how an individual chooses a particular sub-group in order to maximise its fitness in terms of access to resources (Conradt and Roper, 2000; Ramos-Fernandez et al., 2006; van Schaik, 1989). However, little is known about how social relationships may affect these individual choices (Lusseau et al., 2006; Poppa-Lisseanu et al., 2008; Wittemyer et al., 2005). In Japanese macaques [*Macaca fuscata* (Fukuda, 1989)] and Barbary macaques [*Macaca sylvanus* (Ménard et al., 1990)], associations of individuals in sub-groups may occur more or less randomly. In other

species, sub-grouping patterns reflect individual preferences which can be mediated by kinship, or not (Lusseau et al., 2006; Poppa-Lisseanu et al., 2008; Wittemyer et al., 2005). It is a well-documented fact that the social style of macaque species (de Waal and Luttrell, 1989) dictates many social behaviours such as conciliatory tendencies (Thierry et al., 2004), social play (Petit et al., 2008) or decision making (Sueur and Petit, 2008a; Sueur and Petit, 2008b). Similarly, specific social style could influence group fission patterns. In a previous study, we showed that Tonkean macaques (*Macaca tonkeana*) and rhesus macaques (*Macaca mulatta*) collectively decided on the time and the direction of a movement (Sueur and Petit, 2008a). Nonetheless, occasional cases of temporary group fission were observed in both species. The groups split into two sub-groups that went in different directions, and these two sub-groups reunited as one group after a certain time. Therefore, even if there were no long-term interruptions in the social relationships between group members, they still had to choose which sub-group they would join. In the present study we tested four alternative hypotheses regarding which sub-groups an individual would choose during short-term fissions in these two semi-free-ranging groups of Tonkean and rhesus macaques. The four hypotheses tested were as follows: (1) an individual chose a sub-group in which the individuals shared its motivation, regardless of social relationships (Conradt and Roper, 2000; Ramos-Fernandez et al., 2006); (2) an individual chose the largest sub-group; (3) an individual chose the sub-group composed of its relatives (Poppa-Lisseanu et al., 2008; Wittemyer et al., 2005); and (4) an individual chose the sub-group mainly composed of its affiliated individuals (related or non-related individuals) (Lusseau et al., 2006; Sueur and Petit, 2008b; Sueur et al., 2009).

These different hypotheses were tested using a stochastic model which simulates interactions between group members and sub-grouping patterns (Sellers et al., 2007; Sueur et al., 2009). We then compared the observed sub-groups with the simulated sub-groups for each species using social networks analysis (Krause et al., 2007; Sueur and Petit, 2008b; Whitehead, 2009). According to previous studies on social and collective behaviour in macaques (Sueur and Petit, 2008b; Thierry et al., 2004), we expected affiliative relationships to underlie group fission processes in Tonkean macaques whereas kinship relationships should explain the composition of sub-groups in rhesus macaques.

MATERIALS AND METHODS

Subjects and study area

The groups under investigation were bred in the Strasbourg University Centre of Primatology in semi-natural conditions. All group members were born in captivity. Maternal kin relationships are known for both groups. The group of Tonkean macaques (*M. tonkeana* Meyer 1899) was composed of five matriline (with six kin pairs). 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 sub-adult male (3 years old) and three juveniles (2, 1 and 1 year old). The group of rhesus macaques (*M. mulatta* Zimmermann 1780) was composed of two matriline (with 80 kin pairs). At the time of the study (May 2006 to August 2006) it consisted of 22 individuals: two adult males (17 and 8 years old), 11 adult females (16, 14, 12, 11, 11, 11, 8, 7, 7, 7 and 6 years old), two sub-adult females (both 4 years old) and seven infants (<1 year old). The composition of the two groups was comparable to several wild groups (Makwana, 1978; Pombo et al., 2004; Riley, 2007). We did not analyse infant behaviours, as it was not always possible to distinguish these individuals within the group.

The study was therefore based on 10 Tonkean macaque individuals and on 15 rhesus macaque individuals. Each group lived in a park (fenced field of 0.5 ha, i.e. 500 m²) with trees, bushes and grassy areas. Animals had free access to an inside shelter (20 m²) where commercial pellets and water were provided *ad libitum*. Fruit and vegetables were distributed once a week, outside of observation sessions. For both species, groups moved collectively (as a whole group or in sub-groups) between areas devoted to specific activities (Sueur and Petit, 2008a; Sueur and Petit, 2008b).

Definitions

We considered a group fission event to be when a group of individuals in one area split into sub-groups moving in two different trajectories towards two distinct areas (Ramos-Fernandez et al., 2006). We decided to consider a group fission to have occurred if sub-groups had been separated for more than 5 min. Group fission could also be considered when a sub-group stayed in one area while another group moved from this area to another. It was, however, easier to determine the reasons behind an individual's choice to join one of the two sub-groups in the first case (Kerth et al., 2006). This group fission process occurred within the context of simultaneous collective movements in different directions. The mean fission time, and the mean length of interruptions of social relationships between the two sub-groups, was 22.2±6.8 min (range 5.74–34.01 min) for Tonkean macaques and 22.2±3.9 min (range 5.17–36.32 min) for rhesus macaques. We considered two collective movements to be simultaneous and divergent when there was less than 5 min difference between the departures of the first two individuals, and when the angle between the two movement directions was greater than 45 deg. The criterion of 5 min was based on our earlier work (Sueur and Petit, 2008a; Sueur and Petit, 2008b), which describes previous studies of collective movements in macaques. The beginning of a collective movement was defined as the departure of the first individual, walking more than 10 m in less than 40 s. The term 'joiner' (Sueur and Petit, 2008a; Sueur and Petit, 2008b) was used to describe an individual walking more than 5 m in a given direction, forming an angle less than 45 deg. to the direction taken by the first departing individual, and this within 5 min of the first's departure. We considered a collective movement to be over when no further individuals joined the movement within 5 min of departure of the first or of the last joiner (Sueur and Petit, 2008a; Sueur and Petit, 2008b).

Observation procedure

Groups were observed and filmed for 4 h per day between 10:00 h and 16:00 h. Each collective movement was recorded on videotape. Participants (first departing individual and joiners) were observed one by one using video recording. Movements occurring within a context of conflict or sexual consort were not taken into account. Collective movements were only taken into account if more than two-thirds of group members were present in the starting zone (this was the case in 98.3% of movements in Tonkean macaques and 91.9% in rhesus macaques). The remaining tier mainly corresponds to a number of peripheral individuals (Meunier et al., 2006). We considered that the behavioural or social variables were biased, and that it was impossible to explain the collective phenomenon properly if less than two-thirds of group members were in the starting zone. We defined the starting zone to be the area ≤10 m from the starting point of the first individual to depart. With this criterion, both groups were clumped in the majority of cases; the diameter was less than 10 m in both groups, whatever the study group. Previous studies showed that individuals either walked small distances (between 1 and 5 m, considered as foraging or intention movements) or longer

distances during collective movements (with an average of about 20 m) (Sueur, 2008; Sueur and Petit, 2008a). Thus, the departure of the first individual (over a distance of more than 10 m) was an obvious visual signal for other group members (Jacobs et al., 2008; Leca et al., 2003; Sueur and Petit, 2008a; Sueur and Petit, 2008b; Sueur et al., 2009). A map of each park was used to calculate the distance walked by group members.

We scored 146 collective movements for Tonkean macaques and 131 for rhesus macaques. Among these events, we only observed 8 group fissions for the Tonkean macaques, i.e. 16 simultaneous collective movements, and 10 group fissions for the rhesus macaques, i.e. 20 simultaneous collective movements. No group fission involving more than two simultaneous collective movements was observed.

Kinship and affiliative relationships

Two individuals belonging to the same matriline were considered as kin related, whatever their degree of kinship. We chose to consider kinship as binary because several studies have reported the influence of kinship (basically kin or non-kin) on various social behaviours, whatever the degree of relatedness (see Chapais and Berman, 2004). The group of rhesus macaques was only observed by our team from 2004. Whilst we can affirm who belongs to which matriline, we cannot calculate the real degree of relatedness for some pairs of individuals, especially for older individuals. This is the reason why we did not use the degree of relatedness. We tested the influence of kinship by using the degree of relatedness on collective movements in another species (Brown lemurs) (A. Jacobs, C.S., J.L.D. and O.P., submitted) and the result did not change according to which measure was used (binary or degree). Kinship was considered to be a specifically influential factor in the probability of joining an individual or a sub-group of individuals (Sueur and Petit, 2008b; Sueur and Petit, 2010; Sueur et al., 2009).

Affiliative relationships, measured by proximity as well as by grooming between individuals (Chapais et al., 1997; Cords, 2002; Perry et al., 2008; Thierry et al., 2004) [for reviews on association patterns see Whitehead and Croft et al. (Whitehead, 2008; Croft et al., 2008)], reflect a preference for certain group members (kin-related and non-kin-related ones). Using instantaneous sampling every 5 min (Altmann, J., 1974), affiliative relationships were quantified by the number of observations carried out outside of moving contexts. Individuals were observed in proximity (distance less than or equal to 1 m), outside of collective movements of group members, to avoid any confusion between affiliative relationships and associations occurring within a group movement context. We collected 298 scans for Tonkean macaques and 219 for rhesus macaques. We thus calculated the half-weight index (HWI) (Cairns and Schwager, 1987) corresponding to the number of scans in which two individuals were seen together, divided by half of the total number of scans in which the two individuals were seen (not necessarily together). This HWI reflected the quality of inter-individual relationships. We assessed whether affiliation relationships were stable over time and the results showed that affiliation matrices for each observation month were correlated for Tonkean macaques (Dietz *R*-test: $r > 0.47$, $P < 0.00005$) and for rhesus macaques (Dietz *R*-test: $r > 0.51$, $P < 0.00002$), suggesting that the group network for each group did not actually change during the observation session.

The model

According to group composition, the number of individuals (N) was fixed at 10 for Tonkean macaques and at 15 for rhesus macaques.

Individual identities, as well as kinship and affiliative networks, were included in the model. We set the values of kinship at zero for non-kin-related individuals and at one for kin-related individuals, whereas the values of affiliative relationships (the HWI) for each dyad varied between zero (individuals never observed together) and one (individuals always observed together) (Sueur and Petit, 2008b; Sueur et al., 2009). At the beginning of a simulation, all macaques (N) were in an area called the resting area. We then induced the simultaneous departure of the first two individuals. The individuals chosen to be the first to leave in these simulations were those observed to lead in previous group fissions. These individuals went to two different areas qualified as foraging areas. The remaining individuals (resting individuals) had to choose one direction or the other, according to departure probability Ψ (per time unit) in each direction d . An individual decided to move in the direction where its choice probability was the highest (see 'Departure decision and direction decision' in the Appendix for details of the individual decision models). This choice probability was different for each of the following hypotheses.

(1) Random model

The first hypothesis was that an individual would choose a sub-group because it shared the same motivations as individuals within this sub-group and not because of the composition of the sub-group. For this random model, the probability of the n resting macaques (e.g. individual i) becoming a joiner (or the j th moving individuals) in the direction d is:

$$\Psi_{jd} = \lambda n + C \frac{\left(\sum j_d\right)^p}{D}, \quad (1)$$

where

$$n = N - \sum_d \sum j_d. \quad (2)$$

λ represents the intrinsic probability of moving, whatever the direction. In the model, this probability equalled 0.0001 s^{-1} in Tonkean macaques and 0.00007 s^{-1} in rhesus macaques (see 'Analysis of the intrinsic probability λ ' in the Appendix for details of the calculation). C is the mimetic coefficient and equalled 0.002 in Tonkean macaques and 0.003 in rhesus macaques (see 'Determination of the mimetic process' and 'Analysis of distribution for joiners' departure latencies according to these different mimetic coefficients' in the Appendix for definition and calculation details). j_d is the number of individuals moving in the direction d before the departure of the j th individual. p determined the system sensitivity and the influence power for the number of individuals j in the direction d . p was equal to four in Tonkean macaques and three in rhesus macaques (see 'Calculation of the power p ' in the Appendix for definition and calculation details). D is the number of directions. In our study, $D=2$.

As

$$C \frac{\left(\sum j_d\right)^p}{D}$$

was similar for each direction, then the choice probability depended only on λ .

(2) Anonymous model

The second hypothesis specified that an individual would choose the more numerous sub-group. The equation to calculate the

probability of the n remaining macaques becoming the j th moving individual in the direction d under the anonymous model was:

$$\psi_{jd} = \lambda n + (Cj_d)^p. \quad (3)$$

The choice probability therefore mainly depended on the number of individuals j_d .

(3) Kinship model

The third hypothesis tested the influence of kinship. According to previous models, the probability of becoming the j th joiner differed between individuals and depended on their relationships with kin-related individuals already moving in each direction:

$$\psi_{id} = \lambda n + C(k_{id} \times 1 + a_{id} \times 0)^p = \lambda n + C(k_{id})^p. \quad (4)$$

k_{id} is the number of relatives (of the individual i) already moving in direction d . a_{id} is the number of non-relatives (of the individual i) already moving in direction d .

The choice probability depended mainly on k_{id} , $C(k_{id})^p$ always being greater than λ .

(4) Affiliation model

In the affiliation model, we tested how the quality of affiliative relationships could influence the decision to choose a direction. The probability of becoming the j th joiner in direction d would not therefore be the same between individuals, and would depend on their affiliative relationships with the group members who had already left:

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

where $M(k, i)_d$ was the HWI of proximities between individual k and individual i when individual k was already moving in direction d . If individual k was not yet moving in direction d , then $M(k, i)=0$.

The choice probability was mainly dependent on $\sum M(k, i)_d$,

$$C \left(\sum_{k=1}^N M(k, i)_d \right)^p$$

always being superior to λ .

We implemented the four versions of the model (using the four different hypotheses) in Netlogo 3.1.4 (Wilensky, 1999). At each time step (1 s), a number between zero and one was randomly attributed for each resting macaque (i.e. at the resting area); when this number was lower than the theoretical probability ψ_{id1} of moving in direction d_1 , the individual moved in direction d_1 ; when this number was between ψ_{id1} and $\psi_{id1} + \psi_{id2}$, the individual moved in direction d_2 ; if this number was greater than $\psi_{id1} + \psi_{id2}$, the individual did not move. To compare the simulated data with experimental results, we stopped a simulation when no individual joined within 300 s of the departure of the first individual or that of the last joiner (see 'Definitions' above). We set the number of simulations to 1000 for each hypothesis and each set of tested parameters.

Data scoring and calculation

We carried out the same data calculation for both observed and simulated group fissions. The number of joiners was scored in each direction for each group fission. We then scored the identity of the first departing individuals and of every joiner in each direction. Finally, we checked the associations between individuals as measured by the HWI (Cairns and Schwager, 1987). The HWI is the number of events in which two individuals were seen together

(in the same fission sub-group) divided by the total number of events in which each individual participated (Sueur and Petit, 2008b; Whitehead, 2009). These indices ranged between zero (two individuals were never seen in the same sub-group after a fission) and one (two individuals were always seen in the same sub-group after a fission). They were calculated using Socprog 2.3 (Sueur and Petit, 2008b; Whitehead, 2009).

Statistical analysis

We calculated the distribution of the number of individuals choosing one direction for observed and simulated group fissions. This distribution was the relative frequency: we observed the number of events in which n individuals joined a movement in one direction divided by the total number of events. We then compared the observed distribution of the number of individuals moving in one direction with the simulated ones, using Spearman rank correlation tests, in order to know which version of the model fitted better with the observed data (Lehmann et al., 2007; Lockwood et al., 1999; Zou et al., 2003). We used the higher Spearman correlation coefficient to identify which model fitted best with the observed data. The observed and simulated matrices of the HWI of associations (presence in the same sub-group) during group fission were then compared using Dietz R correlation matrices with 10,000 permutations for more accurate and stable P -values (Hemelrijk, 1990; Whitehead, 2009). Finally, the distribution of HWI of associations (frequency of HWI values in a matrix of associations) during group fission was compared using Spearman rank correlation tests to assess which version of the model fitted best correlated to the observed data. The significance level was set at 0.05. Means are presented \pm s.d. Tests were carried out using SPSS 10.0 (SPSS Inc., Chicago, IL, USA) and SocProg 2.3 for matrix correlations (Sueur and Petit, 2008b; Sueur and Petit, 2010; Whitehead, 1997; Whitehead, 2007; Whitehead, 2009).

RESULTS

Distribution of the number of joiners

In Tonkean macaques, Spearman rank correlation tests showed that simulated distributions of anonymous, kinship and affiliation models were positively correlated with the observed distribution of the number of joiners ($N=8$, Spearman rank correlation coefficient $r_s > 0.74$, $P < 0.021$, Fig. 1A; see supplementary material Fig. S1 for illustration of correlations). The best fitting model was that of affiliation ($N=8$, $r_s = 0.96$, $P = 0.00001$, Fig. 1A). The same result was obtained for rhesus macaques ($N=14$, $r_s > 0.56$, $P < 0.034$, Fig. 1B), for which the best fitting model was also that of affiliation ($N=14$, $r_s = 0.74$, $P = 0.002$, Fig. 1B).

Associations of individuals during group fissions

Associations of group members during group fission processes (i.e. composition of sub-groups in terms of identities and associations of group members) are illustrated in Fig. 2. Whatever the study group, we did not observe the same fission sub-group every time, i.e. during group fission events, the sub-group composition varied. Every dyad of individuals was seen together at least once. Matrix correlation tests showed that in Tonkean macaques, the models best explaining group fission processes (i.e. the sub-group composition) were the anonymous and the affiliation models (i.e. the matrices of both these models were positively correlated to the observed matrix of associations; $r = 0.59$, $N = 10$, $P = 0.015$ for the anonymous model; $r = 0.53$, $N = 10$, $P = 0.02$ for the affiliation model). A non-significant tendency of the random model explained group fission processes ($r = 0.30$, $N = 10$, $P = 0.07$). As far as the kinship model is concerned,

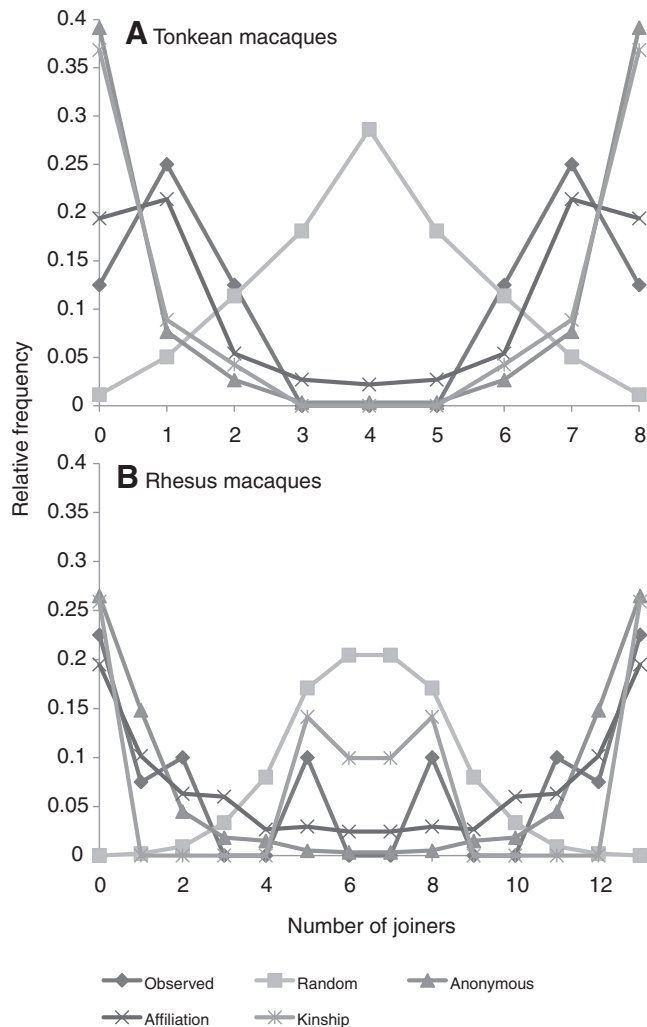


Fig. 1. Distribution of the number of joiners during observed and simulated group fissions for (A) Tonkean and (B) rhesus macaques. We observed a specific number of individuals in one direction, i.e. the number of events in which n individuals joined in one direction divided by the total number of events.

simulated associations were not correlated with the observed models ($r=0.06$, $N=10$, $P=0.321$). Conversely, in rhesus macaques, only the kinship model could significantly explain the associations between individuals during group fissions ($r=0.17$, $N=15$, $P=0.042$). In rhesus macaques, the associations for the affiliation model seemed to correlate with the observed associations, but this correlation remains a tendency ($r=0.16$, $N=10$, $P=0.052$). Both the random and the anonymous model failed to explain them ($r=0.003$, $N=15$, $P=0.483$ for the random model; $r=0.02$, $N=15$, $P=0.411$ for the anonymous model).

Distribution of association indices and group cohesion

In the same way, in Tonkean macaques, only the HWI distribution (i.e. relative frequency of HWI values) for anonymous and affiliation models was positively correlated with the distribution of observed HWI in individual associations after group fission (Fig. 3A; see supplementary material Fig. S2 for illustration of correlations). The best fitting model was the anonymous one ($rs=0.94$, $N=11$, $P=0.00001$), even if the affiliation model fitted with the observed

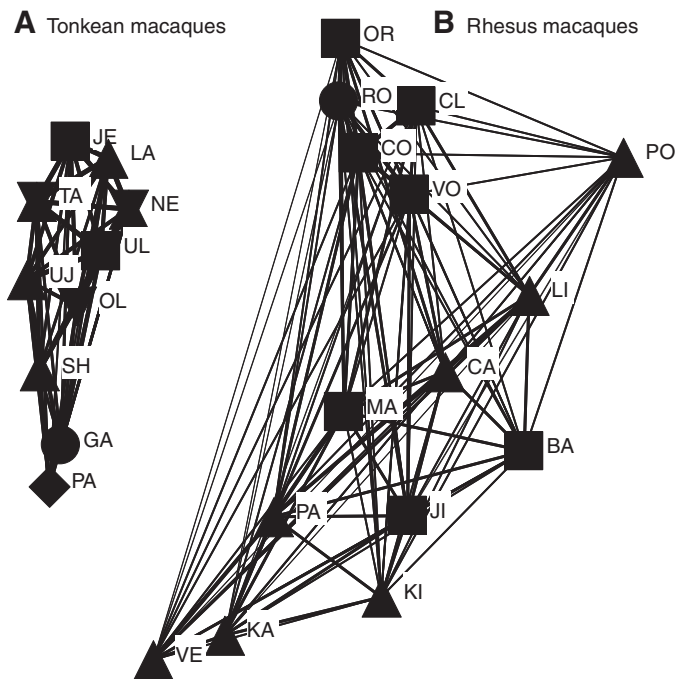


Fig. 2. Representation of inter-individual associations during group fission processes for (A) the Tonkean macaque group and (B) the rhesus macaque group. Social networks were drawn using Netdraw in Ucinet 6.0 (Borgatti et al., 2002). Nodes represent individuals. Distance between individuals represents the half-weight index and was calculated using the Multidimensional Scaling method (Whitehead, 2009). The two graphs are on the same scale (distances between individuals are comparable in the two groups). Similarly, the size of the link between individuals represents the HWI (the more two individuals were seen together, the bigger the link was). For both species, similar shapes characterised individuals belonging to the same matriline. Individual macaques are identified by their initials.

data ($rs=0.63$, $N=11$, $P=0.03$). HWI distribution for both the random and the kinship models was not correlated with the observed distribution ($rs=0.07$, $N=11$, $P=0.838$ for the random model; $rs=0.28$, $N=11$, $P=0.382$ for the kinship model). Group fission patterns in rhesus macaques illustrated that HWI distributions in both the random and the affiliative model were positively correlated with the observed model ($rs>0.66$, $N=11$, $P<0.022$, Fig. 3B). The best fitting model was the affiliative one ($rs=0.73$, $N=11$, $P=0.006$, Fig. 3B). The HWI distribution for the anonymous model was not correlated with the observed one ($rs=-0.47$, $N=11$, $P=0.140$), whilst the HWI distribution of the kinship model was negatively correlated with the observed model ($rs=-0.70$, $N=11$, $P=0.01$). These results may be explained by the affiliative relationships of both groups. As far as these affiliative relationships are concerned, the mean HWI (the sum of all dyad HWI divided by the number of dyads) was found to be 0.13 ± 0.03 (range 0.03–0.44) in the Tonkean macaque group and 0.03 ± 0.01 (range 0–0.35) in rhesus macaques. In Tonkean macaques, all dyads were seen to be in proximity at least once, whilst in rhesus macaques 68.1% of dyads were never observed together. The Tonkean macaques seemed to be more cohesive than the rhesus macaque group (Mann–Whitney: $Z=-6.429$, $P<0.0001$, $N_{\text{Tonkean}}=45$, $N_{\text{rhesus}}=105$; N being the number of dyads in each group). The great cohesion of Tonkean macaques might explain why the group fissions from the anonymous model were correlated to the observed group fissions in this species. The tests showed that the HWI distribution of the anonymous model was correlated to that of the affiliation

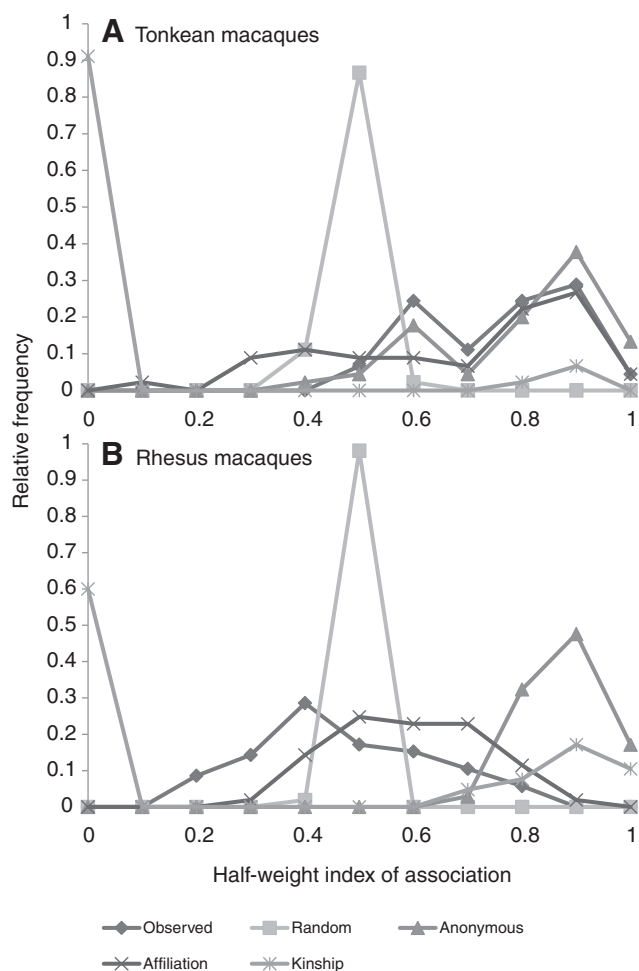


Fig. 3. Distribution of the HWI of associations during observed and simulated group fissions for (A) the Tonkean macaque group and (B) the rhesus macaque group.

model in the Tonkean macaques ($r_s=0.7$, $N=11$, $P=0.014$) and to the kinship model in rhesus macaques ($r_s=0.67$, $N=11$, $P=0.02$). Distributions of other models were not inter-correlated in Tonkean macaques ($r_s<0.322$, $N=11$, $P>0.335$) and rhesus macaques ($r_s<0.55$, $N=11$, $P>0.076$).

DISCUSSION

Group fissions are considered to be scarce in macaques but do exist (Fukuda, 1989; Ménard et al., 1990). This weak rate of fission, showing relatively high cohesion (Aureli et al., 2008), may be the result of two possible effects, namely group structural constraints (Thierry et al., 2004) or few conflicts of interest between group members (Conradt and Roper, 2005). Given that the two species studied are known to have different social styles but that the study groups lived in similar environments, we can confidently suggest that cohesion should therefore be due to limited conflicts of interest. These fissions, whatever their frequency, implied the choice for each group member of joining one sub-group or the other. In this study, we showed that group fissions may be explained by an anonymous process and/or by affiliative relationships in Tonkean macaques. Indeed, each model, both anonymous and affiliative, explained all the measured patterns. On the other hand, affiliation and/or kinship relationships seemed to influence sub-grouping patterns in rhesus

macaques. However, for rhesus macaques, kinship and affiliation explained only two of the three dependent variables. These results are in accordance with our expectations that affiliative relationships could explain group fission processes in Tonkean macaques whereas kinship relationships would underlie these fission processes in rhesus macaques. We note, however, that other models – and therefore other mechanisms – could also explain the composition of the observed sub-groups after fissions, even if affiliation seemed to be the best model to explain fission patterns in both groups. Analysing a greater number of observations could help to assess which model will better explain fission–fusion patterns and thus enable us to understand the possible link between the group structure and the anonymous, affiliation and kinship networks.

Fission–fusion society appears to be a strategy to avoid unnecessary costs of group living (Ramos-Fernandez et al., 2006; Wittemyer et al., 2005). It has been suggested that individuals choose their sub-groups according to similar needs and motivations (Couzin, 2006; Ramos-Fernandez et al., 2006). Ramos-Fernandez and colleagues (Ramos-Fernandez et al., 2006) proposed that social relationships must have developed within the existing grouping patterns that ecological conditions constrain, and that non-random associations among group members can solely arise from the way in which they forage. If individuals were associated according to their motivations, then our random model would be correlated with the affiliation model but, apparently, this was not the case. Whilst affiliation was correlated with the observed data in most results, the random model only correlated once with the observed data in rhesus macaques. Indeed, since we could not simulate observed group fission patterns in either study group using the random model, individual motivations did not seem to be a major influential factor in group fission. Individuals were therefore selectively associated within sub-groups according to their social affinities, and not because of similar needs. Similarly, previous studies on macaques suggested that social behaviours and social relationships of group members were not due to the strength of ecological factors (Thierry et al., 2004).

In the present study, whatever the species, proximities between group members were the best predictor of inter-individual associations during group fission processes. Such an influence of social relationships has been demonstrated for many social behaviours (Sueur and Petit, 2008b; Thierry et al., 2004), information transfer (Voelkl and Noë, 2008) and even permanent group fission (Van Horn et al., 2007). A study in chacma baboons (*Papio hamadryas ursinus*) reported that social relationships influenced fission events: fission was more likely to occur in groups where social ties were weak (King et al., 2008). In their studies on spider monkeys (*Atteles geoffroyi*), Aureli and Schaffner (Aureli and Schaffner, 2007) suggested that fission might reduce conflicts between group members by decreasing intra-group competition and aggressive escalation. As a consequence, sub-groups composed of affiliated individuals would manage better in the case of conflict than sub-groups of non-affiliated ones. They do not have to reassert their affiliative relationships as they belong to the same sub-group, whereas individuals belonging to different sub-groups seem to use embraces to avoid conflict at fusion (Aureli and Schaffner, 2007).

Despite having similar environmental conditions, and the same rate and duration of group fission, the two groups under investigation nevertheless showed some differences during group fission processes. In Tonkean macaques, the anonymous model explained some of the sub-grouping patterns, whereas kinship seemed to influence fission processes in rhesus macaques. These two species are known to have contrasting social styles; Tonkean macaques are tolerant and all individuals can interact with each other whatever their status, whereas

rhesus macaques are more nepotistic (Thierry et al., 2004; de Waal and Luttrell, 1989). In a group such as Tonkean macaques where relationships are egalitarian, it seems coherent that the group fission process appears to be anonymous, even if underlying mechanisms are based on affiliative relationships. In an anonymous system as well as in an egalitarian one, each individual equally influences all other individuals, whatever its social status and whatever its social relationships (in other words, all individuals and all social relationships are considered as similar and equal). The closer a system is to extreme egalitarianism, the more the mechanisms underlying collective phenomena may look like an anonymous process. Moreover, tolerant animals appeared to be more cooperative (Anderson, 2007). In the context of collective movements, cohesion could be interpreted as cooperation between group members and therefore reflecting their social style (Aviles, 1999). Such anonymous mimetism was also found in the relatively tolerant white-faced capuchin monkeys (*Cebus capucinus*) (Leca et al., 2007; de Marco et al., 2008) during induced collective movements showing high group cohesion (Meunier et al., 2006). Moreover, joining the sub-group with the higher number of individuals is a way of maintaining group cohesiveness or advantages in terms of protection or knowledge about resource location (Kerth et al., 2006; Lehmann and Boesch, 2004; Wittemyer et al., 2005). In rhesus macaques, we found that associations during the group fission process were also influenced by kinship, with the emergence of sub-groups composed of kin-related individuals. Due to the nepotism of rhesus macaques, Thierry and colleagues (Thierry et al., 2004) reported that covariance between the affiliative and kin relationships seemed to be higher in this species than in Tonkean macaques. This may explain why the kinship model was sometimes correlated to the observed data. Similar patterns have already been found in rhesus macaques, with sub-groups of related individuals moving together during unidirectional collective movements (Sueur and Petit, 2008b).

The influence of a species' social style could affect temporary and permanent group fission in a similar way to that described above: in a few nepotistic species, affiliation may have a role during the fission process, whereas in some more nepotistic species, sub-groups after group fission would mainly be composed of kin-related individuals (Chepko-Sade and Sade, 1979; Okamoto and Matsumura, 2001; Van Horn et al., 2007). Even if both groups split only a few times and for a short period, we suggest that choosing one sub-group rather than the other, which is mainly dependent on social relationships in the study groups, should follow the same rules whatever the frequency and duration of group fissions. In the same way, the strength and the distribution of affiliative relationships can influence group cohesion, from a highly cohesive group to a more fission–fusion type of group (in terms of the frequency of fusion and composition of sub-groups). In a review of fission–fusion dynamics, Aureli and colleagues (Aureli et al., 2008) explained that social systems are not divided into highly cohesive groups and fission–fusion societies, but rather show a continuum from systems with higher group cohesion stability, lower-FF, to systems characterised by a higher degree of fission–fusion dynamics, higher-FF. Considering their classification, our study groups may be considered as relatively cohesive groups that sometimes show variation in their spatial cohesion and party size (Aureli et al., 2008). However, their party composition remains quite stable and mainly depends on affiliative relationships. Our model only considered two variables: the intrinsic probability λ – corresponding to the physiological (i.e. nutrient requirements) and/or ecological (i.e. foraging areas, predation risk, and so on) constraints of an individual – and its social relationships [$\Sigma M(k, i)$]. This simple rule in the model seems to explicate the link between individual decision making and

short-term collective phenomena (collective movements or fission–fusion process) (Sueur et al., 2009) but could possibly explain more long-term phenomena such as irreversible group fission and consequent changes in population structure (Couzin, 2006; Couzin and Laidre, 2009). It would be interesting to apply our model to wild populations to measure the weight of social influence, compared with that of ecological influence. Coupled with social network analyses, such an approach would be advantageous for managing captive or wild primate populations, as well as other mammals, by enabling an optimal and stable composition of groups (Couzin, 2006; McCowan et al., 2008).

APPENDIX

Departure decision and direction decision

Moving in one direction rather than another corresponds to two decisions: (1) choosing a direction (direction decision); and (2) moving (departure decision).

While the direction decision was influenced by the number of individuals moving in one direction or the other, the departure decision can be influenced by the number of individuals already moving in the direction the individual wanted to follow, or by the total number of individuals having already left, whatever the direction. To assess which process underlies the individual departure decision, we first studied the individual departure latencies of both groups under both assumptions (i.e. departure decision influenced by the number of individuals in one direction and departure decision influenced by the total number of moving individuals). We then compared these latencies with the individual departure latencies when only one direction was proposed. Preliminary analyses showed that departure latencies when considering the number of individuals moving in one of two directions were correlated to departure latencies when only one direction was proposed for Tonkean macaques (Spearman rank correlation, $N=9$, $r_s=0.91$, $P=0.0006$) and rhesus macaques (Spearman rank correlation, $N=11$, $r_s=0.55$, $P=0.036$). However, departure latencies when considering the total number of moving individuals in both directions were not correlated to departure latencies when only one direction was proposed for both Tonkean macaque (Spearman rank correlation, $N=9$, $r_s=0.21$, $P=0.589$) and rhesus macaque groups (Spearman rank correlation, $N=11$, $r_s=-0.072$, $P=0.831$). In our model we followed these results, and therefore considered that the departure probability of an individual could be influenced by the number of individuals already moving in its preferred direction.

We then analysed the survival curves for joiners' departure latencies. The distribution fitted more with an exponential curve than with a linear curve in Tonkean macaques (exponential curve estimation, $F_{1,26}=627$, $r^2=0.96$, $P<0.00001$; linear curve estimation, $F_{1,26}=19.5$, $r^2=0.43$, $P=0.00016$) as well as in rhesus macaques (exponential curve estimation, $F_{1,38}=507$, $r^2=0.93$, $P<0.00001$; linear curve estimation, $F_{1,38}=181$, $r^2=0.83$, $P<0.00001$). These results showed that the probability ψ_{jd} of an individual joining the movement is constant per time unit.

Analysis of the intrinsic probability λ

The survival curve of the departure latencies for the individual departing first fitted more with an exponential curve than with a linear curve in Tonkean macaques (exponential curve estimation, $F_{1,10}=33.1$, $r^2=0.86$, $P<0.00001$; linear curve estimation, $F_{1,10}=22.1$, $r^2=0.69$, $P=0.0008$) as well as in rhesus macaques (exponential curve estimation, $F_{1,14}=298$, $r^2=0.95$, $P<0.00001$; linear curve estimation, $F_{1,14}=46.2$, $r^2=0.77$, $P<0.00001$). These results showed that the probability ψ_{01} of an individual being the first to depart (Eqn A1)

is constant per time unit, and is equal to the log gradient of the theoretical exponential curve (Amé et al., 2006; Meunier et al., 2006; Gautrais et al., 2007):

$$\Psi_{01} = \sum_{i=1}^n \lambda_i, \quad (\text{A1})$$

where $\Psi_{01}=0.001 \text{ s}^{-1}$ in Tonkean macaques and rhesus macaques.

Given that $n=N=10$ in Tonkean macaques, the probability per individual of departing first is $\lambda_f=0.0001 \text{ s}^{-1}$. Given that $n=N=15$ in Tonkean macaques, the probability per individual of departing first is $\lambda_f=0.00007 \text{ s}^{-1}$. We used these probabilities as intrinsic probabilities for joiners.

Determination of the mimetic process

The curve illustrating the inverse of departure latencies (i.e. departure probabilities) followed a cubic function in Tonkean macaques (Spearman rank correlation, $N=9$, $r_s=0.90$, $P=0.001$, $y=-0.0052x^2+0.0453x-0.0016$) and in rhesus macaques (Spearman rank correlation, $N=11$, $r_s=0.69$, $P=0.019$, $y=-0.0044x^2+0.0827x-0.1496$) showing that the studied individuals joined a movement according to a mimetic process (Dussutour et al., 2008).

In this kind of mimetic process, the individual departure probability Ψ_{jd} appeared as:

$$\Psi_{jd} = \lambda n + (Cj)^p. \quad (\text{A2a})$$

The departure latency of the joiner j was:

$$\Delta T_{j-1,j} = \frac{1}{(\lambda + C(j-1))(n - (j-1))}, \quad (\text{A2b})$$

or

$$\frac{1}{\Delta T_{j-1,j}} = (\lambda + C(j-1))(n - (j-1)) = (\lambda - C)(n+1) + j(2C + Cn - \lambda) - Cj^2. \quad (\text{A2c})$$

As the inverse distribution of departure latencies of joiners fitted with a parabolic curve (see above), the departure probability equation for Tonkean macaques was:

$$\frac{1}{\Delta T_{j-1,j}} = -0.0052j^2 + 0.0453j - 0.0016, \quad (\text{A2d})$$

then

$$(\lambda - C)(n+1) + j(2C + Cn - \lambda) - Cj^2 = -0.0016 + 0.0453j - 0.0052j^2.$$

So

$$(\lambda - C)(n+1) = -0.0016, (2C + Cn - \lambda) = 0.0453 \text{ and } C = 0.0052,$$

$$C = -\left(\frac{-0.0016}{(n+1)} - \lambda\right) = 0.0002,$$

or

$$C = \frac{0.0453 + \lambda}{2 + n} = 0.00037$$

or

$$C = 0.0052.$$

C therefore ranged between 0.0002 and 0.005 in Tonkean macaques.

The departure probability equation for rhesus macaques was:

$$\frac{1}{\Delta T_{j-1,j}} = -0.0044j^2 + 0.0827j - 0.1496, \quad (\text{A2e})$$

then

$$(\lambda - C)(n+1) + j(2C + Cn - \lambda) - Cj^2 = -0.1496 + 0.0827j - 0.0044j^2.$$

So

$$(\lambda - C)(n+1) = -0.1496, (2C + Cn - \lambda) = 0.0827$$

and

$$C = 0.0044,$$

$$C = -\left(\frac{-0.1496}{(n+1)} - \lambda\right) = 0.001$$

or

$$C = \frac{0.0827 + \lambda}{2 + n} = 0.0048$$

or

$$C = 0.0044.$$

C was therefore approximately equal to 0.001–0.005 in rhesus macaques.

Analysis of distribution for joiners' departure latencies according to these different mimetic coefficients

The departure probability equation (Eqn A2d for Tonkean macaques and Eqn A2e for rhesus macaques) enabled us to determine a range for mimetic coefficients.

In this analysis, we determined which mimetic coefficient C (from 0.0002 to 0.005 in Tonkean macaques and from 0.001 to 0.005 in rhesus macaques) fitted with the observed mimetic coefficient. The departure latency $\Delta T_{j-1,j}$ of each joiner j was then calculated for each mimetic coefficient as in Eqn A2b.

The results showed that the best fitting mimetic coefficient was equal to 0.002 in Tonkean macaques (Spearman rank correlation, $N=9$, $r_s=0.73$, $P=0.024$) and 0.003 in rhesus macaques (Spearman rank correlation, $N=11$, $r_s=0.92$, $P=0.00003$).

According to these results, we fixed the value C in our model at 0.002 in Tonkean macaques and 0.003 in rhesus macaques.

Calculation of the power p

We tested different values for p in our model (from 1 to 5) and compared the curves for each value of p to the observed curve for the relative frequency of the number of followers in each direction. The results showed that the best fitting curve was that of $p=4$ in Tonkean macaques (Spearman rank correlation, $N=9$, $r_s=0.74$, $P=0.02$) and the curve relating to $p=3$ in rhesus macaques (Spearman rank correlation, $N=11$, $r_s=0.58$, $P=0.029$). Finally, these values were implemented in our model.

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