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Journal of Theoretical Biology

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

Group size, grooming and fission in primates: A modeling approach based on group structure

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ARTICLE INFO

Article history:

Received 29 June 2010

Received in revised form

15 December 2010

Accepted 21 December 2010

Available online 29 December 2010

Keywords:

Social network

Cohesion

Time allocation

Population structure

ODD protocol

ABSTRACT

In social animals, fission is a common mode of group proliferation and dispersion and may be affected by genetic or other social factors. Sociality implies preserving relationships between group members. An increase in group size and/or in competition for food within the group can result in decrease certain social interactions between members, and the group may split irreversibly as a consequence. One individual may try to maintain bonds with a maximum of group members in order to keep group cohesion, i.e. proximity and stable relationships. However, this strategy needs time and time is often limited. In addition, previous studies have shown that whatever the group size, an individual interacts only with certain grooming partners. There, we develop a computational model to assess how dynamics of group cohesion are related to group size and to the structure of grooming relationships. Groups' sizes after simulated fission are compared to observed sizes of 40 groups of primates. Results showed that the relationship between grooming time and group size is dependent on how each individual attributes grooming time to its social partners, i.e. grooming a few number of preferred partners or grooming equally or not all partners. The number of partners seemed to be more important for the group cohesion than the grooming time itself. This structural constraint has important consequences on group sociality, as it gives the possibility of competition for grooming partners, attraction for high-ranking individuals as found in primates' groups. It could, however, also have implications when considering the cognitive capacities of primates.

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1. Introduction

Animals have to balance costs and benefits to be in close proximity to conspecifics (Krause and Ruxton, 2002). On one hand, living in groups may offer the advantage of a lower predation risk and better efficiency when seeking resources. On the other hand, as group size increases, individuals may experience more within-group competition for food and have higher health risks due to the possible spread of contagious diseases (Krause and Ruxton, 2002). Living in group implies interacting frequently with other group members in order to maintain group cohesion (Lehmann et al., 2007). Group cohesion may be defined using three criteria: stability, coordination and proximity. When group size or within-group competition for food increases, disadvantages may outnumber the advantages of group living,

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(Chapman et al., 1995; Janson and Goldsmith, 1995; Ron et al., 1994). As a consequence, group cohesion decreases and the group may split either temporarily (Kerth et al., 2006; Popa-Lisseanu et al., 2008; Wittemyer et al., 2005) or irreversibly (Henzi et al., 1997a, b; Lehman et al., 2007). In social or pre-social animals, irreversible fission is a common mode of group proliferation and dispersion. From ameba to primates, this process may be affected by genetic or social factors (Chepko-Sade and Sade, 1979; Gompper et al., 1998; Lehman et al., 2007; Seppa et al., 2008; Mehdiabadi et al., 2009; Rangel et al., 2009). In primates, irreversible group fissions rarely occur (about every five/ten years) and separation of different sub-groups often takes several months to years (Chepko-Sade and Sade, 1979; Okamoto and Matsumura, 2001; Van Horn et al., 2007).

In primates, grooming is considered to be the most common behavior for the maintenance of close social bonds (Schino, 2001). Previous studies have shown that when an individual regularly grooms a particular partner, it seems to be more tolerant with this partner and more likely to support it during a conflict (without suggesting causality). Likewise, the partner in question typically reciprocates with the same tolerance and support (Henzi and

Barrett, 1999; Dunbar et al., 2009). However, grooming needs time, and time is a limited resource (Dunbar, 1992b; Lehmann et al., 2007; Majolo et al., 2008; Pollard and Blumstein, 2008; Dunbar et al., 2009). In addition to maintaining social relationships, individuals need to rest, forage and move (Pollard and Blumstein, 2008). As a consequence, grooming seldom exceeds 15% of day-time activity for most social species (Dunbar, 1991; Lehmann et al., 2007). Some authors have investigated how an individual manages to maintain its social relationships when grooming time is limited but group size or within-group competition for food has increased (Chapman et al., 1995; Dunbar, 1992b; Janson and Goldsmith, 1995; Lehmann et al., 2007; Majolo et al., 2008; Pollard and Blumstein, 2008; Ron et al., 1994). Lehmann et al. (2007) have suggested that when group size and the number of available partners increase, each individual will have to spend more time grooming until a certain group size for which it is impossible to maintain relationships with all group members (Dunbar, 1992a; Lehmann et al., 2007; Schino et al., 2009). In this case, group cohesion – social proximity and stability – decreases and group members permanently split. This hypothesis implies that an individual tries to develop and maintain bonds with every group member, or at least, the most of conspecifics. However, other studies have shown that whatever the group size, an individual mainly interacts only with certain grooming partners, and does so much more than with other potential partners (Kudo and Dunbar, 2001; Lehmann and Dunbar, 2009). Individuals can therefore be considered to have a relatively fixed number of grooming partners. This is the case, for instance, in blue monkeys (*Cercopithecus mitis*, Cords, 2001), savanna baboons (*Papio ursinus*, Silk et al., 1999), in chimpanzees (*Pan troglodytes*, Watts 2000a,b) and in several macaque species (*Macaca sp.*, Berman et al., 2008; Lin et al., 2008; Nakamachi and Shizawa, 2003). In this case, an individual allocates its grooming time to its preferred partners. Consequently, grooming time should not be dependent on group size as it was found in Majolo et al. (2008).

In this study, we wanted to investigate the dynamic of group cohesion – how group cohesion evolves, from stable groups to groups having a greater probability to fission – according to group size and group structure of grooming relationships. By inducing a variation in the group size and the distribution of grooming time in a stochastic agent-based model, we make predictions about the conditions in which a group will irreversibly split. Most of studies on the link between social structure, grooming and group size (Kudo and Dunbar, 2001; Lehmann and Dunbar, 2009; Lehman et al., 2009) followed standard practices in social network analyses and used a criterion for distinguishing casual from meaningful relationships. Modeling permits, without using this arbitrary criterion for preferred relationships, the simulation of interactions between group members (Seyfarth, 1977; Bryson et al., 2007; Meunier et al., 2006; Sellers et al., 2007; Puga-Gonzalez et al., 2009) and also resulting sub-grouping patterns (i.e. how individuals are sub-grouped; Ramos-Fernandez et al., 2006). We attributed a specific grooming time given by each individual to each other conspecifics. We tested the following three different hypotheses for a range of group sizes (from 2 to 200 individuals): (1) an individual divides its grooming time equally among all other group members; (2) an individual does not divide its grooming time equally among all other group members (i.e. it maintains a social bond with all other group members but these bonds are different depending on the partner concerned) and (3) an individual divides its grooming time among specific individuals (this number is fixed to (a) 5 and (b) 10 partners per individual, see methods for details). This social structure – grooming a specific number of partners – is suggested by several studies (Berman et al., 2008; Cords, 2001; Lin et al., 2008; Nakamachi and Shizawa, 2003; Silk et al., 1999, Watts 2000a,b). Once the social structure was established in the model, individuals made a decision between two states (representing the two potential sub-groups). If less than four

individuals split from the main group at the simulation end, we considered the cohesion maintained (see previous works on fission: Lefebvre et al., 2003; Ron et al., 1994; Van Horn et al., 2007). Then, we observed whether, and if so, how the group divided according to its social structure. According to general rules of cohesion or of mimetism (the probability to do a behavior depends on the number of individuals performing this behavior), we expected that if all individuals are linked together, especially by equivalent grooming relationships (hypothesis 1), the system would lead to amplification process – the more individuals join a group, and the more other ones will join it – and no splitting would be observed (Amé et al., 2006; Dussutour et al., 2005; Nicolis et al., 2003; Meunier et al., 2006). Then, group cohesion would be influenced by grooming time and group size when grooming relationships are not equal and especially when grooming is only given to a small number of partners. The simulated data were compared to observed data in order to assess which model most closely corresponds to the observed distribution of group sizes in primates (Lehmann et al., 2007). This comparison allowed us to understand which is the best rule affecting group structure and then population structure. We also tested how increased within-group competition – leading to grooming time decrease by a foraging time increase – influences group cohesion, and whether changes in group cohesion are similar according to group size. We eventually used a path analysis to investigate the relationships (direct and/or indirect) between group size, group structure and group cohesion.

2. Material and methods

2.1. Data

2.1.1. Empirical data

We used published data about group size and grooming time in order to compare them to our simulation data. Data is taken from 40 published studies on Old World primate species/populations (see Lehmann et al., 2007 for details) and are summarized in Table 1.

2.1.2. Theoretical data

We created theoretical networks using UCINET 6.0 (Borgatti et al., 2002). Groups contained 2–200 individuals (2, 5, 10, 20, 40, 60, ..., 200). We set networks as random (Erdos–Renyi random graph, with a linear distribution of links). The social structure is different for each generated random network. We did not set networks as scale-free since recent primate studies showed that social networks were not scale-free (i.e. with a power distribution of links) but random (see Flack et al., 2006; McCowan et al., 2008; Sueur and Petit, 2008; Kasper and Voelkl, 2009; Ramos-Fernandez et al., 2009 for studies on primate social networks; see Wasserman and Faust, 1994 for social network theory). We can observe on Fig. 1 that some individuals are only groomed by one partner whilst other ones are groomed by 7 or 8 partners, even if one individual can only groom 5 partners. Then, some social characteristics such as dominance of individuals may be taken into account by considering the network having an Erdos–Renyi random structure. For instance, individuals groomed by a lot of partners on Fig. 1 might be high-ranking individuals or matriarchs. Indeed, it was shown that these individuals are more groomed than other ones (Nakamachi and Shizawa, 2003; Schino, 2001; Silk et al., 1999).

2.2. Definitions of parameters

We defined a bond (or a link) in a network as the time one individual groomed another one. Then the relationship is directed and does not need to be reciprocal. The grooming time per

Table 1
Data (Genus, species, group size and grooming time) and references of data used in this study.

Genus	Species	Group size	Grooming time (%)	Reference(s)
<i>Avahi</i>	<i>laniger</i>	2	2	Harcourt (from Dunbar,1991)
<i>Cercocebus</i>	<i>galeritus</i>	27	5.5	Homewood (1976)
<i>Cercopithecus</i>	<i>ascanius</i>	26.75	3.45	(Struhsaker, 1980; Cords, 1986)
<i>Cercopithecus</i>	<i>campbelli</i>	9	2.8	Buzzard (2004)
<i>Cercopithecus</i>	<i>diana</i>	28.75	2.48	(Whitesides 1989; Buzzard, 2004)
<i>Cercopithecus</i>	<i>mitis</i>	22.65	7.18	Struhsaker and Leland (1979) (Butynski 1990; Lawes 1991) Cords (1995, 2002) Kaplin and Moermond, (2000) (Dunbar, 1974; Lee, 1981) Baldellou and Adan (1997, 1998)
<i>Chlorocebus</i>	<i>aethiops</i>	19.7	9.17	Bocian (1997)
<i>Colobus</i>	<i>angolensis</i>	18	5.25	Dunbar and Dunbar (1974) (Oates 1977a,b; Bocian 1997)
<i>Colobus</i>	<i>guereza</i>	9.04	5.52	Fashing (2001)
<i>Colobus</i>	<i>polykomos</i>	12.5	3.49	Dasilva (1989)
<i>Colobus</i>	<i>satanas</i>	12	5.51	McKey and Waterman (1982)
<i>Gorilla</i>	<i>gorilla</i>	11	0.09	Doran (from Lehmann et al., 2007)
<i>Gorilla</i>	<i>G. beringei</i>	6	1	Fossey and Harcourt (1977)
<i>Hylobates</i>	<i>agilis</i>	4.4	0	Gittins and Raemakers (1980)
<i>Hylobates</i>	<i>klossii</i>	3.8	0	Whiten (1980)
<i>Hylobates</i>	<i>lar</i>	3.4	2.1	Ellefson (1974) Gittins and Raemakers (1980)
<i>Indri</i>	<i>indri</i>	4.3	1	Pollock (1977)
<i>Lemur</i>	<i>catta</i>	12.2	7.18	Sussmann (1977)
<i>Lemur</i>	<i>fulvus</i>	15.33	7.98	Sussmann (1977)
<i>Lophocebus</i>	<i>albigena</i>	15	5.8	Struhsaker (1979)
<i>Macaca</i>	<i>fascicularis</i>	82.45	7.98	Van Noordwijk (1985) Son (2004)
<i>Macaca</i>	<i>fuscata</i>	36.5	10.7	Maruhashi (1981) Seth and Seth (1986)
<i>Macaca</i>	<i>mulatta</i>	32	15	Teas et al. (1980)
<i>Pan</i>	<i>paniscus</i>	27.8	5.7	White (1992)
<i>Pan</i>	<i>t. Schweinfurthi</i>	59.2	11.67	(Wrangham, 1977; Nishida, 1990) White and Chapman (1994) Matsumoto-Oda and Oda (1998) Fawcett (2000)
<i>Pan</i>	<i>t. verus</i>	40.33	8.27	Tutin et al. (1983) Yamakoshi (1998, 2004) Boesch and Boesch-Achermann (2000) (Nagel, 1973; Eley et al., 1989)
<i>Papio</i>	<i>anubis</i>	58.8	8.3	Henzi et al. (1997b)
<i>Papio</i>	<i>ursinus</i>	28.07	12.64	Nagel (1973)
<i>Papio</i>	<i>hamadryas</i>	51	13.5	R. Noe and H. Korstjens (from Lehmann et al., 2007)
<i>Ptilocolobus</i>	<i>badius</i>	42.5	4.5	Decker (1994)
<i>Ptilocolobus</i>	<i>rufomitratu</i>	16.16	0.83	Starin (1991)
<i>Ptilocolobus</i>	<i>temminckii</i>	26.2	5.4	(Clutton-Brock 1974, 1975; Stanford, 1998)
<i>Ptilocolobus</i>	<i>tephrosceles</i>	51.67	4.99	Struhsaker and Leland (1979) Chapman and Chapman (2000)
<i>Pongo</i>	<i>pygmaeus</i>	1	0	Mackinnon (1974)
<i>Presbytis</i>	<i>entellus</i>	33	4.4	Sugiyama (1976)
<i>Presbytis</i>	<i>rubicunda</i>	7	0	Davies (1984)
<i>Procolobus</i>	<i>verus</i>	3	3.58	R. Noe and H. Korstjens (from Lehmann et al., 2007)
<i>Propithecus</i>	<i>verreauxi</i>	5.1	4.7	Howarth et al. (1986)
<i>Trachypithecus</i>	<i>leucocephalus</i>	10	11.71	Li and Rogers (2004)
<i>Theropithecus</i>	<i>gelada</i>	144.7	17.4	Iwamoto and Dunbar (1983)

individual $T(G)_i$ was defined as the time an individual spends grooming, whatever the number of groomed partners n . According to observed data (see Table 1) in this study, we considered grooming to represent no more than 15% of total day-time activity.

For hypotheses 1 (an individual equally grooms all group members) and 2 (an individual non-equally/randomly grooms all group members), the mean strength of social relationships (i.e. dyad's social bonds) was equal to the grooming time divided by the number of group members. For hypothesis 1, all grooming time is equal to $T(G)_i/n$. For hypothesis 2, minimum and maximum of grooming time are, respectively, 0.4% and 5.4% in a group of 5 individuals and 0.01% and 0.7% in a group of 200 individuals.

As far as hypothesis 3 is concerned (i.e. an individual grooms a fixed number of partners), we carried out simulations with two

numbers of groomed partners, $n_1=5$ and $n_2=10$. These correspond to the average and to the maximum numbers, respectively, of groomed partners found in experimental studies regardless of the group size or the species (Berman et al., 2008; Cords, 2001; Lin et al., 2008; Nakamachi and Shizawa, 2003; Silk et al., 1999; Watts 2000a,b; Kudo and Dunbar, 2001; Lehmann and Dunbar, 2009). These studies revealed that the time taken by an individual to groom a non-preferred group member could be considered unimportant compared to the time taken to groom its preferred partners. Previous studies have reported that even if individuals groomed a specific number of individuals, high-ranking individuals or matriarchs can be groomed more than others (Nakamachi and Shizawa, 2003; Schino, 2001; Silk et al., 1999). We took into account these results to build the theoretical group

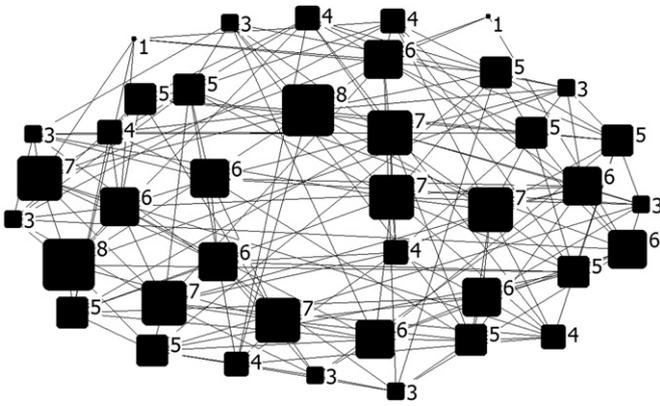


Fig. 1. Illustration of a social network with 40 individuals (squares). Number labels indicated the number of group members by which an individual is groomed (*indegree*, Wasserman and Faust (1994)). We showed from this graph that even if the number of partners groomed by the same individual was fixed at 5, an individual can be groomed by more (or less) than 5 grooming partners in the model. We built this network via Netdraw in UCINET 6.0 (Borgatti et al., 2002). Distance between individuals represents the strength of associations, and was calculated using multidimensional scaling (Whitehead 2009; Sueur and Petit, 2008).

structure. Even if the number of partners an individual grooms is fixed to (5 and 10), an individual can be groomed by more (or less) than 5 or 10 grooming partners (see Fig. 1 for an example).

In our model, we decided to simulate an increased within-group competition by reducing grooming time in steps of 20% (i.e. –20%, –40%, –60%, –80% and –100%). We attributed the new social bonds equally for hypothesis 1 and randomly for hypothesis 2. For hypothesis 3, we deleted one partner at each step (i.e. 4, 3, 2, 1 and 0 partner). Indeed, previous studies reported that decreased grooming time seems to have differing effects on an individual's social bonds: in the case of high within-group competition, social bonds were mainly observed amongst kin, and an attraction was observed towards the highest-ranking individuals (Berman et al., 2008; Majolo et al., 2008; Schino, 2001; Watts 2000a,b). We created the networks varying using UCINET 6.0 (Borgatti et al., 2002; Krause et al., 2007; Wey et al., 2008).

Group fission was considered to have occurred when the group irreversibly split into two sub-groups (i.e. daughter groups, Ron et al., 1994) containing more than three individuals each. This criterion of three individuals was based on group fission studies (Lefebvre et al., 2003; Ron et al., 1994; Van Horn et al., 2007). It is suggested that if the number individuals leaving the group is inferior to three individuals (as dispersing males, females with juveniles), it is more considered as dispersion than fission.

2.3. The model

We described the model according to the ODD protocol (i.e. Overview, Design concepts and Details; Grimm et al., 2006).

2.3.1. Purpose

The purpose of the model is to assess how group structure in terms of group size and distribution of grooming between individuals (hypotheses 1–3) leads to group fission or allow group cohesion (see Section 2.2 for definitions). In our model, each individual has to choose between two sub-groups according to the social relationships it has with each individual in each sub-group. Then, the global variable we observed – group fission or group cohesion – is based on the sum of individual decisions.

2.3.2. State variables and scales

The model is based on rules of mimetism/cohesion (Markov chain process) described in several studies on collective phenomena (Amé et al., 2006; Gautrais et al., 2007; Dussutour et al., 2005). In this model, the probability of an individual joining a collective movement in one direction (the future sub-group) depends on the number but also the strength of relationships it has with the individuals already in this direction. The number of individuals, individual identities and the network of affiliative relationships of each theoretical social network are included in the model. Then, an individual is only characterized by its affiliative relationships, based on grooming time he gave and received from its conspecifics. This model was already used in Sueur et al. (2010). In this study, authors explained how Tonkean and rhesus macaques joined a sub-group during short-term fissions. For both species, the affiliative relationships (i.e. the social network, based on contact between individuals) explain the sub-grouping patterns. Even if individuals are all connected together (one individual was at least observed once with each group member), strength of social relationships leads to fission. In this study, it means that the group fission or cohesion will not only depend on the group size but also on how individuals are connected (hypotheses 1–3).

2.3.3. Process overview and scheduling

Each group is characterized by its size (number of individuals per group) and its structure (how individuals are connected). Individuals are characterized by their social relationships depending on the three tested hypotheses and by a state S . At the start of a simulation all group members are in state s_0 (i.e. group 0, initial group). Then, all individuals will have to choose between state s_1 (i.e. sub-group 1) and s_2 (i.e. sub-group 2) according to their own social relationships. This process based on social network will lead to the group cohesion or the group fission. This is the only measure we took into consideration at the end of a simulation. Simulations stop when all group members have changed from state s_0 to states s_1 or s_2 . Groomed partners for each group member were attributed randomly (see Data for details). The model was then implemented in Netlogo 3.14 (Wilensky, 1999). We set the number of simulations to 10,000 for each hypothesis and for each set of tested parameters.

2.3.4. Design concepts

Emergence: the only phenomenon emerging from individual decisions in the model is the group fission or cohesion.

Fitness: we did not measure fitness of individuals in this study.

Interaction: individuals are linked to another one by the grooming time they give or they receive (see Section 2.2 for details).

Sensing: to change state s (1 or 2), individuals take into account an intrinsic probability λ_{is} and the relationships they have with individuals already in the state s .

Stochasticity: the model is stochastic. At each time step, a number is randomly attributed to each individual and this number will determine if individual will change of state and for which state, according to the probabilities to be in each state.

Collectives: collectives are represented as social groups of primates. Collectives occur as phenomena emerging from individual behavior, specifically from the way to choose one sub-group (i.e. state) or another one according to the relationships an individual has in each sub-group (i.e. each state). The collective phenomenon emerging from this choice is the group fission (or the group cohesion).

Observation: we set the number of simulations to 10,000 for each hypothesis and for each set of tested parameters (i.e. group size). Then, for each hypothesis and each group size, we obtained

a value of group cohesion (how much time the group staid cohesive up on the 10,000 simulations).

2.3.5. Initialization

At the start of a simulation all group members are in state s_0 (i.e. group 0, initial group). We then induce a change of state in two randomly chosen individuals: state s_1 (i.e. sub-group 1) for one individual and state s_2 (i.e. sub-group 2) for the other. These two individuals are therefore the basis of the formation of the two sub-groups.

2.3.6. Input

At each time step, a number between 0 and 1 is randomly attributed to all other individuals i in state s_0 ; when this number is lower than the theoretical probability ψ_{is_1} ($P_1 = [0, \psi_{is_1}]$) the individual changes from state s_0 to s_1 ; when this number is comprised between ψ_{is_1} and $\psi_{is_1} + \psi_{is_2}$ ($P_2 =]\psi_{is_1}, \psi_{is_1} + \psi_{is_2}]$), then the individual changes from state s_0 to s_2 ; however, no change of state occurs if this number is superior to $\psi_{is_1} + \psi_{is_2}$ ($P_3 =]\psi_{is_1} + \psi_{is_2}, 1]$), with $P_1 + P_2 + P_3 = 1$.

If $\sum r(k, i) = 0$ for an individual i , it changed of state according to its intrinsic probability λ .

The probability ψ_{is} for an individual i in state 0 to turn into state s (1 or 2) was

$$\psi_{is} = \lambda_i + \left(\sum_{k=1}^{N-1} r(k, i)_s \right)^p$$

where λ_i was the intrinsic probability to change state. We considered that all group members had the same intrinsic probability. $\lambda_i = 0.0001$.

p determined the degree of non-linearity in the response shown by individual i . The higher the value of p was, the higher was the resulting discrimination between the both directions (i.e. the higher the individual probability Ψ to go into state s), suggesting a deterministic response in this study (Amé et al., 2006; Dussutour et al., 2005; Nicolis et al., 2003). $p = 5$.

λ_i and p were chosen according to previous studies using similar models in primates (Meunier et al., 2006; Petit et al., 2009; Sueur et al., 2009, 2010; Jacobs et al., In press).

$r(k, i)_s$ was the social bond of i towards k when individual k was already in state s . If individual k was not yet in state s , then $r(k, i)_s = 0$.

$\sum r(k, i)_s$ represented the sum of social bonds for individual i in state s .

2.3.7. Submodels

Hypothesis 1. (an individual grooms all group members equally)

$$r(k, i)_s = \omega_{k,i} * T(G)_i$$

where $\omega_{k,i}$ is the weight (strength of social bonds) between individual i and individual k and $T(G)_i$ is the grooming time per individual.

For this hypothesis,

$$\forall i, \omega_{k,i} = 1/(N-1) \quad (\text{all } r(k, i)_s \text{ were equal}).$$

N is the number of individuals in the group.

$$T(G)_i = 0.15$$

Hypothesis 2. (an individual does not groom all group members equally)

$$r(k, i)_s = \omega_{k,i} * T(G)_i$$

with all $\omega_{k,i}$ were attributed randomly according to a normal distribution in order that $\omega_{k,i} > 0$ and $\sum \omega_{k,i} = 1$ for each individual of each group.

$$T(G)_i = 0.15$$

For this second hypothesis, an individual groomed all other group members but almost all the $r(k, i)_s$ were seen to be different (see Data for details).

Hypothesis 3. (an individual grooms a fixed number n of partners)

$$\forall k \in G_i, \omega_{k,i} = 1/n$$

$$\forall k \notin G_i, \omega_{k,i} = 0$$

where n is the number of groomed partners (see Definitions of parameters for explanation) and G_i the group of G partners groomed by the individual i .

2.4. Group structure analyses

Group structure was analyzed using the social networking approach (Krause et al., 2007; Wasserman and Faust, 1994; Wey et al., 2008; Whitehead 2009). We used two indexes to determine a group structure.

Group density: number of observed bonds divided by the number of possible bonds in the group.

Group mean path length: an average number of all paths (shortest number of connections between two individuals) between all pairs of individuals in the group. For the same density (i.e. same number of social bonds in a group), group mean path length can be different. This depends on how individuals are connected (see Wasserman and Faust, 1994 for details on social network theory; see Flack et al., 2006; McCowan et al., 2008; Sueur and Petit, 2008; Kasper and Voelkl, 2009; Ramos-Fernandez et al., 2009; for studies on primate social networks).

We calculated these indices using UCINET 6.0 (Borgatti et al., 2002).

2.5. Statistical analyses

The relationship between group size and group structure i.e. group mean path length and density, was determined for the three hypotheses. Curve estimation tests were used to assess whether the density and the group mean path length of a given group depends on group size, and to establish the relationship between these variables (linear, logarithmic and exponential) (Newman et al., 2006). The same curve estimation tests were used to assess the dynamics of group cohesion for each hypothesis according to group size. In order to understand the relations between group cohesion and group size, we finally verified for each hypothesis how group cohesion is affected by group density and group mean path length.

Distributions of group sizes after simulations were compared to observed distribution (data from 40 studied groups, see Data for details) using the Kolmogorov–Smirnov test with Monte–Carlo significance estimation (the number of simulations for this test was set at 10,000). This allows to assess if simulated dynamics of group cohesion/fission fits with global patterns observed in the wild. The theoretical values were obtained by dividing the number of cohesive groups (i.e. that have not split) in each group size by the total number of cohesive groups.

A Mann–Whitney test was used to assess how increased within-group competition – a decrease in the grooming time – influences group cohesion within our model. The initial condition – 15% of grooming time – was compared to each other condition (12%, 9%, 6%, 3% and 0%). Analyses were performed using SPSS 10 (SPSS Inc., Chicago, USA).

Path analysis was used to assess direct and indirect effects between group size, group structure and group cohesion. Path analyses and diagrams were carried out using AMOS5 software (AMOS Development Corporation, Spring House, PA, USA.) with

maximum likelihood estimations (for non-parametric analyses). This analysis was the most suitable for obtaining the best model of possible relationships and causal effects between variables (identified using AIC – Akaike Information Criterion – values, a measure a goodness of fit of a model).

α was set at 0.05. Means were Standard Error (\pm SE). Tests are two-tailed.

3. Results

3.1. Dynamics of group cohesion

3.1.1. Relationship between group structure and group size

Group mean path length. For both hypotheses 1 (an individual grooms all other group members equally) and 2 (an individual does not groom all other group members equally), the group mean path length was constant (1.00) whatever the group size (Fig. 2a). For hypothesis 3 (an individual grooms a fixed number of partners), the best-fit equation between the group mean path length and the group size was logarithmic, whatever the number of groomed partners (5 or 10) ($N=13$ tests group sizes, $F_{1,11} \geq 195.945$, $R^2 \geq 0.947$, $P < 0.000001$; Fig. 2a), showing that

path length and, thus connectivity between individuals highly vary for small group size (until about 40 individuals per group) whilst it is more constant for large group sizes.

Group density. For hypotheses 1 and 2, the density was constant (1.00) whatever the group size (Fig. 2b). For hypothesis 3, the best fit equation between the group mean path length and the group size was logarithmic, whatever the number of groomed partners (5 or 10), ($N=13$, $F_{1,11} \geq 96.611$, $R^2 \geq 0.898$, $P < 0.000001$; Fig. 2b).

3.1.2. Relationship between group cohesion and group size

For hypothesis 1, group cohesion (defined as the ratio of the number of cases where “one of the sub-groups containing three individuals or less” divided by the total number of simulations) was a constant (1.00; Fig. 2c). For hypothesis 2, the best fit equation between group cohesion and group size was logarithmic ($N=13$, $F_{1,11} = 24.255$, $R^2 = 0.68$, $P = 0.0004$; Fig. 2c). The decrease in group cohesion was only seen to be $0.085 \pm 0.004\%$ in groups of 10–200 members. For hypothesis 3, whatever the number of groomed partners (5 or 10), the best fit equation between the group cohesion and the group size was exponential ($N=13$, $F_{1,11} \geq 327.615$, $R^2 \geq 0.967$, $P < 0.000001$; Fig. 2c).

These results suggest that when an individual has social bonds with all other group members, whatever the quality of these social bonds, group size has little influence on group cohesion and consequently on group fission probability.

3.1.3. Relationship between group cohesion and group structure

Group mean path length. For hypotheses 1 and 2, group cohesion was constant (1.00) whatever the group mean path length. For hypothesis 3, the best fit equation between mean path length and group cohesion is negatively linear, whatever the number of groomed partners (5 or 10) ($N=13$, $F_{1,11} \geq 219.38$, $R^2 \geq 0.952$, $P < 0.000001$).

Group density. For hypotheses 1 and 2, the group cohesion was constant (1.00) whatever the density. For hypothesis 3, the best fit equation between density and group cohesion is logarithmic, whatever the number of groomed partners (5 or 10) ($N=13$, $F_{1,11} \geq 471.13$, $R^2 \geq 0.977$, $P < 0.000001$).

The equation best describing the relationship between density (and the group mean path length) and group cohesion for 5 partners was similar to that calculated for 10 partners (Table 2). These results suggest that group size seems to not directly influence group cohesion, but it seems to indirectly do it through group structure, and only in the case of hypothesis 3. However, this hypothesis needs to be statistically tested a test allowing to describe direct and indirect effects of variables (see. Section 3.2 in Results).

3.1.4. Comparison of observed group distribution and simulated group distributions

For the observed data, and for each hypothesis, we calculated the relative distribution of group sizes. The best fit equation for the observed distribution was exponential ($N=6$, $F_{1,4} = 21.29$, $R^2 = 0.852$, $P = 0.008$; Fig. 3). For hypotheses 1 and 2, there was no relationship between relative frequency and group size ($N=11$, $F_{1,9} \leq 1.74$, $R^2 \leq 0.16$, $P \geq 0.215$; Fig. 3). Their distributions significantly differed from the observed distribution ($N_{\text{observed}}=6$, $N_{\text{simulated}}=11$, $z=1.314$, $P \leq 0.021$). For hypothesis 3, whatever the number of groomed partners (5 or 10), the best fit was exponential ($N=11$, $F_{1,9} \geq 720.55$, $R^2 \geq 0.98$, $P < 0.000001$; Fig. 3). For 5 and 10 partners, the simulated distribution did not significantly differ from the observed distribution ($N_{\text{observed}}=6$, $N_{\text{simulated}}=11$, $z=0.806$, $P=0.356$ for 5 partners; $N_{\text{observed}}=6$, $N_{\text{simulated}}=11$, $z=1.134$, $P=0.086$ for 10 partners; Fig. 3). However, P -values suggested that there was less difference between the observed distribution and the

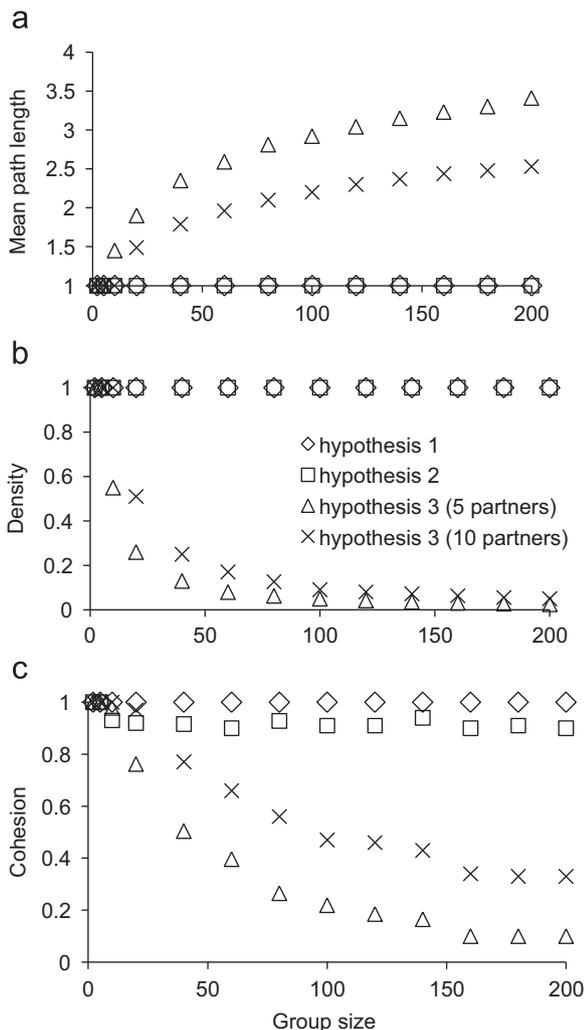


Fig. 2. Influence of group size on group structure ((a) on group mean path length and (b) on density) and on group cohesion (c) for each hypothesis. For hypotheses 1 and 2, where an individual groomed all other group members, there is no relationship between group size and group structure, nor between group size and group cohesion, contrary to hypothesis 3 (where an individual groomed a fixed number of partners).

Table 2 Equations of relationship between mean path length and group cohesion and between density and group cohesion, for 5 and 10 partners. Tests showed that the equations are similar for 5 and 10 partners. We used a comparison test for two linear regressions (transformation from logarithmic to linear for the relations between density and number of partners). We first used a Snedecor test to compare variances of each distribution ($df_1 = df_2 = 11, f \leq 0.75$). Then, we tested if variable ($b_{15 \text{ partners}} - b_{110 \text{ partners}}$, $df = 22, T \leq 0.27$) and variable ($\text{constant}_{5 \text{ partners}} - \text{constant}_{10 \text{ partners}}$, $df = 22, T \leq 0.21$) followed a Student law ($df = 22$).

N=13	Group cohesion							Similar functions	
	5 partners			10 partners					
	Function	Constant	b1	Function	Constant	b1			
Group mean path length	Linear	1.51	-0.45	Linear	1.48	-0.42	Yes	$P < 0.05$	
Density	Logarithmic	1.03	0.23	Logarithmic	1.05	0.26	Yes	$P < 0.05$	

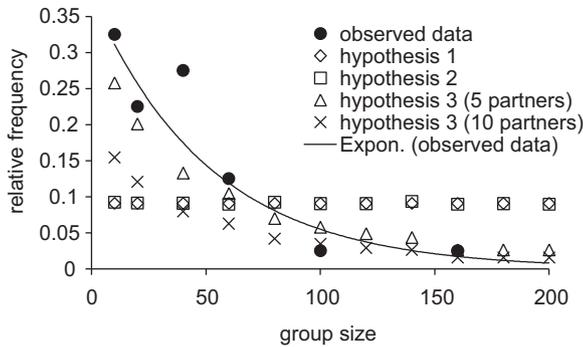


Fig. 3. Relative distribution of group size for observed data and under each hypothesis. The curve line is the best-fit model explaining the distribution of observed data and corresponds to an exponential law.

Table 3 Influence of grooming time on mean group cohesion for each hypothesis.

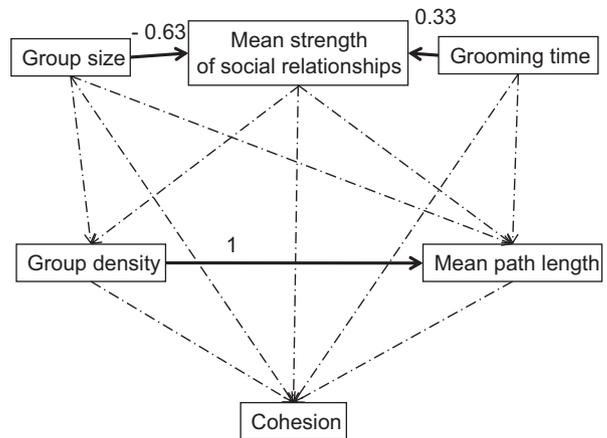
Grooming time (% per day time)	Initial time Decrease (%)	Mean group cohesion		
		Hypothesis 1	Hypothesis 2	Hypothesis 3
15 (initial time)	-0	1.00	0.93	0.44
12	-20	1.00	0.93	0.33
8	-40	1.00	0.92	0.27
6	-60	1.00	0.93	0.22
3	-80	1.00	0.92	0.17
0	-100	0.00	0.00	0.00

distribution for 5 partners than for 10 partners. The “5 partners” condition seemed the best model to explain how an individual attributed grooming time to group-mates.

3.2. How does an increase of within-group competition affect group cohesion?

When within-group food competition increased, group members had to spend more time foraging (and therefore to move from one patch to another). As a consequence, grooming time decreased (Berman et al., 2008; Lehmann et al., 2007; Sterck et al., 1997). For hypotheses 1 and 2, a decrease in grooming time did not affect group cohesion, whatever the group size (Mann–Whitney test: $U \geq 68.5, P \geq 0.418$; see Table 3 for means), except when grooming time is null (Mann–Whitney test: $U < 0.001, P < 0.00001$, Table 3). For hypothesis 3, a decrease in grooming time (represented by a decrease in the number of partners) from 40% (3 partners) to 100% (0 partner), influenced group cohesion (Mann–Whitney test: $U \leq 46, P \leq 0.048$). This effect followed an exponential law ($N = 13, F_{1,11} \geq 31, R^2 \geq 0.74, P \leq 0.0001$). We can therefore conclude that according to group size, group cohesion was affected non-linearly by decreased grooming time and a decreased number of partners.

a. Hypotheses 1 and 2



a. Hypothesis 3

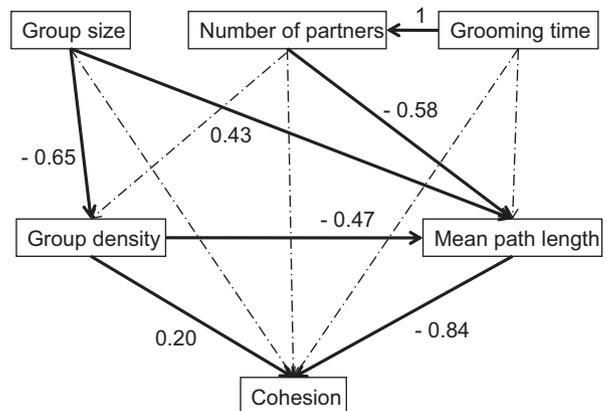


Fig. 4. Path diagram indicating causal relations between group size, grooming time and group structure, i.e. mean strength of social relationships (a), number of partners (b), density and group mean path length, and group cohesion. Rectangles indicated observed variables. Arrows indicated presumed causal relations: solid arrows represented the best model based on AIC value, using AMOS5; dotted arrows represented the relations we included in the analysis but not selected in the best model.

3.3. Causal relations between group size, grooming time, group structure and group cohesion

The most likely causal relations among the different variables previously tested were assessed using path analyses. For hypotheses 1 and 2, the most parsimonious causal model showed that grooming time and group size did not affect group cohesion either directly or indirectly ($AIC = 18; df = 2; P = 1$; Fig. 4a). These results confirmed what we expected below. In the case of hypothesis 3, grooming time and group size affected group cohesion but did so indirectly through

the group structure and especially through the group mean path length ($AIC=38$; $df=2$; $P=0.021$; see Fig. 4b for details about different influences).

4. Discussion

Time is a finite resource and grooming time, therefore, has to be limited if an individual also wishes to forage, rest or move (Dunbar, 1992b; Lehmann et al., 2007; Majolo et al., 2008; Pollard and Blumstein, 2008). Nevertheless, grooming may be the most important behavior used by primates for maintaining social relationships (Henzi and Barrett, 1999; Schino, 2001). As a consequence, the time an individual attributes to grooming will likely influence the quality and/or the quantity of its social bonds (Dunbar, 1991, 1992b; Lehmann et al., 2007). If the grooming time of an individual decreases, the quality and/or the quantity of its social bonds should also decrease. Moreover, the structure of social networks – the number of partners per individual and the strength of these connections – may influence group fission probability and therefore group size if the group splits (Koyama, 2003; Van Horn et al., 2007). As a consequence, grooming time should logically influence group cohesion and also thus group size. Our study suggests that the relationship between grooming time, group size and group cohesion depends on the way an individual distributes its grooming time to its specific social partners. If an individual grooms all its conspecifics, in an equal way or not, group size does not affect group structure and then group cohesion. If grooming time is, however, distributed to a specific number of partners, group structure and then group cohesion are affected.

It has previously been shown that the time primates invest in grooming increases with group size (Dunbar, 1991). Nevertheless, Lehmann et al. (2007) suggested that when group size increases, each individual should spend more time grooming until a certain group size (about 40 individuals) for which individuals cannot devote more time to maintain relationships with all group members (Dunbar, 1992a; Lehmann et al., 2007; Schino et al., 2009). As a consequence, group cohesion decreases and the group splits (Henzi et al., 1997a, b). This hypothesis implies that individuals should be expected to try to maintain social bonds with (i.e. to groom) all, or at least most of, group members. Our results, by contrast, suggest that if this assumption is applied (hypotheses 1 and 2 in our study), group cohesion is not influenced by grooming time, even if time for this activity decreases when group size increases. In the same way, within-group competition is not predicted to affect group cohesion when an individual grooms all its partners, but does have an effect when an individual has a specific number of partners which it grooms. This result may be explained by the fact that, as all individuals were linked to each other in one way or another (whatever the quality/strength of these social bonds), group cohesion was high and therefore the probability of the group splitting was low. This result is not dependent on our model but directly influenced by social network and sociality of individuals. For instance, Amé et al. (2006) showed that when several shelters are proposed, cockroaches (*Blatta germanica*) always aggregate together in only one shelter if this one is able to host all individuals. Even if fission is possible, the group cohesion of individuals does not lead them to split. Sueur et al. (2010) also showed that in macaques, the highest the group cohesion is (more contacts between individuals, less clustered), the lowest the probability to split is. An alternative to grooming all other group members is to groom a specific number of partners (hypothesis 3). Several authors have shown that individuals do not groom all available partners but rather a fixed number of individuals, whatever the group size (Silk et al., 1999; Cords, 2001; Nakamachi and Shizawa, 2003; Berman et al., 2008; Lin et al., 2008; Watts, 2000a,v). Under this hypothesis and as found in Majolo et al. (2008),

the grooming time an individual devotes to another is not directly dependent on group size. However, the study of Majolo et al. (2008) was the only one to propose this indirect link before our study and this result needs to be checked. Our model suggests that group size, grooming time and group cohesion are linked when an individual grooms only a specific number of partners. In this scenario, group cohesion decreases when group size increases and/or grooming time decreases. Kudo and Dunbar (2001) also showed that structure of small and large groups differ. Indeed, large groups seem to be more sub-structured. This sub-grouping might be because animals deliberately invest their grooming in core coalition partners (Kudo and Dunbar, 2001; Lehmann and Dunbar, 2009). Indeed, a theoretical study on social network graphs showed a similar decrease of connectivity according to nodes' number (Wu, 2005). Moreover, we showed that this relationship between group cohesion and group size is non-linear: when group size exceeded 40 individuals, group cohesion was almost null. This link was however indirect: as (1) group size and grooming time directly influenced group structure, and (2) group structure directly influenced group cohesion (in our study the inverse probability that a group splits in two sub-groups), therefore (3) group size and grooming time influenced group cohesion. To confirm this result and to understand how the group structure evolved according to both group size and the number of groomed partners, it would be interesting to study groups at the same size but with a different number of partners per individual.

Moreover, Lehmann et al. (2007) showed for instance that female dispersion and sex ratio influenced grooming: species with female philopatry spend more time grooming than species with female dispersal. Even if social characteristics such as philopatric sex or the sex ratio, that represent the variability of a social structure, are already included in the different random networks we tested with our model, we did not identify them. However, it would be interesting to assess how these characteristics influence the social network and then the group cohesion.

The distribution of the number of groups staying cohesive according to group size was similar, in our model with a fixed number of 5 partners, to that based on observed data. Previous studies have confirmed that, on average, an individual preferentially grooms 5 partners (Berman et al., 2008; Cords, 2001; Lin et al., 2008; Nakamachi and Shizawa, 2003; Silk et al., 1999; Watts 2000a,b), giving further support for our hypotheses. Even if an individual grooms 5 preferred partners, it can still be groomed by more or less individuals than 5 congeners itself, since grooming is not necessarily reciprocal (Nakamachi and Shizawa, 2003; Schino, 2001; Silk et al., 1999). This pattern has important consequences on group sociality: it allows competition for grooming partners, attraction to high-ranking individuals (Schino, 2001) and may allow the emergence of phenomena such as the biological market (i.e., exchanges of commodities according to supply and demand; Fruteau et al., 2009). On the other hand, if an individual grooms all its partners, this kind of competition for partners could not emerge. Kinship may also constrain the relationships of individuals: they will groom their relatives. In these conditions, the two new sub-groups will be more composed on kin related individuals (Chepko-Sade and Sade, 1979; Van Horn et al., 2007). This influence did not affect, however, our results, since groups having an influence of kinship can also be represented using random networks as the ones we used in this study (Flack et al., 2006; McCowan et al., 2008; Sueur and Petit, 2008; Kasper and Voelkl, 2009; Ramos-Fernandez et al., 2009). Grooming a specific and low number of partners could also be of interest when managing time (individuals do not need to change their grooming time when group size increases) but could also have implications when considering cognitive capacities. Several authors (Dunbar 1992a, 1996; Lehmann et al., 2007; Stevens et al., 2005) have suggested that there is a relationship between the cognitive capacities (measured as the neocortex ratio) and the number of

relationships an individual can keep track of. Remembering the grooming relationships for 5 partners would be the easiest solution for an individual, and would be a more parsimonious process than having to remember its ties with all group members. Moreover, grooming 5 partners rather than all group members may favor sub-grouping patterns and reduce within-group conflict by regrouping individuals with similar social/physiological affinities (Aureli and Schaffner 2007; Couzin and Laidre, 2009; Ramos-Fernandez et al., 2006).

We believe that a relationship may exist between group size and grooming time but that this relationship would probably be indirect: an increase in group size could result in more food competition between group members (Majolo et al., 2008). As a consequence, an individual would have to increase its foraging time and therefore decrease its grooming time. The consequence is not due to a higher number of partners, but to lower food availability. We did not directly test the relation between food competition and group size in our model, but several studies have already supported this hypothesis (Berman et al., 2008; Dittus, 1988). Moreover, group size and grooming time, elements that can be influenced by ecological factors such as food competition or predation (Lehmann et al., 2007; Majolo et al., 2008; Pollard and Blumstein, 2008), did not directly influence the probability that a group would split. Social relationships directly influenced group fission probability. And these social relationships are resultants of the combined influence of group size and food competition, but also of other factors as internal or structural constraints (Thierry et al., 2004).

This study was based on grooming interactions but we suggested that similar results may be obtained for any positive interaction such as proximities, contacts or frequency of lips-making for instance. Even if our model did not test all factors having a potential influence on the structure of social relationships, it does show that the key characteristic of group cohesion and stability is group structure (Wey et al., 2008). It is interesting to note that the probability to find large group sizes decreases exponentially with group size in the context of stable groups after irreversible fission but also in fission–fusion populations (Couzin and Laidre, 2009). We do not think that a group splits irreversibly in one event as it does in our model. This irreversible fission might be long, from several months to several years (Chepko-Sade and Sade, 1979; Okamoto and Matsumura, 2001; Van Horn et al., 2007). We still lack of data about dynamic of fission. It should be interesting to conduct more studies about dynamical processes allowing a group to split. General principles seem to underlie rules of group cohesion at different time scales. All factors, whether social or ecological, seem to influence group cohesion through its structure. In the end, group fission probability may not depend on the sum of individual decision-making based on physiological states and/or on their complex interactions (Schino, 2001; Tomasello and Call, 1997), but may simply depend on the properties of the social structure, as observed in several self-organized systems (Camazine et al., 2001; Couzin and Krause, 2003).

Acknowledgements

We are grateful to J. Munro for the language editing and N. Poulain, biostatistician at the DEPE, IPHC, for his help on analyses. This work was supported by the Wallonia Brussels International, the Belgian National Funds for Scientific Research, the Franco-American Commission, the Alsace Region and the Fyssen Foundation.

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