

Collective decision-making and fission–fusion dynamics: a conceptual framework

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Sociality exists in an extraordinary range of ecological settings. For individuals to accrue the benefits associated with social interactions, they are required to maintain a degree of spatial and temporal coordination in their activities, and make collective decisions. Such coordination and decision-making has been the focus of much recent research. However, efforts largely have been directed toward understanding patterns of collective behaviour in relatively stable and cohesive groups. Less well understood is how fission–fusion dynamics mediate the process and outcome of collective decisions making. Here, we aim to apply established concepts and knowledge to highlight the implications of fission–fusion dynamics for collective decisions, presenting a conceptual framework based on the outcome of a small-group discussion INCORE meeting (funded by the European Community's Sixth Framework Programme). First, we discuss how the degree of uncertainty in the environment shapes social flexibility and therefore the types of decisions individuals make in different social settings. Second, we propose that the quality of social relationships and the energetic needs of each individual influence fission decisions. Third, we explore how these factors affect the probability of individuals to fuse. Fourth, we discuss how group size and fission–fusion dynamics may affect communication processes between individuals at a local or global scale to reach a consensus or to fission. Finally, we offer a number of suggestions for future research, capturing emerging ideas and concepts on the interaction between collective decisions and fission–fusion dynamics.

A social group is usually defined as aggregation of individuals interacting with one another in space and time more often than with other individuals of the same species (Kummer 1971). Group living brings advantages to individuals such as a decreased risk of predation, enhanced food searching efficiency, or better access to potential mates for reproduction, but group living also implies some disadvantages, such as increased transmission of pathogens or competition with group members for food or mating partners (Krause and Ruxton 2002). How social groups make collective decisions has received increasing attention (Conratt and Roper 2005, Couzin et al. 2005, Conratt and List 2009). In particular, efforts have been directed towards understanding how groups achieve collective changes in activity states (e.g. from resting to moving: Dostalkova and Spinka 2007 Stueckle and Zinner 2008, Sueur et al. 2009, 2010). These events are crucial if individuals are to benefit from synchrony with other group

members (Conratt 1998, Ruckstuhl 1999, King and Cowlshaw 2009a), and are generally easier to identify than collective decisions occurring within a single activity state, such as a decision to change direction when moving (Byrne et al. 2009; Dyer et al. 2009, Sueur et al. 2010). Researchers have tended to focus on relatively cohesive groups, where membership and cohesiveness among group members are usually stable. This is, however, quite a rare situation (Jacobs 2010). For most species, group membership, the degree of synchrony across individuals, and their spatial cohesion can be highly variable (Kerth 2010). This variability can be summarized in terms of the degree to which groups fission and fuse, i.e. their fission–fusion dynamics (Aureli et al. 2008). Social systems that exhibit high levels of fission–fusion dynamics are well described in a variety of vertebrates (reviewed by Aureli et al. 2008). Individuals do not always reach a 'consensus' (i.e. all group members following the same

action: Conrard and Roper 2007) concerning the timing of their activity (time decision) or direction of their movement (space decision), and fission can be viewed as an adaptive outcome where individuals' interests conflict, or simply they are not able to stay together (Kerth et al. 2006).

The distinction between time and space decisions is relevant to the study of collective behaviours in fission–fusion settings. While individual compromises concerning decisions about activity timing are often (but not always: Conrard and Roper 2010) plausible – as preferences can be traded or averaged – compromises concerning spatial decisions are often less feasible (King and Cowlishaw 2009b, List et al. 2009, Conrard and Roper 2010). The following example illustrates this point. Consider a group deciding whether to move to a food patch immediately or in one hour. Assume that half of the group members would prefer to leave immediately, the other half in one hour. The average preferred leaving time (i.e. leaving in half an hour) would be a compromise that would meet everybody's needs halfway. In contrast, consider a group deciding between moving to food patch A or to food patch B, one of which lies to the north of the location of the group, the other to the east. Again, assume that half of the group members prefer the first option (patch A), the other half the second option (patch B). No group member would benefit from travelling into the average preferred direction (i.e. towards northeast), if the group would end up halfway between food patches A and B in unsuitable habitat. Where the costs of maintaining cohesion become too high, a group can temporarily split, offering a strategy to balance the costs and benefits of group living (Kummer 1971, Ruckstuhl 1999, Aureli et al. 2008), and this might be more likely in spatial than in timing decisions. Even when all individuals ultimately benefit from cohesion, individuals may not reach consensus because no individual is ready to cooperate and 'give in'. The outcome is a temporary fission (see Table 1 for an example). Therefore, in a number of situations fission–fusion dynamics become crucial to patterns of collective decision making. This factor has largely been overlooked by those studying group decision-making since researchers assume, a priori, that it always pays for individuals to reach a consensus decision and remain as a cohesive group (but see Kerth et al. 2006).

Here we consider the implications of fission–fusion dynamics for the study of collective decisions. We focus on the individual costs and benefits of grouping – an

Table 1. Game in which A and B are two individuals, and each of them has a different preferred location. If they coordinate their behaviour and go together to either individual's preferred location, the individual with a preference for that location gets a pay-off of 10, and the follower a pay-off of 4. However, if they go alone to their own preferred location, each individual receives a pay-off of 5. If the two individuals in this 'game' compromise, half the time visiting each other's preferred location their expected pay-off would be 7 each. If neither individual compromised, they would always receive 5. This is a classic prisoner's dilemma situation, and serves to illustrate how decisions to remain cohesive or to fission, are important to individual fitness.

	A	B
A	5, 5	10, 4
B	4, 10	5, 5

approach common to studies of collective decision-making (Conrard and Roper 2003, King et al. 2008) and fission–fusion dynamics (Conrard and Roper 2000, Ramos-Fernandez et al. 2006, Asensio et al. 2009, Sueur et al. 2010) – allowing us to combine these largely disparate research areas (for a rare study combining both areas see Kerth et al. 2006). Our aim is to suggest ways in which research can address the dearth in empirical evidence and theoretical insight. To achieve this aim we first consider 1) how the degrees of variability and uncertainty in the environment shape social flexibility and therefore the type of decisions individuals make in different social settings. We then try to disentangle the relative roles of 2) social relationships and 3) information acquisition and dissemination for social decisions where groups exhibit different degrees of fission–fusion dynamics. The review of these three aspects of the interaction between collective decisions and sociality leads us to a number of suggestions for future research that can be pursued with empirical and theoretical work.

Environmental variability and uncertainty

The social environment can often be considered a reflection of the ecological environment. If there is little or no spatial variability in the ecological environment (e.g. if all productive food patches contain resources of similar quality and quantity, and they are associated with similar predation risks) then there is little reason for conflict between group members in spatial decisions, and we would expect frequent consensus decisions and little fission into subgroups (left hand side of Fig. 1a). Group size would mainly be determined by the size and quality of food patches and by predation risks. The frequency of consensus decisions should increase further, and the rate of group fission decrease, if there is high environmental temporal variability and uncertainty added to the low spatial variability (e.g. if it is difficult to predict which food patches are productive at any one time, but those which are productive are very similar to each other), since the animals then benefit from information pooling by making shared consensus decisions.

In contrast, if there is high spatial variability in the environment (e.g. food patches differ widely in quality or quantity of resources, or in associated predation risks: right-hand side of Fig. 1a), then the situation becomes more complicated. There is now wide scope for conflict between group members, and the costs and benefits of sociality are likely to differ between individuals. This could result in partial or complete segregation of individuals into (sub)groups according to their requirements (e.g. in segregation of the sexes, age classes, body size classes, etc., Conrard and Roper 2000, Ruckstuhl and Kokko 2002, Krause and Ruxton 2002), and potentially into relatively smaller group sizes than expected in a more homogeneous environment. However, this in itself does not necessarily lead to a high level of fission–fusion dynamics, since segregated groups could be very stable in size and composition. In particular, if spatial variability of the environment is very high, consensus costs in heterogeneous groups, consisting of individuals with different requirements, are also expected to be very high (Conrard 1998), and might outweigh the grouping benefits in heterogeneous groups.

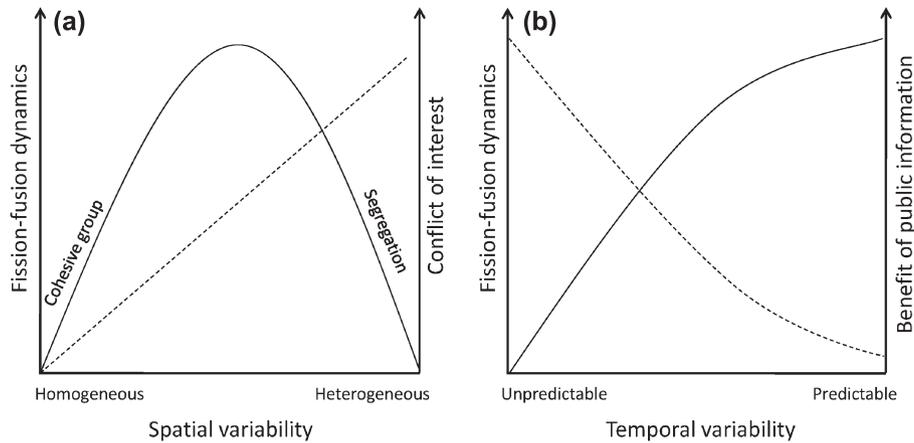


Figure 1. Influence of spatial (a) and temporal (b) variability of the environment on fission–fusion dynamics (continuous line). The relationship between conflict of interest and spatial variability (a) and the relationship between the benefit of public information and temporal variability (b) are also represented (dashed line).

As a consequence, heterogeneous groups might no longer be stable, resulting in a high degree of segregation of individuals with different requirements within the population into relatively homogeneous groups, so that individuals with different requirements would dwell more or less permanently in separate groups, and use different parts of the environment. Fission events are expected to be relatively rarer in homogeneous than in heterogeneous groups, because individuals in such groups have similar environmental requirements. Thus, additional fission events are likely to be relatively rare once individuals with different requirements are segregated. Therefore, the most interesting, and for fission–fusion dynamics most relevant, situation arises if spatial variability of the environment is intermediate.

If spatial variability of the environment is intermediate, there is scope for conflict between group members with different requirements, but consensus costs are no longer forbiddingly high (mid-point of x-axis in Fig. 1a). Thus, consensus costs can at times be lower than grouping benefits, allowing the formation of larger groups that are heterogeneous in composition. It is such heterogeneous groups in intermediately spatially variable environments that are most likely to show high levels of fission–fusion dynamics. Here, sometimes grouping benefits outweigh consensus costs and it pays for groups to fuse and stay cohesive by making consensus decisions. At other times, consensus costs outweigh grouping benefits, leading to group fissions into separate subgroups consisting of individuals with similar requirements.

The temporal variability of the environment also plays a role in fission–fusion dynamics in environments with intermediate spatial variability. Where this variability is predictable to some extent (i.e. changes predictable by day, season, or year: right hand side of Fig. 1b), individuals would do well to show high flexibility in their sociality, fissioning and fusing according to the current state of the ecological environment. This occurs in African elephants *Loxodonta africana* (Wittemyer et al. 2005), spider monkeys *Ateles geoffroyi* (Asensio et al. 2009) and Guinea baboons *Papio papio* (Patzelt et al. 2011) where seasonality affects subgroup size: subgroups are smaller during dry seasons, when food is more

scattered. Similarly, in red deer *Cervus elaphus*, social and spatial segregation between the sexes vary seasonally, and peak in winter when food is scarce (Conradt 1998). However, food availability and breeding patterns are not the only seasonal parameters affecting fission–fusion dynamics. For example, Bechstein’s bats *Myotis bechsteinii* adapt their roosting group sizes according to seasonal ambient temperatures in order to maximize the benefits of social thermoregulation through clustering (Pretzlaff et al. 2010).

Where the variability in the ecological environment is unpredictable individuals face uncertainty. Under this condition (and where group living is beneficial), we would expect individuals to exhibit relatively low levels of fission–fusion dynamics (left hand side of Fig. 1b), and collective decisions achieved by consensus are likely to be common for at least three reasons. First, if resources are not predictable in space and time, fission may be costly since individuals run the risk that social cohesion could not easily be restored once it became desirable again. Indeed, it would be extremely difficult to coordinate fusion where resources (e.g. sleeping sites or food sources) are not predictable in space or time. Second, one can expect reduced opportunity for developing divergent preferences and goals, since (potentially conflicting) options are uncertain and individual information gathering may be scarce (Mettke-Hofmann et al. 2002) given that the value of information (defined as the difference in payoff of a decision between an informed and an uninformed individual; Gould 1974) is low in a stochastic and variable environment. Third, where gathering ‘personal information’ is costly, the benefits of information pooling – either by aggregating information across all group members, or adopting the decision of those individuals with the most information – are likely to be large (see Katsikopoulos and King 2010 for a model and discussion). Therefore, large diversified groups are likely to outperform small, less diversified groups in terms of decision-making accuracy, while fission potentially reduces the diversity within a (sub)group in terms of information or expertise. However, this information-pooling benefit of larger diversified groups is predicted to diminish as group size exceeds more than 20 individuals (King and Cowlshaw 2007). Thus, we hypothesise that in unpredictable ecological

environments, three factors favour consensus decisions and low levels of fission–fusion dynamics: 1) an increased risk that social cohesion cannot be restored; 2) reduced divergent preferences and goals; and 3) the advantages of information pooling and diversity in cohesive groups.

To summarize the effects of environmental variability and uncertainty, as a consequence of decision-making processes, fission–fusion dynamics are predicted to be most frequent in environments with intermediate spatial variability and to increase with the (temporal) certainty and predictability of the environment.

Social relationships

The conceptual framework we present above describes the varying degrees of fission–fusion dynamics that one would expect based on the variability and predictability of the ecological environment. Where the degree of fission–fusion dynamics is high, there is a challenge for individuals attempting to coordinate their actions with group members of similar or different age, sex or size, or with whom they share specific genetic or social affiliation. In this section, we examine the influence of relationships between group members on subgroup composition, a critical component of fission–fusion dynamics (Aureli et al. 2008), and its implications for reaching consensus or splitting into smaller subgroups. Following Hinde (1976), we define a social relationship based on the content and quality of the interactions between two individuals and the relative frequencies and patterning of those interactions over time. The unique history of interactions between two individuals therefore characterizes their social relationship.

Since social relationships, which often are based on kinship, can confer lifetime fitness benefits (Silk et al. 2003, 2009, Frere et al. 2010), it is no surprise that fission–fusion patterns can be influenced by such relationships. For example, macaque species (*Macaca mulatta* and *M. tonkeana*) split and form subgroups according to their affiliative relationships (Sueur et al. 2010; Fig. 2), and the stability of social relationships influence fission–fusion dynamics in chimpanzees *Pan troglodytes* (Mitani and Amstler 2003, Lehmann and Boesch 2004, Le Hellye et al. 2010) and hamadryas baboons *Papio hamadryas* (Abegglen 1984, Schreier and Swedell 2009). Similar patterns are described in Bechstein's bats *Myotis bechsteinii* where individuals maintain long-term relationships that can partially be explained by kinship and that can persist over several years despite high daily fission–fusion dynamics (Kerth and König 1999, Kerth et al. 2011). Thus, in several species social relationships affect fission–fusion patterns, but the frequencies of fissions and fusions and the association patterns in subgroups also influence, in a feedback loop, the social relationships between group members.

Fission–fusion patterns can also be structured in groups that are considered to show little or no evidence of social relationships, that is, animals do not individually recognize all other group members and are broadly undifferentiated (mostly due to the large group size; Krause and Ruxton 2002, Conradt et al. 2005). For example, dietary preferences are known to affect shoaling decisions in the Trinidadian guppy

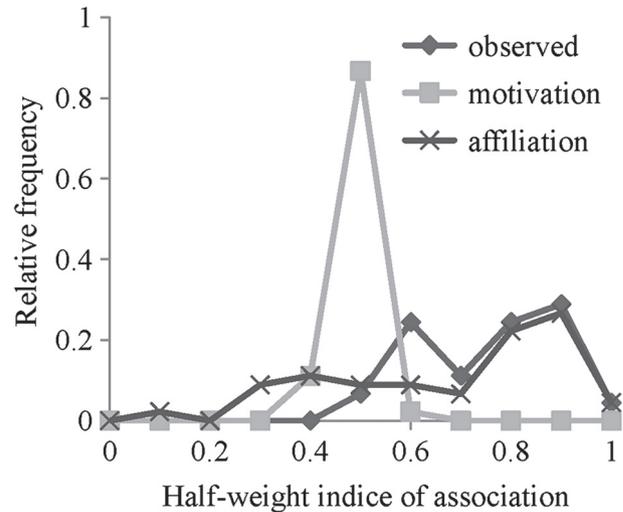


Figure 2. Subgroup patterns (observed curve) of Tonkean macaques after fission. The motivation curve is the distribution of the strength of associations during fission obtained by a model when individuals follow individuals having the same motivation (e.g. same energetic state). The affiliation curve is the distribution of the strength of associations during fission obtained by a model when individuals follow individuals according to their affiliative relationships. The half-weight index represents the number of cases two individuals were seen in the same subgroup divided by half of the total number of cases in which the two individuals were observed. The graph shows that simulated patterns of association according to affiliative relationships are similar to the observed patterns. Data from Sueur et al. 2010.

(e.g. *Poecilia reticulata*: Morrell et al. 2005), and in several species displaying fission–fusion dynamics, individuals show high levels of attraction toward conspecifics of similar size, resulting in the formation of shoals of size-matched individuals (reviewed by Krause and Ruxton 2002). More often than not, these different processes at the basis of subgroup formation and composition may not be independent. For example, individuals with similar feeding preferences may aggregate at the same feeding sites, but may also associate preferentially with kin or affiliative partners to reduce the negative consequences of feeding competition (Ventura et al. 2006, King et al. 2010). Simple models now exist that allow researchers to disentangle the relative influence of similar motivation (e.g. equivalent energetic state) and the strength of social relationships on fission–fusion patterns (Ramos-Fernández et al. 2006, Sueur et al. 2010; Fig. 2), and we expect these to be extremely useful for uncovering the proximate mechanisms (individual choice rules) that result in subgroup formation and composition.

Studies of fission–fusion dynamics that aim to determine the strategies animals use to maximise individual benefits have traditionally focused on fission, but the dynamics of fusion are perhaps more interesting from a collective-decision perspective. Take the example of animals returning to a sleeping site or roost at the end of the day. Animals could be obliged to fuse every night if only one sleeping site exists within their home range (e.g. *Papio hamadryas*: Kummer 1968). Under these circumstances, no ‘real’ spatial coordination is required, social relationships do not likely come into consideration (all individuals associate at the same site), and only a decision about timing is needed. However, where

multiple sleeping sites are available individuals must coordinate their decisions of where and when to fuse, and may preferentially associate with kin or affiliated individuals (e.g. in bats that roost in different tree cavities or bat boxes each day; Kerth 2008, Kerth et al. 2011).

The aforementioned examples underline the different role of information transfer for fusion decisions. For decisions that require spatial coordination (e.g. multiple sleeping sites available), some form of explicit communication is needed and this may depend on social relationships (Aureli et al. 2008). For example, in African elephants the ‘greeting rumble’, the ‘contact call’ and the ‘let’s go rumble’ are vocal exchanges that function in maintaining cohesion and coordination between family and bonded group members (Poole et al. 1988, McComb and Reby 2005). In chimpanzees, pant-hoots are used to maintain contact between group members that are separated and are exchanged more often between individuals with stronger relationships (Mitani and Nishida 1993). Finally, in Bechstein’s bats, colony members follow each other to new day roosts (Kerth and Reckardt 2003) and calls may facilitate the coordination during the decision for a communal roost (Schöner et al. 2010). This evidence highlights the importance of information transfer and acquisition to collective decision-making in groups with a high degree of fission–fusion dynamics, which is the focus of our next section.

Information acquisition and transfer

The distinction that we make above between groups with differentiated social relationships and aggregations in which members are broadly undifferentiated (and therefore no or few stable relationships exist) can be linked to the distinction between local and global communication (Camazine et al. 2001, Conradt and Roper 2005, Ballerini et al. 2008, Ramseyer et al. 2009, Nagy et al. 2010, Fischer and Zinner 2011). In small groups, individuals can develop and

maintain stable social relationships with all group members, and can similarly communicate with them by sending information, but also by receiving and processing it, representing a situation where global communication is possible. However, in larger groups it is more difficult for one individual to develop relationships or communicate with all other group members, and there is therefore the possibility to restrict communication to a local scale (Fig. 3). Although individuals can modulate the scale at which they can broadcast, in many species the biological limit to this modulation is well above the grouping scale (McGregor and Peake 2000). An alternative is for the communication process to be structured hierarchically, e.g. only one particular individual of each stable subgroup needs to communicate with other such individuals in other subgroups (decision making in hamadryas baboons where leader males of individual harem subgroups, or one male units, ‘negotiate’ the direction of travel: Kummer 1968, Stolba 1979).

We might therefore predict heterogeneity or even loss of information as groups grow larger or become more dispersed; such groups may be better placed to coordinate their movements at the level of the subgroup, and consequently the probability of fission is expected to increase with group size (Kerth and König 1999, Conradt and Roper 2005, Focardi and Pecchioli 2005, Voelkl and Noë 2008, Kerth et al. 2011, Sueur et al. 2011). For example, under the scenario that one individual can only communicate with its five closest neighbours (Couzin et al. 2005, Ballerini et al. 2008), when group size increases, density (i.e. an index of group cohesion, Sueur et al. 2011a, 2011b) decreases (Fig. 4), and the propagation of information decreases too (Wu 2005, Voelkl and Noë 2008). It may therefore be advantageous if information was transferred between subgroups via particularly connected individuals (‘brokers’: Lusseau and Conradt 2009, Kerth et al. 2011; or ‘leaders’: Sueur and Petit 2008, McComb et al. in press, Sueur et al. 2011b). In this way, fission and fusion can occur so that an individual ‘X’ received information from co-members of subgroup i

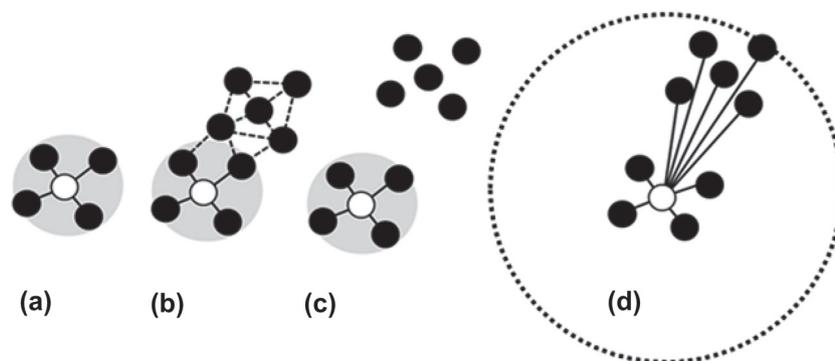


Figure 3. Flow of information between group members depending on group size and inter-individual distance, given a potential transmission range. Individuals are represented as circles, with signallers in white and potential receivers in black. Potential receivers within signal range are indicated by the greyed area. Direct transfer of information between individuals is shown by an unbroken link, and indirect information transfer (i.e. information transmitted by an individual other than the original signaller) shown by a dashed link. A visual signal may allow information to reach directly all group members in a small group (a), and so this visual signal can be described as a global signal. In a larger group the same visual signal is received only from those individuals in the signaller’s immediate surroundings (i.e. local scale: (b)). The information may still propagate through the social network, if information can pass indirectly to those out of signal range. However, if individuals are spaced so that the information cannot pass through the social network (c), then an alternative signal with a larger communication range (dotted line) would be required, e.g. vocal signal, allowing communication directly with all individuals, and enabling global communication (d).

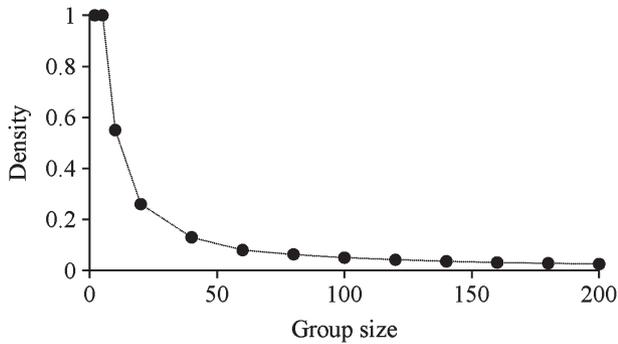


Figure 4. Density (i.e. the number of observed links divided by the number of possible links; here a link is the possibility for an individual to communicate with another individual) depending on group size (from 2 to 200) when one individual can only communicate with its five closest neighbours. We set the number of relationships n to five for each individual. Then, the number N_o of observed relationships is $n * G$, G being the group size (number of individuals per group). The number N_p of possible relationships is $G * (G - 1)$, $G - 1$ because one individual does not have relationships with itself, only with other group members, i.e. $G - 1$. The density equals N_o / N_p .

from which it subsequently split and then fused with subgroup j . Then, the information that 'X' has may be advantageous in deciding what subgroup j should do next and therefore it would be to the advantage of 'X' to share this information (by whichever means, i.e. passively or actively)

because it could do what is 'best' at that time for itself and at the same time retain subgroup membership benefits (Lusseau 2007). There is evidence of such behaviour in a population of bottlenose dolphins *Tursiops truncatus* with high levels of fission–fusion dynamics (Lewis et al. 2010). Lewis and colleagues found that a small number of specific individuals lead group travel (by initiating successful direction changes) regardless of the size of the (sub)group. The problem, however, is whether conspecifics should 'trust', in the most liberal sense of the word, 'X'. Trust is achieved when 'X' holds a structural bottleneck position in the social network (Lusseau and Conradt 2009), that is it belongs to a given group but also spends time with a number of other groups or subgroups (Fig. 5). In these situations 'X' is more likely to have information that other members of its (sub)group do not, and when it displays motivation to change activity, others will follow its decision (Kummer 1968, Stolba 1979, Lusseau and Conradt 2009). Importantly, this process need not rely on complicated cognitive abilities, as an individual need only identify a 'broker' (i.e. an individual holding a structural bottleneck position on the social network) from others belonging to its group. This only requires that an individual follows the actions of conspecifics in its current (sub)group based on how recently it has shared interaction (Anderson and Schooler 1991), and this may be facilitated by differentiated signals (McCowan and Reiss 2001) where these are used to initiate changes in group activity (Lusseau and Conradt 2009).

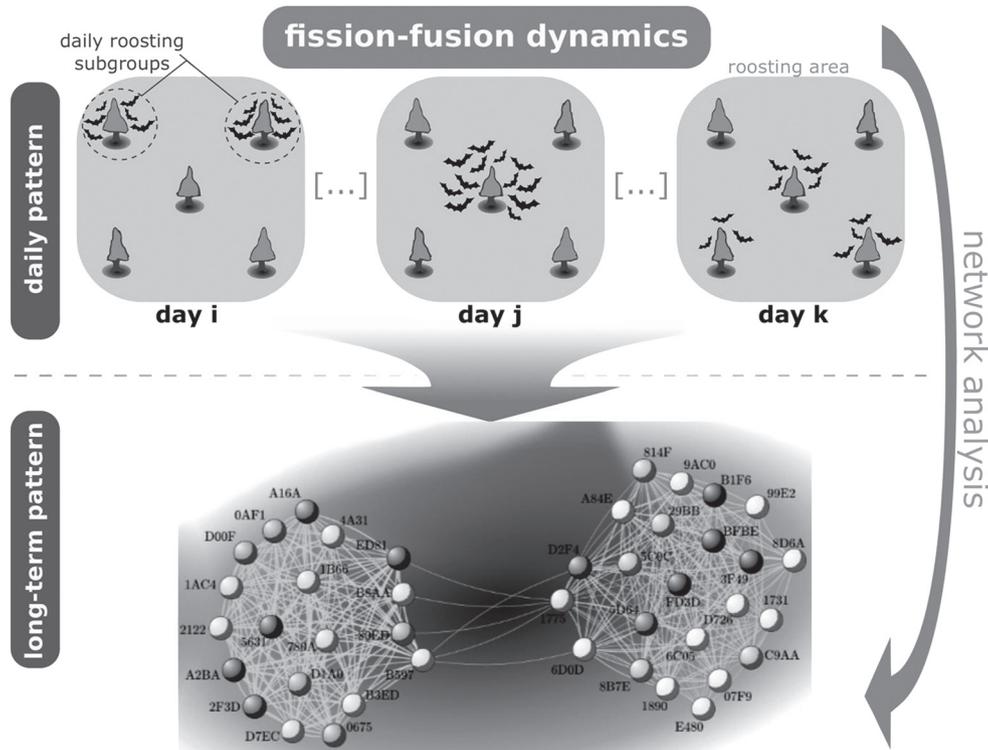


Figure 5. Fission–fusion dynamics and social networks in Bechstein's bats. The upper part shows a schematic representation of the fission–fusion dynamics of a representative Bechstein's bat colony, with a typical daily roost occupation pattern (1 to 3 subgroups occupying different day roosts) on three randomly chosen days (i, j, k). The lower part shows the corresponding social networks in a real colony (GB2, Kerth et al. 2011) based on the daily roosting associations of the bats measured over an entire breeding season (ca 150 days). The social network is fully connected as all pairs of bats roosted together at least once; however, for clarity only strong links are shown here. The colony GB2 forms two distinct communities. The bats (nodes of the network) are identified by their PIT-tag numbers (individually identifiable chips that were read when a bat entered a roost). Different shades of the nodes depict different matrilineal within the colony (modified from Kerth et al. 2011).

This ‘information distribution strategy’ becomes particularly advantageous when the groups that compose a population can overlap in space (i.e. no territoriality) and share membership of (sub)groups (Connor et al. 1998, Lusseau et al. 2003) as is common in cetaceans and ungulates and birds. In these instances, it becomes highly probable that these ‘brokering’ individuals offer a substantial amount of new information that others from their groups cannot reach (Lusseau and Conradt 2009). This idea mirrors the central concept of the information centre hypothesis (Ward and Zahavi 1973, Danchin 1990, Danchin and Wagner 1997): by fusing together, whatever the location, individuals may share information about their environment. Such a hypothesis is difficult to test, but an ingenious study by Wright et al. (2003) offers insight on which future research can build. Wright and colleagues placed sheep carcasses at varying distances from raven *Corvus corax* communal roosts (ravens feed on rich but ephemeral carcasses of large animals). The carcasses were baited with colour-coded plastic beads, which were ingested by the ravens, and regurgitated in pellets back at the roost. Aggregations of beads at the roost grew daily with an increasing radius centred upon the first pellet per carcass, and groups were led to carcasses by a single bird (which were dominant at the carcass) roosting centrally within the aggregation. Interestingly, it appears that roost-mates did not have to identify those birds with information, or track previous interactions with these informed birds, since the latter signalled their departure with a series of acrobatic display flights.

Conclusions and future research

Three factors that influence the role of fission–fusion dynamics on collective decisions were explored: 1) the degree of environmental variability and uncertainty; 2) the social relationships with other group members, and 3) potential ways individuals garner information about their environment. First, we hypothesized that when there is an intermediate degree of spatial variability in an environment, which is nevertheless predictable in the way it changes, a high level of fission–fusion dynamics is more likely and a low rate of consensus decision making occurs. Fission–fusion dynamics are expected to increase with the (temporal) certainty and predictability of the environment. In contrast, when the environment is stable or there is unpredictable variability individuals should have a high rate of consensus decision-making and be less likely to engage in fission–fusion dynamics, due to the influence of three factors: 1) an increased risk that social cohesion cannot be restored; 2) reduced divergent preferences and goals; and 3) the advantages of information pooling and diversity in cohesive groups. These are novel theories that arise from the synthesis of research on fission–fusion dynamics and collective decision making. They give us clear predictions that can be tested empirically. However, to date no empirical research is available that measures at the same time all the relevant factors (i.e. the environmental variability and predictability, fission–fusion dynamics, the incidence of successful consensus decisions, the distribution of relevant environmental information between individuals, the difference in preferences and goals between individuals,

and the likelihood of reunions after splits). Therefore, empirical studies that endeavor to measure most or all of these factors simultaneously are urgently required. Moreover, we would like to encourage experimental studies that systematically manipulate some of these factors in order to test the above hypotheses. There is also a place for theoretical studies that investigate the implications of the above hypotheses in more detail, in particular by investigating the relative importance of different factors (e.g. preferences and goals, information distribution, risk of not being able to restore social cohesion) on fission–fusion dynamics and consensus decision making.

Second, the extent to which social relationships are important in determining subgroup composition and how this feeds into reaching a consensus or splitting into smaller subgroups was also explored. We hypothesized that for species with a high degree of fission fusion dynamics and individualized social relationships that the quality of the social relationship and the internal state (e.g. energetic needs) of individuals may both play a role in fission decisions. However, we placed more emphasis on examining fusion decisions and how individuals may coordinate coming together as a useful direction for future research. Again, empirical studies that test these hypotheses are urgently needed.

Finally, we hypothesized mechanisms through which such decisions might be communicated on a local or global level depending on group size and the pattern of fission–fusion dynamics, and the potentially significant role of ‘broker’ individuals to group coordination and decision-making in social systems with a high degree of fission–fusion dynamics.

We believe that the degree of environmental variability and uncertainty is a key focus for new theoretical and empirical research that will allow researchers to bring the two largely disparate – but explicitly linked – research topics of fission–fusion dynamics and collective decisions together. Furthermore, we endorse an approach that incorporates contributions from modelling, experiments and naturalistic observational techniques. For example, agent based modelling in conjunction with field data on spider monkeys has been employed previously to disentangle the respective roles of social relationships quality and similar energetic state in fission decisions (Ramos-Fernandez et al. 2006). Information about individuals might be estimated by measuring key variables, such as age of individuals, their frequencies of initiations leading to group fission, whether individuals are the philopatric or dispersing sex and their energetic state, and incorporated into such an approach. Furthermore, we can begin to understand the extent to which key group members are important for communicating information by evaluating how the absence of an individual affects the probability of a subgroup to go in one specific direction, using observations or natural experiments (for instance how individuals change patterns of movements in the absence of key subgroup members). These approaches will increase our understanding of the extent to which individuals of species with a high degree of fission–fusion dynamics employ consensus decisions.

We also need to develop new approaches to better understand the dynamic nature of social interactions and how they play a role in the decision-making process of individuals. One

avenue is to expand techniques available at the dyadic scale, such as lagged association rate analyses (Whitehead 1998), to social network statistics (Kerth et al. 2011, Sueur et al. 2011b). This will help us assess the extent to which social networks impact fission–fusion patterns and the impact fission–fusion dynamics have on the social relationships. The understanding of this feedback loop between social relationships and fission–fusion dynamics may help us understand why we observe a continuum from highly cohesive groups to groups with a high degree of fission–fusion dynamics to irreversible group fissions. Indeed, under the assumptions that social relationships have an influence on fission processes and that fissions have an influence on social relationships (e.g. the more often individuals are together in the same subgroup, the more likely they might develop strong social relationships), we might expect that a simple social amplification process depending on social relationships underlies collective decision-making in different species (Gautrais et al. 2007, Petit et al. 2009, Sueur et al. 2009, Jacobs et al. 2011). When the probability to move in one direction or the probability to stay in the same area depends on the social relationships with individuals already moving or still resting, then the social network of a group could lead, by its heterogeneous structure, cliquishness and density, to different patterns of collective decisions.

The behaviour of individuals is the outcome of the interactions between a number of internal processes and life history strategies (McFarland 1975), such as physiological needs, information and social relationships (as measured through social interactions: Hinde 1976). We can employ simulations to start developing contrasting hypotheses of the ways in which these processes and strategies at the individual level work together to ultimately lead to collective decisions and fission–fusion dynamics. Comparing the outcomes of these simulations to large datasets based on empirical observations would then help tease apart more plausible hypotheses and therefore generate predictions that can iteratively be tested in the field (Bonabeau et al. 1999, Couzin and Laidre 2009). Indeed we have the statistical tool to fit such hidden process models to behavioural observations thanks to recent advances in state space modelling methods (Zucchini et al. 2008).

Finally, we support a comprehensive comparative approach to studying the extent to which consensus decision-making operates in species living with different degrees of fission–fusion dynamics, a task that cannot be easily accomplished by a single researcher or research group. More coordinated experimental and theoretical studies need to be done in order to bridge the gap between individual decisions and population structure such as fission–fusion dynamics. Bridging this gap is crucial if we want to better understand whether and how simple and local interactions drive population structure and ecological systems.

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