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Aggression and conflict management at fusion in spider monkeys

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In social systems characterized by a high degree of fission–fusion dynamics, members of a large community are rarely all together, spending most of their time in smaller subgroups with flexible membership. Although fissioning into smaller subgroups is believed to reduce conflict among community members, fusions may create conflict among individuals from joining subgroups. Here, we present evidence for aggressive escalation at fusion and its mitigation by the use of embraces in wild spider monkeys (*Ateles geoffroyi*). Our findings provide the first systematic evidence for conflict management at fusion and may have implications for the function of human greetings.

Keywords: aggression; conflict; embrace; fission–fusion; greeting; grooming

1. INTRODUCTION

Conflicts of interest between group members over resources, travel decisions or allocation of time to different activities are unavoidable, but they may compromise the cooperative benefits of group living, especially when they escalate into aggression (Aureli *et al.* 2002). Group-living animals are therefore expected to use various behavioural mechanisms to manage their conflicts (Aureli & de Waal 2000; Wittig & Boesch 2003; Flack *et al.* 2005). Most attention has been given to post-conflict behaviour after aggressive interactions (Arnold & Aureli 2006), but a more efficient means of conflict management would be to prevent aggressive escalation in the first place.

A possible way to reduce intragroup competition and aggressive escalation is to adjust group size to local resource availability (Janson 1988). The adjustment can also occur within the same group resulting in the temporary formation of smaller subgroups based on fission–fusion dynamics (Kummer 1971; Wrangham 1979). Thus, whereas fissions into smaller subgroups are likely to reduce conflicts over resources and decisions, fusions may create such conflicts among individuals from joining subgroups. If so, mechanisms for mitigating the negative consequences of fusion are likely to have evolved, but no previous study has investigated this aspect of conflict management.

The aims of the present study were to document whether fusions were characterized by aggressive escalation and to examine whether post-fusion affiliative interactions play a role in conflict management. We carried out the study on wild spider monkeys (*Ateles geoffroyi*), one of the primate species with the highest degree of fission–fusion dynamics (Symington 1990).

2. MATERIAL AND METHODS

Subjects of the study were the adult, subadult (thereafter labelled together as (sub)adult) and juvenile members of two communities (eastern and western) of spider monkeys living in the forest surrounding the Punta Laguna lake, Yucatan peninsula, Mexico (Ramos-Fernandez *et al.* 2003). During the 2002–2003 study period, the eastern community included 4–6 (sub)adult males, 5–7 (sub) adult females and 0–4 juveniles, and the western community included 8–10 (sub)adult males, 12–14 (sub)adult females and 5–7 juveniles.

Although subgroups were usually separated by distances of hundreds of metres, visibility constraints forced us to use a conservative definition of subgroup. Individuals were not considered to be in the followed subgroup if they were not observed at a distance less than or equal to 30 m from at least one current subgroup member for more than 30 min. The cut-off distance of 30 m for this chain rule was derived from previous data on the same communities (Ramos-Fernandez 2005). Fusion was recorded when one or more individuals from another subgroup came within 30 m from any member of the followed subgroup.

Each subject was observed for approximately 160 h in the eastern community and 40 h in the western community. All occurrences of aggressive interactions including conspicuous patterns, such as chases, physical contact and loud vocalizations, were recorded along with ad libitum sampling of approaches within an arm's reach of another individual, grooming and embraces (i.e. a monkey wraps one or two arms around another individual's back and/or performs pectoral sniff and cheek-to-cheek contact; Schaffner & Aureli 2005).

Each subject was involved on average in 164 fusion events in the eastern community and 31 in the western community. Analyses were carried out at the individual level and compared the likelihood of social interactions in the first 5 min following fusion with baseline rates. Since preliminary analyses revealed that interactions clustered just before fissions and after fusions, baseline periods for each subject were obtained by excluding the 5 min preceding fissions and the 5 min following fusions from the total time the individual was observed in a subgroup. Hourly aggression rates were calculated for the individual initiating the interaction. The proportion of approaches that were followed by either embraces or grooming was calculated for each subject that approached others in the first 5 min following fusion and at baseline in at least three separate occasions for more reliable estimates. When sample size allowed, separate statistical analyses were carried out for the two communities. As the results were highly consistent, we report the results for the combined dataset of the two communities. Data that were not normally distributed based on the Kolmogorov–Smirnov test were square-root transformed. One-way repeated measures ANOVA with correction for sphericity (followed by Bonferroni *post hoc* tests) and paired *t*-tests with two-tailed probabilities were used to compare hourly rates and proportions of approaches at the individual level with an alpha level of 0.05.

3. RESULTS

The rates of aggressive interactions were affected by fusion events (figure 1; $F_{2,52}=15.95$, $p=0.00004$). *Post hoc* tests revealed that during the 5 min following fusion, spider monkeys behaved aggressively against members of joining subgroups more often than against members of the subgroup they were in before the fusion ($p=0.001$) and at baseline ($p=0.0001$). In contrast, rates of post-fusion aggression between individuals that were in the same subgroup before fusion did not differ from baseline rates ($p=0.114$).

The proportion of approaches followed by grooming between individuals from joining subgroups (mean$\pm$s.e.: 0.13 ± 0.05) was significantly lower in the first 5 post-fusion minutes than at baseline (0.41 ± 0.05; $t_{11}=4.49$, $p=0.001$). In contrast, the proportion of approaches followed by embraces between such individuals was higher in the first 5 post-fusion minutes (0.55 ± 0.10) than at baseline

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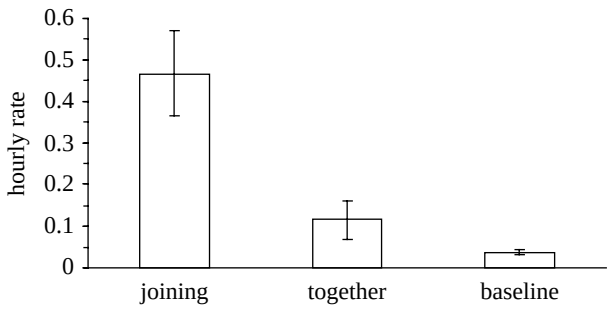

Figure 1. Mean (±s.e.) hourly rate of aggressive interactions in the 5 min post-fusion period between individuals from joining subgroups, between individuals that were together in the same subgroup before the fusion and at baseline.

(0.17±0.03; $t_{11}=4.80$, $p=0.001$). This result was confirmed as the 95% bootstrap confidence interval (1000 replicates) for the mean of the difference between the 5 min pre- and post-fusion embraces for all individuals involved in fusions did not include zero (0.50, 1.27). Embraces, like aggression, were usually initiated only by one or two individuals per fusion and thus only a minority of the potential dyads from the joining subgroups were involved.

All 15 individuals for whom we recorded at least one post-fusion embrace with a member of the joining subgroup did not display or receive any aggressive behaviour after the post-fusion embrace (in one case there was aggression before the embrace). This is in contrast with the mean hourly post-fusion aggression rate of 0.56 (±0.11) for the same 15 individuals when no embrace occurred. As post-fusion aggression rate was highest in the first minute and post-fusion embraces occurred on average within the first minute, we calculated the post-fusion aggression rate only for 2–5 min. Even when using this conservative estimate, there was a consistent decrease in post-fusion aggression rate after embraces took place compared with when there was no embrace (0.0±0.0 versus 0.21±0.05; $t_{14}=4.23$, $p=0.001$).

4. DISCUSSION

Our study shows that spider monkeys' fusion events are potentially risky situations in which aggression is more likely to occur than at other times. Fusions did not create situations in which aggression occurred indiscriminately as a reflection of generalized tension or increased number of group members because aggressive interactions were selectively increased between members of joining subgroups. Fusions were also characterized by increased affiliation as members from joining subgroups engaged in embraces, which appeared to be one way to reduce the likelihood of post-fusion aggression. These results were obtained despite using a conservative definition of subgroup, biasing against finding such effects of fusion events, and a small number of subjects, predominantly (sub)adults, for the analyses on affiliation. Although increased levels of aggressive and affiliative interactions after fusion were reported in other studies (see below), this is the first systematic evidence for post-fusion conflict management.

Previous studies described that chimpanzees (*Pan troglodytes*) and spider monkeys display aggressive behaviour when subgroups join one another (Klein 1974; Bauer 1975; Fedigan & Baxter 1984; Nishida *et al.* 1999; Muller 2002). In chimpanzees, grooming and other affiliative behaviour (no study focused specifically on embraces or other brief friendly contacts) seem more probable after fusion between the members of joining subgroups (Bauer 1975; Nishida *et al.* 1999; Okamoto *et al.* 2001). As in our study, spider monkeys seem to exchange more embraces, but not grooming, after fusion in the wild or at reunion after separation in captivity (Klein & Klein 1971; van Roosemalen & Klein 1988; Schaffner & Aureli 2005). Given that only a few individuals exchange embraces during a given fusion event, further research needs to focus on their possible bond-testing function as has been shown for male baboons' (*Papio* populations) greetings in contexts other than reunions (Whitham & Maestripieri 2003).

The prevalence of embraces at fusion may be related to the quick nature of the exchange relative to grooming. Embraces can therefore be more effective in appeasing or reassuring others when rapid action is needed to reduce the likelihood of aggression at fusion. Rapid contacts at reunion have been reported in other species that experience high rates of fission and fusion, such as spotted hyenas, *Crocuta crocuta* and bonobos, *Pan paniscus* (East *et al.* 1993; Hohmann & Fruth 2000; G. Hohmann 2006 personal communication). This is in contrast with the long and elaborate reunion displays of capuchin monkeys (*Cebus* spp.) in which separations are rare events (Matheson *et al.* 1996; Manson & Perry 2004). Interestingly, humans exchange rapid friendly contact, such as handshakes, embraces, nose rubbing and kisses, when they are reunited with familiar individuals and such greetings have been interpreted as a 'disclaimer of aggression' (Firth 1972; Kendon & Ferber 1973). As human societies are also characterized by frequent fissions and fusions (Rodseth *et al.* 1991), our results suggest that research on the potential function of such greetings in reducing tension and facilitating tolerance at reunions may contribute to the understanding of human conflict management.

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