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Article

Should I stay or should I go?
How activity synchronization affects fission decisions

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Abstract (max 200 words)

Group-living animals need to deal with conflicting interests to maintain cohesion. When the costs of doing so outweigh the benefits, the group may (temporarily) split into two or more subgroups. Conflicting interests can concern the activity to pursue or the direction of travel. Temporary group separation is a common feature in species with a high degree of fission-fusion dynamics. We investigated the role activity synchronization played in fission decisions in a spider monkey group living in the Otoch Ma'ax Yetel Kooh Nature Reserve, Yucatan, Mexico. For 21 months, we recorded every fission event occurring in the followed subgroup, as well as the subgroup activity. We classified the activity as "synchronized" when at least the 75% of subgroup members performed the same activity (resting, foraging, socializing or travelling); otherwise, we classified it as "non-synchronized". We found that fission events occurred more often when the activity was non-synchronized. In addition, when the activity was synchronized, fission events occurred more often when spider monkeys were travelling than when they engaged in other subgroup activities. Our findings highlight the role of conflicting interests over the activity to pursue and travel direction on fission decisions.

Key words: activity synchronization; fission-fusion dynamics; decision making process; Ateles.

Introduction

Most studies on decision-making processes in group-living animals focus on collective decisions, i.e. when a group of individuals coordinate their behaviour [1], to maintain the benefits of group living (e.g. safety from predation: [2,3]). Collective decisions are usually studied when individuals try to reach a consensus on when to move [4,5], where to move and where to eat [6-10].

To stay in the same group, members need to compromise their different needs and synchronize activities. If the cost of synchronization outweighs the benefits, the lack of consensus may result in a (temporary) break-up of the group [11-13]. For example, red deer (*Cervus elaphus*) are rarely in mixed-sex groups outside the breeding season probably due to the difference in the length of the foraging-resting bouts between males and females [14,15]. Furthermore, consensus needs to be reached not only for the activity, but also for the travel direction. The lack of consensus over travel direction may result in a leader change during the travelling bout [16], a delay in the decision-making process [17], or the temporary break-up of the group [9,18,19].

In several species temporary formation of subgroups occurs several times a day. This is the case for species with a high degree of fission-fusion dynamics [20], in which subgroups frequently change their size and composition [21]. The decision to fission into smaller subgroups is a trade-off between the need to reduce feeding competition [22-26] and the need to decrease the risk of predation [25,27,28]. However, other ecological and social factors may affect fission decisions, such as food characteristics [29], the quality of social relationships [30-32], the location within the home range [33], and the degree of human disturbance [34]. Here we investigate whether the degree of synchronization of subgroup members' activity could affect individual fission decisions in wild Geoffroy's spider monkeys (*Ateles geoffroyi*), a species with a high degree of fission-fusion dynamics [35].

We focus on fission decisions related to conflicting interests over the activity to pursue and travel direction. We have two predictions. First, when the degree of activity synchronization among subgroup members is lower, we expect fission to be more likely (Prediction 1). Individuals may also face conflicting interests over travel direction based on differences in the location to be reached. Thus, our second prediction is when the activity is highly synchronized, we expect a higher likelihood of fission when subgroup members travel rather than when they engage in other activities (Prediction 2).

Methods

Field site and study subjects

The field site is near the Punta Laguna lake within the natural protected area of Otoch Ma'ax Yetel Kooh, Yucatan Peninsula, Mexico (20°38’ N, 87°38’ W, [36]). We studied 22 adult and subadult individuals of a group of Geoffroy’s spider monkeys living in the protected area (6 adult males, 10 adult females, 1 subadult male, 5 subadult females). The study group has been the focus of a continuous long-term project since 1997 [37]. All monkeys are fully habituated to human observers and individually recognized by facial features, scars and fur coloration.

Data collection

Data were collected from January 2013 to September 2014. While following a subgroup, the first author continuously recorded any change in each subgroup member’s activity in a digital voice recorder with the help of field assistants spread in the area occupied by the subgroup, so that every subgroup member could be monitored (see Supplementary information for a detailed description of data collection). We considered the following four activities: resting (individual in a stationary position either lying, sitting or hanging), foraging (individual actively searching, manipulating and/or ingesting food items), social (individual involved in social interactions, e.g., grooming) and travelling (individual moving together with other subgroup members in the same direction).

Subgroup membership was continuously updated as we recorded the identity of every member of the initially encountered subgroup and all changes due to fission and fusion events. An individual was considered part of the followed subgroup if it was <30 m from a subgroup member according to a chain rule established for this study site ([38], see [39] for the concept of the chain rule). Fission was defined as individuals from the followed subgroup separating from one another into different subgroups and was recorded when one or more individuals were not seen within 30 m from any member of the followed subgroup for 30 min [40].

Data analyses

To test Prediction 1, we considered the subgroup activity as synchronized when at least 75% of subgroup members performed the same activity [41]. Otherwise, we considered it non-synchronized. We tested Prediction 1 in two ways. The first consisted of considering the number of fission events occurring during a given day, depending on whether the subgroup activity was synchronized or non-synchronized. We used a generalized linear mixed model (GLMM) in which the dependent variable was the number of fission events occurring when the activity was synchronized or non-synchronized during a given day. Activity duration was entered with the "offset" function. Activity synchronization (synchronized or non-synchronized) was the predictor variable, whereas the maximum subgroup size recorded during the duration of the activity was entered as a control variable, as the number of individuals in the subgroup may affect the likelihood of activity synchronization [42], and thus fission events [43]. We included the month in which the data were collected as a random factor to control for multiple data points during the same month.

The second way we tested Prediction 1 was to consider the number of fission events depending on the time spent in synchronized activity during each observation hour. We used a GLMM in which the dependent variable was the number of fission events occurring in an hour and the time spent in a synchronized activity during that hour as the predictor variable. We also included the maximum subgroup size recorded during the observation hour and the subgroup type (only males, only females or mixed-sex subgroup) as control variables because they may affect the likelihood of fission events, as individuals are more often in same-sex subgroups [44]. Given the frequent variation in subgroup composition, we could include the subgroup type as control variable only in this model because of the shorter temporal scale (i.e. 1 hour in this model instead of 1 day in the previous model). When subgroup composition type changed during an observation hour, the subgroup composition type occurring for most of the time was selected (we excluded the few cases in which more than one subgroup composition type occurred for most of the time). We included the day in which the data were collected as a random factor to control for multiple data points during the same day.

To test Prediction 2, only periods with synchronized activities were considered. We used a GLMM in which the dependent variable was the number of fission events that occurred during the same activity type in each observation day and activity duration was entered with the "offset" function. The type of activity (travelling or non-travelling) was the predictor variable, the maximum subgroup size recorded during the duration of the activity was entered as a control variable, and the month was entered as a random factor (Data available: see [45])

We ran all the GLMMs using the lme4 package [46] in R (version 3.6.0, R Core Team 2019). We compared full models with null models, which included only the random factor and the control variables, using a likelihood ratio test with the function anova [47]. We checked model assumptions using the “performance” package [48].

Results

Prediction 1 that fission would be more likely when the activity of subgroup members was not synchronized was supported. The rate of fission events was higher when the subgroup activity was non-synchronized compared to when it was synchronized at the temporal unit of observation day (Table 1, Fig 1). A similar result was found at the temporal unit of observation hour (Table 2).

Table 1: Results of the GLMM showing the association between the number of fission events (dependent variable) and whether the subgroup activity was synchronized or non-synchronized throughout the observation day.

Fixed effects	Estimate	Std. Error	z value	p
(Intercept)	-4.74479	0.15885	-29.869	<0.0001
Activity synchronization	-0.55263	0.11839	-4.668	<0.0001
Maximum subgroup size	0.01427	0.01569	0.909	0.363

The model was significantly different from the null model (likelihood ratio test: N= 416; χ^2= 73.056; p<0.0001). The negative estimate of activity synchronization means that there were fewer fission events when the activity was synchronized than when the activity was non-synchronized.

Table 2: Results of the GLMM showing the association between the number of fission events (dependent variable) and the time spent in synchronized subgroup activity in each observation hour.

Fixed effects	Estimate	Std. Error	z value	p
(Intercept)	-0.669354	0.217579	-3.076	0.002
Time in synchronized activity	-0.009286	0.003516	-2.641	0.008
Maximum subgroup size	0.017826	0.020084	0.888	0.375
Subgroup type (only males)	-0.126567	0.204421	-0.619	0.536
Subgroup type (mixed)	0.318309	0.151351	2.103	0.036

The model was significantly different from the null model (likelihood ratio test: N= 682; χ^2= 6.613; p<0.010). The categories of Subgroup type “only males” and “mixed” were compared with “only females”.

(FIG 1 here)

Prediction 2 that fission would be more likely when the subgroup activity was travelling compared to non-travelling was also supported (Table 3, Fig 2).

Table 3: Results of the GLMM showing the association between the number of fission events (dependent variable) and the time of travelling throughout the day.

Fixed effects	Estimate	Std. Error	z value	p
(Intercept)	-5.12511	0.19544	-26.223	< 2e-16
Activity type	-0.38841	0.14141	-2.747	0.0060
Maximum subgroup size	0.02466	0.01938	1.272	0.2033

The model was significantly different from the null model (likelihood ratio test: N= 432; χ^2= 55.994; p<0.0001). The negative estimate of Activity type means that there were fewer fission events when the activity was non-travelling than when the activity was travelling.

(Fig 2 here)

Discussion

Overall, we found that subgroup activity played an important role in influencing fission decisions in wild spider monkeys. We found a higher fission rate when the subgroup activity was non-synchronized compared to when it was synchronized (Prediction 1). When activity was synchronized, we found a higher fission rate when the subgroup was travelling compared to when subgroup members engaged in other activities (Prediction 2).

We found that the fission rate was higher when the subgroup activity was not synchronized than when it was synchronized at two temporal scales: several hours up to the entire observation day and each observation hour, supporting Prediction 1, although a note of caution is warranted due to the effect of subgroup size may have on activity synchronization [42]. Whereas most studies on activity synchronization focus on the need for individuals to forage and subsequently travel or fission depending on group cohesion level [13,14], our findings suggest that the lack of activity synchronization is sufficient to promote subgroup fission. As individuals of species with a high degree of fission-fusion dynamics do not need to reach a consensus on the activity to pursue [11,13], the difference in the activities performed (e.g., an individual already foraged and needs to rest) may promote fissioning from other subgroup members.

Another possible complementary explanation is related to the quality of social relationships between group members, such as affiliation and compatibility [49]. The relation between synchrony and affiliation is evident in humans [50] and other animals [51-53]. Spider monkeys' tendency to associate in subgroups with the most compatible group members [34] likely results in more shared activities. Thus, non-synchronized subgroup activity may be a predictor of the presence of subgroup members with social relationship characterized by low compatibility, which may lead to fission.

Prediction 2 was also supported. Our findings showed that fission rates were higher when the subgroup activity was travelling than when subgroup members were engaged in other activities. Given that we compared the likelihood of subgroup fission during travelling bouts with the likelihood of subgroup fission during other synchronized activities, we interpret this result as the outcome of conflicting interests over the travel direction rather than over the next activity to pursue, which may occur during any of the synchronized activities. In cases of conflict over travel direction, individuals of some species adopt strategies to maintain group cohesion [16,17], whereas others fission into subgroups [9,18,19]. Thus, it is likely that spider monkeys adopt the latter strategy. Conflict over travel direction is likely due to three reasons: differing nutritional needs [29]; engaging in different activities (e.g., feeding vs sleeping); and, males and females experience different travel costs [54] and therefore may not travel as far as males [55].

Overall, our study contributes to understanding fission decisions, highlighting the important role played by activity synchronization in species with a high degree of fission-fusion dynamics. Staying together when group members experience conflict over activity to pursue and travel direction is not the only option, as individuals can temporarily fission from other group members. Our findings support this view, providing further evidence about fission being a mechanism for conflict management [56].

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