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Unraveling fission-fusion dynamics: how subgroup properties and dyadic interactions influence individual decisions

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Abstract Many species show fission-fusion group dynamics because it has clear advantages for flexibly exploiting heterogeneous environments. However, the mechanisms by which these dynamics arise are not well known. We used a hierarchical Bayesian model to disentangle the different influences on spider monkey (Ateles geoffroyi) individual fissions and fusions, including the three dimensions of fission-fusion dynamics (subgroup size, dispersion, and composition). Furthermore, we considered the influences of other individuals also leaving or joining a subgroup at the same time. We found that the most important influence on individual fissions and fusions is whether other individuals are also doing the same. Subgroup size and dispersion did not have clear effects on the probability that an individual fissioned or fusioned, while individuals tended to leave subgroups that were biased toward the opposite sex and to join subgroups that were biased toward their own sex. The networks constructed by the interindividual influences during fissions and fusions were cohesive and did not show assortativity by sex or by degree. Individuals had a similar degree in both networks and each was influenced by a different set of individuals, suggesting a high fluidity in the social networks. We suggest that these networks reflect the way in which information about the

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environment flows as individuals follow one another during fissions and fusions.

Keywords Spider monkeys · Hierarchical Bayesian models · Social networks · Information sharing · Collective decision-making

Introduction

Fission-fusion dynamics (FFD) refers to the variation in interindividual dispersion and subgroup size and composition present in animal groups (Aureli et al. 2008). Variability in the size and dispersion of foraging groups is considered to be advantageous in exploiting food resources, which are often distributed heterogeneously in time and space (Kinzey and Cunningham 1994; Chapman et al. 1995). There is good evidence that FFD does improve foraging efficiency by reducing feeding competition (Symington (1988a) in spider monkeys *Ateles paniscus*, Shaffer (2013) in bearded sakis *Chiropotes sagulatus*, Asensio et al. (2009) in spider monkeys *A. geoffroyi*, and Smith et al. (2008) in spotted hyenas *Crocuta crocuta*).

Much less is known about the mechanisms underlying FFD (Kerth 2010a; Sueur et al. 2011), both at the level of individual behavior and at the level of interactions between individuals. The group-level properties that define FFD are clearly the result of individual decisions, which in turn can be affected by FFD themselves. However, this feedback loop is not necessarily present as FFD could emerge from interactions between individuals that behave according to relatively simple, local rules (Kerth 2010b). In order to address this question, Ramos-Fernandez et al. (2006) built an agent-based model which showed that subgroups of varying size could be formed by individuals behaving independently according to simple foraging rules. These subgroups could

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split, depending on the different information that agents could have about the location of food sources, or join, when more than one agent considered the same food patch as convenient. Within a certain parameter space, this model could mimic the size frequency distribution observed in spider monkeys' subgroups. Yet, in many cases, when an individual joins a subgroup and increases its size, it also modifies the decisions of other subgroup members to stay together or split. This recursive relationship between group- and individual level phenomena is recognized as a source of complexity and unpredictability in animal collective patterns (Couzin and Krause 2003). One important question is whether individuals take into account global properties such as subgroup size or the general degree of subgroup dispersion in their decisions.

Furthermore, individual decisions to leave or join a subgroup must also be influenced by social relationships, another arena where social interactions both influence and are influenced by group-level properties such as the social structure (Hinde 1976).

In species with a high degree of FFD, the time that two individuals spend in the same subgroup is closely related to the quality of social interactions between individuals (Tokuda et al. (2012) in Northern muriquis *Brachyteles hypoxanthus*, Wakefield (2013) in chimpanzees *Pan troglodytes*, and Wittemyer et al. (2005) in African elephants *Loxodonta africana*). In spider monkeys (*Ateles* spp.), association networks show the sex-segregated pattern typical of these species (Ramos-Fernandez et al. 2009)—males are closely associated among each other, interacting mostly affiliatively, while female-male bonds are the weakest, consistent with the mostly neutral or agonistic relationships between the sexes (Fedigan and Baxter 1984; Slater et al. 2009).

A key ingredient in the relationship between decisionmaking processes and FFD, particularly for species living in large, heterogeneous habitats, is the information that can be shared by individuals: if there are asymmetries in the information that individuals have about their environment (location of important resources, for example), then we would expect informed leaders to be followed by non-informed individuals (Sueur et al. 2011; Lewis et al. 2013). The possibility of pooling information with other group members is predicted to promote grouping, particularly when personal information is accurate (King and Cowlishaw 2007). In the case of FFD, this tendency to follow knowledgeable individuals could promote the fission of groups into subgroups consisting of knowledgeable individuals and their immediate followers.

Knowing which factors affect individual decisions to fission from a subgroup is relevant, given the prevailing view about collective decision making in which fission is seen as a lack of consensus due to group members having different priorities (Conradt and Roper 2005). An alternative view of fissions as a solution to a conflict has been proposed by Kerth (2010a), who argues that by forming temporary subgroups, individuals in groups with high FFD can fulfill their different needs better than they would if they traveled as a cohesive unit.

Here we investigate the factors underlying FFD using data from behavioral observations and subgroup properties in spider monkeys (A. geoffroyi). We focus on individual fission and fusion events and evaluate the influence of the three dimensions of FFD (subgroup size, dispersion, and composition) on the probability that an individual will leave or join a subgroup. In other words, we test how subgroup properties such as the number of individuals, their spatial dispersion, and sex ratio influence individual tendencies to leave the subgroup or be joined by other group members who are outside the subgroup. Given the different association tendencies by the different sexes in the spider monkey society, we also tested for differences in the probabilities to fission or fusion between males and females. Finally, we tested whether particular individuals would influence the probabilities of others to either fission or fusion. We use a hierarchical Bayesian model that explicitly takes into account the fact that individuals can vary in their response to covariates, thus estimating effects at the individual and global levels. We also use social network analysis to explore the patterns of inter-individual influences on fission and fusion tendencies.

Methods

Study site and animals

Observations were conducted from August 2009 to July 2010 in the Otoch Ma'ax Yetel Kooh protected area (also known as Punta Laguna; 5,367 ha), in the Yucatan Peninsula, Mexico (20° 38' N, 87° 38' W, 14 m elevation; mean annual temperature is around 25 °C). The area has a seasonally dry climate (1,500 mm mean annual rainfall, 70 % between May and October). The study group was habituated to human presence and studied continuously by trained field assistants long before this study began (Ramos-Fernández et al. 2003). We identified all its members by their facial marks and other unique features. During the study period, the group included 10 adult females and 7 adult males, all distinguished from the 6 juvenile or infants by their darker faces and sexual maturity. The analysis presented here focuses only on adults, because juveniles and infants are not independent from their mothers in their decisions to fission or fusion (group size, G=17).

Data collection

Data consisted of instantaneous scan samples taken by experienced observers every 20 min over an average of 7.3 h per day (min=40 min, max=18 h) for 177 days and a total of 3.916 scan samples (1.305 h in total). Each sampling day, a focal subgroup was located according to a priority list of individuals which helped to homogenize the number of samples per individual (min=100, max=1,847, mean=1,002.3). Once a focal subgroup had been chosen, observers registered the identity and location of all its members in each scan sample (subgroup size min=1, max=14, mean=4.47). A subgroup included all adult individuals that in a particular scan sample were found within the empirically determined threshold of 30 m or less of any other (Ramos-Fernandez 2005; Aureli et al. 2012). Individuals outside the subgroup were not monitored specifically. Observers registered a fission when one or more individuals left the subgroup and were not present for the two subsequent scan samples (size of the smallest subgroup after a fission min=1, max=7, mean=1.88). Similarly, observers registered a fusion when one or more individuals that were not previously part of the focal subgroup were present in two consecutive samples (size of the smallest subgroup before a fusion min=1, max=5, mean=1.68). After fissions, observers chose the resulting subgroup to follow based on the same criteria of sample size homogeneity per individual. The 20-min sampling period was chosen based on our previous experience describing FFD in the same study system (Ramos-Fernandez et al. 2009), and it allowed us to reliably detect all fission and fusion events, which seldom occurred at a faster rate (mean fission rate, 0.13 events/scan; mean fusion rate, 0.18 events/scan).

We defined subgroup dispersion as the distance separating the two most distant individuals in the subgroup at a given scan sample. We defined the female bias as the proportion of adult females out of the total number of adults in the subgroup. In the analyses that follow, individuals that could fission from a focal subgroup were those in the subgroup, while individuals that could fusion to a focal subgroup were those individuals in the group that were not part of the focal subgroup. We performed separate analyses on fissions and fusions, using the same modeling framework and covariates.

Hierarchical Bayesian model

We used a hierarchical Bayesian (HB) model to estimate the probabilities of individual fissions and fusions and the effect of the different covariates. Bayesian inference uses conditional probability rules to estimate the probability of a parameter given the data (Box and Tiao 1973). For this, it updates the prior probability of a parameter θ , $p(\theta)$, with the likelihood of the observed data given the parameter, $p(y|\theta)$, producing a posterior probability of the parameter given the data, $p(\theta|y)$:

 $p(\theta|y) \propto p(y||\theta) p(\theta)$

Compared to traditional maximum likelihood methods, Bayesian estimations yield the full probability distribution of all parameters, providing, among other things, a measure of the uncertainty around parameter values after looking at the data. In our case, θ could represent, for example, the probability that an individual leaves its current subgroup in a particular time interval. In simple models, the posterior uncertainty shrinks as sample size increases. However, HB models allow for the possibility that some model parameters depend on other (hyper)parameters (Clark 2005; Clark and Gelfand 2006). For example, θ_1 could depend on θ_2 :

 $p(\theta_1, \theta_2|y) \propto p(y|\theta_1) p(\theta_1|\theta_2) p(\theta_2)$

 θ_2 in this example could refer to the mean of the populationlevel distribution from which the values of the individuallevel θ_1 are taken (e.g., the values corresponding to all individuals of a given group or sex). In this case, the variability in its posterior distribution $p(\theta_1, \theta_2|v)$ is due to variability in the population (i.e., the set of individuals from the same group or sex), not to uncertainty. The main advantage of a HB model is that it allows for a realistic assignment of sources of variation: we do not expect all individuals in a population to respond in exactly the same way but we also recognize that they are part of a population and hence not fully independent.

We assume that a fission (or fusion) by individual *j* in observation *t* is the outcome of a Bernoulli trial with success probability p_{tj} . In model I, we use a logit link to model this probability as a function of subgroup size, dispersion, and composition:

$$\operatorname{logit}(p_{tj}) = \beta_{0j} + \beta_{1j}(s_t) + \beta_{2j}(d_t) + \beta_{3j}(b_t)$$

where β_{0j} is the basal probability of a fission (or fusion) by individual *j* in sample *t*. Parameters β_{1j} , β_{2j} , and β_{3j} refer to the effect of subgroup size (*s*), dispersion (*d*), and female bias (*b*) in sample *t* on p_{tj} , respectively. These variables were centered by subtracting the mean and standardized by dividing by the standard deviation. The values of β_0, \ldots, β_3 for each individual *j* are taken from a population-level normal distribution with mean μ_0, \ldots, μ_3 and standard deviation $\sigma_0, \ldots, \sigma_3$. These are the hyperparameters for parameters β_0, \ldots, β_3 . To allow for the possibility that males and females could show consistent differences, we assumed that the parameters come from different distributions, in the case of males with means μ_0, \ldots, μ_3 and in the case of females $\mu_0 + \mu_{f0}, \ldots, \mu_3 + \mu_{f3}$ (Fig. 1).

Model I assumes that each individual *j* will decide to fission or fusion independently of the decisions of other individuals. In model II, we chose to explicitly account for possible inter-



Fig. 1 Diagram for model I. A fission (or fusion) event by individual *j* in observation *t* occurs with probability p_{ij} (the probability in the Bernoulli trial that defines whether an event occurs or not). This probability is assumed to be an inverse logistic function of parameters β_0 , β_1 , β_2 , and β_3 , which in turn take their values from normal distributions with

individual influences on fission and fusion events, by adding another parameter β_{4ij} :

$$\operatorname{logit}(p_{ij}) = \beta_{0j} + \beta_{1j}(s_t) + \beta_{2j}(d_t) + \beta_{3j}(b_t) + \sum_{\substack{i = 1 \\ for \\ i \neq j}}^{G} \left(\beta_{4ij}f_{ij}\right)$$

This parameter evaluates the interaction between individuals *i* and *j* in each sample. If *j* does not fission or fusion (an individual event denoted by *f*) in sample *t* (i.e., when $f_{ij}=0$), then the term in the sum above becomes 0, while for $f_{ij}=1$ it evaluates whether another individual *i* is fissioning (or fusioning) at the same time as *j*. Because β_{4ij} evaluates the influence of *i* over *j* for all $i \neq j$, there are as many β_{4ij} parameters as the number of directional dyadic influences in the group (where the influence of individual *i* over *j* is not the same as that of *j* over *i*). Thus, we produced a 17×17 matrix of β_{4ij} for all pairs of individuals *i* and *j*, referring to the effect of *j*'s fission on *i*'s tendency to fission (or fusion). These parameters take their values from a normal (population level) distribution with different mean for males and females and the same standard deviation for both sexes (Fig. 2).

All parameters and hyperparameters are assigned a prior distribution, and the HB model updates these prior distributions in light of the data, estimating posterior distributions. In all cases, we used vague prior distributions for the hyperparameters μ (normal distribution with mean=0 and standard deviation=32) and σ (uniform distribution with mean=0 and standard deviation=100). We fitted the two models above

corresponding hyperparameters μ for the mean and σ for the standard deviation. Plates indicate whether an observation or estimation is iterated over observations, individuals, or over the set of all adult males (*blue plate*) or all adult females (*red plate*). The two sexes differ in the mean of the normal distribution from which the parameters values are taken

using Markov Chain Monte Carlo techniques implemented in the WinBUGS software v.1.4.3 (Lunn et al. 2000). We ran three chains for 50,000 iterations each and checked for convergence using the ratio of between- to within-chain variation, which stabilized to 1 in all cases. We ran all other analyses in R (R Core Development Team 2013).

Models I and II were compared using the Deviance Information Criterion (DIC), a generalization of the Akaike Information Criterion for hierarchical models (Spiegelhalter et al. 2002).

Network analysis

We constructed binary directional networks by linking two individuals *i* and *j* whenever the value of β_{4ij} and its 95 % highest posterior density (HPD) credible intervals were above zero (Supplementary Information). We calculated degree (number of links per node) and assortativity by degree and sex (how closely linked are individuals of similar degree or same sex compared to pairs of different degree or sex; Newman 2002) using the *igraph* package in R (Csardi and Nepusz 2006).

Results

Comparison of different models

Model II was clearly superior in explaining the probability of fissions ($DIC_{Model II}$ =5,074 vs. $DIC_{Model I}$ =7,257) and fusions

Fig. 2 Diagram for model II. Same as in model I, but with an additional parameter, β_{4ij} , which refers to the influence of individual *i* on *j*'s fissions or fusions. The estimation of this parameter is iterated over all possible dyads between individuals *i* and *j*, creating a 17×17 matrix of values



(DIC_{Model II}=7,254 vs. DIC_{Model I}=10,174). Therefore, in what follows, only results from model II will be shown (the relevant results from model I can be found in the Supplementary Information).

Probability of fission and fusion events

The mean basal probability of an individual fission (estimated by the inverse logit of parameter μ_0) was low (Fig. 3a). Males had a higher probability of fissioning than females, and there was more variability among individuals (Fig. 3a). With regard to fusions, the basal probability that an individual would join a subgroup was lower than in the case of fissions, and the opposite pattern was observed with respect to the different sexes—females outside the focal subgroup were more likely to join it than males and there was more variability among individuals (Fig. 3b). Effect of subgroup covariates

Figure 4 shows the posterior probability distribution of the population-level parameter μ_1 , which estimates the effect of subgroup size on the probability of individual fission (Fig. 4a) or fusion (Fig. 4b) events, as a function of subgroup size. There is no clear effect of subgroup size on the probability that an individual fissions from a subgroup for neither sex. In the case of fusions, as the number of individuals in a subgroup decreases, there is a higher probability that a female (but not a male) will join it. In the case of model I, there was an increase in the probability of fissions, especially by males, with the size of subgroups (Fig. S1 in Supplementary Information).

In the case of subgroup dispersion, individuals of either sex were somewhat more likely to fission from subgroups that were more cohesive than from more dispersed ones (Fig. 5a),

Fig. 3 Posterior probability densities for individual fissions (a) and fusions (b), corresponding to hyperparameter μ_0 in the case of females and $\mu_0+\mu_{f0}$ in the case of females (see Fig. 2). This hyperparameter corresponds to the mean basal probability of an individual fissioning or fusioning



Fig. 4 Posterior probabilities of fission (**a**) and fusion (**b**) as a function of subgroup size and the number of individuals outside the subgroup, respectively. These probabilities correspond to the hyperparameters μ_1 in the case of males and $\mu_1 + \mu_{/1}$ in the case of females and their 95 % HPD credible interval. These hyperparameters represent the effect of subgroup size on the probability of an individual fissioning or fusioning



while they were more likely to join subgroups that were more dispersed than more cohesive ones, particularly in the case of females, although the variation between individuals is large (Fig. 5b). Model I showed similar patterns, although it showed a higher probability of fusions as subgroup dispersion increased (Fig. S2 in Supplementary Information).

The last subgroup covariate we tested was composition, as summarized by the female bias. We found a clear, opposite pattern with respect to sex—males were more likely to split from a subgroup that was composed in its majority by females, while females were more likely to split from a subgroup that was composed mostly by males (Fig. 6a). In the case of fusions, each sex was more likely to join a subgroup if its composition was biased toward its own sex (Fig. 6b).

Effect of other individuals

The probabilities of leaving or joining a subgroup as others do so are much higher than the basal probabilities shown in Fig. 3 and the probabilities estimated with respect to the other covariates (Figs. 4, 5, and 6). Figure 7 shows the values of hyperparameter

Fig. 5 Posterior probabilities of fission (a) and fusion (b) as a function of the dispersion of the focal subgroup. These probabilities correspond to the hyperparameters μ_2 in the case of males and $\mu_2 + \mu_{/2}$ in the case of females and their 95 % HPD credible interval. These hyperparameters represent the effect of subgroup dispersion on the probability of an individual fissioning or fusioning



Fig. 6 Posterior probabilities of fission (a) and fusion (b) as a function of the composition of the focal subgroup, measured by the bias toward adult females. These probabilities correspond to the hyperparameters μ_3 in the case of males and $\mu_3 + \mu_{f3}$ in the case of females and their 95 % HPD credible interval. These hyperparameters represent the effect of female bias on the probability of an individual fissioning or fusioning





 μ_4 , which refers to the mean of the probability distribution of parameter β_{4ij} , and evaluates the interaction between individuals *i* and *j* in each sample. Males have a higher probability of fissioning as others do so than females (Fig. 7a), and, in the case of fusions, there is no difference between sexes (Fig. 7b).

Probability of fission in 20' period

0.20

0.05 0.10 0.15

0.00

0.0

0.2

Networks of influence during fissions and fusions

As we considered the possibility of asymmetries in how individuals could affect each other, we estimated 272 β_{4ii} coefficients ($G \times G - G$). In order to highlight those pairs of individuals that had a clearly positive or negative influence on each other, we identified those values of β_{4ij} that had a 95 % HPD above or below zero. This yielded 77 pairs with clearly positive influences for fissions and 59 for fusions. There were only three pairs that had β_{4ij} values below zero in the case of fusions and none in the case of fissions (Fig. S3 in Supplementary Information).

We used these unambiguous positive influences to construct directional, binary networks linking two individuals when one clearly influences the fissions (Fig. 8a) or fusions (Fig. 8b) of another. These networks show no clear pattern

Fig. 7 Posterior probability densities for the effect of other individuals on individual fissions (a) and fusions (b), corresponding to hyperparameter μ_4 in the case of males and $\mu_4 + \mu_{f4}$ in the case of females (see Fig. 2). This hyperparameter represents the overall effect of others on the probability of an individual fissioning or fusioning





with respect to sex, as there are individuals of both sexes with high and low degrees. We searched for patterns in residency status, but there was no clear relationship (data not shown).

Fig. 8 Networks constructed with the clearly positive influences of other individual on fissions (a) and fusions (b). A clearly positive influence was one in which the posterior value of parameter β_{4ij} and its 95 % HPD credible interval was above zero (Supplementary Information). *Nodes* represent adult individuals, females in *red* and males in *blue. Arrows* represent directional influences from individual *i* on individual *j* and are colored depending on whether they join two females (*red*), two males (*blue*), or two individuals of different sex (*purple*). The size of nodes is proportional to its degree, i.e., the number of interactions (in both directions) in which it is involved in. c The degree of individuals in both networks (the line represents the linear regression: adj R²=0.528; *p*<0.001)</p>

Individuals with a high degree in the network of fission influences tend to be the same as those in the network of fusion influences (Fig. 8c).

Both fission and fusion networks showed a negative, close to zero assortativity by sex (fissions, -0.1247; fusions, -0.0959) implying that individuals of each sex tend to be equally linked to both sexes, and by degree (fissions, -0.0648; fusions, -0.1139), implying no separation or clustering of individuals by their degree.

Discussion

We used a hierarchical Bayesian model to disentangle the different influences of subgroup properties and the behavior of other individuals on individual fissions and fusions. These models allow variability to be decomposed at different levels by conditioning each component on those elements that affect it directly (Clark 2005). We have assumed that the probability that each individual decides to fission (or fusion) is dependent on three subgroup-level properties which correspond to the three dimensions of FFD-subgroup size, dispersion, and composition (Aureli et al. 2008). The analysis allows us to assign a portion of the variability in the probability of fission and fusion events to each covariate. In addition, the analysis evaluates how these effects of covariates on the probability of individual fissions depend upon the variability existing among individuals in the group and their sex. In this way, we obtained estimations of the importance of each factor for all individuals of a given sex as well as for each individual.

An important assumption of all models that use a binomial process (or a Bernoulli process for a single trial, as in our case) is that individual decisions are independent—in a given time sample, each individual would be deciding independently of the others whether to fission or, in the case of those individuals outside the focal subgroup, to join it. This may not be realistic, neither for many ecological processes such as fruit removal at a plant, survival of siblings, etc. (Williams 1982), nor for a social process such as subgroup formation. Our analysis explicitly considers this potential lack of independence by introducing a set of coefficients that account for the influence of all other individual fissions (or fusions) on a given individual's decision.

In fact, we have found that the most important influence on individual fissions and fusions is whether other individuals are also doing the same. Given that our observations consist of instantaneous samples taken at 20-min intervals, it is difficult to determine causality in these inter-individual influences. This is because we have no information on the sequence of events that led to each individual's decision to fission (or fusion). In other words, a clearly positive influence of individual i's fissions on those of individual i does not imply that during the interval between two instantaneous samples *i* influenced j's decision to fission because i was the first one to move out of the subgroup, or who showed an intent to depart (Sueur et al. 2009; King et al. 2011). All we know from our observations is that both individuals fissioned (or fusioned) together during the same interval. However, there is directionality in the interactions that we have found a positive influence by *i*'s fissions on those by *j* implies that out of all individuals who may have influenced *j*, *i* was a particularly important one. This does not imply the reverse, i.e., that out of all individuals who may have influenced *i*, *j* was necessarily important. This is the reason why our matrices of inter-individual interactions are asymmetrical and consequently, the networks of interaction are directed.

Neither subgroup size nor dispersion had strong effects on individual fissions or fusions. In model I, which did not explicitly account for individual interactions, subgroup size had a positive influence on the probability of individual fissions, but not on that of fusions, and this effect was larger for males than for females (Supplementary Information). In model II, this effect became unimportant in comparison to the very salient effect of specific individual's fissions. This may be because the most important influence on whether an individual fissions is the behavior of particular others, which are more likely to be present in large than in small subgroups. These findings do not imply that feeding competition, and particularly the local and habitat-wide food abundance, are not important determinants of FFD (Symington 1988a; Asensio et al. 2008, 2009). Aggressive interactions, satiation levels, or the presence of important feeding areas could be causing these fissions in the first place. Similarly, fusions could be more likely in large feeding areas, consistent with interpretations of FFD as a way to adjust subgroup size to local food availability (Asensio et al. 2009). What our results do suggest is that spider monkeys are paying attention not to global properties of their subgroup such as their size and dispersion in order to decide whether to split from it, but simply to the behavior of particular others. It can be argued that in groups with high FFD, much of the pattern emerging at the subgroup level, even if it results in a functional adaptation, is not really "coded" in the individual but rather results from interactions between specific individuals (Couzin and Krause 2003; Couzin 2006).

This finding should be taken into account in other studies of FFD in species with individual recognition and differentiated social relationships.

Sex had an important influence on individual fissions and fusions. Males had a higher probability of fissioning than females, and the opposite was true for fusions. This is consistent with the known patterns of higher mobility, longer day ranges, and larger individual core areas by males compared to females in Ateles spp. (Symington 1988b; Shimooka 2005; Wallace 2008)-males would be fissioning more often from stationary subgroups due to their high mobility, while females would be more likely to join focal subgroups as they would share their core areas with more individuals in the group. Moreover, our results on subgroup composition show that individuals of each sex tended to split from subgroups that were predominantly composed by the opposite sex and join those that were composed of individuals from their own sex. This is consistent with known patterns of sex segregation in spider monkeys (Fedigan and Baxter 1984; Ramos-Fernandez et al. 2009). Taking all our results together, subgroup composition seems to be the most important subgroup property that individuals consider in their decisions to fission or fusion.

The networks of inter-individual influences on fissions and fusions were cohesive. This is especially important given that we used a stringent criterion to link two individuals—values of the interaction parameter that were clearly positive. It was then possible that some individuals would be left out of the network or that isolated clusters would form which included only a subset of the adults in the group. The fact that all individuals were included in the same cluster implies the degree distribution is not greatly skewed (it ranged from 5 to 13 in the fission network and from 4 to 12 in the fusion network; Fig. 8). Indeed, these networks do not show a central individual that has a greater degree than all the rest. Rather, they show some individuals of both sexes with the highest degrees, and interestingly, each individuals in the network.

Our assortativity results show that females and males are influencing each other similarly than pairs of individuals of the same sex. When we compare these interaction networks with the association networks, in which a link represents the extent to which pairs of individuals spent time in the same subgroup (Ramos-Fernandez et al. 2009; Pinacho-Guendulain and Ramos-Fernández 2013), they are quite different. Association networks show a clear segregation by sex, while the fission and fusion networks showed null or even slightly negative degrees of assortativity by sex, implying that the two sexes were highly integrated in the network. If we consider association networks as an approximation to the social relationships existing among group members (Brent et al. 2011), these differences between both networks would suggest that, in the case of fissions and fusions, it is not long-term affiliative relationships that are necessarily driving each individual's decisions.

The networks that we have uncovered here could represent how information about the environment is flowing between individuals as they follow each other during fissions and fusions. In a classical study in social network analysis, Zachary (1977) attributed the fission of a human group to different information flowing in different sections of the network. More recent research in social networks has made it clear that many of the structural properties of social networks affect information flow between the nodes (Easley and Kleinberg 2010). Information transmission within the group increases through collective action, where group members interact with each other and exchange information about the environment (Couzin 2009), as well as by social facilitation, where individuals pay attention to what others do and act accordingly (Fischer and Zinner 2010). As in other species with high FFD, constant leadership in spider monkeys is not expected (Sueur et al. 2011), given that subgroups range independently of one another (Ramos-Fernández et al. 2011) and perhaps have access to different information about the environment. If this is so, it is possible that the network structure is being driven by individuals following other knowledgeable individuals. If correct, this interpretation would imply that fissioning with others would be the result of each individual following someone else who in a certain moment appears to know where to go, without long-term affiliative relationships playing such an important role. Thus, an apparently adaptive feature of high FFD such as a variable subgroup size would be the result of simple but highly dynamic interactions between individuals. An intriguing possibility is that high FFD improves foraging efficiency not only by reducing feeding competition, but also by improving the transfer of information about resource locations.

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Ethical standards The experiments comply with the current laws of Mexico.

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