



## No Evidence of Coordination Between Different Subgroups in the Fission–Fusion Society of Spider Monkeys (*Ateles geoffroyi*)

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**Abstract** Flexibility in spatial cohesion allows species with high fission–fusion dynamics to exploit variable habitats and decrease the costs of feeding competition. However, coordination among highly dispersed group members becomes problematic. In spider monkeys (*Ateles* spp.), individuals can spread over wide areas, forming several subgroups that appear to travel independently from each other. To explore their relative travel patterns, we compare the distance between different subgroups with the distance predicted by a null model of independent travel. Observations of distance between subgroups come from simultaneous follows of  $\geq 2$  subgroups in 2 different groups of spider monkeys in Punta Laguna, Mexico. We estimated space use using the kernel method, which produces areas with a given probability of presence of the subgroups, based on the frequency with which they were observed in each location. The null model consisted of the frequency distribution of distances between randomly chosen pairs of points within the home range, choosing each point independently with a probability proportional to the corresponding observed probability of presence. In all cases, the observed distances between subgroups were very close to those predicted by the null model, which suggests that subgroups do not coordinate their relative travel patterns. Also, the distance separating 2 individuals when in different subgroups was not affected by their sex or association index. These findings underscore the low cohesiveness

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between group members in species with high fission–fusion dynamics and challenge us to find the mechanisms by which groups maintain their social structure.

**Keywords** *Ateles geoffroyi* · Group coordination · Fission–fusion · Null models · Spatial cohesion

## Introduction

Fission–fusion dynamics in animal societies are characterized by the degree of variation in 3 different dimensions: group size, composition, and spatial cohesion (Aureli *et al.* 2008). In species with high fission–fusion dynamics, such as chimpanzees (*Pan* spp.) and spider monkeys (*Ateles* spp.), groups are divided into subgroups that vary greatly in size and composition within short timescales, and may also spend long periods of time separated from others in the group (Symington 1990). Individuals in the same subgroup have the option of following others or splitting from them, which adds to the complexities of group coordination and decision making (Kerth 2010). A decision to split from others may reflect the lack of a shared consensus, but may also represent an optimal decision if individuals can gain advantages by foraging in smaller units. In spider monkeys, a variable subgroup size has been shown to decrease the costs of feeding competition, by allowing individuals in a group to feed at widely separated food patches (Asensio *et al.* 2009; Chapman *et al.* 1995; Symington 1988a). At the same time, forming subgroups poses a challenge for the maintenance of social bonds among group members, which has been hypothesized to be an important selective pressure on the cognitive abilities of primates, including human ancestors (Aureli *et al.* 2008; Barrett *et al.* 2003).

Of the 3 dimensions of fission–fusion dynamics, spatial cohesion has received the least attention, despite the fact that it is the dimension that can show the greatest variation within and between species. Some primate species are highly cohesive, with group members in continuous visual contact with one another (as in most species of savanna-dwelling, cercopithecine monkeys; Melnick and Pearl 1987), whereas others can show high degrees of variation in spatial cohesion, even within a day (as in desert and montane baboons, which can become separated by several kilometers throughout the course of a day and then come together at the same sleeping site; Stambach 1987). Aureli *et al.* (2008) suggested that spatial cohesion is an important source of flexibility in grouping patterns, and predicted that the spatial distribution of resources, e.g., food, sleeping sites, would be matched by the spatial distribution of individuals (Aureli *et al.* 2008, pp. 631).

Groups of spider monkeys can vary from 15 to 55 individuals (Shimooka *et al.* 2008a) and occupy home ranges of 95–390 ha (Wallace 2008). Groups, in turn, are divided into subgroups that can vary in size from a solitary individual to up to 30 group members (van Roosmalen and Klein 1987). These subgroups can be separated by several hundred meters, traveling in what seems to be an independent fashion (Ramos-Fernandez 2005). However, the poor visibility conditions in tropical forests make it difficult to study cohesion at scales larger than a few tens of meters. Therefore, to capture patterns of cohesion at larger spatial scales, it is necessary to perform simultaneous follows of different subgroups (Shimooka *et al.* 2008b). We

here present the first systematic analysis of intersubgroup cohesion patterns in a species with high fission–fusion dynamics. We use 3 sets of data from 1997–1999 and 2009–2010 in 2 groups living around the Punta Laguna lake in the Yucatan peninsula, Mexico.

Although subgroups of spider monkeys seem to travel independently from each other, a priori there are several reasons why this may not always be the case. First, individuals in different subgroups could use long-distance communication to coordinate their distances, approaching or avoiding individuals in other subgroups depending on their social relationships (Ramos-Fernandez 2005). Second, the use of a limited number of feeding or resting sites by different subgroups (van Roosmalen and Klein 1987) would make it more likely that subgroups would coincide in these sites at certain times of day than if their travel patterns were completely independent. Our goal here is to evaluate whether subgroups coordinate their relative distances or whether they can be considered to travel independently from each other. To address this question, it is necessary to explore what a pattern of independent travel would look like. This null model approach was advocated by Aureli *et al.* (2008) when delineating a research framework on the socioecology of fission–fusion dynamics (pp. 629–632 and Supplement E). Here we develop a null model consisting of the frequency distribution of the distance between subgroups that would be expected if the relative movements of 2 different subgroups were independent from each other. For this purpose, we calculate the distance between pairs of points randomly and independently chosen from the areas within the home range used by the monkeys during the observations, each point being drawn with a probability equal to the probability of presence as estimated by the kernel method. Then we compare the observed distances between subgroups with those predicted by the model. We also analyze the influence of individual sex and association index between selected pairs of individuals in different subgroups, to explore whether particular pairs show signs of coordination when traveling in different subgroups. If a mechanism for intersubgroup coordination exists, we predict that 1) female–male dyads will maintain a greater distance than female–female dyads, given the generally low tendencies of male–female dyads to be found in association, which suggests mutual avoidance (Ramos-Fernandez *et al.* 2009), and the high levels of aggression of males toward females (Asensio *et al.* 2008), and 2) dyads with higher association indices will maintain a shorter distance than those with lower association indices.

## Methods

### Study Site and Subjects

Data come from 2 free-ranging, habituated groups of black-handed spider monkeys (*Ateles geoffroyi*) living around the lake of Punta Laguna, in Yucatan, Mexico (20° 38'N, 87°38'W, 14 m altitude). Their habitat consists of a mosaic of several fragments of semi-evergreen medium forest, with trees no taller than 25 m, in a matrix of vegetation in different stages of secondary succession, with trees no taller than 15 m (see Garcia-Frapolli *et al.* 2007 for more details about the landscape structure of the area). A system of trails allowed us to follow spider monkey

subgroups closely and register their position accurately with the use of a GPS or with respect to known trees and other landmarks. Visibility conditions for observers on the ground are very good, as monkeys use the canopy at heights from 5 to 25 m.

We identified individuals by their facial marks and other unique features, distinguishing adults from other age classes by their darker faces and, in the case of males, by their fully descended testes. Data reported here come from 2 different periods, June 1997 to February 1999 (period 1) and August 2009 to June 2010 (period 2). In period 1, we studied 2 different groups: the MX group, which by June 1997 contained 8 female and 2 male adults, plus 9 dependent young (juveniles and infants of the 2 sexes), for a total of 19 individuals; and the EU group, which contained a total of 18 female and 7 male adults, plus 13 dependent young, for a total of 38 individuals. In period 2, we studied the MX group only, which by August 2009 contained a total of 9 female and 7 male adults, plus 6 dependent young, for a total of 22 individuals. For the remainder of this article, we refer to these 3 data sets as MX1, MX2, and EU.

### Observation Procedure

Observations were performed by G. Ramos-Fernández (period 1), B. Pinacho-Guendulain (period 2), and 4 trained field assistants (both study periods). In both study periods, simultaneous follows consisted of instantaneous scan samples obtained from 2 or 3 subgroups simultaneously, every 20 min for an average of 2.5 h per observation per day. We sampled all daily hours equally in both study periods. In each sample, we noted the identity and location of all independently moving individuals, i.e., all age classes except for infants, as well as their activity and position with respect to landmark trees or paths located  $\leq 30$  m from the closest individual in the subgroup. We mapped these landmark trees and paths using a GPS ( $\pm 7$  m accuracy, on average). Only during period 2, we also performed focal observations, so the position of the subgroup corresponds to the position of a focal individual, obtained by placing the GPS directly below it. During this period, we followed a given pair of focal individuals for up to 6 h in a given day, and distributed observations equally among all adults in the group. During this period, the majority of observed subgroups were composed of several females with infants (41% of observations) and of males and several females with infants (33% of observations). Other subgroups consisted of lone females (14%), several adult males (6%), lone males or estrous females (4%), and several estrous females with males (2%).

We defined a subgroup using a chain rule of 30 m; i.e., we considered all individuals  $\leq 30$  m of every other as part of the same subgroup and therefore in association for a particular instantaneous sample. We derived the cutoff distance of 30 m for the chain rule by choosing, at the beginning of the study, 1 adult monkey and noting its distance to all other individuals within a 200 m radius. We repeated this procedure 5 times and selected a cutoff as the shortest distance at which the distribution of the number of individuals with respect to distance showed a steep decline. We employed this operational definition of subgroup throughout the study as it proved to be consistent with the tendencies of individuals in a subgroup to travel together and to coordinate their activities (Ramos-Fernandez 2005).

We obtained a total of 1212 pairs of simultaneous scan samples for the MX group (275 pairs in period 1 and 937 in period 2) and 305 for the EU group (period 1 only). Thus, the sample size  $N$  for the MX1, MX2, and EU data sets is 275, 937, and 305, respectively. Field observations complied with the relevant laws in Mexico.

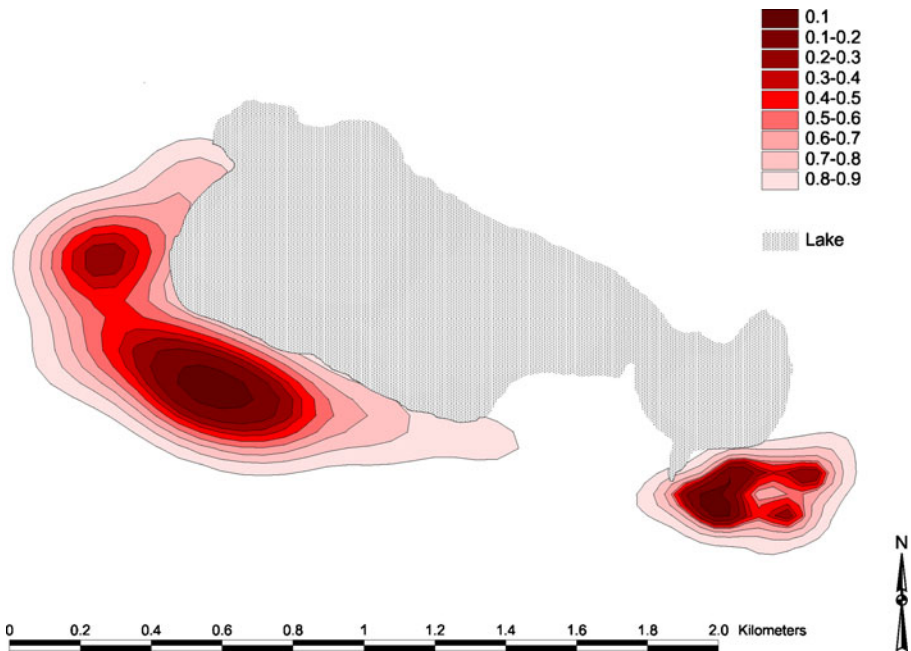
## Data Analysis

We measured the distance between subgroups using the UTM coordinates of either the subgroups' position (period 1: using the coordinates of the closest landmark) or the focal individuals' position (period 2: UTM coordinates measured directly with the GPS below the focal subject). Owing to the unequal sample size of the 3 data sets, we used survival curves, i.e., the fraction of distances larger than  $x$  as a function of  $x$ , to represent the frequency distributions of the distance between subgroups.

We calculated association indices for a larger data set, involving both simultaneous and nonsimultaneous scan samples (Ramos-Fernandez *et al.* 2009; Pinacho-Guendulain in preparation) using the number of samples in which two individuals were seen together, divided by the sum of the number of samples where each was observed without the other and the number of samples they were seen together (simple ratio association index: Cairns and Schwager 1987).

To estimate the intensity of use of different areas within the home range, we fed the locations from the simultaneous follows into the kernel density estimation procedure available in the Home Range Extension for ArcView 3.1 (Rodgers *et al.* 2007). We used all locations from the simultaneous follows, in spite of the temporal autocorrelation that could have existed in the positions, following the suggestion by De Solla *et al.* (1999) that as long as the time intervals between subsequent positions are maintained relatively constant, the temporal autocorrelation should not affect the validity of kernel density estimation. Briefly stated, this method (Worton 1989) places a probability density distribution, i.e. a kernel, around each observation point and for each point in the plane adds the value of the individual kernels present. The kernels' shape is determined by a smoothing factor, estimated by the software through the *href* procedure, which takes into account the variances in the  $x$  and  $y$  coordinates of the locational data. We chose *href* instead of other alternatives such as least-squares cross validation (LSCV) because for large data sets that contain multiple observations in identical or nearby locations, such as ours, the LSCV method produces overly small values of the smoothing factor, underestimating the true home range (De Solla *et al.* 1999, pp. 224; Hemson *et al.* 2005, pp.460; Kie *et al.* 2010, pp. 2223). The *href* procedure determined the following values of the smoothing factor, for the MX1, MX2, and EU data sets, respectively: 0.325, 0.291, and 0.386.

The output of a kernel estimation of space use is a set of contours, each of which defines an area inside which the monkeys can be found with some known probability, given the set of points where they were observed. In this case, we obtained 9 contours corresponding to 0.1–0.9 probabilities, in increments of 0.1 (Fig. 1). Because external probability contours actually contain the internal ones, the outermost contour (0.9) represents the total area where it is most likely to find the subgroups, the next most internal one represents a 0.8 probability, and so on. Because of the increments of 0.1 from one contour to the next one, each of the



**Fig. 1** Results of the kernel analysis of space use for the EU (left) and MX1 (lower right) data sets. The different shades of gray correspond to areas with a given probability of finding the monkeys, given the set of locations where they were observed. Each ring corresponds to the area where this probability increases by 0.1, from the innermost (darker) to the outermost (lighter) ring. Therefore, the probability to find a subgroup in a ring of a given color is 0.1. The results for the MX2 data set are not shown due to the high overlap of the resulting area with those of the MX1 data set.

colored rings in Fig. 1, in between two successive probability contours, also corresponds to that area where there is a 0.1 probability of finding a subgroup. In the analyses, we ignored the remaining positions located outside the 90% contour.

### Null Model Construction

The null hypothesis assumed that the positions of any pair of subgroups were spatially independent, or did not correlate to each other. Specifically, given two subgroups A and B with identical patterns of space use (described by an equal, a priori nonuniform probability of being found at a given location), the position of A at any given moment has no effect on the position of B, and vice versa. In other words, at a single time, ignoring the position of subgroup B and knowing the position of A does not bring any additional information on where B might be. Such independence does not mean that temporal autocorrelations are absent; however, the position of a given subgroup is generally a variable autocorrelated in time, as is the distance between 2 subgroups with known positions. A simple example to illustrate this temporal autocorrelation is the case of 2 random walks in a bounded domain. Although these 2 walks represent by definition 2 independent sets of movement decisions, the distance between them correlates temporally: if both walkers are seen close to each other at a given time, they will probably still be close after a small time increment, but these correlations eventually decay after a large number of movement

steps. In general, if 2 subgroups, which do not need to be random walkers and may take movement decisions using more or less sophisticated cognitive skills, are independent, the frequency distribution of intersubgroup distances, aggregated over a long time period, i.e. several months, will be indistinguishable from that given by pairs of points randomly and independently chosen according to the probabilities determined by the rings in Fig. 1.

Before describing this procedure, we make the following comment regarding the sampling rate. The intersubgroup distance distribution, if it is stationary, is independent of the sampling rate and thus each distance, instead of being measured every 20 min, could also be determined from a pair of positions well separated in time from the previous pair, so that successive pairs are temporally uncorrelated. Provided that the data collection period is long enough, a stationary frequency distribution does not depend on the temporal autocorrelations in the data. Hence, the model picks a pair of positions independently from the previous pair, which mimics a low sampling rate, i.e., the time interval between measurements is larger than the time over which autocorrelations decay. What makes ours a null model of independent travel is the key assumption that the *same-time* positions are independent, i.e., do not spatially correlate. The present model has no tuning parameters because it only requires the knowledge of probability contours.

Using the multiagent platform Netlogo (version 4.1.2; Wilensky 1999), we grouped all points (pixels) of a given ring (color) of Fig. 1 into the same category. To obtain a first position, we chose 1 of the 9 categories at random (because they are equiprobable) and then randomly selected a point inside that category. Then we repeated the procedure for the second position, choosing 1 of the 9 categories at random again and selecting at random a point inside that category. We measured the Euclidean distance between these 2 independently selected points. The scale was 30.5 pixels for 100 m. This selection process was repeated for 100,000 independent pairs for each set of probability contours (EU, MX1, and MX2), leading to the predicted average survival curve of separation distances for each data set.

In the aforementioned procedure, although all rings (categories) are chosen with equal probability, the points belonging to a ring of smaller area are chosen (occupied) more often on average. Therefore, the model reproduces the nonuniform probability of presence in the home range. To evaluate the importance of the internal structure of these probability contours on the separation distances, we compared the aforementioned prediction with what would be obtained assuming independent movements, as earlier, but with a uniform use of space. For this purpose, we chose the points randomly inside the 90% contour (the outermost in Fig. 1) assuming that any point could be selected with equal probability and thus ignoring the structure of the internal contours. Similarly, we obtained an average survival curve in this case for each set of probability contours from 100,000 pairs.

### Statistical Tests

We determined 2-tailed 95% confidence intervals (CI) of the theoretical survival curves by randomly generating a large number (10,000) of data sets with each of the 2 variants of the model (nonuniform and uniform space use), every set containing the same number of distances  $N$  as the corresponding observational data set. We

determined the survival curve of each generated set, and therefore obtained 10,000 values (at a given distance  $x$ ) for the fraction of pairs with distances larger than  $x$ . At fixed  $x$ , we eliminated the 2.5% highest and 2.5% lowest values, yielding the confidence interval of the survival probability at that  $x$ . We repeated this procedure varying  $x$ , giving the CI curves (Frey 2009).

We also determined the  $p$ -value for each model using the Kolmogorov-Smirnov (KS) statistic, defined as the maximum absolute difference between 2 survival curves as  $x$  is varied (Clauset *et al.* 2009). We defined the  $p$ -value as the proportion of generated data sets with a difference to the average curve larger than the difference between the empirical data and the average curve (high values of  $p$  indicate that the model can explain the observations). As evident in the results, a low  $p$ -value does not necessarily call for rejecting a model; however, more information on its goodness can be gained by evaluating the fraction of the observed curve that falls between the CI curves.

The simultaneous follows that produced the MX2 data set contain information on the exact position of 1 focal adult monkey that was followed in each subgroup. To explore the distance between focal individuals in this data set, we used a Mantel test with 10,000 permutations to compare the distance matrix with a distance in which 3 different ordinal values were assigned to each dyad type (female–female, female–male, and male–male). We also used a Mantel test with the same number of permutations to explore the association between the matrix of interindividual distances and the matrix of association indices.

## Results

Figure 2 shows the box plots of the distance between subgroups for the 3 data sets analyzed (MX1, MX2, and EU). Although 10 years passed between the first and second study periods, subgroups in the MX group remained at a remarkably similar distance (mean  $\pm$  SD, MX1: 183.39 $\pm$ 110.42 m, MX2: 178.39 $\pm$ 103.3 m). Subgroups in the EU group were at a significantly larger distance than those in MX (EU: 373.21 $\pm$ 214.53 m; Welch ANOVA for unequal variances:  $F=117.46$ ;  $p<0.0001$ ; Tukey HSD test: MX1 vs. MX2,  $p>0.5$ ; MX1 vs. EU,  $p<0.0001$ ; MX2 vs. EU,  $p<0.0001$ ).

**Fig. 2** Box plot showing the range, upper and lower quartiles, and medians for the distance between subgroups in the 3 data sets.

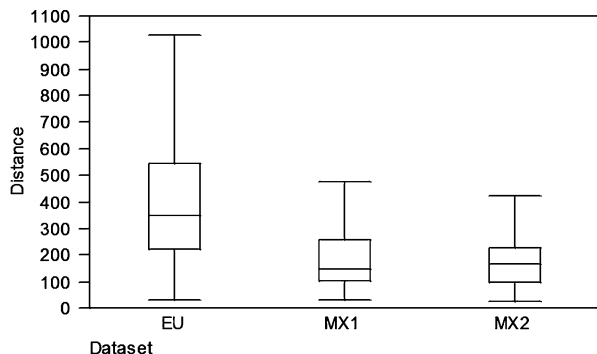
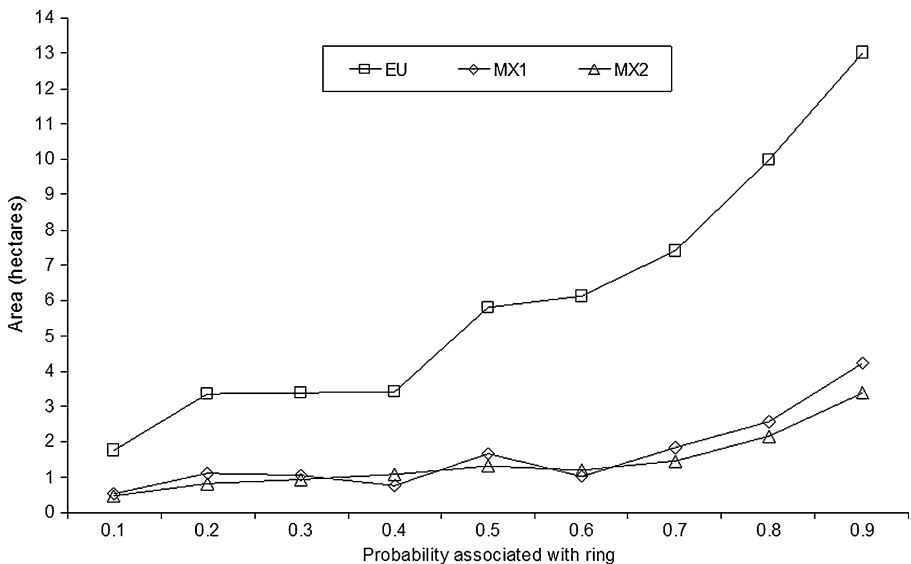


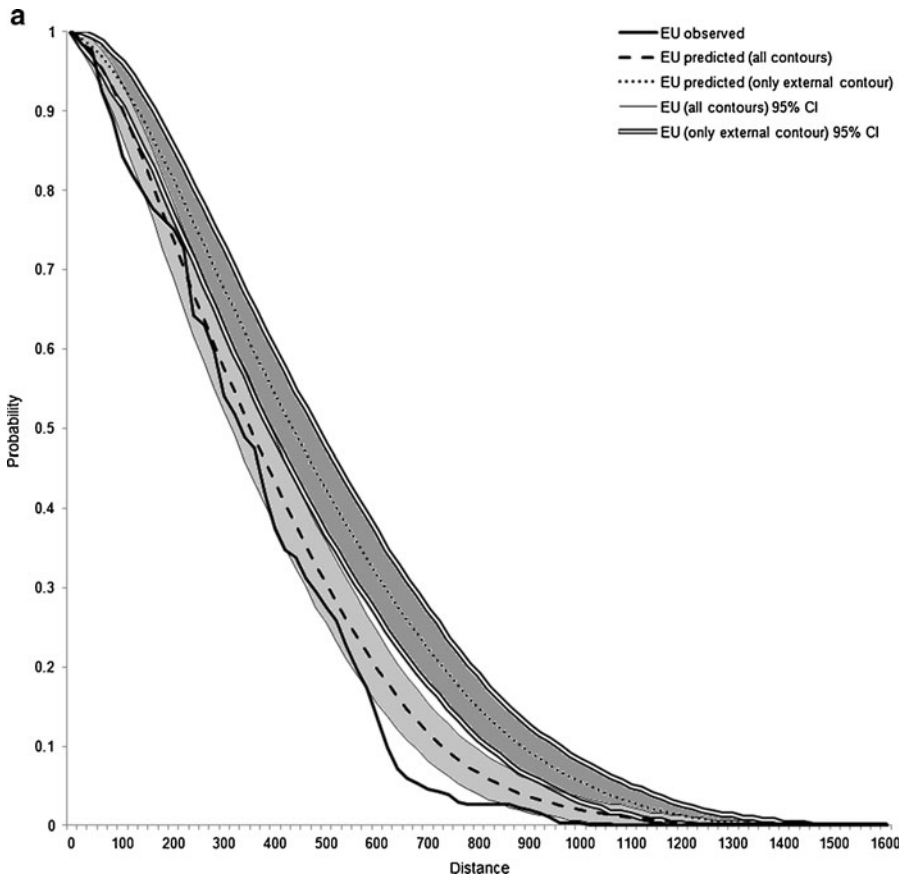


Figure 1 shows the contours generated by the kernel method (Worton 1989, 1995), corresponding to a 0.1–0.9 probability of finding the subgroups in each data set. Each visible area in Fig. 1 corresponds to an increment of 0.1 in the probability of finding the subgroups, from the internal to the external areas. Figure 3 shows the area corresponding to each probability ring, i.e., the areas delimited by 2 successive contours, in the 3 data sets. The more external rings are larger and thus used less intensively by the monkeys, i.e., it is equally likely to find the monkeys in these larger areas as in the more internal and smaller rings. Because contours actually include one another, the total sum of the areas covered by each ring corresponds to the total area enclosed by the 0.9 (outer) contour, i.e., 54.9, 14.7, and 12.8 ha for the EU, MX1, and MX2 data sets, respectively. This could be considered the home range, as estimated from the sets of simultaneous observations.

Figure 4 shows the survival frequency distribution of the distances between subgroups as generated by the models and in the field observations, for each of the 3 data sets. A great extent of the observed distributions falls within the confidence intervals for the distribution predicted by the null model that takes into account a heterogeneous use of space. Based on the fact that the confidence intervals of the model include the observed distribution for most of the distance ranges, we can conclude that the model constitutes a good description of the data. However, the 3 data sets differ in how well the observations agree with the model. The agreement is particularly good for MX2, where the KS test gives  $p=0.25$ . For MX1, 93% of the observed curve lies within the CIs, which is also a good agreement. This data set has a lower  $p$ -value, however ( $p=0.02$ ). The most noticeable discrepancy in MX1 is a slight overestimation by the predicted survival curve in the range 120–160 m, which is sufficient to produce a low  $p$ -value. In the case of EU, the hypothesis of independent travel works very well up to distances of 600 m. Only the distances



**Fig. 3** Area of the different rings as a function of their probability, for each of the 3 data sets: MX1, MX2, EU.



**Fig. 4** Survival distribution curves for the observed distances between subgroups (solid lines) and those predicted by the null model that selected points using all probability contours in Fig. 3 (dashed lines) or only the external one in Fig. 3 (dotted lines). Shadings around the predicted curves correspond to 95% confidence intervals. **a** EU data set. **b** MX1 data set. **c** MX2 data set.

between subgroups  $>600$  m are much less numerous than what the model predicts, also leading to a low  $p$ -value ( $p < 0.0001$ ).

Overall, the results show that the null model provides a consistent description of most of the data. In contrast, the model in which distances were drawn by assuming no internal probability contours showed a poor agreement with the data, given that the overlap between the observed curve and the confidence intervals of that model was close to 0% in all 3 cases (in addition, the KS test gave  $p < 0.0001$ ). We base our conclusions mainly on the confidence intervals and not on the KS tests, which do not detect regions of good agreement and can give low values only due to a particular distance range at which the model is inconsistent with the data.

When we analyzed the distances for particular dyads of focal individuals that were in different subgroups, we found that female–female dyads were separated by a mean distance of  $161.9 \text{ m} \pm 68.2 \text{ SD}$  ( $N=23$ ), female–male dyads by  $188.58 \text{ m} \pm 71.8 \text{ SD}$  ( $N=19$ ), and the only male–male dyad studied by 203 m. Members of different dyad types remained at a similar distance (Mantel test,  $r=0.208$ , 2-sided  $p > 0.3$ ) and

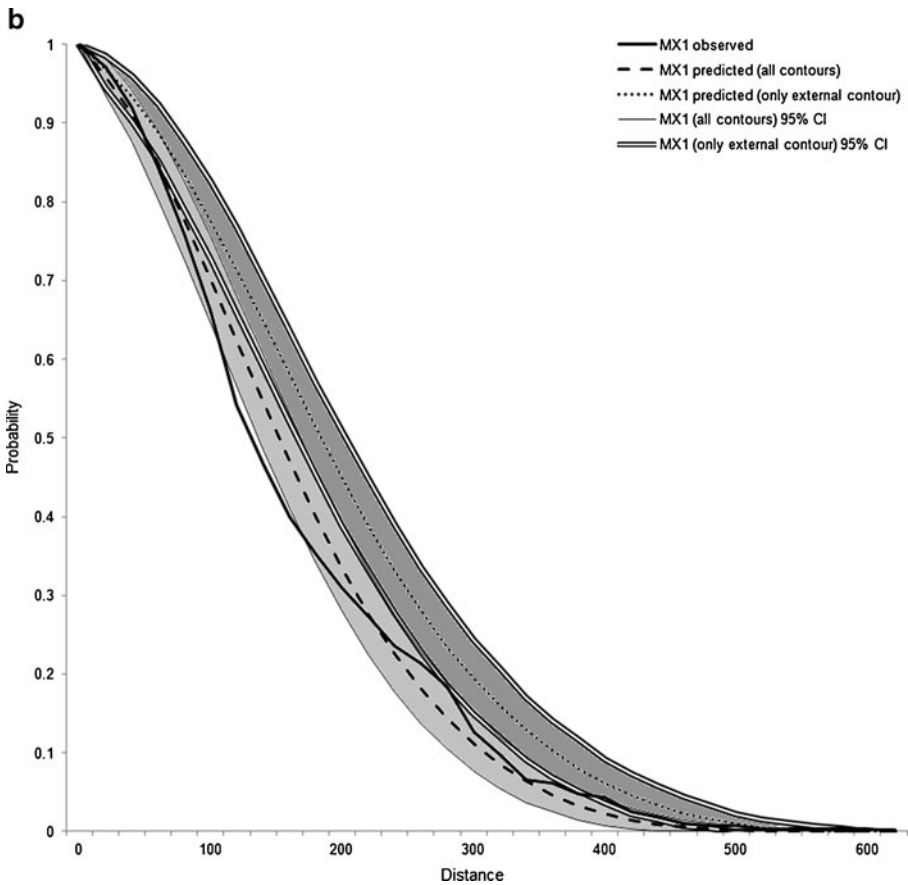


Fig. 4 (continued).

the association index between the different dyads does not significantly correlate with the average distance at which their members remained (Mantel test,  $r=-0.163$ ,  $p>0.4$ ).

## Discussion

We have found that the distribution of distances between different spider monkey subgroups is practically indistinguishable, particularly at short-to-intermediate distances, from that predicted by a null model of independent use of space. We constructed our model by drawing space use contours with the same locations used to measure the distances between subgroups, but ignoring the fact that those locations came from simultaneous follows of 2 subgroups. By selecting pairs of points at random within those contours, giving more weight to those areas in which subgroups spent more time, we have considered the fact that habitat use by spider monkeys is not homogeneous (Shimooka 2005; Wallace 2008). Thus, the distance between pairs of points in the model corresponds to that which would separate 2

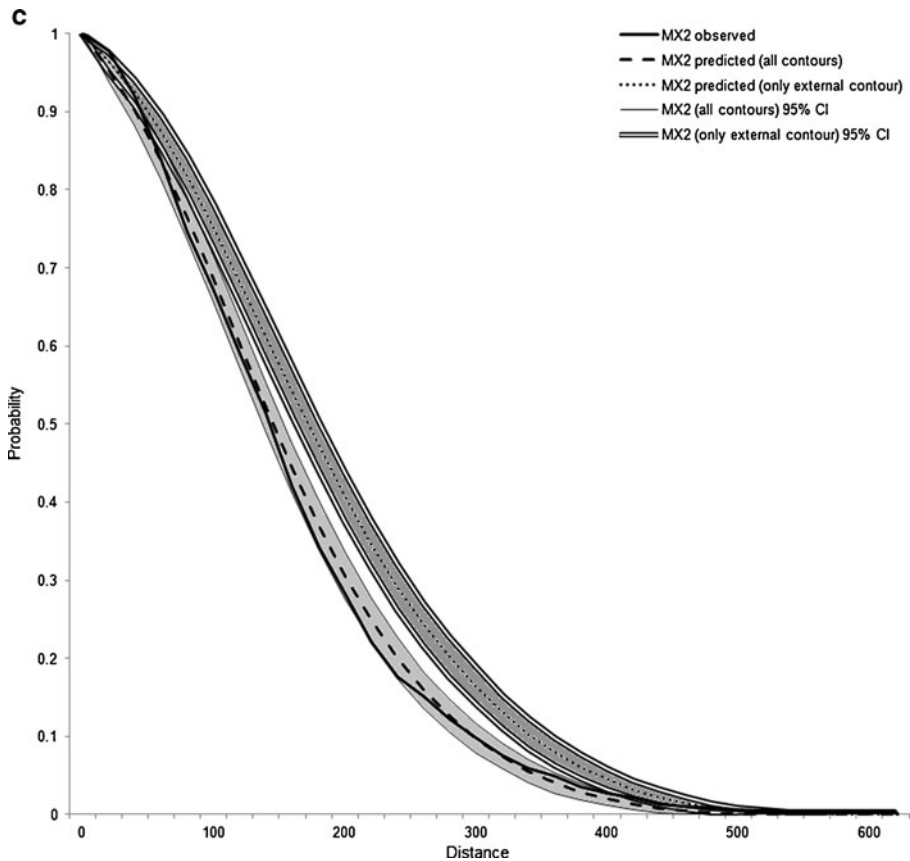


Fig. 4 (continued).

subgroups if their travel routes covered space as in the real observations but were independent from each other.

Our approach is similar to the gas model Waser (1976) used to explore the frequency of intergroup encounters in gray-cheeked mangabeys (*Cercocebus albigena*), and the subsequent iteration of that approach by Barrett and Lowen (1998). In the original study by Waser (1976), a null model of random movement, consisting of a Brownian random walk, was used to generate a prediction about the frequency of encounters between moving particles and their mean square displacement after a given number of steps. Because mangabey groups moved less than what the model predicted, the author concluded that there existed some kind of site attachment process. Similarly, because the observed frequency of intergroup encounters was lower than that predicted by the model, Waser (1976) concluded that groups avoided each other. Barrett and Lowen (1998) modified the previous study by introducing boundaries in the model, which produced lower net displacements and lower encounters between independently traveling groups. This study concluded that in both Waser (1976) original data and the authors' own data from a different study population, mangabey movement patterns were as expected from the random walk model (*cf.* Hutchinson and Waser 2007). In contrast to the gas model approach,

however, the test of coordination between moving subgroups that we have adopted here has the double advantage of not requiring an explicit movement model, e.g., a Brownian random walk, and of incorporating the observed heterogeneous occupation of space of the subgroups. Had we not incorporated this heterogeneity in the use of space and simply measured the distance between randomly chosen pairs of points inside the domain bounded by the 0.9 contour, for instance, the model would have predicted significantly larger distances between subgroups.

Our finding of independent travel by different subgroups is consistent with the results of the analysis of the possible effect of some social factors on the distances between individuals in different subgroups. We found no effect of the type of dyad (female–female vs. female–male), which suggests that the mutual avoidance shown by females and males (Ramos-Fernandez *et al.* 2009) is not reflected in their relative travel patterns. Nor did we find a significant effect of the association index on the distance between individuals when in different subgroups. This suggests that there is no mechanism for intersubgroup coordination that allows dyads with higher association indices to remain closer than those with lower associations.

The 2 study groups differed in several important aspects: the EU group was larger and used a larger area than the MX group. Accordingly, we found subgroups in EU at a significantly longer distance from each other. However, we found similar patterns of independent travel in both groups. A possible exception is the distances >600 m in the EU group, for which the observations are less frequent than predicted by the model. Thus, we cannot exclude that EU subgroups coordinate their movements in some way at large scales not to move too far away from each other.

If spider monkeys were using some mechanism of coordination that was dependent on a maximum distance between subgroups, we would expect to find stronger evidence for coordinated travel in the MX group, simply because of the shorter distances at which subgroups were found, vs. those in the EU group. In a study on vocal communication using the same study groups, Ramos-Fernandez (2005) proposed that whinnies, the most common vocalization in spider monkeys, could serve to maintain individuals in contact when in different subgroups, based on 2 sources of evidence: 1) whinnies were exchanged between individuals in different subgroups; and 2) pairs of subgroups that traveled within the active space of whinnies, i.e., 300 m, tended to approach each other more than pairs of subgroups that were separated by longer distances, at which whinnies were assumed not to be perceived by spider monkeys. In the present work, we used the entire frequency distribution of distances between subgroups. For the MX2 data set, it seems clear that subgroups do not appear to coordinate their relative distances at any distance range, while the other 2 data sets showed deviations from the predicted distances at some distance ranges, thus lowering the *p* value when comparing the observations with the model. However, given that these deviations did not occur at the shorter distance range, i.e., <120 m, they do not necessarily suggest that a call that travels for a maximum of 300 m would be involved in the decrease of the distances in the observations compared to the model.

Long-distance communication, i.e., occurring over >1 km, could be playing a role in maintaining individuals in different subgroups aware of each other's location. This is suggested by the fact that spider monkeys respond to whinnies when in different subgroups (Ramos-Fernandez 2005), but also by the existence

of long-distance screams, given mainly by males at dusk, when already in their sleeping tree (Eisenberg 1976; Ramos-Fernandez 2008). These screams can be heard over long distances and be followed by whinnies emitted by several individuals in different subgroups (Ramos-Fernandez, *pers. obs.*). It is possible that spider monkeys use long-distance vocal signals to stay in touch with close associates when in different subgroups, but that they seldom do something about it immediately. In other words, by using these signals they can find out who is around, and may even find close associates when they did not know their whereabouts. Spider monkeys range in a well known area, as is suggested by the fact that the location of the MX home range changed little in the course of 10 years (Wallace 2008). Individuals in different subgroups may simply rely on this passive form of coordination, counting on the fact that their associates are somewhere around and maintaining contact through the use of periodical vocal signals. This form of coordination could explain the fewer distances at which subgroups in the EU group remained for the  $\geq 600$  m distance range vs. the model predictions. The apparent absence of coordination between different subgroups at relatively short distances, however, could also imply that encounters between subgroups are somewhat surprising for the monkeys involved. This highlights the importance of those social interactions taking place specifically when 2 subgroups join each other, such as vocal exchanges, grooming, and embraces, believed to reduce tension and avoid escalation of aggression (Aureli and Schaffner 2007).

Spider monkey subgroups may travel independently from each other despite the fact that subgroups in the sample showed clear preferences for certain areas within their home range. The use of preferred sleeping trees or feeding areas and the existence of individual core areas within the group's home range (Shimooka 2005; Symington 1988b), as well as the use of travel routes (Valero and Byrne 2007), suggested to us that perhaps typical distances would separate subgroups, provided they spent a large proportion of their time in these areas. However, the areas highlighted as preferred in Fig. 1 are large enough to contain several preferred sleeping or feeding trees. Moreover, we do not know whether a number of preferred sites or travel routes used at different times by different subgroups would produce dependent or coordinated travel as we define it in this study. Perhaps a more explicit study of the temporal relationships between 2 trajectories (Polansky and Wittmyer 2010) could allow us to explore the coordination on short time scales between individuals when in different subgroups. This approach could be complemented by an agent-based approach such as the one used in Ramos-Fernandez *et al.* (2006), generating independent trajectories when agents share common information or preference for sites or routes.

Low cohesiveness between group members in fission–fusion societies may be a result of the structure of the foraging environment (Ramos-Fernandez *et al.* 2006) and may even be an optimal solution to the problem of exploiting a variable resource base (Asensio *et al.* 2008). In turn, species with low cohesiveness, by virtue of often being out of contact with group members, would require the use of special signals and cognitive processes to resolve uncertainties in their social relationships (Aureli *et al.* 2008; Barrett *et al.* 2003). The results reported here underscore the low cohesiveness of spider monkey grouping patterns and suggest that spider monkeys do not actively coordinate their spatial relationships when traveling in different

subgroups. The mechanisms, cognitive and in terms of social interactions, by which they maintain a social structure in such a loose and flexible grouping pattern remain elusive.

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