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Association networks in spider monkeys (*Ateles geoffroyi*)

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Abstract We use two novel techniques to analyze association patterns in a group of wild spider monkeys (*Ateles geoffroyi*) studied continuously for 8 years. Permutation tests identified association rates higher or lower than chance expectation, indicating active processes of companionship and avoidance as opposed to passive aggregation. Network graphs represented individual adults as nodes and their association rates as weighted edges. Strength and eigenvector centrality (a measure of how strongly linked an individual is to other strongly linked individuals) were used to quantify the particular role of individuals in determining the network's structure. Female–female dyads showed higher association rates than any other type of dyad, but permutation tests revealed that these associations cannot be distinguished from random aggregation. Females formed tightly linked clusters that were stable over time, with the exception of immigrant females who showed little association with any adult in the group. Eigenvector centrality was higher for females than for males. Adult males were associated mostly among them, and although their strength of association with others was lower than that of females, their association rates revealed a process of active companionship. Female–male bonds were weaker than those between same-sex pairs, with the exception of those involving young male adults, who by virtue of their strong connections both with female and male adults, appear as temporary brokers between the female and male clusters of the network. This analytical framework can serve to develop a more complete explanation of social structure in species with high levels of fission–fusion dynamics.

Keywords Social networks · Fission–fusion ·
Spider monkeys · Centrality

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Introduction

Hinde (1976) defined animal social structure as the content, quality, and patterning of social relationships. In doing so, he drew a distinction between two meanings of "social structure". The *surface structure* of a particular animal group is determined from empirical data on social interactions and relationships. This is to be distinguished from the *structure* (in the sense of norm or essential structure) of all groups of a given species, which corresponds to the combined regularities in the content, quality, and patterning

of social relationships across individuals and groups, independent of the particular individuals concerned. The distinction is an important one, for knowledge about the social structure of a given species is dependent upon a series of empirical studies of the surface structure of many groups. Clearly, in order to develop unifying explanations for empirical data, these studies should be carried out under a common analytical framework.

Since Hinde's (1976) seminal paper, much progress has been made in describing the wide variety of structures that can be found among social vertebrates (e.g., primates, Smuts et al. 1987; cetaceans, Mann et al. 2000). However, the application of analytical techniques aimed at uncovering unifying principles for the described societies has lagged behind the accumulation of data (Whitehead 2009). The concept of social dominance (e.g., Bernstein 1981; de Waal 1987) is one of the few general principles that have been demonstrated to govern social relationships in many different animals, particularly primates. But a full explanation of social structure requires concepts and analytical frameworks that consider social interactions and relationships other than those observed in conflict situations. Even Hinde (1976, pp.1) warned primatologists that they should escape from the "strait-jacket" of social dominance.

The fission–fusion dynamics of many animal societies (Aureli et al. 2008) pose a particularly difficult challenge to the description and analysis of social structure (Whitehead 1997). In these societies, members of a large group fission and fuse into smaller subgroups. Spatial cohesion, as well as subgroup size and composition can be widely variable over time, such that recurrent patterns of social interactions among particular dyads can be difficult to observe and quantify. Recently highlighted by Aureli et al. (2008) as one of the hallmarks of fission–fusion dynamics, this "temporal patterning" of social interactions and relationships was considered by Hinde (1976) as one of the essential elements of a species' social structure (cf. Kappeler and van Schaik 2002).

Recently, two different analytical frameworks have been used in studies of species with a high degree of fission–fusion dynamics, showing a promising start toward the development of a more complete explanation of their social structure. One of these is the statistical approach developed by Whitehead (2008). Here, Monte Carlo probabilistic approaches have been used to distinguish random aggregation from active processes of companionship and avoidance. These methods have been used to study groups of marine mammals (Gowans et al. 2001; Owen et al. 2002), as well as bats (Vonhof et al. 2004) and elephants (Wittemyer et al. 2005). The other promising analytical framework is the social network approach, in which recent developments in social network theory (e.g., see review by Newman 2003) have begun to be applied to the analysis of social structure of animal groups (e.g.,

Lusseau and Newman 2004; Croft et al. 2004; Henzi et al. 2009; Krause et al. 2009).

In this paper, we applied the two analytical frameworks outlined above to investigate the social structure of spider monkeys (*Ateles geoffroyi*), a species with a high degree of fission–fusion dynamics. Association data from 8 years of continuous study of one group were used in the analyses. Association patterns have been examined in spider monkeys before (Klein 1972; Fedigan and Baxter 1984; Chapman 1990), but no study has explicitly distinguished observed association rates from null expectation (Whitehead and Dufault 1999). Also, while spider monkey association patterns have been studied using dendrograms and clustering techniques (Chapman 1990), no study has used network graphs and statistics to characterize these patterns.

Methods

Study site and animals

A group of black-handed spider monkeys (*A. geoffroyi*) has been studied continuously since June 1996 in the Otoch Ma'ax Yetel Kooh protected area (5,367 ha), in the Yucatan Peninsula, Mexico (20°38′ N, 87°38′ W, 14 m elevation; Ramos-Fernandez et al. 2003). The area is characterized by seasonally dry tropical climate, with mean annual temperature of about 25°C and mean annual rainfall around 1,500 mm, 70% of which is concentrated between May and October. Most observations occurred within a 200-ha fragment of medium semi-evergreen forest surrounding the Punta Laguna lake (2×0.75 km). This fragment is one of many similar fragments lying within a matrix of secondary successional forest about 30–50 years old (Garcia-Frapolli et al. 2007). Spider monkeys use both of these vegetation types although they spend more than 50% of their daily time and every night in the medium forest.

The study group was habituated to human presence long before the study began. All monkeys were identified by facial marks and other unique features. Adults were defined by their darker faces and sexual maturity (e.g., fully descended testes in the case of males). Juveniles were independently locomoting individuals that had not yet reached adult age. All monkeys could be reliably identified by the end of 1996. Since then, data have been gathered by four trained field assistants and various graduate students, as well as authors GRF, FA, and LV. Data reported here include 8 years (January 1997–December 2004, 4,755 h of observation in total; mean=594, range 337–809 h per year).

The number of adult and juvenile individuals varied from 18 in 1997 to 23 in 2004 due to maturation of young and the immigration of four adult females between 2002 and 2004, as well as disappearances and confirmed deaths (Ramos-

Fernandez et al. 2003; Valero et al. 2006). As 1 year was the maximum interval chosen for the analysis of association patterns (see "Results"), changes in size and composition of the study group are reported for yearly periods (see Table 1). The number of days in which every individual was observed every year varied from 1 to 193 (mean across individuals and years=60.1 days, SD=45.8). Data from individuals observed for fewer than 20 days were discarded for a given year. For reasons that will be clear below, two analyses used data from adults and juveniles (temporal analyses and permutation tests), while association networks were constructed by taking into account adults only.

Definition of association

Data were derived from 20-min instantaneous scan samples taken over periods of 1–8 h while following subgroups. For each sample, the identity and location of all adults and juveniles was noted. A subgroup was defined using a chain rule of 30 m, that is, all individuals within 30 m or less of any other were considered as part of the same subgroup and therefore in association with one another for a particular 20-min sample. The cutoff distance for the chain rule was originally derived by choosing one adult monkey and noting its distance of to all other individuals within a 200-m radius. This procedure was repeated five times, and a cutoff was selected as the shortest distance at which the frequency distribution of the inter-individual distances showed a steep decline (Ramos- Fernandez 2005).

Association indices

For the analysis of dyadic association indices, the 20-min scan data were re-sampled with a period equivalent to a day. Thus, for two individuals to be considered in

association, they had to be observed together in at least one scan sample during a given day. In other words, if individuals A and B were observed in the same subgroup in at least one scan sample during a day, that day counted as an observation of A with B. Conversely, if A and B were not observed together in any scan during the day, but A was observed without B, that day counted as an observation of A without B. Association indices were calculated using the number of days two individuals were seen together divided by the sum of the number of days each was observed without the other and the number of days they were observed together (simple ratio association index: Cairns and Schwager 1987).

The daily sampling period was chosen to highlight those associations that occur frequently (or infrequently) across days. This period is long enough to observe several associations for each dyad, but avoids overestimating the frequency of association between individuals that remain together for several 20-min samples simply because of foraging in the same food patch (Whitehead 1995).

Temporal analyses

The temporal analysis module of the SOCPROG2 software (Whitehead 2009) was used to determine the maximum scale over which to analyze temporal variation in association patterns (or the maximum time lag over which associations appear meaningful). Lagged association rates were calculated for all pairs of juveniles and adults in the study group (see methods in Whitehead 1995). This rate represents the probability that if any two individuals are found together at one point in time, they will be found together again after different lag times. In a group with a constant membership, this probability would be equal to 1, while in a group with members that separate and come together at high rates, this probability would fall exponentially with time lag toward a low value (Whitehead 1995). Juveniles were included in this analysis due to the fact that as they develop, their association with their mother changes over the scale of two or more years (Shimooka et al. 2008).

Lagged association rates were calculated by dividing, for different time lags and summing across all individuals, the observed number of repeat associations (i.e., the number of associates with whom an individual was observed at the beginning and end of a given time lag) over the potential number of repeat associations (i.e., the number of associates with whom an individual could have been observed again after a given time lag if subgroup membership was constant).

Null association rates represent the expected value of lagged association rates under the assumption of no preference for repeating associations among individuals. The calculation of these rates considers the number of associates and the number of observations for each

Table 1 Number of individuals of each age (adults, A; juveniles, J) and sex (females, F; males, M) class in the study group during each year of study

Composition of study group

Year	Age/sex class				
	AF	AM	JF	JM	Total
1997	6	1	7	4	18
1998	7	3	5	3	18
1999	9	4	2	3	18
2000	6	5	6	2	19
2001	6	6	5	2	19
2002	11	6	2	3	22
2003	13	4	2	3	22
2004	13	6	2	2	23

individual, but assigns the identity of its associates randomly (with a probability proportional to the inverse of the group size minus 1). Lagged and null association rates are compared in the same graph. In order to obtain the best displays, lagged and null association rates for lag increments of 1 day were averaged using a moving average window of 3 days. Standard errors were calculated using a jackknife procedure with 400–500 groupings of the data, each time removing one sample from the complete set (Whitehead 1995).

Permutation tests

An explicit way of testing whether association indices differ significantly from what would be expected if each individual was associating with others at random consists in generating random sets of data and comparing the results with the real set. The random set of data is generated by permutations of the original set of data, keeping the number of observations per individual and the total number of individuals with whom each individual was seen the same as in the original set. It is important to note that this procedure can identify which associations, among the many held by a given individual, are more frequent than would be expected by chance, *given his/her tendencies to associate with others*. So, if an individual associates with many individuals at high rates but more or less equally with all, none of these associations will be higher than would be expected by chance. Conversely, fewer associations of similarly high rates of another, less sociable individual will tend to be more significant. In this analysis, both adults and juveniles were included. Because juveniles spend most of their time in the same subgroup as their mother, mother–juvenile associations would tend to be detected as higher than random expectation, thus providing a point of comparison for the associations between adults (see "Results").

Permutation tests were performed using SOCPROG2, with methods described in Bedjer et al. (1998) and modified by Whitehead (1999). Random sets of data were generated in which every individual was in the same number of subgroups and with the same number of associates as in the original data, so that only the identities of the associates were randomly assigned. A total of 1,000 random sets of data were generated, each of which contained 100 "flips". A flip consists of the exchange of individuals A and B between two subgroups: one in which A was present but not B and another where B was present but not A. By permuting randomly chosen pairs of individuals among randomly chosen subgroups in this manner, subgroup size and the total number of observations per individual remain constant in all permuted versions. No more permutations of the original data were necessary as the P values were stabilized at 1,000 permutations with 100 flips each.

A mean association index, its coefficient of variation (CV; standard deviation over the mean) and a cumulative P value were generated for the original and permuted data sets and then used to compare the two data sets. As Whitehead et al. (2005) suggest, when the CV is larger in the original data set than in the permuted sets, even if the mean association index is not different, there is evidence for active companionship (or avoidance) because some dyads might be associating more (or less) than would be expected by chance. Thus, for each dyad, a random expectation of association was generated, which could also be compared to the original using P values that referred to the probability that their association index would have arisen by chance. A two-tailed level of significance of 0.05 was used throughout the tests.

Association networks

In order to obtain graphical representations of the association networks, association indices were used to draw weighted association networks using Netdraw (Borgatti 2002). In these networks, nodes represent individuals and edges (or links) represent association indices. The weight of a link between two nodes was defined as the association index between these two nodes. The width of each link corresponded to the association index value, distinguished in seven categories: 1=close to the mean association index for that year, 7=close to unity. For clarity of presentation, only adult individuals were represented as nodes. Because juveniles spend most of their time in close association with their mother, they tend to associate with others according to her associations, so their inclusion in the network provides little extra information. Also, for clarity, association indices below the mean for each year were not represented as links. Therefore, while some individuals might have had measurable association indices with some of the individuals of the network, if the value of all of these indices was below the mean for the group, the individual was not represented as a node. The "spring embedding" algorithm with node repulsion was used for laying out the nodes' positions (Borgatti 2002).

While the graphical representation of association patterns as a network is mostly a qualitative exercise, in conjunction with the results of the permutation tests and the quantification of network metrics (see below), it is a powerful tool to identify consistent association patterns that may underlie the species' surface social structure.

Association network metrics

The weighted networks that resulted from the association patterns for each year were quantitatively analyzed using the network statistics module of SOCPROG2. In contrast to

the graphical representation of association networks (see above), this analysis considered all association indices among adults, regardless of whether the association index was below or above the mean association index for that year. However, the analysis did consider the weight of edges between nodes (Newman 2004). Again, the exclusion of juveniles in this analysis is due to the fact that they tend to be associated most strongly with their mother (see "Permutation tests" in "Results"), and so, their position in the network is highly dependent on their mother's.

Two metrics related to the structure of the network were estimated for the association networks of each year (Newman 2004). The first one was *strength* or the sum of all association indices of an individual with all other group members. An individual with high strength is associated with many other group members and/or has very high association indices with a few group members. Strength was calculated for each individual considering all his/her associations or only those with a particular sex class (see "Results"). The second network metric was *eigenvector centrality*, which is an individual's component in the first eigenvector of the matrix of association indices. This is a measure of how central an individual is to the network, either by being strongly linked to many others or by being directly linked to highly central individuals.

Results

Lagged association rates

Figure 1 shows the lagged and null association rates for all individuals studied between 1997 and 2004. The probability of finding any given pair of individuals together after ever longer time lags decreases, but does so slowly up to an interval of about 300–400 days, after which this probability decreases much faster. This means that an interval of 300–400 days was a "natural break" in the temporal pattern of associations among spider monkeys and thus was chosen as the maximum time interval to take into account in order to analyze the association patterns in further detail. Therefore, all the following analyses of association patterns were performed on 1-year periods.

Figure 1 also shows that after lags of about 1,100 days (or about 3 years), the probability that two individuals are still associated is indistinguishable from the null probability, in which an association is assumed to be independent of all previous associations.

Permutation tests

Mean association indices of the real and random data did not differ for any of the study years (Table 2). The
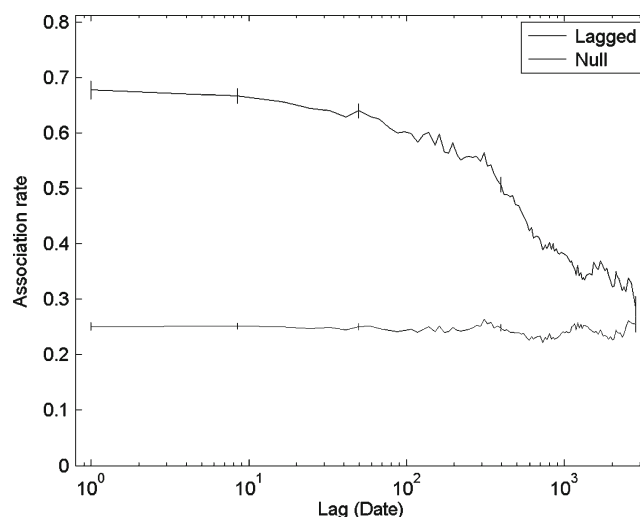

Fig. 1 Lagged and null association rates for all adult and juvenile individuals in the group, in the period 1997–2004. Lags increasing by 1 day were smoothed with a moving average window of 3 days. Error bars correspond to the jackknifed variation estimates, using one sampling unit as the grouping factor

coefficients of variation, however, were higher in the original than in the random set, in all study years. This suggests that some associations were either more or less frequent than would be expected by random association (as indicated by the $P > 0.99$ in all study years; Table 2). However, because the mean association indices and their variances reduce a set of possibly dissimilar dyads to a single average value, they carry limited information (Whitehead 1999). In order to focus on particular dyads, we performed a different analysis.

Over each 1-year period, it is possible to estimate a random expectation of association for every pair, so that it can be compared with the real association index and the probability that this value could have arisen purely by chance can be estimated. This procedure identifies those pairs for which there is evidence for active companionship (with a higher association index than the random expectation) or active avoidance (with a lower association index than the random expectation). Pairs that associated more than would be expected by random association (Table 3) included pairs of adult males (36 times in 8 years, out of the 55 possible pairs, or 65%) and mother–juvenile offspring pairs (36 times in 8 years out of the 71 possible pairs or 51%). Together, these two types of dyad constitute 70.5% of the total number of pairs that had a significantly high association index ($N=102$). Adult females formed significantly high associations only in 11 occasions during the 8 years of study (4% out of the 313 possible pairs). Other significantly high associations included juvenile siblings and, to a lesser extent, other combinations of adults and juveniles.

Pairs that associated less than would be expected by chance (Table 4) included pairs of female and male adults (in 19

Table 2 Mean and coefficient of variation of the association indices obtained for all independently locomoting individuals (adults and juveniles) in each year of study

Year	Permutation test results						Total number of pairs
	Association index (mean±CV)		P values for the CV	Number of pairs with values different from random			
	Observed	Random		Higher	Lower	Total	
1997	0.276±0.785	0.275±0.744	0.999	8	3	11	153
1998	0.369±0.526	0.368±0.499	0.999	15	7	22	153
1999	0.275±0.758	0.276±0.724	0.999	5	0	5	153
2000	0.322±0.653	0.320±0.622	0.999	18	7	25	153
2001	0.318±0.688	0.317±0.648	0.999	20	23	43	171
2002	0.189±1.316	0.188±1.286	0.999	12	3	15	253
2003	0.160±1.144	0.159±1.130	0.999	13	4	17	231
2004	0.191±1.252	0.190±1.246	0.992	11	6	17	253

Shown are the observed values and the values obtained through 1000 permutations of the original data set (see "Methods"). P values indicate the probability that the coefficient of variation is different between the observed and the randomly expected value. Also shown are the total number of pairs that, according to the permutation tests, showed an association that was higher or lower than the association expected by random association and the total number of pairs analyzed in each year

times over the 8 years out of the possible pairs or 6%) and adult males and juveniles (12 times over the 8 years out of the 211 possible pairs or 6%). Together, these two types of dyads constitute 58% of the total number of pairs that had a significantly low association index ($N=53$). Seven pairs of adult females (2% out of the possible pairs) were observed to associate less than would be expected by chance.

Association networks

Association networks for each of the 8 years of study are shown in Fig. 2a–h. We recall that the links shown are only those above the average weight. If all links were repre-

sented, the network would appear much denser and harder to visualize (although the network metrics presented below are calculated with all the links—see below). The general pattern that emerges in these graphs is that of a sex-segregated structure. The network for 2000 (Fig. 2d) shows this more clearly as a clear separation of the sexes in two clusters, a pattern that can be seen in most of the other networks (Fig. 2a shows no males because PA, the only adult male in the group in 1997, was not associated with any adult female with an index that was higher than the mean and therefore was not represented in the diagram).

In addition to the segregation by sex, the networks show that, in general, female–female links are stronger than

Table 3 Number of pairs of individuals from different sex–age classes that, according to the permutation tests, had an association index that was higher than the randomly expected one ($P<0.025$ in all cases)

Year	AM–AM	AF–AF	AF–adult daughter	AF–juv.	AF–AM	Juv–juv	Juv–juv sibs	AM–juv.	Mother–juvenile	Mother–AM	Total
1997								2	6		8
1998	1	1					3	1	8	1	15
1999	1								3	1	5
2000	6		1			1	3		7		18
2001	11		1	1			1		6		20
2002	8								4		12
2003	4	8			1						13
2004	5	2		1	1				2		11
Total	36	11	2	2	2	1	7	3	36	2	102

Juveniles in AF–juv pairs are not the adult female's offspring

AM adult male, *AF* adult female, *juv.* juvenile, *Mother* adult female that is the mother of the other individual in the pair

Table 4 Number of pairs of individuals from different sex–age classes that, according to the permutation tests, had an association index that was lower to the randomly expected one ($P < 0.025$ in all cases)

Juveniles in AF–juv pairs are not the adult female's offspring

AM adult male, *AF* adult female, *juv.* juvenile

Year	Pairs with a value lower than random							
	AM–AM	AF–AF	AF–juv.	AF–AM	Juv–juv	Juv–juv sibs	AM–juv.	Total
1997		1	2					3
1998		2	2	1	1		1	7
1999								
2000		1	2	1	1	1	1	7
2001		1	3	9	1		9	23
2002				2			1	3
2003		1		3				4
2004	2	1		3				6
Total	2	7	9	19	3	1	12	53

male–male links, and these in turn are stronger than mixed sex links. This can be most clearly seen in the network for 2002 (Fig. 2f), where bonds can be classified in three different width classes: those between females were the widest, then those between males and the thinnest were those between females and males. This difference in strength can be shown quantitatively by calculating the strength of each node in the networks (see "Methods"). Figure 3 shows the strength for particular individuals and how it changed in the different years of study. Females had a higher strength than the males and, over the years, more equally distributed among them. The results of the permutation tests (Tables 3 and 4), which had already shown that females are not selective in the identities of their associates, are also consistent with their similar strength values for a given year. In the case of males, the association networks in Fig. 2a–h suggested that their bonds were more variable than those among females, and the permutation tests showed that often they have significantly high association rates with some individuals, particularly other males (Table 3). Accordingly, strength values for individual males (Fig. 3b) although showing somewhat similar patterns over the years, were more variable than those among individual females. Altogether, the analysis of individual strength values (Fig. 3) showed a significant effect of year and sex (two-way ANOVA with year and sex as factors, $F = 16.63$; $P < 0.0001$; type III sum of squares analysis for year, $F = 13.75$, $P < 0.0001$; sex, $F = 53.07$, $P < 0.0001$).

There are some interesting exceptions to the general patterns outlined above. The first results from the process of immigration/emigration by female spider monkeys. In 2003, three new adult females immigrated into the group (KL, KR, and HE). The network for this year (Fig. 2g) shows that these females maintained associations mostly among themselves, with the exception of KL, who associated at equal rates with an adult male and the other

adult females. In this network, four distinct clusters appeared: the immigrating adult females, the resident females (forming the closest associations), the adult males associating more among themselves than with the females, and the emigrating adult females (see below). The initial strength values of the immigrating females, as expected, are lower than the long-term resident females' (Fig. 3), but they also show a substantial increase from the first year to the second year of being in the study group. The fourth cluster included KA and MI, young adult females that emigrated or disappeared from the group the following year. These two females associated less with the rest of the females. Consistent with the fact that the network for this year showed a wider variation in the strength of female–female bonds and therefore a higher degree of selectivity, permutation tests for this year revealed eight adult female pairs as being higher than random expectation (Table 3).

The second exception to the general patterns of sex segregation is the males' transition to adulthood, when they change from being more attached to their mothers and the adult females to associating strongly with some adult males. This can be observed clearly by comparing the network position of DA and BE in 1998 (when they were young adults; Fig. 2b) and their position in subsequent networks (Fig. 2c–h). The same can be said about LI's position in the network in 2001 (Fig. 2e) with the subsequent networks. An analysis of the strength values for five adult males, distinguishing the strength of links to males and the strength of links to females, revealed these patterns in a more quantitative manner (Fig. 4). Each graph corresponds to a male's strength values in each year of study when he was an adult divided by the number of potential association partners of each sex for a given year (the number of adults of each sex class in Table 1 minus one). Weighed in this manner, the values of strength toward males tended to be higher than those of strength toward females, implying that
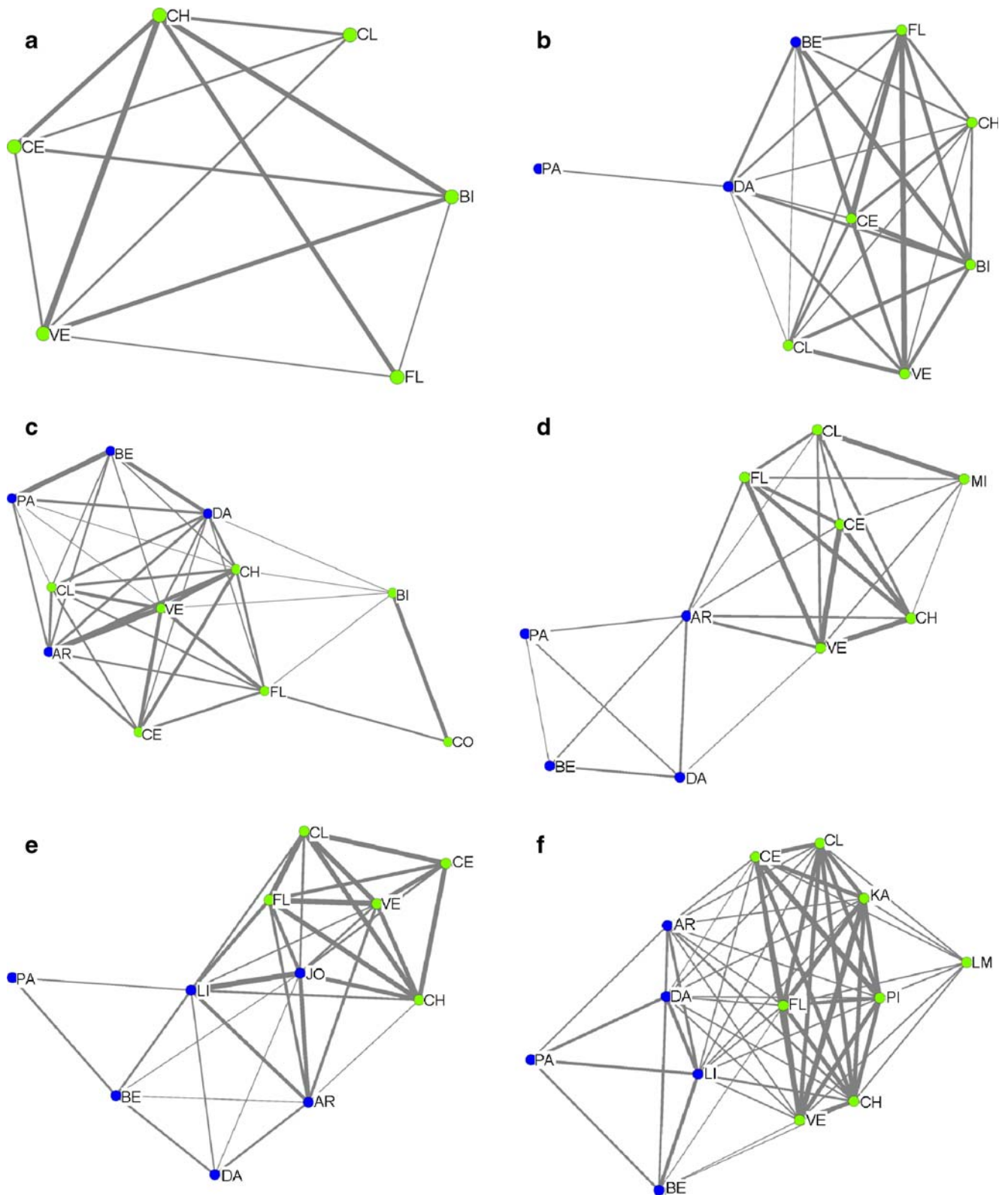
Fig. 2 Diagrams of the association networks among the adults in each year of study (**a–h** correspond to 1997–2004). *Light gray* [or *green*] *circles* represent females, while *darker gray* [or *blue*] represent males. Links vary along seven possible values, depending on the value of the association index between two individuals during the corresponding year (thus, 1= close to the mean value; 7=close to unity). Only association indices larger than or equal to the mean of all observed association indices for each year were drawn. Also, individuals that did not have any link higher than this mean were not represented. For example, in **a**, PA, the only adult male in the group in 1997, was not associated with any adult female with an index that was higher than the mean and thus is not represented in the diagram. Observed mean association indices are in Table 2
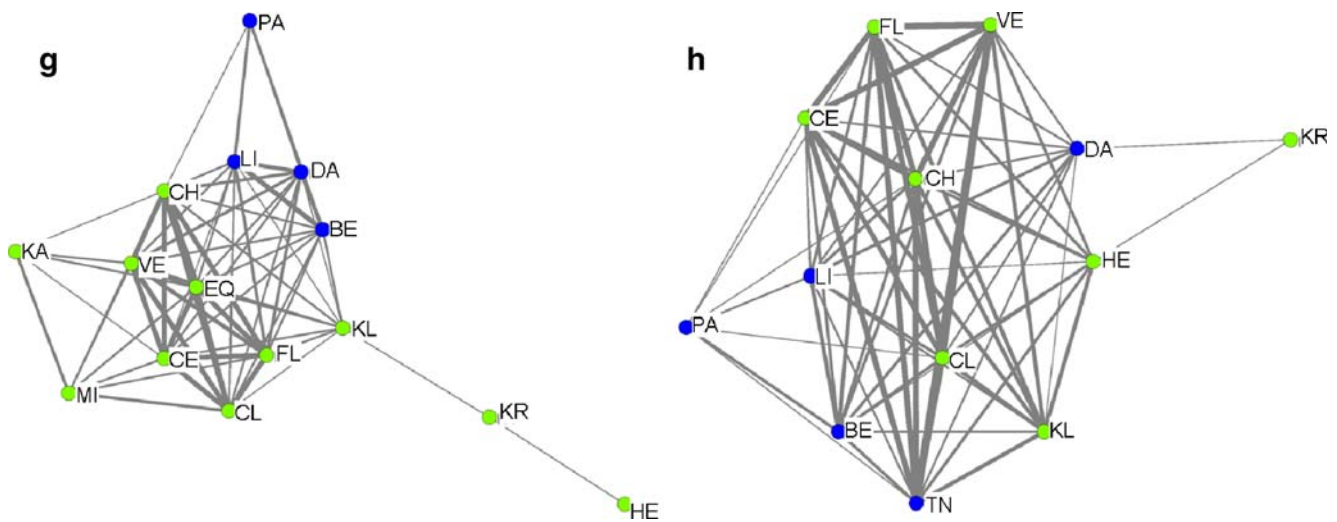
Fig. 2 (continued)

the strength of a given bond from a male to a male was higher than a given bond from a male to a female. What is more interesting, however, is how these values of strength change across time, particularly the opposite tendencies of bonds toward females and males during the males' first 2 years as adults. In three of the four males who became adults during the study period, BE, DA, and LI, the strength of bonds toward females showed a large decrease from the first to the second year, while the strength of their bonds towards males increased. This is a reflection of these males' integration into the male–male alliances and their decreasing tendency to associate with females, particularly with their mother. In the case of PA, the only adult male who was present in the study group in 1997, it is not surprising to observe increasing strength values for the bonds with males during 1998–1999, simply because the number of adult males was increasing too. The same increase in number of association partners explains the apparent increase in BE and DA's strength of association with females toward the end of the study period.

Another network metric that illustrates the role that particular individuals might play in the association network is eigenvector centrality. An individual can have a high eigenvector centrality either because it is strongly linked to many others or because it is directly linked to highly central individuals. Figure 5 shows the eigenvector centrality values for the five adult females who resided as adults in the group for the entire study period, as well as for six adult males observed in at least two consecutive years. Adult females had a higher eigenvector centrality than males (two-way ANOVA with year and sex as factors, $F=13.49$; $P<0.0001$; type III sum of squares analysis for year, $F=2.4$, $P=0.03$; sex, $F=77.78$, $P<0.0001$). Among them, females had quite similar centrality values. In the case of males,

their centrality values decreased as they matured as adults, in a similar way as their strength did (Fig. 4). PA, the oldest adult male, again had the lowest centrality value.

The centrality analysis confirms that females, on the one hand, form a more central cluster in the association networks, being more numerous and more strongly associated with each other than the males (albeit not in a selective manner; see "Permutation tests"). Males, on the other hand, tend to be in the periphery of this central cluster, associating little with females and less strongly with each other. Maturing males seem to fulfill an important role in maintaining the two clusters together, as they switch from being in the more central cluster of females to associating with the other males. For example, in the network for 2000 (Fig. 2d), which shows a clear segregation by sex, it is only through young male AR and, to a lesser extent, DA (AR's elder brother), that many of the males were linked to any female in the network, particularly with VE, the mother of DA and AR. Accordingly, AR's eigenvector centrality for 2000 is the highest among the males in that year (Fig. 5). The same occurs if we compare DA and PA's position in the network in 1998, which is reflected in DA having a much higher eigenvector centrality than PA (Fig. 5). Another young male with a high eigenvector centrality is JO in the network for 2001 (Fig. 2e), where he is strongly bonded to several females (including his mother, CH) and to two adult males (LI and AR). JO's eigenvector centrality for that year was the highest for all males throughout the study period (Fig. 5). Interestingly, JO was killed in early 2004 by a series of coalitionary attacks from PA, BE, and DA (Valero et al. 2006). His strength value (Fig. 3b) and his eigenvector centrality value (Fig. 5) showed a large decrease from 2001 to 2002 (he was not observed often enough for analysis during 2003).
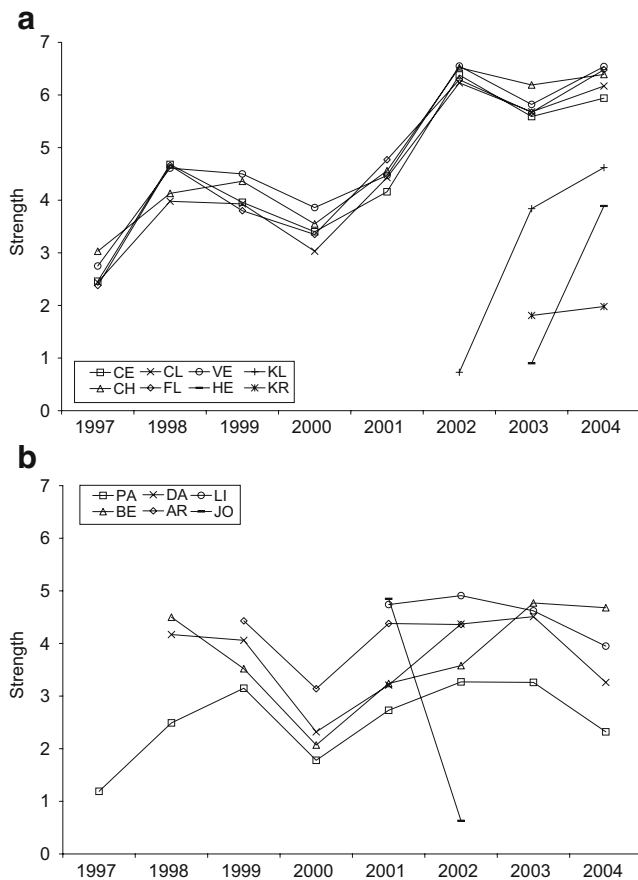
Fig. 3 Strength or the sum of all association indices for each individual in the networks (identified with the same code as in Fig. 2) for each study year. **a** Adult females; **b** adult males. Strength was calculated for all adult individuals in an unfiltered weighted network (as opposed to the networks represented in Fig. 2)

Discussion

We have analyzed association patterns of spider monkeys using two different and complementary methods, permutation tests and social network analysis. The first method allowed us to identify associations that were more or less frequent than random expectation and therefore the result of processes of active companionship and avoidance as opposed to simply random aggregation at feeding or resting areas. The second method allowed us to graphically represent the patterns of association of all group members, thus allowing us to analyze the way in which many dyadic relationships were integrated into a network of individuals. We quantified some aspects of the structure of this network, such as the strength with which individuals were linked to all others and the degree of centrality that each individual had within the network and how these parameters change over time.

In general, results of the association network analysis suggest that it is the adult females that actually form the core of the social network, being more connected to most

other individuals in the network, especially among themselves. The spider monkey social structure has been described as a sex-segregated system (Fedigan and Baxter 1984; Chapman 1990), based principally on the finding that male–male bonds are stronger than female–female or mixed sex bonds, as well as the less gregarious nature of females (Symington 1987; Chapman 1990; Aureli and Schaffner 2008). By focusing on the totality of links in the network and not simply on a comparison between different types of dyads, our results suggest that females, by virtue of their higher and more stable association, are central to the social structure of spider monkeys. The analysis of network metrics confirms that adult females have higher eigenvector centrality values, i.e., they are linked strongly to more individuals who are strongly linked themselves.

However, closer inspection of the association patterns among resident females reveals that even when their association indices are higher overall than those among males, they also show little selectivity in terms of who associates with whom. Results of the permutation tests revealed that females associate with each other more frequently than random expectation only in 4% of all possible cases throughout the 8 years of study (11 pairs; Table 3). Eight of these associations took place in 2003, the year when various females immigrated or emigrated. This shows that immigration and emigration of females had a large effect upon the female–female association patterns.

It is important to note that a high association index value does not necessarily imply that it is more likely than random expectation (Whitehead et al. 2005). The dyadic P values that the permutation tests use to determine whether a pair has a higher or lower association rate than would be expected by random aggregation are sensitive to the degree of selectivity or differentiation of an individual's associations with others. If an individual is strongly linked to many individuals but with more or less the same strength, randomizing its associates will maintain the same association indices with all those associates, such that none of the associations in the original data set will have a significantly high or low P value. On the contrary, if an individual is strongly linked with some individuals but not with others, randomizing the identities of his/her associates will affect the association patterns with those few individuals, which in turn will place a higher P value on the few strong links in the original data set.

Thus, our results suggest that most associations among females cannot be distinguished from what would be expected if they simply aggregated at random, i.e., they do not differentiate between female partners. This suggests that simply by virtue of passively aggregating with other females, they form a distinct and central cluster. One way in which this hypothesis could be further tested is by analyzing, for different individuals, their use of feeding
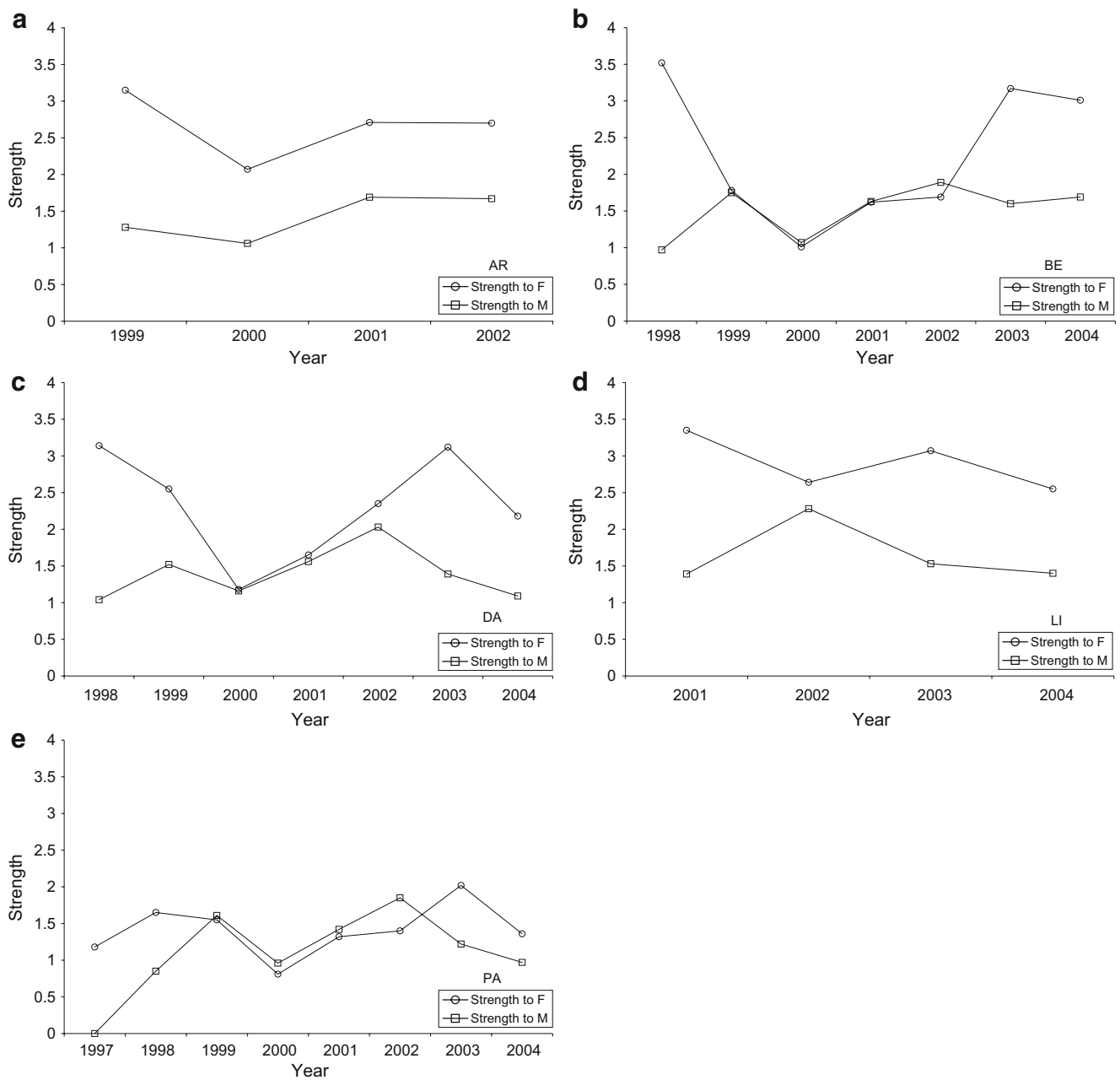
Fig. 4 Strength for adult males, calculated by considering only those associations with adult females or those with adult males, for each study year divided by the number of potential association partners of each sex (number of adults of each sex minus one). Individual males: **a** AR, **b** BE, **c** DA, **d** LI, **e** PA

areas and relating it to their association patterns: If females are passively aggregating at large feeding areas, we would predict that females would associate more with others when these areas were scarce than when they were abundant, as females could disperse over different feeding areas. This prediction is supported by the results of other studies: Henzi et al. (2009), using a network approach similar to the one used here, found that female chacma baboons (*Papio hamadryas ursinus*) associated in tighter and more connected networks when food was scarce than when it

was abundant. Also, Sugardjito et al. (1987) found that orangutans (*Pongo pygmaeus*) formed temporary aggregations in scarce fig trees. Finally, Ramos-Fernandez (2001) used a subset of the observations reported here and found a negative relationship between the size of spider monkey subgroups and the proportion of a hyper-abundant resource in their diet, suggesting that subgroups are partly the result of aggregation at limited feeding areas.

The process of randomly aggregating at feeding or resting areas can produce rich patterns of association, as

Fig. 5 Eigenvector centrality or each individual's component in the eigenvector for the association index matrix for each study year. Shown are the values for the five adult females that were adults in the study group for the duration of the study and for the six adult males who were adults in the study at least two consecutive years. *Continuous lines with full symbols* correspond to females, while *dotted lines with empty symbols* correspond to males. Eigenvector centrality was calculated for all adult individuals in an unfiltered weighted network (as opposed to the networks represented in Fig. 2)
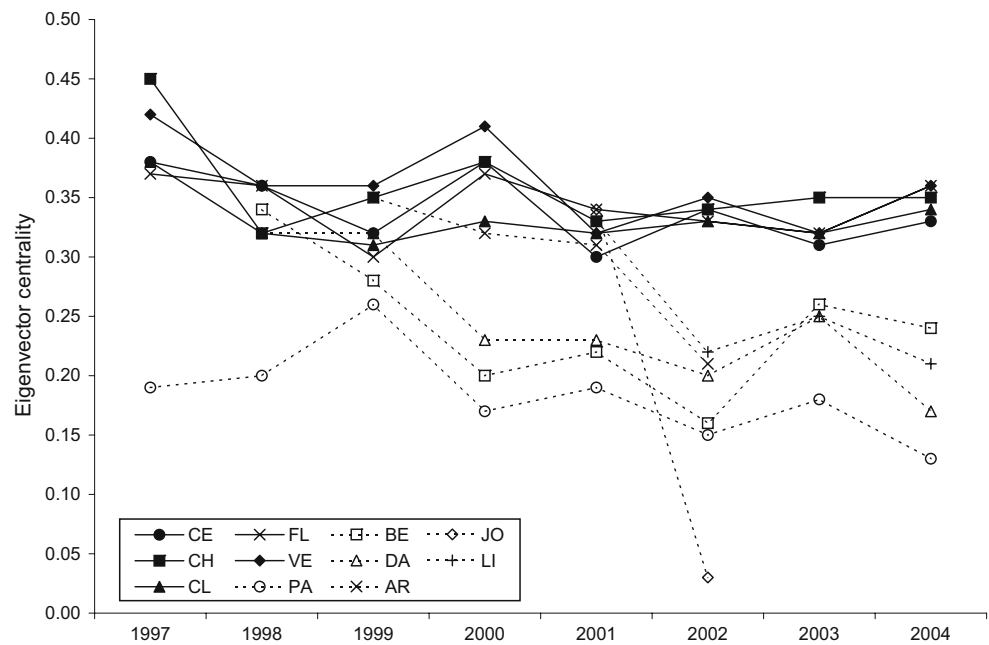
has been demonstrated in an agent-based model by Ramos-Fernandez et al. (2006). In this model, agents forage according to simple efficiency rules in an environment where feeding patches vary in size. By simply coinciding at those feeding patches that are large but neither too scarce nor too abundant, agents in the model (1) formed groups of size that resembled that of spider monkey subgroups, (2) associated more or less with particular others, and (3) formed an association network in which weak and strong links could be distinguished. One may compare the females in this study to one of the clusters of strong links relatively equal in weight produced by the model. The nodes of these clusters are connected through weak links with the rest of the network. Thus, the results reported here, especially for the female–female links, are consistent with a null model of network formation, in which individuals passively aggregate due to ecological reasons and not as a result of the particular social relationships among them. Again, the results by Henzi et al. (2009) suggest that female baboons did not seem to be very selective in their choice of association partners as only a few of the dyads showed significantly high association for two consecutive food scarce seasons.

Adult males, unlike adult females, are peripheral nodes in the network in most years, maintaining close bonds only with a few individuals, mostly among themselves and only with a few females. Male–male social relationships in spider monkeys have been characterized as cooperative (Symington 1987; Chapman 1990). Although the present analysis defines bonds based only on one social interaction (association in the same subgroup), the general pattern that arises is that of strongly bonded males. Permutation tests revealed that a substantial proportion of the male–male

associations is higher than would be expected by chance, thus suggesting that their association patterns are the result of active companionship. Also, the analysis of how strongly linked males are to individuals of different sex (Fig. 4) revealed that, in general, they are indeed more strongly bonded among themselves than to the females.

Another interesting pattern that arises from the present analysis of male association patterns is that the young adult males, just coming out of juvenile age, have stronger associations with females than older males, possibly as a result of their mother's position in the network. As they mature, they become more linked with other adult males than with females. The fact that the eigenvector centrality of these young adult males decreases as they mature is consistent with a switch in their association with the highly connected cluster of females to associating with the less strongly connected cluster of males. This switch in their association patterns is consistent with the known dynamics of social interactions between young adult males and the older males in their group: While initially adult males do not tolerate young adult males, over time, they interact more affiliatively (Aureli and Schaffner 2008; Vick 2008).

Thus, male–male association patterns seem to be the result of a process of active companionship, more than random aggregation, and this is reflected as a distinct cluster in the network in several years. Although this network is less tightly linked than that of females, it contains links that are statistically more significant as they involve fewer individuals that maintain a lower and weaker association strength with the group overall. The process by which new individuals are incorporated into this male–male cluster implies that during certain periods, it is the young adults that appear to play the role of "brokers" between the

female and the male clusters in the network, in a manner akin to the dolphin network studied by Lusseau and Newman (2004).

Compared to males, the only cases in which adult females were peripheral, maintaining close bonds only with a few individuals, was when they were new immigrants. Such is the case of adult females KR, KL, and HE, who immigrated into the MX group in 2002 and 2003. As is clear from the association network from those years, their position in the network is very different from that of the long-term resident adult females. In their first year as immigrants, these females associated equally with males and females and among these showed more selectivity than the resident females. This is consistent with the immigration process described for spider monkeys, in which new immigrant females are more tolerated by resident males than by the females (Aureli and Schaffner 2008; Asensio et al. 2008).

One important caveat regarding the results of this study is that only one group was analyzed. This particular group only had one adult male in 1997, which is uncommon for spider monkeys (Shimooka et al. 2008). As the number of males increased over the years, one male (JO) was killed by the males in his own group, which is also rare for what is known about spider monkey species (Valero et al. 2006). In addition, the total size of the study group increased, from 18 individuals in 1997 to 23 in 2004. This may be due to the fact that during this time, the spider monkey population was in a period of recovery from habitat disturbances, as the vegetation at the study site has been subject to periodical fires, both accidental and induced, over the past 30 years (Garcia-Frapolli et al. 2007). Whether these circumstances produce an "unrepresentative" surface social structure can only be determined with more studies on the same species in similar and different habitats. In such studies, use of the same analytical framework would help to determine the actual regularities that constitute the social structure of the species.

Another important caveat is that, as mentioned earlier, this study used association in the same subgroup as the only dimension for links nodes in the network. Thus, the association networks cannot be considered the equivalent of social structure, even in the sense of the "surface" social structure coined by Hinde (1976). This is because a social relationship (i.e., a link between two nodes of the network, if it were equivalent of the social structure) is supposed to be the long-term pattern of all the meaningful social interactions between two individuals. When studying animals in which a detailed description of social interaction is difficult, it is assumed that association patterns (in the case of spider monkeys, being in the same subgroup) are a proxy for social interactions (Whitehead and Dufault 1999). Of course, a more thorough description and analysis of

social structure would require that we used multiple dimensions of social interaction between pairs of individuals (e.g., rates of grooming, embraces, aggression, and coalitions). In that case, the network would be a more accurate representation of Hinde's (1976) surface social structure. However, social interactions such as grooming, aggression, and coalition occur at very low rates in spider monkeys compared to other primate species, particularly among females (Symington 1987; Slater et al. 2007). This makes it difficult to obtain sufficient data for each year in order to complement the association networks presented here. But, the fact alone that these social interactions occur so infrequently, at least among the females, supports the interpretation that their association patterns are mostly the result of simple aggregation.

The weighted network approach considered here (Newman 2004) takes advantage of the fact that association indices, in themselves, contain information not only about whether two individuals are associated or not but also about the strength with which they are associated. If we were to simplify the networks by turning them into binary networks, with links that appear or not depending on some threshold in the association indices, we would be losing a lot of information about the actual association between individuals. The network for 2002 (Fig. 2f), for example, is a case in which the weight of the edges, in addition to their presence linking different individuals, provided important information on the association patterns. In this network, the links can clearly be classified in three categories according to their weight, which also coincides with the sex class of the pairs of nodes that they link: The highest links are those between two females, then the links between males, and finally the links between females and males. In this context, the recommendation by James et al. (2009), that in order to remove the effects of random processes of aggregation, binary networks should be filtered before being analyzed, is less important. This is because in a binary network, the decision on whether to draw a link or not is a more crucial one than the decision on whether to leave out a weighted link or not. In a weighted network, weak links contribute less than strong links to metrics such as those used here. Note that in this study, links were filtered out only for the purposes of graphical representation, using the average association index as a threshold below which links would not be represented, but when measuring strength and centrality, all links were considered.

One of the main applications of network theory has been on understanding and predicting how information flows between the nodes of a network by virtue of being linked to one another in a complex way (reviewed in Newman 2003; Krause et al. 2009). In the case of a network of animals with a high degree of fission–fusion dynamics, the structure of the association network may have important consequences for the way in

which information flows among individuals that are seldom together, but that still require to have common knowledge about their surroundings (food and shelter as the most important). The association networks studied here show that through weak links, most individuals belong to one "giant cluster", i.e., even if some pairs have a null association index, they are nevertheless linked to every node in the network through indirect paths that include other pairs of individuals showing some degree of association. This "strength of weak ties" (Granovetter 1973) may allow information about the social and ecological environments to be shared easily while at the same time maintaining the flexibility in grouping patterns that seems to be necessary for foraging successfully in these environments.

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