

Social Networks Predict Group Fission, with Implications for the Management of Northern Muriquis (*Brachyteles hypoxanthus*)

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Abstract: The size and composition of primate groups affect dispersal and reproductive opportunities, and thus have implications for the conservation and management of endangered species. Group fissions that increase dispersal options can reduce close inbreeding, particularly in small, isolated populations that are candidates for translocation and other forms of management. While the impact of group size on permanent group fissions has been well documented in matrilineal societies, less is known about the process of permanent fission in patrilineal primates. Here, we use social network analyses of four years of scan-sample data (2011–2014) to retrospectively investigate whether membership in a newly fissioned group of northern muriquis (*Brachyteles hypoxanthus*) at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala, Caratinga, Minas Gerais, Brazil, could be predicted from prior social relationships. Modularity metrics indicated the start of the Matão group fission during the 2012–2013 mating season, with a distinct subgroup of individuals that formed the new Nancys group being evident. Dyadic associations were significantly stronger and eigenvector centrality values were significantly higher among the individuals that formed the Nancys group than among those that remained in the Matão group. One mother and her four adult sons were among the founders of the Nancys group, but other mother-adult son families did not fission together. Our analyses add to the literature on permanent fissions in patrilineal societies. They also suggest that the modularity metric of social network analyses can be useful in identifying the best timing for implementing management programs that take social preferences into account. Such considerations can contribute to informed decisions about translocations, reintroductions, and the rehabilitation of groups or subgroups in the conservation management of endangered primates such as muriquis.

Key words: Social network analysis, patrilineal primates, conservation management, translocation, reintroduction

Introduction

Wildlife conservation management often focuses on protecting habitat and connecting fragmented areas. However, conservation management decisions also benefit from considering the species' social behavior (Snijders *et al.* 2017), especially in instances of reintroductions (Renan *et al.* 2018) and translocations (Goldenberg *et al.* 2019). In socially complex species such as primates, social dynamics strongly influence fitness, including survival, reproduction, and longevity (Silk *et al.* 2003, 2010). Female chacma baboons (*Papio ursinus*) that form long-lasting social bonds, for example, live significantly longer than those that maintain fewer stable bonds (Silk *et al.* 2010).

Primate social structures, like those of other social animals, are built upon social relationships, or social networks,

which result from repeated interactions and associations among individuals (Hinde 1976; Whitehead 1997; Wey *et al.* 2008). Patterns of social interactions and associations are influenced by the availability and identities of social partners, which fluctuate because of demographic processes such as births, deaths, immigrations, emigrations, and development (Rubenstein *et al.* 2015; Shizuka and Johnson 2020). In some social networks, central individuals serve as connectors among other individuals and the removal of these central individuals through death or dispersal can disrupt relationships, and thereby affect how the remaining individuals associate with one another (Kanngiesser *et al.* 2011; Flack *et al.* 2006; Modlmeier *et al.* 2014; Alvarado *et al.* 2020). Similarly, the maturation of juveniles or recruitment of immigrants into adult social networks have the potential to alter existing social networks (Ilany and Akçay 2016). In

bottlenose dolphins (*Tursiops truncatus*), for example, adult male social networks change as subadult males mature in their natal groups and become connectors with other individuals (Lusseau *et al.* 2006). The maturation and immigration of individuals can also shift adult sex ratios and therefore affect the number and identities of potential social partners (e.g., northern muriquis, *Brachyteles hypoxanthus*: Strier *et al.* 2002; spotted hyenas, *Crocuta crocuta*: Turner *et al.* 2018). Increases in group size can reduce hierarchical stability (moor macaques, *Macaca maura*: Furuya 1969; Barbary macaques, *Macaca sylvanus*: Prud'Homme 1991; chimpanzees, *Pan troglodytes*: Feldblum *et al.* 2018), dilute kinship (rhesus macaques, *Macaca mulatta*: Chepko-Sade and Sade 1979), increase levels of resource competition (moor macaques: Furuya 1969; toque macaques, *Macaca sinica*: Dittus 1988; chacma baboons, *Papio ursinus*: Ron 1996), weaken social bonds (yellow baboon, *Papio cynocephalus*: Henzi *et al.* 1997), result in smaller, flexible subgroups with fission-fusion dynamics to reduce intragroup competition (northern muriquis, Dias and Strier 2003), or permanently fission into separate groups (e.g., Sueur and Maire 2014).

Permanent group fissioning has been documented in matrilineal (e.g., toque macaques: Dittus 1988; yellow baboons: Henzi *et al.* 1997) and patrilineal primate societies (e.g., chimpanzees: Goodall 1986; northern muriquis: Strier *et al.* 1993, Tokuda *et al.* 2014; white-bellied spider monkeys, *Ateles bezeluth*: Alvarado *et al.* 2020). When permanent fissions occur, social variables such as affiliative relationships, social rank, and kinship influence which group individuals join (Silk 2007; Van Horn *et al.* 2007; Silk *et al.* 2010). It can be difficult, however, to anticipate the timing of group fissions from these social variables alone.

Less is known about patterns of permanent fission in patrilineal groups than in matrilineal groups. In one population of northern muriquis, two permanent fission events were suspected of being stimulated by increases in group size (Strier *et al.* 1993, 2006) and in one case, group fission also coincided with a male-biased sex ratio in the parent group (Tokuda *et al.* 2014). Similarly, in chimpanzees, a retrospective analysis of a historical (1973) community fission event also identified a strongly male-biased sex ratio in addition to prolonged dominance struggles in the parent group prior to the fissioning event (Feldblum *et al.* 2018). However, neither the muriqui nor chimpanzee analyses considered other factors, such as affiliative relationships and maternal kinship, which are known to influence patterns of fissioning in matrilineal societies (Van Horn *et al.* 2007).

Critically Endangered northern muriquis maintain egalitarian relationships and exhibit fission-fusion dynamics in their patrilineal societies (Strier *et al.* 2002). Females typically disperse from their natal groups at 5–7 years old (Strier *et al.* 2015), while males integrate into the adult social network (Strier *et al.* 2002, 2006). Nonetheless, like other Critically Endangered primates, some remaining northern muriqui populations are restricted to isolated social groups

that are highly vulnerable to extinction (Strier *et al.* 2021). Management efforts including the translocations of individuals between some of these populations have been underway (Tabacow *et al.* 2021), but simultaneous translocations or reintroductions of multiple individuals or mixed-sex subgroups into the wild have not yet been attempted. Social network analyses may provide insights that could inform and increase the success of future management programs involving multiple individuals if they are deemed necessary (Valença-Montenegro *et al.* 2021).

Here, we use social network analyses to retrospectively evaluate the most recent permanent fission of one muriqui group (Matão) at the Reserva Particular do Patrimônio Natural – Feliciano Miguel Abdala (RPPN-FMA), a small forest fragment in the Brazilian Atlantic Forest for which long-term data on individual life histories and maternal kinship are available (Strier and Mendes 2012; Strier 2021). Because of their fluid, fission-fusion social dynamics, it was difficult to identify precisely when the process of fissioning had begun or whether social preferences and maternal kinship networks might have influenced the process. We therefore investigated whether the metrics of social networks could quantify the timing of the onset of group fission and corroborate the identities of which individuals ultimately fissioned together. We predicted that individuals would fission if they had associated more consistently with one another in subgroups and had higher connectivity (measured by eigenvector centrality) and stronger social associations with one another compared to individuals that remained in the parent group, where associations and connectivity might be diluted by the greater number of potential associates. We also examined whether group fissioning might have been affected by the deaths or disappearances of individuals.

Methods

Study site and subjects

The study was conducted at the RPPN-FMA, a 1,000-ha seasonally deciduous forest fragment (Boubli *et al.* 2011), located in Caratinga, Minas Gerais, Brazil (19°44'S, 41°49'W). Rainfall is seasonal, with 80% of the annual 1168 ± 286 mm rainfall occurring between November and April (Strier *et al.* 2001). Mating is concentrated during the rainy months from November–April and births are concentrated during the dry months from May–October (Strier *et al.* 2001; Strier *et al.* 2006).

This isolated population grew from two mixed-sex groups with 50–60 individuals in 1983 to five mixed-sex groups with a maximum of 356 individuals in 2015 (Strier 2021). Groups maintain distinct but overlapping home ranges with intergroup encounters occurring mostly in the areas of home range overlap (Lima *et al.* 2019). Dispersing females may visit different groups, but none have moved after the onset of sexual activity (Strier *et al.* 2015).

Data for this study were collected from individuals in the Matão group, which has been under long-term observation

since 1983. The birthdates and full maternal histories of all but the oldest individuals in this group are known. Only adults and subadults (≥ 5 years of age) are included in our analyses (Strier *et al.* 2017). In May 2011, the Matão group consisted of 73 adult and subadult individuals. By April 2014, the Matão group had 69 adults and subadults, and the daughter group, the Nancys group, had 15 adult and subadult members.

Data collection

Behavioral data used in this study were collected on a near daily basis from May 2011 to December 2014 by trained observers of the Projeto Muriqui de Caratinga (Strier 2021). Muriquis could be individually identified from their distinct facial pigmentations and other physical characteristics, except when poor visibility due to lighting or dense vegetation allowed for only the use of more generic, age-sex classifications. Different parts of the group were followed by different observers using the same systematic methods of behavioral observation. Scan samples were conducted at 30-min intervals, during which the nearest neighbor(s) up to a 5-m radius of each visible individual were recorded.

All data were collected non-invasively and followed the methods described in Lima *et al.* (2019). Methodology was approved with a Wildlife Waiver submitted through the University of Wisconsin Animal Resources and Compliance office and research adhered to legal requirements of the Brazilian government.

Data analyses

Scan-sample data were accessed through MBED: the Muriqui Behavioral Ecology Database (https://mbed.ssc.wisc.edu/easy_db/user/views/mbed_demo_overview.html). Demographic information on individual age, maternal kinship, births, and deaths or disappearances from the group were compiled through access to the muriqui life-history data housed in the Primate Life History Database (Strier *et al.* 2010).

A total of 89,983 records were obtained during the Matão group scan samples from May 2011 through December 2014. We excluded 11,253 records, or 12.5% of individuals that could not be identified in the scan samples and an additional 154 cases where an individual mistakenly appeared as being its own nearest neighbor in the database. Following Tokuda *et al.* (2014) and Lima *et al.* (2019), we separated the daily scan samples by observer, and considered animals to be members of the same subgroup if they were observed by the same observer on that day. While these daily subgroups did not allow us to evaluate the amount of time individuals spent together, they did provide a consistent basis for evaluating changes in subgroup composition over a multi-year study (Tokuda *et al.* 2014). To avoid redundancy, when one or more individuals were recorded by different observers on the same day, only the scan samples collected by the observer with the greatest number of different individuals were included for that day (Lima *et al.* 2019). Thus, our

analyses were based on the 959 subgroups extracted from the scan samples conducted over the eight seasons spanned by this study period (Table 1).

We divided the 2011–2014 study period into eight seasons by separating the mating (November–April) and birth (May–October) seasons (Strier 1997; Strier *et al.* 2001). We calculated Simple Ratio Indices (SRIs) (Cairns and Schwager 1987) for individual dyads in SOCPROG 2.9 (Whitehead 2019). This index was selected because associations were defined by their presence in the same group and all individuals included in the analyses could be identified (Whitehead 2019). The SRI evaluates the proportion of time two individuals were observed to associate with one another relative to the number of times each individual was observed (Cairns and Schwager 1987; Whitehead 2008). All SRI values were corrected for gregariousness (SRIG), as proposed by Godde *et al.* (2013), such that the SRIG of individuals A and B was equal to the SRI between individuals A and B divided by the sum of the SRIs involving A and the sum of those involving B, multiplied by the sum of all the SRIs.

We used the SRIGs to calculate group modularity and two other social network metrics, eigenvector centrality and betweenness centrality, and to identify preferred dyadic associations. Modularity is defined as the difference between the observed and expected proportion of the total associations within subgroups (Whitehead 2019; Newman and Girvan 2004). We employed the modularity metric in SOCPROG 2.9 (Whitehead 2019) to identify the individuals involved in the fission by examining changes in the composition of the subgroups over seasonal periods. The coefficient of modularity (Q) ranges from 0 to 1.0, with $Q > 0.3$ considered to be indicative of notable clustering within subgroups (Newman and Girvan 2004). We therefore considered the first period with $Q > 0.3$ to be the period during which group fissioning began.

Eigenvector centrality measures an individual's connectivity both through their own associations, based on the number of associates and the strength of their bonds, and to whom they are connected to, such that an individual with a high eigenvector centrality value should be strongly connected to others in its subgroup (Whitehead 2008). We

Table 1. Total number of subgroups across sample days, based on nearest-neighbor data.

Seasonal Period	Subgroups	Days
2011 Birth Season	160	158
2011-2012 Mating Season	121	117
2012 Birth Season	167	163
2012-2013 Mating Season	125	123
2013 Birth Season	138	136
2013-2014 Mating Season	104	103
2014 Birth Season	144	142
Total	959	942

predicted that eigenvector centrality values would be higher among individuals that fissioned to form the Nancys group because of their more frequent and consistent associations with one another, compared to the eigenvector centrality values of individuals that remained in the Matão group, where a larger number of weak associations in this group would dilute the strong associations. Statistical analyses were conducted using R 4.0.2 software (R Core Team 2019). We recalculated and weighted our eigenvector centrality scores for individuals using the R package ‘igraph’ (Csardi and Nepusz 2006) and reformatted those data using the R packages ‘reshape2’ (Wickham 2007) and ‘data.table’ (Dowle and Srinivasan 2019) so that they were in a more usable format for statistical analyses. We conducted Kruskal-Wallis tests with Bonferroni corrected Wilcoxon signed-rank tests for pairwise comparisons in R package ‘ggpubr’ (Kassambara 2020) to evaluate whether the eigenvector centrality of individuals differed between these groups in the periods leading up to the fission, following Tokuda *et al.* (2014). We gathered descriptive statistics using the R package ‘tidyverse’ (Wickham 2019).

To evaluate whether individuals were more likely to fission with their closest associates, we conducted Mantel tests in SOCPROG 2.9 (Whithead 2019) with 10,000 permutations to compare the SRIGs of dyads that ended up remaining together in the Matão group or remaining together and fissioning into the Nancys group or splitting up such that one individual remained in Matão and the other joined the Nancys group (mixed-group dyads). We further evaluated SRIGs using a Kruskal-Wallis test with Wilcoxon signed-rank pairwise comparisons and Bonferroni correction in R

package ‘ggpubr’ (Kassambara 2020) to identify if there were differences among SRIGs when comparing all dyad types.

We used UCINET 6.7 (Borgatti *et al.* 2002) to calculate betweenness centrality (betweenness), which measures the importance of an individual in connecting other individuals together. An individual with high betweenness has strong associations with at least two individuals that rarely interact with one another and can serve as a bridge between them (Whitehead 2008). We used betweenness to investigate whether the disappearances (and presumed deaths) of any of the seven males that occurred prior to or during the 2013–2014 mating season may have influenced which individuals fissioned.

Results

Modularity analyses confirmed that adults and subadults in the Matão group were associated as a single network during the 2011 birth season ($Q = 0.159$), the 2011–2012 mating season ($Q = 0.119$), and the 2012 birth season ($Q = 0.195$). During the 2012–2013 mating season, however, modularity increased, indicative of increasingly distinct subgroups ($Q = 0.316$) that persisted through the rest of the study period (Fig. 1). We thus considered the 2012–2013 mating season to mark the onset of the Matão group fission (Fig. 2), when most of the individuals that ultimately established the Nancys group were identified by their associations in a distinct subgroup that persisted for the duration of the study (Table 2). Among these individuals were four maternal brothers (NE, NI, NO, NR) and their mother (NY),

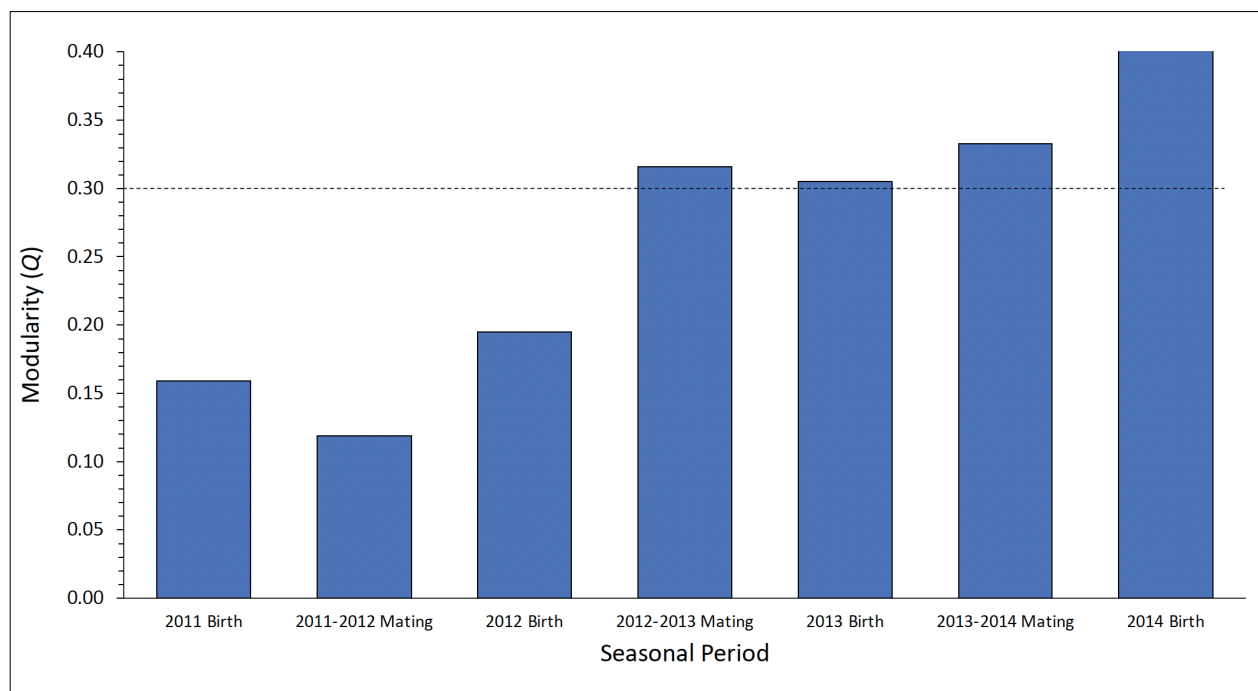


Figure 1. Modularity across seasons. Modularity (Q) > 0.3 (dotted horizontal line) indicates distinct clustering of individuals. The Nancys group fission began during the 2012–2013 mating season, and clustering persists for the remaining seasons.

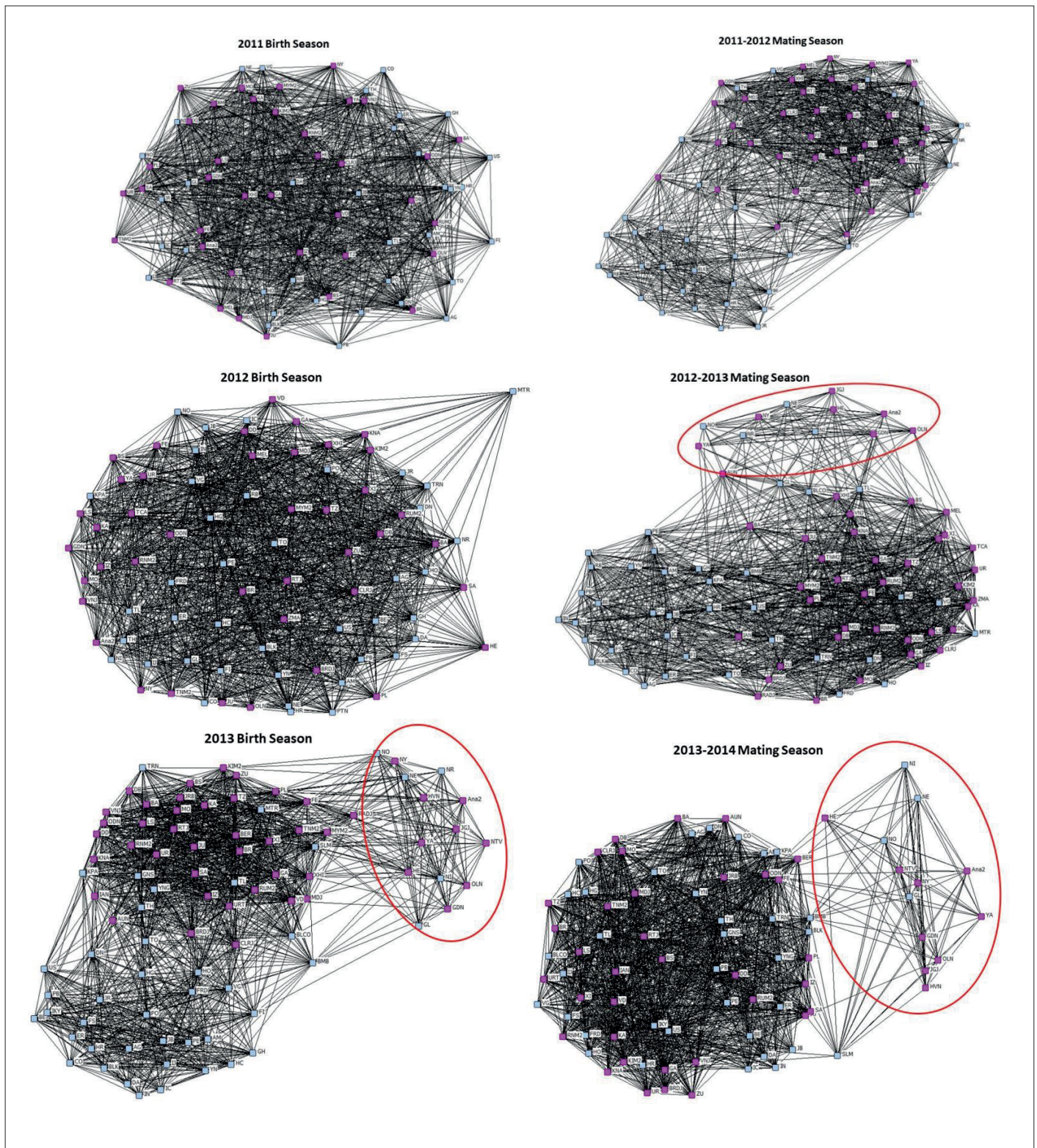


Figure 2. Social network diagrams based on SOCPROG SRIGs. Diagrams created in UCINET NetDraw (Borgatti *et al.* 2002). Pink squares represent females, blue squares represent males, black lines represent the presence of an association between two individuals. Dyads with fewer than two proximity associations within a seasonal period have been removed for clearer sociograms. Individuals that fissioned to form the Nancys group are circled in red.

which together accounted for five of the founding members (Table 2). However, two mothers (HE and YA) fissioned with the Nancys group without their sons, which remained in the Matão group.

Three females associated with the Nancys subgroup during a single season before returning to the Matão group where they remained (Table 2). One male (SLM) associated with the Nancys group when he turned 5 years of age, appeared in our analyses during the 2013–2014 mating

Table 2. Composition of the Nancys group across seasonal periods, according to modularity metrics. Superscripts (F) = female, (M) = male; (+) = mothers with one or more offspring present in this group; parentheses indicate immature offspring during that period that were not included in the analyses until they reached subadulthood, shown without parentheses. One individual (SLM) appeared in the Nancys group when he reached subadulthood (shown in *italics*).

Year and Season			
2012-2013 Mating	2013 Birth	2013-2014 Mating	2014 Birth
Ana2 ^F + (AMA ^M)	Ana2 ^F + (AMA ^M)	Ana2 ^F + (AMA ^M)	Ana2 ^F + (AMA ^M)
GD-N ^F + (GOD ^M)	GD-N ^F + (GOD ^M)	GD-N ^F + (GOD ^F)	GD-N ^F + (GOD ^F)
	GL ^M	GL ^M	GL ^M
HE ^F + (HVN ^F)	HE ^F + HVN ^F	HE ^F + HVN ^F	HE ^F + HVN ^F + (HOR ^M)
NE ^M	NE ^M	NE ^M	NE ^M
NI ^M	NI ^M	NI ^M	NI ^M
NO ^M	NO ^M	NO ^M	NO ^M
NR ^M	NR ^M		
NY ^F + (NTV ^F)	NY ^F + NTV ^F	NY ^F + NTV ^F	NY ^F + NTV ^F
OL-N ^F + (ORP ^M) + (ORE ^M)	OL-N ^F + (ORP ^M) + (ORE ^M)	OL-N ^F + (ORP ^M) + (ORE ^M)	OL-N ^F + ORP ^M + (ORE ^M)
YA ^F + (YAM ^M)	YA ^F + (YAM ^M)	YA ^F + (YAM ^M)	YA ^F + (YAM ^M)
JG-J ^F	JG-J ^F	JG-J ^F	JG-J ^F
		<i>SLM^M</i>	<i>SLM^M</i>
AU-N ^F			
	MY-M2 ^F		
	RAD-J ^F		

season, while his mother (SA) remained in the Matão group. Three other juveniles moved with their mothers (HE, NY, and OL-N), founders of the Nancys group, but only appeared in the analyses after they reached 5 years of age, which was in the 2013 birth season (HVN, NTV) and the 2014 birth season (ORP), respectively (Table 2).

Median eigenvector centrality values were significantly higher among individuals that ultimately fissioned to form the Nancys group than those that remained in the Matão group throughout the study period. The differences were especially evident beginning in the 2012–2013 mating season, when the Matão group's eigenvector centrality values declined and remained low (Fig. 3).

Mantel tests revealed that the SRIGs of same-group dyads (Matão–Matão or Nancys–Nancys) were significantly higher than between group dyads (Nancys–Matão) across all seasonal periods (all P values ≤ 0.05), except the 2012 birth season. However, the Kruskal-Wallis test with adjusted pairwise Wilcoxon sign-rank comparisons using Bonferroni Correction indicated that the SRIGs of dyads that fissioned to the Nancys group were significantly higher than the SRIGs of same group Matão dyads or mixed group dyads across all seasonal periods (Fig. 4).

Betweenness scores for all individuals fluctuated widely across seasons. There was no consistent pattern in the betweenness scores of the six males that died during the study period, but all of those males were present through the

2012–2013 mating season when the individuals that formed the Nancys group fissioned (Table 3). Of these six males, one (NR) was a founding member of the Nancys group.

Discussion

Social network analyses proved to be reliable in retroactively identifying the individuals that ultimately fissioned from the original study group. Specifically, the Matão group displayed no distinct modularity until the 2012–2013 mating season, when the core founders of the Nancys group formed a consistent module across the remaining seasonal periods. Two of the three females that associated temporarily with the Nancys group during a single season may have been in the process of dispersal, when females sometimes ‘shop’ between groups (Strier *et al.* 2015). Indeed, the overall consistency of the Nancys group membership, as identified by the modularity metric, supports the idea that social network analyses can be applied retroactively to quantify temporal changes in this process (e.g., Tokuda *et al.* 2014).

We found significantly higher median eigenvector centrality values among the Nancys group members beginning with the 2011 birth season. However, while these values remained high for the Nancys group, they declined sharply and remained low for Matão group members beginning with the 2012–2013 mating season, when the modularity metric indicated the group had fissioned. This differs from

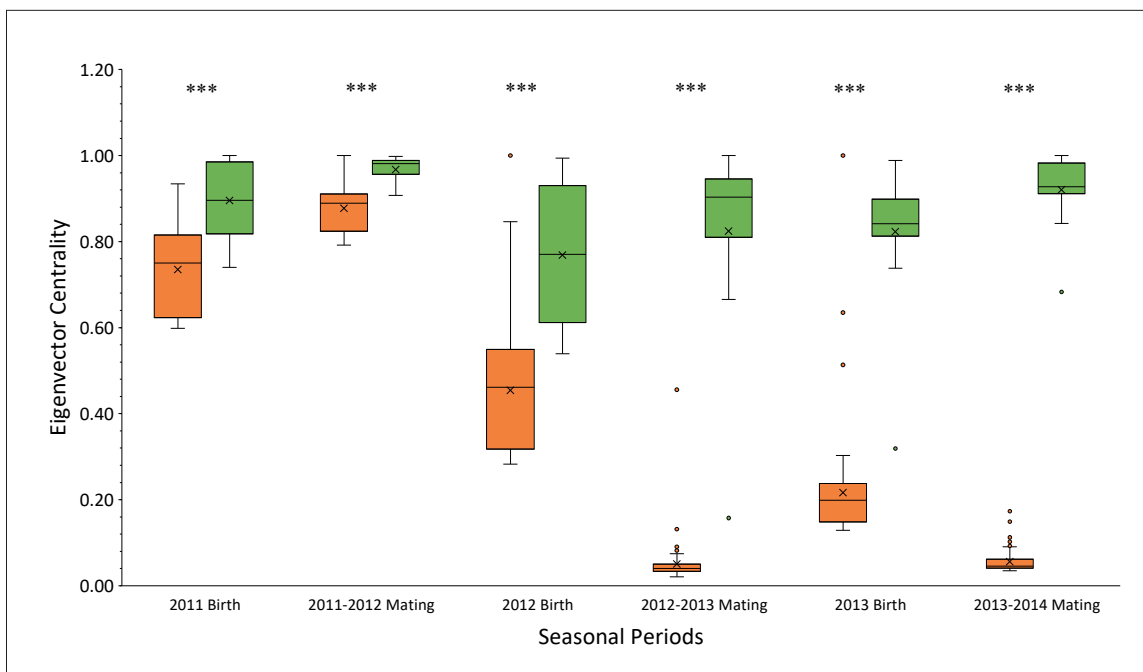


Figure 3. Individual eigenvector centrality based on final group membership across seasonal periods. Orange = Matão group; Green = Nancys group. Box plots show mean (x), median (horizontal line), 1st and 3rd quartile (box limits), minimum and maximum (lines), and outliers (circles). Asterisks correspond to significant differences ($P < 0.001 = ***$). Kruskal Wallis test ($H(2) = 119.92, P < 0.0001$) and Wilcoxon signed-rank pairwise comparisons with Bonferroni Correction: 2011 birth season: $N_{\text{Matão}} = 63, N_{\text{Nancys}} = 12, P < 0.001$; 2011–2012 mating season: $N_{\text{Matão}} = 63, N_{\text{Nancys}} = 11, P < 0.001$; 2012 birth season: $N_{\text{Matão}} = 70, N_{\text{Nancys}} = 11, P < 0.001$; 2012–2013 mating season: $N_{\text{Matão}} = 74, N_{\text{Nancys}} = 12, P < 0.0001$; 2013 birth season: $N_{\text{Matão}} = 77, N_{\text{Nancys}} = 14, P < 0.0001$; 2013–2014 mating season: $N_{\text{Matão}} = 69, N_{\text{Nancys}} = 15, P < 0.0001$.

the significantly lower eigenvector centrality values found among members of another muriqui group in the same population that previously underwent fissioning before and during the first season that modularity was detected (Tokuda *et al.* 2014). Such different patterns of eigenvector centrality could reflect different underlying causes for the groups' fissions, or to our use of SRIGs, which corrected for gregariousness in these analyses.

Consistent with our prediction, we found significantly higher SRIGs among dyads that ultimately fissioned into the Nancys group as early as the 2011 birth season, corresponding to their higher eigenvector centrality values. A similar pattern in the strong associations corresponding with group membership after fission has been found in matrilineal primates that fissioned along matrilineal lines (e.g., olive baboons (*Papio anubis*: Nash 1976; Japanese macaques (*Macaca fuscata*: Sugiyama 1960, Yamagiwa 1985), and in communities of patrilocal white-bellied spider monkeys (Alvarado *et al.* 2020) and Indo-Pacific dolphins (*Tursiops aduncus*) (Nishita *et al.* 2015). In our study, however, significant modularity indicative of group fissioning was delayed by more than a year, providing additional information about the timing of the fissioning process that would not have been evident from the association data alone.

Although maternal kinship is known to play a major role in group membership during permanent fissions in matrilineal societies such as those of savannah baboons (*Papio cynocephalus*: Van Horn *et al.* 2007) and spotted hyenas

(*Crocuta crocuta*; Holekamp *et al.* 1993), our findings were mixed. On the one hand, five of the original founders of the Nancys group were comprised of a mother (NY) and all four of her adult sons. On the other hand, none of the five adult or subadult sons of the other two founding females accompanied their mothers into the Nancys group, and their SRIGs tended to be lower in each period compared to those that NY had with most of her sons. These differences are not surprising, considering that variation in the relationships between mothers and their adult sons has previously been described among members of the Matão group (Tolentino *et al.* 2008).

We found no evidence that deaths or disappearances led to fissioning. Although six males disappeared and were presumed to have died during our study period, none of them did so prior to the start of the fissioning event in the 2012–2013 mating season. Indeed, some of these males had high betweenness scores up until and after the onset of group fissioning. This finding is in sharp contrast with a similar study of white-bellied spider monkeys, where the disappearance of some males decreased group cohesion and coincided with the fission (Alvarado *et al.* 2020).

This study highlights the usefulness of social network analysis in quantifying the process of permanent group fissions, and adds to the limited literature documenting the dynamics of permanent fissions in patrilocal primate societies. It also has implications for understanding the social correlates of intra- and intergroup dynamics, which are especially important in small populations where the risks of inbreeding are high.

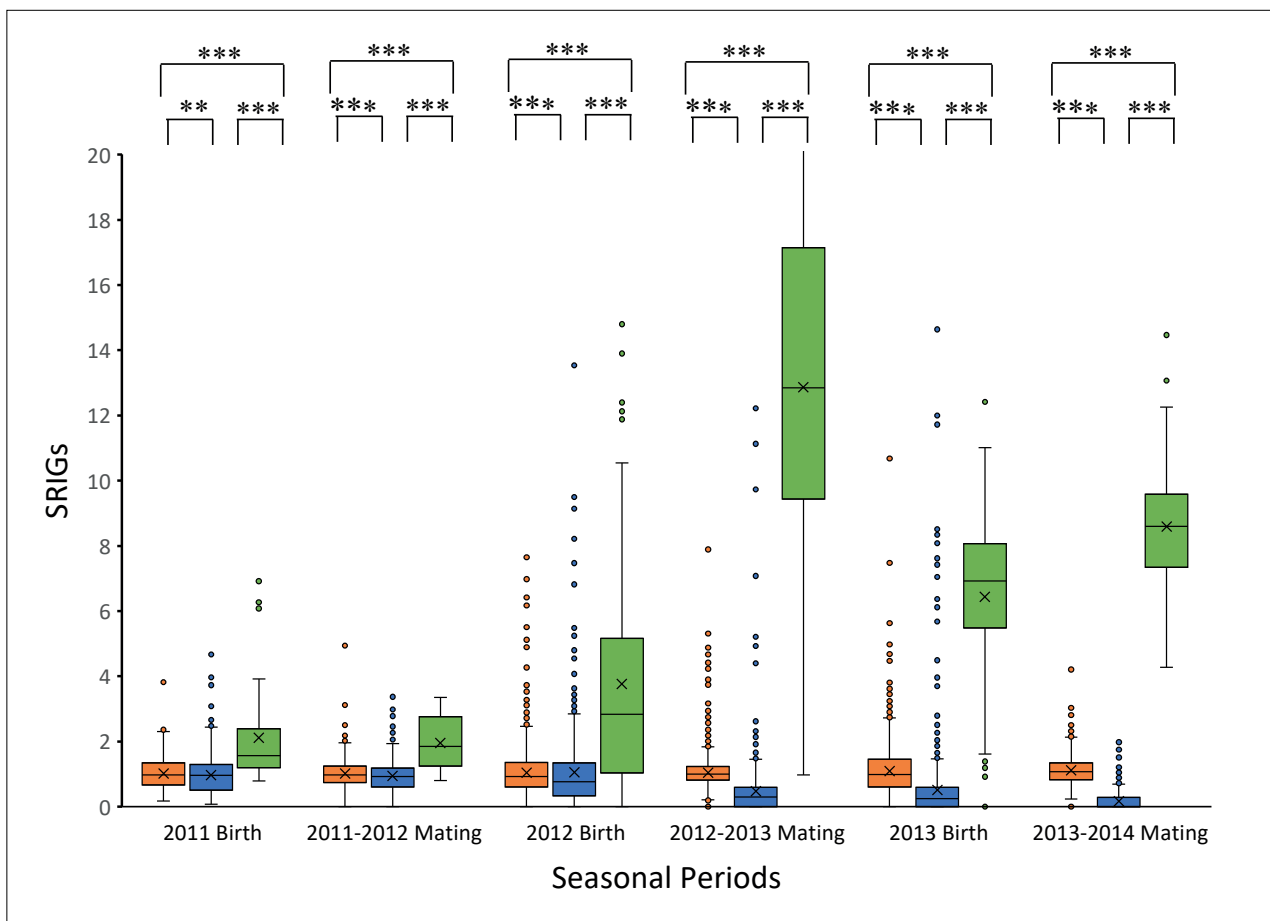


Figure 4. SRIGs by group members across seasonal periods. Orange bars = Matão group dyads; blue bars = mixed group dyads; green bars = Nancys group dyads. As per Figure 3, box plots show medians, means, quartiles, and max and min values; dots signify outliers. Asterisks correspond to significant differences ($P < 0.001 = ***$). Kruskal-Wallis test: $H(5) = 3600.20, P < 0.0001$. Comparisons between groups are as follows for results from the Wilcoxon Signed-Rank tests with $N =$ number of dyads per group: 2011 birth season: $N_{\text{Matão}} = 1830, N_{\text{Mixed}} = 732, N_{\text{Nancys}} = 66$; Matão \times Mixed: $P < 0.001$; Matão \times Nancys: $P < 0.0001$; Mixed \times Nancys: $P < 0.0001$; 2011–2012 mating season: $N_{\text{Matão}} = 1953, N_{\text{Mixed}} = 693, N_{\text{Nancys}} = 55$; Matão \times Mixed: $P < 0.0001$; Matão \times Nancys: $P < 0.0001$; Mixed \times Nancys: $P < 0.0001$; 2012 birth season: $N_{\text{Matão}} = 2415, N_{\text{Mixed}} = 770, N_{\text{Nancys}} = 55$; Matão \times Mixed: $P < 0.0001$; Matão \times Nancys: $P < 0.0001$; Mixed \times Nancys: $P < 0.0001$; 2012–2013 mating season: $N_{\text{Matão}} = 2701, N_{\text{Mixed}} = 888, N_{\text{Nancys}} = 66$; Matão \times Mixed: $P < 0.0001$; Matão \times Nancys: $P < 0.0001$; Mixed \times Nancys: $P < 0.0001$; 2013 birth season: $N_{\text{Matão}} = 2926, N_{\text{Mixed}} = 1078, N_{\text{Nancys}} = 91$; Matão \times Mixed: $P < 0.0001$; Matão \times Nancys: $P < 0.0001$; Mixed \times Nancys: $P < 0.0001$; 2013–2014 mating season: $N_{\text{Matão}} = 2346, N_{\text{Mixed}} = 966, N_{\text{Nancys}} = 91$; Matão \times Mixed: $P < 0.001$; Matão \times Nancys: $P < 0.0001$; Mixed \times Nancys: $P < 0.0001$.

Table 3. Betweenness centrality of males that died during the study period.

Males that died during the study period	2011 Birth season	2011-2012 Mating season	2012 Birth season	2012-2013 Mating season	2013 Birth season	2013-2014 Mating season
FI	0.00	0.64	0.90	6.47	0.15	Died
GH	0.00	0.69	0.90	2.45	0.00	Died
JR	0.00	0.69	3.28	4.70	4.50	Died
NR--Fissioned	0.00	0.69	3.07	2.81	0.70	Died
PTN	Juvenile	Juvenile	0.79	0.00	Died	Died
RB	0.00	0.03	0.82	4.70	Died	Died
Mean \pm SD (range) for these males (N = 6)	0.00 \pm 0.00 (0.00 – 0.00)	0.55 \pm 0.260 (0.03 – 0.69)	1.88 \pm 1.17 (0.79 – 3.28)	3.52 \pm 2.26 (0.00 – 6.47)	1.34 \pm 2.13 (0.00 – 4.50)	Died
Mean \pm SD (range) for all group members	0.00 \pm 0.00 (0.00 – 0.00, N = 75) Absence of Betweenness in network – No intermediary needed for relationships	0.42 \pm 0.32 (0.00 – 0.69, N=74)	1.41 \pm 1.15 (0.00 – 3.28, N=81)	4.01 \pm 2.18 (0.00 – 7.96, N=86)	5.74 \pm 3.26 (0.00 – 13.07, N=91)	6.92 \pm 8.13 (0.01 – 24.87, N=83)

Group fission, in particular, offers important considerations for conservation management, because it can create new groups that provide dispersal opportunities in small populations, as well as reduce resource competition in forest fragments (Dittus 1988; Strier 2009). Although our findings that social network analyses can identify which dyads are likely to fission together are not unique, our retrospective results from the modularity metric provide original insights into the timing of group fissioning and the identities of the founding group members, which may have practical implications for conservation management programs. Specifically, informed decisions about social compatibility are critical to the success of translocations, rehabilitations, and reintroductions that involve multiple individuals (Tabacow *et al.* 2021). Social compatibility is also essential to the success of newly formed reproductive groups in both captive and wild contexts. Whenever possible, the inclusion of social network analyses is highly recommended to increase the success of primate management programs involving multiple individuals or groups.

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