Social cliques in male northern muriquis *Brachyteles hypoxanthus*

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Abstract Analyses of spatial relationships and social interactions provide insights into the social structure of animal societies and the ways in which social preferences among and between dyads affect higher order social relationships. In this paper we describe the patterns of spatial associations and social interactions among adult male northern muriquis in order to evaluate the dynamics of their social networks above the dyadic levels. Systematic observations were made on the 17 adult males present in a multi-male/multi-female group from April 2004 through February 2005, and in July 2005. Analyses of their spatial relationships identified two distinct male cliques; some adult males (called “N” males) were more connected to the females and immatures than other adult males (“MU” males), which were more connected to one another. Affiliative interactions were significantly higher among dyads belonging to the same clique than to different cliques. Although frequencies of dyadic agonistic interactions were similarly low among individuals within and between cliques, MU males appeared to be subordinate to N males. Nonetheless, there were no significant differences in the copulation rates estimated for MU males and N males. Mutual benefits of cooperation between MU and N cliques in intergroup encounters might explain their ongoing associations in the same mixed-sex group [Current Zoology 58 (2): 342–352, 2012].

Keywords *Brachyteles hypoxanthus*, Male northern muriquis, Social relationship, Social clique, Social network analysis

The study of animal societies involves the description of social systems and their underlying factors (e.g. Wilson, 1975; Kappeler and van Schaik, 2002). According to the framework proposed by Robert Hinde (1976, 1983), the sociality of group living animals should be described in terms of interactions, relationships and structure. By definition, a group’s social structure is the network of relationships distinguished by the nature, quality, and patterning of interactions among group members.

Contemporary applications of Hinde’s approach to understanding higher order relationships have been facilitated by the development of Social Network Analyses (SNA) (Whitehead, 2008; Sueur et al., 2011), a set of methods that permit the social network description, quantification, and comparison of social relationships of individuals in a group (Croft et al., 2008, 2011; Sueur et al., 2011). SNA also allow the visualization of sub-structure of social groups, making them especially useful tools for studies of species that form subgroups of variable size and composition within their fission–fusion societies (Whitehead, 1997; e. g. bottlenose dolphins *Tursiops* spp., Lusseau et al., 2006, 2008). In this study, we employ SNA to analyze male relationships of a group of northern muriquis *Brachyteles hypoxanthus*.

The northern muriqui is a Neotropical primate species in the subfamily Atelinae. Males are philopatric, form strong affiliative bonds, and spend a high proportion of time in close proximity (Mendes, 1990; Strier, 1994, 1997a; Strier et al., 2000, 2002). The lack of overt competition among males for access to fertile females (Strier, 1997b) and the absence of hierarchical relationships are remarkable characteristics of male northern muriqui behavior. They are considered to be extremely peaceful primates because of the low rates of aggression observed among group members (Strier, 1994). Moreover, northern muriqui males cooperate with other members of their groups during agonistic intergroup encounters, which can include chases and extended vocal exchanges (Mendes, 1990; Strier, 1990, 1994; Boublí et al., 2005).

Typically, northern muriquis live in large multi-male/multi-female social groups. Social groups in our study population were originally cohesive, but with increasing
population size the groups began to split up routinely into fluid subgroups of variable size and composition (Strier et al., 1993; Dias and Strier, 2003). Previous studies have shown that despite their egalitarian relationships, some male dyads have stronger relationships than others (Strier, 1997a; Strier et al., 2002). Here, we investigate whether males exhibit consistent partner preferences above the dyadic level, similar to those observed in other species with fission-fusion dynamics and strong male bonds (e.g., chimpanzees Pan troglodytes: Mitani and Amsler, 2003; bottlenose dolphins: Lusseau, 2007).

Affiliative bonds play an important driving force in the social structure of animal societies (Sussman et al., 2005), explaining individual social preferences and patterns of subgrouping formation (Lusseau et al., 2006; Bezzanson et al., 2008). Affiliative behaviors and spatial associations have been used to detect bonds among dyads and at higher order levels in several species of primates (Kudo and Dunbar, 2001; Mitani and Amsler, 2003; Schreier and Swedell, 2009) and other mammals including African elephants Loxodonta africana (Moss and Poole, 1983; Wittemyer et al., 2005), bottlenose dolphins (Lusseau et al., 2006; Connor et al., 2011), Columbian ground squirrels Spermophilus columbianus (Manno, 2008), meerkats Suricata suricatta (Madden et al., 2009), and giant noctule bats Nyctalus lasiopterus (Popa-Lisseanu et al., 2008). In general, subsets of individuals within a social group that form stable bonds are classified as members of a clique (Kudo and Dunbar, 2001; Mitani and Amsler, 2003; Scott and Lockard, 2007; Bezzanson et al., 2008; Wakefield, 2008). Therefore, social relationships among members of the same cliques are expected to be stronger than those between members of different cliques.

We used data on proximity and the affiliative and agonistic interactions among male northern muriquis to evaluate whether their social relationships are structured above the dyadic level into cliques. In addition, we examined copulation patterns to investigate the possible factors that underlie interactions between male subgroups. We predicted that particular sets of individuals would be found to associate in proximity and to engage in affiliative interactions more often with one another than with other sets of individuals, consistent with the social dynamics of cliques in other animals. However, because of their high level of tolerance toward other group members, we predicted low frequencies of intra- and inter-clique agonistic interactions and similar rates of copulation, reflecting their lack of interference in one another’s copulations (Strier et al., 2000).

1 Material and Methods

1.1 Subjects and study site

Our study was conducted at the Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala (RPPN-FMA; previously known as the Estação Biológica de Caratinga), a 957 ha forest located in the municipality of Caratinga, Minas Gerais, Brazil (19°44’S, 41°49’W). During the present study period, from April 2004 through February 2005, and July 2005, the forest supported more than 200 muriquis divided into four bisexual groups during the present study period (Strier et al., 2006). Study animals were free-ranging and completely habituated to the presence of researchers. Individual identification was attained by distinct facial pigmentation and other physical characteristics.

Since 1982, the northern muriqui population at the RPPN-FMA has grown from its two original groups (Matão group and Jaó group) to four mixed-sex social groups. The Jaó group has fissioned twice, resulting first in the creation of the Matão II group by 1991 (Strier et al., 1993) and second in the creation of the Nadir group by 2003 (Strier et al., 2006; Boublí et al. in prep.). Our study focuses on the Nadir group, which included from 54 to 67 animals (17–18 adult males, 3 subadult males, 18 adult females, 2–3 subadult females and 13–21 infants/juveniles) during this study period. One adult male (MV) was present in April 2004, but disappeared and is presumed to have died by June 2004, and is therefore excluded from our analyses (Table 1). Prior to 2002, systematic data on demography, life-history, and behavior were collected only on the Matão group whereas only opportunistic observations were made on the other social groups. Thus, we did not know the ages and relatedness of our study subjects in the Nadir group at the time of this study.

1.2 Data collection

The behavioral data were collected by MT on the 17 adult males in the Nadir group. Following previous studies conducted at the RPPN-FMA (Printes and Strier, 1999; Strier et al., 2002; Possamai et al., 2007) focal males were observed for 10 continuous minutes, and their spatial relationships and affiliative interactions (e.g., embraces, touches, and play) were recorded on-the-minute during the sampling periods (Altmann, 1974). Samples with fewer than 8 on-the-minute observations were not included in the analyses to minimize potential biases associated with the contexts that might have led to lack of visibility of the study subject. The
Table 1  Distribution of focal subjects and sample sizes

| Male ID | Clique | n Focal samples | Mean n focal samples per month (SD) | n Focal hours | Mean n focal hours per month (SD) | n months sampled |
|---------|--------|----------------|-------------------------------------|---------------|----------------------------------|-----------------|
| GO-N    | MU     | 51             | 4.3±5.3                             | 8.3           | 0.7±0.9                          | 7               |
| JU-N    | MU     | 103            | 8.6±3.6                             | 16.9          | 1.4±0.6                          | 12              |
| MV      | MU     | 12             | 1.0±2.9                             | 2.0           | 0.2±0.5                          | 2               |
| OT-N    | MU     | 97             | 8.1±4.6                             | 16.0          | 1.3±0.8                          | 11              |
| PI-N    | MU     | 110            | 9.2±4.3                             | 18.1          | 1.5±0.7                          | 11              |
| QUI-N   | MU     | 106            | 8.8±4.1                             | 17.4          | 1.4±0.7                          | 11              |
| RD-N    | MU     | 108            | 9.0±4.0                             | 17.7          | 1.5±0.7                          | 11              |
| SN-N    | MU     | 101            | 8.4±3.4                             | 16.7          | 1.4±0.6                          | 12              |
| VE-N    | MU     | 101            | 8.4±3.8                             | 16.5          | 1.4±0.6                          | 11              |
| BU-N    | N      | 91             | 7.6±3.7                             | 14.9          | 1.2±0.6                          | 12              |
| DA-N    | N      | 102            | 8.5±3.2                             | 16.7          | 1.4±0.5                          | 12              |
| IN-N    | N      | 107            | 8.9±3.7                             | 17.5          | 1.5±0.6                          | 12              |
| UL-N    | N      | 93             | 7.8±3.4                             | 15.3          | 1.3±0.6                          | 12              |
| BT-N    | N      | 69             | 5.8±4.4                             | 11.2          | 0.9±0.7                          | 9               |
| DP-N    | N      | 69             | 5.8±4.6                             | 11.3          | 0.9±0.8                          | 8               |
| FB-N    | N      | 63             | 5.3±4.4                             | 10.4          | 0.9±0.7                          | 8               |
| JE-N    | N      | 68             | 5.7±4.3                             | 11.1          | 0.9±0.7                          | 9               |
| KD-N    | N      | 75             | 6.3±4.5                             | 12.4          | 1.0±0.8                          | 9               |
| TOTAL   |        | 1,514          |                                     | 248.4         |                                  |                 |

focal animal observations were balanced as much as possible across times and days each month. All focal animals were sampled a maximum of three times for each hour during each month, and the subjects were selected from a predetermined sequence to balance observations. Altogether, a total of 1,514 focal subject samples was conducted, corresponding to 248.4 hours of observation, and a mean ± SD of 14.6 ± 3.1 hr of observation per focal male (Table 1).

The identities of all individuals that were within a 5 m radius of the focal male, and all affiliative interactions (e.g., embraces, touches, and play) in which the focal male participated were recorded. Rare events such as copulations and agonistic interactions (e.g., chases, displacements, threats and grabs) were recorded ad libitum (Altmann, 1974). During affiliative and agonistic interactions, the identities of the participants were noted and distinguished by whether they were initiators or recipients whenever possible.

1.3 Data analyses

We analyzed the spatial associations using a simple ratio association index (Cairns and Schwager, 1987), the Jaccard’s Similarity Index ($S_J = a/a + b + c$, where $a$ is the frequency with which individuals A and B were observed in proximity, i.e. within a 5 m radius, $b$ is the frequency with which A was observed without B and $c$ is the frequency with which B was observed without A. An interaction index of affiliation and agonism was calculated similarly to the association index. In this case, $a$ is the frequency with which individuals A and B were observed in interacting, $b$ is the frequency with which A was observed interacting with another individual and $c$ is the frequency with which B was observed interacting with another individual. We calculated the spatial association index for all adult and subadult individuals, and the affiliative and agonistic indices were calculated only for adult males.

We produced dendrograms using the average-linkage hierarchical cluster analysis to display the matrices of spatial association and affiliative interactions indices. The index values were organized into matrices (one for each index) that were then input into SOCPROG (Whitehead, 2009). We assessed the degree to which clusters represented the observed data using the co-
phenetic correlation coefficient (CCC). CCC values above 0.8 indicate an accurate representation of the matrices (Bridge, 1993). We used Newman’s modularity coefficient \( Q \) to detect how well clusters were defined in the dendrograms (controlling for the gregariousness of individuals). Modularities greater than 0.3 are often considered to represent useful group divisions, whereas those lower than 0.3 can probably be ignored (Newman, 2004).

In order to obtain a graphical representation of spatial associations and interactions to detect cliques, we drew spatial association, affiliation and agonistic networks using Netdraw (Borgatti, 2002). In weight network analysis, edges represent indices that connect nodes, or individuals. In the sociogram, the thickness of the edges is proportional to the index values, and only edges with values equal to or higher than the mean group value were included in the sociogram.

In our analyses of spatial associations and affiliative interactions we used only the data obtained during the 10-min focal subject samples. However, we used all occurrences of agonistic interactions and copulations, because, typical of rare events, most of these were observed outside of the systematic focal subject samples. Polyadic agonistic interactions, which included up to three individuals, were divided into their dyadic components following Strier et al. (2002). To supplement our comparisons of affiliative and agonistic behaviors, we estimated rates of interactions per dyad by dividing the frequency of affiliative or agonistic interactions between two males by the frequency with which the same two males were observed in proximity with one another. To determine whether patterns of association, affiliation, or agonism differed between and within male cliques, we performed the Mantel test, with 1000 permutations. For a two-tailed test, we considered values of \( P < 0.025 \) and \( P > 0.975 \) to be significant (Whitehead, 2008).

We calculated copulation rates in a similar way, except these were based on the time males spent in proximity to females. Thus, the frequency of copulations between male-female dyads was divided by the frequency of proximity of the same dyads. To determine whether copulation rate was related to clique membership, we constructed a hypothesis matrix where “0” was attributed to dyads between MU males and females, and “1” was attributed to dyads between N males and females. With this hypothesis matrix and the matrix of copulation rate, we performed the Mantel test with 1000 permutations. For a one-tailed test, significance was set at \( P < 0.05 \). All of these analyses were conducted using SOCPROG (Whitehead, 2009).

In addition, we followed Printes and Strier (1999) by dividing the frequency of copulations by the sum of focal observation hours for each male during the months that any copulations were observed (September, October, November and December 2004, January and February 2005). This method permits us to estimate the variation in the rates of male sexual activity relative to the amount of time each male was observed during the mating season months. We employed BioEstat 3.0 software for data analysis (Ayres et al., 2003). Non-parametric statistics Mann-Whitney was used for comparisons of samples. Significance was set at \( P < 0.05 \) (two-tailed probabilities).

2 Results

2.1 Inter-individual distances

Analysis of the associations among all subadult and adult group members in the Nadir group revealed five distinct clusters (CCC = 0.94; \( Q = 0.50; AI = 0.01 \)). Two clusters of males were apparent; some adult males were more connected to the females and immatures than to other adult males, who were more connected to each other than to females and immatures (Fig. 1A and 2A).

The division of males into two cliques was more evident when we analyzed only male-male associations (Fig. 1B and 2B; CCC = 0.97; \( Q = 0.49; AI = 0.03 \)). Adult males in the Nadir group could be segregated into two cliques, as follows: “N males” (BU-N, DA-N, IN-N, UL-N, BT-N, DP-N, FB-N, JE-N, KD-N); and “MU males” (GO-N, JU-N, OT-N, PI-N, QUI-N, RD-N, SN-N, VE-N). We found significant differences in the patterns of associations between and within cliques (Mantel test: \( r = 0.77, P = 1 \)). Association frequencies within cliques were significantly higher than those between cliques (Table 2).

2.2 Affiliative interactions

Similar to male spatial associations, the male affiliative network could be divided into two cliques (CCC = 0.85; \( Q = 0.48; AI = 0.03 \); Fig. 1C and 2C). A total of 193 dyadic affiliative interactions between adult males was observed during the focal subject samples, of which 6% (\( n = 12 \)) occurred between N-MU males, 38% (\( n = 73 \)) between N-N males, and 56% (\( n = 108 \)) between MU-MU males. There were significant differences in the pattern of affiliative behavior depending on male clique membership, as measured by the affiliative interaction index (Mantel test: \( r = 0.69, P = 1 \)). The affiliative interaction indices were significantly higher within cliques than between cliques (Table 2).
Fig. 1 The Average-linkage Cluster Dendrograms based on dyadic index values
A. Spatial associations for all adult and subadult individuals in the Nadir group. Five clusters are evident: 1) from RD-N to AM-N, 2) from BU-N to CI-N, 3) from BRIS to SB, 4) GA-N and INS, and 5) GLO-N and NTH-N. B. Spatial association for adult males only. C. Affiliative interactions for adult males only.

By contrast, rates of affiliative interactions (interactions per time spent in proximity) did not differ among dyads of males within and between cliques (Table 2; Mantel test: \( r = 0.09, P = 0.82 \)). However, this result was due to one N-MU dyad (males OT-N and JE-N) that was observed in proximity only twice and interacted affiliatively on both observations, thus resulting in an affiliation rate of 1.00. Closer examination of the distribution of affiliation rates showed that this dyad was the most extreme outlier of a total of six extreme outlier dyads of the 136 possible dyads (Fig. 3). When we excluded the most extreme outlier, we found significant differences in the dyadic rates of affiliative interactions depending on male clique membership (Mantel test: \( r = 0.23, P = 0.998 \)); the difference was even greater when all six of the extreme outliers were excluded (Mantel...
Fig. 2  Sociograms of association networks
A. Spatial association network for all adults and subadults. B. Spatial association network for adult males. C. Affiliative social network for adult males. D. Agonistic social network for adult males. The thickness of the lines represents the values of association and interactions index. The node positions were set by the spring embedding algorithm with node repulsion. White circle: adult females; white diamond: subadult females; white triangle: subadult males; black square: MU adult male; grey square: N adult male.
Table 2  Comparisons of dyadic spatial and social relationships within and between cliques

| Behavioral measure          | Cliques* | Mean ± SD | Median | Range   |
|----------------------------|----------|-----------|--------|---------|
| **Spatial association index** |          |           |        |         |
| MU-MU                      | 0.153±0.047 | 0.139     | 0.059–0.272 |
| N-N                        | 0.061±0.031 | 0.061     | 0.060–0.157 |
| N-MU                       | 0.003±0.005 | 0         | 0–0.02  |
| **Affiliative interaction index** |          |           |        |         |
| MU-MU                      | 0.063±0.038 | 0.055     | 0.01–0.14 |
| N-N                        | 0.049±0.039 | 0.04      | 0–0.17  |
| N-MU                       | 0.004±0.008 | 0         | 0–0.03  |
| **Agonistic interaction index** |          |           |        |         |
| MU-MU                      | 0.009±0.033 | 0         | 0–0.14  |
| N-N                        | 0.026±0.059 | 0         | 0–0.25  |
| N-MU                       | 0.042±0.09  | 0         | 0–0.50  |
| **Rates of affiliation**   |          |           |        |         |
| MU-MU                      | 0.04±0.049 | 0.03      | 0–0.24  |
| N-N                        | 0.055±0.081 | 0.03     | 0–0.38  |
| N-MU                       | 0.032±0.13  | 0         | 0–1     |
| **Corrected Rates of affiliation** |          |           |        |         |
| MU-MU                       | 0.036±0.03  | 0.03     | 0–0.12  |
| N-N                         | 0.036±0.04  | 0.03     | 0–0.13  |
| N-MU                        | 0.007±0.03  | 0         | 0–0.13  |
| N-MU†                      | 0.018±0.07  | 0         | 0–0.13  |
| **Rates of agonism**       |          |           |        |         |
| MU-MU                       | 0.000±0.001 | 0         | 0–0.0065 |
| N-N                        | 0.005±0.014 | 0         | 0–0.03  |
| N-MU                       | 0.010±0.01  | 0         | 0–0.5   |

*Bold font indicates significant differences were found in behavioral comparisons within versus between cliques, as described in the text.

* The number of dyads compared is as follows: MU-MU, n = 28 dyads; N-N, n = 36 dyads; N-MU, n = 72 dyads.

† The six extreme outlier dyads values were excluded from analyses (1 outlier among MU-MU dyads, 2 outliers among N-N dyads, 3 outliers among N-MU dyads).

++ Only the most extreme outlier (N-MU dyad) was excluded from the analysis.

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Fig. 3  Distribution of rates of affiliative interactions
Minimum and maximum values and quartiles are shown. The median and lower quartile are superimposed. Open circles indicate outliers. Asterisks indicate extreme outliers (i.e., values that exceed 3 inter-quartile intervals; Norusis, 1998), that may be legitimately excluded if they distort statistical inferences (Miller, 1993). See text and Table 2.

test: r = 0.42, P = 1). Rates of affiliative interactions were significantly higher within cliques than between cliques (Table 2).

Cooperation between MU and N males was observed during three of the 26 intergroup encounters that occurred when males from both cliques were traveling together. In one of these cases, MU and N males chased some individuals of another neighboring multi-male/multi-female muriqui group. The other two encounters were restricted to vocalizations, and in both cases, MU and N males stayed in close proximity to one another and emitted agonistic vocalizations in response to another bisexual group. In 88% (n = 23) of the intergroup encounter events one of the two cliques was out of view of the observer. Of the intergroup encounters involving members of a single clique, 60% (n = 14) involved only N males, and 40% (n = 9) involved only MU males.
2.3 Agonistic interactions

There were no significant differences in the patterns of agonism between and within cliques (Mantel test: $r = -0.16$, $P = 0.028$), but of the 32 dyadic agonistic interactions in which the identities of both participants were observed, 72% ($n = 23$) occurred between N-MU males, 22% ($n = 7$) between N-N males, and 6% ($n = 2$) between MU-MU males. MU males were the recipients of agonism in 96% ($n = 22$) of the interactions involving N-MU dyads. Rates of agonistic interactions per time spent in proximity did not differ among dyads of males within and between cliques (Table 2; Mantel test: $r = -0.08$, $P = 0.261$). In the sociogram of agonistic relationships (Fig. 2D), individuals of the same clique were not grouped together as they were in the sociogram of affiliative relationships.

An additional 21 agonistic interactions were observed in which multiple males from different cliques participated in the interactions but specific dyads could not be distinguished. Nonetheless, in all 21 cases, N males jointly threatened one or more of the MU males, who either were evicted by N males or else avoided them. For example, on 21 May 2004, MU males and some Nadir group females were feeding in the same tree, when some N males approached quickly while emitting agonistic vocalizations. The MU males left the feeding tree and moved away from the N males. On 7 October 2004, three MU males descended to the ground, traveling and looking around carefully after some N males approached them; on 12 October 2004, one MU male exhibited the same avoidance behavior.

2.4 Copulations

We observed a total of 63 copulations in Nadir group during this study period. Thirty-nine of these (62%) involved N males, and 24 (38%) involved MU males. N males had an average frequency of $4.3 \pm 3.0$ (mean $\pm$ SD) copulations per individual (median = 4, range = 1–11), and MU males had an average frequency of $3.0 \pm 2.9$ copulations per individual (median = 2, range = 0–8). N males copulated with an average of $3.0 \pm 1.2$ different females (median = 3, range = 1–5), and MU males with an average of $2.0 \pm 1.2$ different females in the Nadir group (median = 2, range = 1–4).

Estimated copulation rates averaged $0.63 \pm 0.41$ copulations per hour of observation (median = 0.7) for N males, and $0.44 \pm 0.40$ copulations per hour of observation (median = 0.3) for MU males. There were no significant differences in the estimated copulation rates per hour of observation of N males and MU males ($n_1 = 9$, $n_2 = 8$; Mann-Whitney test: $Z = 0.818$, $P = 0.413$), and copulation rate was not related to clique membership (Mantel test: $r = -0.07$, $P = 0.095$). Two-thirds ($n = 16$) of copulations by MU males were observed when they were associating with the mixed Nadir group, and 33.3% ($n = 8$) occurred when the couple was out of view of other members of the Nadir group. All copulations of N males were recorded when they were in the mixed large group.

3 Discussion

Our hypothesis that the social preferences of northern muriquis would represent social subgroups, or cliques, was supported by our findings. We observed two distinct patterns of male social interactions corresponding to within-versus between-cliques dynamics. Specifically, within-clique interactions were marked by relatively high levels of spatial proximity and affiliative interactions. By contrast, between-clique interactions were characterized by clear spatial segregation and low levels (frequencies and rates) of affiliative interactions. Previous analyses of dyadic relationships among male northern muriquis at the RPPN-FMA have shown that some male dyads have stronger affiliative relationships than others (Strier, 1997a; Strier et al., 2002). However, differentiated relationships at the level of male cliques have not previously been described.

Patterns of spatial association and affiliative interactions might indicate social preferences and correspond to the strength of relationships among group members (Hinde, 1983; Silk, 2002; Beazanson et al., 2008; Ramos-Fernández et al., 2009). However, it is difficult to identify what influenced the individual social preferences that defined their membership in the MU and N cliques. In other species, factors such as age, rank, and kinship have been found to explain variation in the strength of social bonds (Silk, 2002; Chapais, 2006; Van Horn et al., 2007). For example, Mitani and Amsler (2003) suggested that the social integration of adolescent male chimpanzees into the adult male network may be difficult in the unusually large Ngogo community at Kibale National Park, Uganda, and therefore the males’ subgrouping behavior may be a consequence of both the large numbers of males and of age segregation. Previous studies of male northern muriquis social relationships concluded that older adult males were more valued as associates by younger adult males on the basis of age-biases in the dynamics underlying male spatial relationships (Strier, 1997a; Strier et al., 2002). Thus, although we do not know the ages of MU and N males, there is reason to suspect that age might be an important factor in determining the structure of male social groups.
factor underlying male muriqui subgrouping behavior as it is thought to be in chimpanzees.

Our findings of low rates of dyadic agonistic interactions among males within and between cliques in the Nadir group are similar to those described previously in this population (Mendes, 1990; Strier, 1994, 1997a; Strier et al., 2000, 2002). However, in contrast to previous studies, we found that males in the MU clique appeared to be subordinate to those in the N clique. On most occasions, N males directed agonism towards MU males, causing the latter to retreat to the periphery of the group. Considering the effect of social status on foraging success and levels of food intake in other species (Janson, 1985, 1990), MU males might be expected to have experienced some ecological stress.

Despite the apparent social dominance of N males over MU males, males from both cliques were observed to cooperate in encounters against another social group when the cliques were traveling together. This cooperation between male cliques may serve the same function, cooperative female defense, attributed to male alliances in other species of mammals (e.g. chimpanzees: Watts, 1998; bottlenose dolphins: Connor et al., 1992, 2000; Lusseau, 2007; lions, Panthera leo: Packer et al., 1991). Although rare, such cooperation between MU and N males in intergroup encounters might benefit members of both cliques if together they can defend their group of females against males from other groups more effectively than either of the cliques could have done alone (Strier, 1992, 1994). At the RPPN-FMA, the value of cooperating with related allies may be increased due to the frequency of intergroup encounters in an increasingly saturated habitat (Strier, 2008).

The similarities in the copulation patterns of males from both cliques are consistent with our hypothesis that males benefit by acting collectively during intergroup encounters. Males of both cliques attained comparable rates of copulation, and consistent with previous studies (i.e., Strier, 1997b; Possamai et al., 2007) we did not observe overt competition among male cliques for access to fertile females. Indeed, on one occasion, an MU male (PI-N) copulated while an N male (FB-N) was resting within seven meters, but did not display any agonistic behavior.

In conclusion, we found that male northern muriqui relationships were structured above the dyadic level into cliques, which may represent a higher order level of social bond within groups. We hypothesized that the formation of subgroups was driven by social preferences, as observed in other primates (Bezanson et al., 2008; Sueur et al., 2009, 2010) and mammals (Wittenmyer et al., 2005; Archie et al., 2006; Lusseau et al., 2006; Popa-Lisseau et al., 2008). Affiliative bonds above the level of dyads might be common in many animal societies, and might be more evident in specific ecological and demographic conditions. For example, affiliative subgroups might emerge naturally when group size increases. Comparative data from other groups and populations of northern muriquis under different ecological and demographic conditions are necessary to evaluate whether the intragroup social dynamics we observed among males are typical or atypical for this species.

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References

Altmann J, 1974. Observational study of behaviour: Sampling methods. Behaviour 49: 227–267.

Archie EA, Moss CJ, Alberts SC, 2006. The ties that bind: Genetic relatedness predicts the fission and fusion of groups in wild African elephants Loxodonta africana. Proc. R. Soc. B. 273: 513–522.

Ayres M, Ayres JrM, Ayres DL, Santos AS, 2003. BioEstat 3.0: aplicações estatísticas nas áreas das ciências biomédicas. Belém: Sociedade Civil Mamirauá.

Bezanson M, Garber PA, Murphy JT, Premo LS, 2008. Patterns of subgrouping and spatial affiliation in a community of mantled howling monkeys Alouatta palliata. Am. J. Primatol. 70: 282–293.

Borgatti SP, 2002. Net Draw: Graph Visualization Software. Harvard: Analytic Technologies.

Boubli JP, Tokuda M, Possamai C, Fidelis J, Guedes D et al., 2005. Dinâmica intergrupal de muriquis-do-norte, Brachyteles hypoxanthus, na Estação Biológica de Caratinga, MG: o comportamento de uma unidade de machos (all male band) no vale do Jaó. Livro de Resumos XI Congresso Brasileiro de Primatologia: 41.

Bridge PD, 1993. Classification. In: Fry JC ed. Biological Data Analysis. Oxford, UK: Oxford University Press, 219–242.

Cairns SJ, Schwager SJ, 1987. A comparison of association indi-
ces. Anim. Behav. 35: 1454–1469
Chapais B. 2006. Kinship, competence and cooperation in primates. In: Kappeler PM, van Schaik CP ed. Cooperation in Primates and Humans: Mechanisms and Evolution. Berlin: Springer, 47–64.
Connor RC, Smolker RA, Richards AF, 1992. Two levels of alliance formation among male bottlenose dolphins (Tursiops sp.). Proc. Natl Acad. Sci. USA 89:987–990.
Connor RC, Wells RS, Mann J, Read AJ, 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. In: Mann J, Conner RC, Tyack PL, Whitehead H ed. Cetacean Societies: Field Studies of Dolphins and Whales. Chicago: University of Chicago Press, 91–126.
Connor RC, Watson-Capps JJ, Sherwin WB, Krützen M, 2011. A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins (Tursiops sp.). Biol. Lett. 7: 623–626.
Croft DP, James R, Krause J, 2008. Exploring Animal Social Networks. Princeton, NJ: Princeton University Press.
Croft DP, Madden J, Franks DW, James R, 2011. Hypothesis testing in animal social networks. Trends in Ecology and Evolution 26 (10): 502–507.
Dias LG, Strier KB, 2003. Effects of group size on ranging patterns in Brachyteles arachnoides hypoxanthus. Int. J. Primatol. 24: 209–221.
Hinde RA, 1976. Interactions, relationships and social structure. Man 11: 1–17
Hinde RA, 1983. Primate Social Relationships. Oxford: Blackwell Scientific Publications.
Janson CH, 1985. Aggressive competition and individual food consumption in the brown capuchin monkey Cebus apella. Behav. Ecol. Sociobiol. 18:125-138.
Janson CH, 1990. Ecological consequences of individual spatial choice in foraging brown capuchin monkeys Cebus apella. Anim. Behav. 38:922–934.
Kappeler PM, van Schaik CP, 2002. Evolution of primate social systems. Int. J. Primatol. 23: 707–740.
Kudo H, Dunbar RMJ, 2001. Neocortex size and social network size in primates. Anim. Behav. 61: 711–722.
Lusseau D, 2007. Why are male social relationships complex in the Doubtful Sound bottlenose dolphin population? PLoS ONE 2(4): e348. doi10.1371/journal.pone.0000348
Lusseau D, Wilson B, Hammond PS, Garellick K, Durban JW et al., 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. J. Anim. Ecol. 75: 14–24.
Lusseau D, Whitehead H, Gero S, 2008. Incorporating uncertainty into the study of animal social networks. Anim. Behav. 75: 1809–1815.
Madden JR, Drewa JA, Pearce GP, Clutton-Brock TH, 2009. The social network structure of a wild meerkat population: 2. Intragroup interactions. Behav. Ecol. Sociobiol. 64: 81–95.
Manno TG, 2008. Social networking in the Columbian ground squirrel Spermophilus columbianus. Anim. Behav. 75: 1221–1228.
Mendes FDC, 1990. Aflição e hierarquia no muriqui: o grupo Matão de Caratinga. Master’s thesis. University of São Paulo, São Paulo.
Miller JN, 1993. Outliers in experimental data and their treatment. Analyst 118: 455–461.
Mitani J, Amsler S, 2003. Social and spatial aspects of male subgrouping in a community of wild chimpanzees. Behaviour 140: 869–884.
Moss CJ, Poole J, 1983. Relationships and social structure of African elephants. In: Hinde RA ed. Primate Social Relationships: An Integrated Approach. Oxford: Blackwell Scientific, 315–325.
Newman MEJ, 2004. Analysis of weighted networks. Phys. Rev. E 70: 056131
Norusis MJ, 1998. SPSS 8.0 Guide to data analysis. Upper Saddle River, New Jersey: Prentice-Hall.
Packer C, Gilbert DA, Pusey AE, O’Brien SJ, 1991. A molecular genetic analysis of kinship and co-operation in African lions. Nature 351: 562–565.
Popa-Lisseanu AG, Bontadina F, Mora O, Ibanez C, 2008. Highly structured fission-fusion societies in an aerial-hawking carnivorous bat. Anim. Behav. 75: 471–482.
Possamai CB, Young RJ, Mendes SL, Strier KB, 2007. Socio-sexual behavior of female northern muriquis Brachyteles hypoxanthus. Am. J. Primatol. 69: 766–776.
Printes RC, Strier KB, 1999. Behavioral correlates of dispersal in female muriquis Brachyteles arachnoides. Int. J. Primatol. 20: 941–960.
Ramos-Fernández G, Boyer D, Aureli F, Vick LG, 2009. Association networks in spider monkeys Ateles Geoffroyi. Behav. Ecol. Sociobiol. 63: 999–1013.
Schreier AL, Swedell L, 2009. The fourth level of social structure in a multi-level society: Ecological and social functions of clans in hamadryas baboons. Am. J. Primatol. 71: 948–955.
Scott J, Lockard JS, 2007. Competition coalitions and conflict interventions among captive female gorillas. Int. J. Primatol. 28: 761–781.
Silk JB, 2002. Kin selection in primate groups. Int. J. Primatol. 23: 849–875.
Strier KB, 1990. New World primates, new frontiers: insights from the woolly spider monkey, or muriqui Brachyteles arachnoides. Int. J. Primatol. 11: 7–19.
Strier KB, 1992. Causes and consequences of nonaggression in the woolly spider monkey, or muriqui Brachyteles arachnoides. In: Silverberg J, Gray P ed. Aggression and Peacefulness in Humans and Others Primates. New York: Oxford University Press, 100–116.
Strier KB, 1994. Brotherhoods among atelins: Kinship, affiliation, and competition. Behaviour 130: 151–167.
Strier KB, 1997a. Subtle cues of social relations in male muriqui...
monkeys *Brachyteles arachnoides*. In: Kinzey WG ed. New World Primates: Ecology, Evolution, and Behavior. New York: Aldine de Gruyter, 109–118.

Strier KB, 1997b. Mate preferences of wild muriqui monkeys *Brachyteles arachnoides*: Reproductive and social correlates. *Folia Primatol.* 68: 120–133.

Strier KB, 2008. The effects of kin on primate life histories. *Annu. Rev. Anthropol.* 37: 21–36.

Strier KB, Mendes FDC, Rimoli J, Rimoli AO, 1993. Demography and social structure of one group of muriquis *Brachyteles arachnoides*. *Int. J. Primatol.* 14: 513–526.

Strier KB, Carvalho DS, Bejar NO, 2000. Prescription for peacefulness. In: Aureli F, de Waal FBM ed. Natural Conflict Resolution. Los Angeles: University of California Press, 315–317.

Strier KB, Dib LT, Figueira JEC, 2002. Social dynamics of male muriquis *Brachyteles arachnoides hypoxanthus*. *Behaviour* 139: 315–342.

Strier KB, Boubli JP, Possamai CB, Mendes SL, 2006. Population demography of northern murikus *Brachyteles hypoxanthus* at the Estação Biológica de Caratinga/Reserva Particular do Patrimônio Natural-Feliciano Miguel Abdala, Minas Gerais, Brazil. *Am. J. Phys. Anthropol.* 130: 227–237.

Sueur C, Petit O, Deneubourg JL, 2009. Selective mimetism at departure in collective movements of *Macaca tonkeana*: A theoretical and experimental approach. *Anim. Behav.* 78: 1087–1095.

Sueur C, Petit O, Deneubourg JL, 2010. Short-term group fission processes in macaques: A social networking approach. *J. Exp. Biol.* 213: 1338–1346.

Sueur C, Jacobs A, Ambland F, Petit O, King AJ, 2011. How can social network analysis improve the study of primate behavior? *Int. J. Primatol.* 71:1–17.

Sussman RW, Garber PA, Cheverud JM, 2005. Importance of cooperation and affiliation in the evolution of primate sociality. *Nat. J. Phys. Anthropol.* 128: 84–97.

Van Horn R, Buchan J, Altman J, Alberts S, 2007. Divided destinies: Group choice by female savannah baboons during social group fission. *Behav. Ecol. Sociobiol.* 61:1823–1837.

Wilson EO, 1975. *Sociobiology: The New Synthesis*. Cambridge, Massachusetts: Belknap Press.