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Network Analysis as A Tool to Understand Social Development in Spider Monkeys

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Abstract

The emerging field of network science has demonstrated that an individual's connectedness within their social network has cascading effects to other dimensions of life. Like humans, spider monkeys live in societies with high fission–fusion dynamics, and are remarkably social. Social network analysis (SNA) is a powerful tool for quantifying connections that may vary as a function of initiating or receiving social behaviors, which has been described as shifting social roles. In primatology, the SNA literature is dominated by work in catarrhines, and has yet to be applied to the study of development in a

platyrrhine model. Here, SNA was utilized in combination with R-Index social role calculation to characterize social interaction patterns in juvenile and adult Colombian spider monkeys (*Ateles fusciceps rufiventris*). Connections were examined across five behaviors: embrace, face-embrace, grooming, agonism, and tail-wrapping from 186 hr of observation and four network metrics. Mann–Whitney *U* tests were utilized to determine differences between adult and juvenile social network patterns for each behavior. Face-embrace emerged as the behavior with different network patterns for adults and juveniles for every network metric. With regard to social role, juveniles were receivers, not initiators, for embrace, face-embrace, and grooming ($p < .05$). Network and social role differences are discussed in light of social development and aspects of the different behaviors.

1 INTRODUCTION

The burgeoning field of network science demonstrates that social relationships emerge from structural connections that together form a social network. Throughout the life of an individual, these connections change dynamically, and an individual's connectedness within its social networks has cascading effects to other dimensions of life (Hawkley & Capitanio, **2015**; Ponzi, Zilioli, Mehta, Maslov, & Watson, **2016**; Wrzus, Hänel, Wagner, & Neyer, **2013**). Among primates, a social network is most readily measured by observing pairwise interactions that are used to represent links in the social network. These links are quantified and graphically represented through social network analysis (SNA; Wasserman & Faust, **1994**). The application of SNA within primatology has a long history (Beisner, Jackson, Cameron, & McCowan, **2011**; Flack, Girvan, De Waal, & Krakauer, **2006**; McCowan, Anderson, Heagarty, & Cameron, **2008**; McCowan et al., **2011**; Sade, **1972**; Sade, Altmann, Loy, Hausfater, & Breuggeman, **1988**), but only adopted new software platforms for complex network analytics within the last decade (Brent, Lehmann, & Ramos-Fernández, **2011**; Puga-Gonzalez, Sosa, & Sueur, **2019**). The application of SNA within areas of primatology has included documenting patterns of disease transmission (Gómez, Nunn, & Verdú, **2013**; Griffin & Nunn, **2012**; MacIntosh et al., **2012**; Nunn, **2012**; Rimbach et al., **2015**; Rushmore et al., **2013**), characterizing the structure of adult social interactions (Barrett, Henzi, & Lusseau, **2012**; Kasper & Voelkl, **2009**; Lehmann & Ross, **2011**; Sueur, Jacobs, Amblard, Petit, & King, **2011**), modeling fission–fusion dynamics (Ramos-Fernández & Morales, **2014**; Ramos-Fernández, Boyer, Aureli, & Vick, **2009**; Shimooka, **2015**; Smith-Aguilar, Aureli, Busia, Schaffner, & Ramos-Fernández, **2019**; Wakefield, **2013**), and assessing structure of captive social groups (Clark, **2011**; Dufour, Sueur, Whiten, & Buchanan-Smith, **2011**; Levé, Sueur, Petit, Matsuzawa, & Hirata, **2016**; Rodrigues & Boeving, **2019**; Schel et al., **2013**). These important studies apply established network techniques with roots in the mathematical field of graph theory across multiple different software platforms and network metrics with the common goal of understanding the structure and organization of social phenomena.

Given the utility of SNA to characterize the organization of social processes, and the focus of social development on describing the emergence of these social processes, SNA may be particularly useful in studying social development. An individual's social network position can provide opportunities or constraints on social behavior. Network analytics provides the tools to unpack how different types of interactions and connections are linked to network position. The concept of centrality has been widely applied to characterize dimensions of social connection using centrality network metrics (c.f., Brent et al., **2011**). Centrality measures comprise a group of direct and indirect social network metrics. Degree

centrality measures the number of direct connections and can be used to measure actual social participation within a network. Betweenness centrality is an indirect measure that indicates the control or prominence a node may have within a network. Closeness centrality measures the cumulative number of shortest paths to reach other nodes. A node high in closeness has a short distance to other nodes and achieves a more efficient network. As a whole, these three centrality measures are derived from the dyadic level, but measures assessing higher order sub-groupings require assessment of triadic connections. Clustering coefficient is a community detection metric that measures the tendency for nodes to cluster together, and can be utilized to assess group cohesion. Employed in conjunction, these social network metrics allow for a multidimensional assessment of social network development.

These four network metrics, and others, have specifically been applied to social development studies in chimpanzees and catarrhine monkeys. Shimada and Sueur (2014) reported that juvenile chimpanzees were fully integrated into social play networks, but not grooming and alliance formation networks. They used the network metrics of degree centrality, clustering coefficient, density, and diameter. This finding contrasts with research in vervet monkeys where juveniles engage with multiple partners and integrate themselves into grooming networks early in development (Jarrett, Bonnell, Young, Barrett, & Henzi, 2018), a pattern the authors characterized by differentiating occurrences given and received by individuals. Liao, Sosa, Wu, and Zhang (2018) utilized measures of centrality (degree, betweenness, and eigenvector) in conjunction with a social role measure to assess differences in initiating and receiving interactions and found that juvenile rhesus macaques achieved network centrality due to high frequencies of initiating grooming interactions. Thus, primate developmental patterns vary across species and SNA can be utilized to elucidate the structure of these differences. However, a network approach has not been used to characterize the development of social interaction patterns in platyrrhines or strepsirrhines, which could be especially important for understanding how patterns vary across more distantly related species. Moreover, studying species that are distantly related, but socio-ecologically similar could provide an opportunity to identify convergent evolution. This opportunity may be possible in studying a platyrrhine species such as spider monkeys given that they live in societies with high levels of fission–fusion social dynamics.

Only a handful of primate species exhibit highly fluid fission–fusion dynamics, including humans, chimpanzees, and spider monkeys (Aureli et al., 2008; Chapman, Chapman, & Wrangham, 1995; Symington, 1990). Such fission–fusion dynamics allow spider monkeys to flexibly cope with social and ecological challenges (Chapman, 1990; Chapman et al., 1995; Rodrigues, 2017; Schaffner, Rebecchini, Ramos-Fernandez, Vick, & Aureli, 2012; Symington, 1990). Fission–fusion is characterized by an ebb and flow of splitting into subgroups and reuniting, which is in stark contrast to cohesive societies (Aureli et al., 2008). Along with this ebb and flow of social movement comes greater likelihood of variation in social interaction partners and low stability in social hierarchy. In addition, spider monkeys are characterized by male philopatry with female dispersal, and sex-segregated association patterns (Chapman, 1990; Di Fiore & Campbell, 2007; Fedigan & Baxter, 1984; Hartwell, Notman, Bonenfant, & Pavelka, 2014; Rodrigues, 2014; Symington, 1990). In wild foraging contexts, older, resident individuals are more likely to be followed, and males, as well as central individuals, lead followers to new patches (Palacios-Romo, Castellanos, & Ramos-Fernandez, 2019). In the wild, such relationships may also assist females in learning the locations of key fruit patches.

Although spider monkeys are more phylogenetically distant from humans compared with the more widely studied chimpanzees and catarrhine monkeys (Eizirik, Murphy, Springer, & O'Brien, **2004**), it is the strong similarity to human social dynamics that makes them an ideal species to investigate social processes, particularly with regard to evolutionary and developmental convergence. Furthermore, spider monkeys have a long developmental period relative to their body size, which may be related to the need to develop social and ecological competence (Milton & Hopkins, **2006**; Rodrigues, **2007b**; Schmitt, **2010**; Vick, **2008**). Spider monkeys engage in broad social behaviors that are known to occur in other primate species, such as grooming, but also engage in species-specific social interactions (Klein & Klein, **1971**; Schaffner & Aureli, **2005**). These interactions are characterized as multimodal contact gestures, and include embrace, face-embrace, and tail-wrapping (Klein & Klein, **1971**). Behaviors such as grooming may be related to social bonding, which is typical in other primates (di Bitetti, **1997**; Dunbar, **1991**; Henzi & Barrett, **1999**), whereas multimodal contact gestures may play a role in signaling benign intent or managing social risks (Aureli & Schaffner, **2007**; Boeving & Nelson, **2018**; Klein & Klein, **1971**; Rebecchini, Schaffner, & Aureli, **2011**; Schaffner & Aureli, **2005**; Slater, Schaffner, & Aureli, **2007**). No study to date has used a network approach to examine the development of these social behaviors in spider monkeys.

Previous work examining age-related differences in grooming patterns in spider monkeys indicates that juveniles receive significantly more interactions than they initiate (Ahumada, **1992**). However, juveniles' roles in social networks beyond grooming are still not well understood. Here, we employed network analytics to characterize developmental differences in social dynamics in a group of Colombian spider monkeys across five behaviors (i.e., grooming, embrace, face-embrace, tail-wrapping, and agonism). For each behavior, we assessed age-related differences across four social network metrics that represent different aspects of social life. Degree centrality was chosen as a direct measure of interactions, representing participation in behavior. Betweenness centrality was chosen as an indirect measure that represents an individual as a social broker or facilitator; those with high scores typically bridge connections to individuals on the periphery of a network to those more centrally connected. Closeness centrality was chosen as a measure of efficiency since individuals with high closeness values can quickly interact with others without going through other intermediaries. Clustering coefficient was chosen as a measure of community detection because it allows for the assessment of individuals that tend to cluster together and are thus interconnected. This measure can be utilized to determine cohesion in behaviors (Makagon, McCowan, & Mench, **2012**). Given previous literature from spider monkey and chimpanzee grooming interactions, we hypothesized that overall juvenile and adult grooming networks would differ, and predicted that across all network metrics, adults would be more connected, achieving higher centrality and clustering coefficient values than juveniles for grooming. As there is limited evidence regarding patterns of agonism and multimodal contact gestures among juvenile spider monkeys, we then explored age and sex-based patterns within the four network metrics for agonism, tail-wrapping, face-embraces, and embraces. Additionally, we explored the social roles juveniles and adults play in social networks. We define social role in terms of sequential processes, meaning that for every interaction, there is both an initiator and a receiver. Given that degree centrality is a direct measure of social participation, in-degree (interactions received) and out-degree (interactions initiated) were computed for all behaviors and subjected to a social role R-Index calculation to determine if adults and juveniles play different social roles within the

networks. For grooming, we predicted the low frequency of initiating interactions would influence degree of social network connectedness such that juveniles would not achieve centrality. Finally, to explore potential between-behavior relationships, we examined dyadic interaction patterns to determine if individuals interacted across multiple behaviors, and if there were overall differences in these patterns between juvenile and adult spider monkeys.

2 METHODS

2.1 Subjects

Social interactive data were collected from dyads (i.e., two monkeys interacting) May 2015 to August 2015 from 15 Colombian spider monkeys (*Ateles fusciceps rufiventris*). Monkeys were housed with group members in an outdoor enclosure with adjoining rooms in view of the public at the wildlife park Monkey Jungle in Miami, FL. The main enclosure measured 8.84 m × 3.96 m × 4.47 m. The adjoining room measured 3.30 m × 1.92 m × 1.77 m and was connected directly to an indoor night house, which measured 3.30 m × 1.09 m × 2.72 m. The group consisted of nine females and six males aged <1 year to 48 years old. Paternal kinship was not known, however four adult females in the group were known maternal kin. Mints is the mother of Sunday, Mason, and Jasper. CJ is the mother of Dusky, Cleo, Uva, and Molly. Molly is the mother of Marley. The enclosure was equipped with multiple horizontal and vertical structures for the monkeys. Because spider monkeys reach sexual maturity age at 5 years (Aureli & Schaffner, 2010), monkeys <5 years of age were classified as juveniles ($N = 4$) and monkeys >5 years of age were classified as adults ($N = 11$). One monkey was wild-caught and the remaining monkeys were captive-born. Water was freely available. Monkeys were fed commercial chow (Purina LabDiet® 5045) and a mixture of fruits and vegetables.

2.2 Procedures

The study followed a three-step methodological procedure including behavioral data collection, utilization of network software and computation, and social role calculation. A pipeline of these procedures is presented in Figure 1.

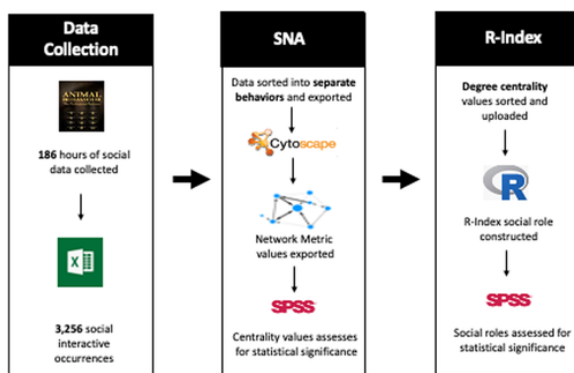


Figure 1 The three-step method and data pipeline is presented. The first step is behavioral data collection, second is social network analysis, and the third is the social role calculation. The substeps contained within are pictured

2.3 Behavioral data collection

Data were collected using Apple iPod 5th generation with the Animal Behaviour Pro mobile iOS application (Newton-Fisher, 2012). The application was programmed with the behavioral ethogram

such that actor, behavior, and receiver were recorded upon occurrence as three data points. Data were collected using the continuous sampling method for 90-minute sessions, across three intervals throughout the day: 9:30 a.m.–11:30 a.m., 12:30 p.m.–2:00 p.m., and 4:00 p.m.–5:30 p.m. The All-Occurrence recording method was used given the interest in recording five targeted dyadic social behaviors across match-to-time samples. A subset of the data identifying side biases for three of the behaviors, and network-level differences in laterality have previously been reported but did not include juveniles (Boeving & Nelson, **2018**; Boeving, Belnap, & Nelson, **2017**). Embrace was recorded when individuals wrapped arms around the body, placing the head down toward the shoulder or trunk of the body, and was often accompanied with the whinny vocalization. Face-embrace was recorded when individuals articulated their heads such that their cheeks touched. Tail-wrapping was recorded when individuals locomoted side-by-side or one behind the other with tails intertwined. Grooming was recorded when individuals used the hands or mouth to pick or mouth the fur of another individual. Agonism was recorded when individuals attempted or carried out biting, scratching, or noncontact aggression such as chasing (Klein & Klein, **1971**).

2.4 Social network construction and analysis

All data sessions were exported and pooled into Excel.csv files. These files were then uploaded to Cytoscape (<http://www.cytoscape.com>; Version 3.7.1; Shannon et al., **2003**), an open source software project for modeling interaction networks. For each behavior, one complete network measuring the direction of the interactions (totaling five networks) were computed. The network metric of *degree centrality* was chosen given our interest in creating social networks from observable actions representing participation within a social network, and degree of connectedness. The network metric of *betweenness centrality* is an indirect measure of sociality, reflecting the control a node exerts over the interactions of other nodes and is reported with values between 0 and 1. We included this network metric to help determine within network differences of social facilitation between juveniles and adults across the five behaviors. Weighted degree centrality provides a composite score of social interactions. Whole networks depict degree centrality for each individual, which can be further specified as initiated behaviors directed toward an individual (i.e., out-degree) and behaviors received from other individuals (i.e., in-degree). These composite scores were used to construct directed network graphs, and to determine if juveniles occupy a different position (e.g., central, peripheral) in each network compared to adults. The “Kamada-Kawai Algorithm” is a force-directed program that formats network graphs such that the most connected nodes are placed about the center of the graph, and least connected nodes are placed about the perimeter (Kamada & Kawai, **1989**). In addition, nodes (e.g., individuals) differ in size, such that nodes with high degree centrality values are larger, and nodes with lower degree values are smaller. Individuals with the highest betweenness centrality scores were denoted with a diamond shape.

Edge weights, denoted by thick lines, indicate a high-frequency occurrence of a behavior between two individuals and thin edges denote few occurrences of a given behavior between two individuals. The edge weights are meant to indicate frequency of interaction among dyads relative to the rest of the group within a given behavior, not between behaviors relative to total occurrence. The direction of interactions was represented by weighted arrows connecting edges and nodes between two individuals. Large arrows reflect high occurrences of initiating or receiving and small arrows reflect lower occurrences of initiating and receiving. Within the following network results, adult nodes were

depicted with spheres, and juveniles were indicated with the outline of squares surrounding each juvenile node. Males were depicted as green and females were depicted as blue. Each node was labeled with a unique individual ID number (Table 1).

Table 1. In-degree (In) and out-degree (Out) centralities for each individual

ID name	Groom		Tail-wrap		Face-embrace		Embrace		Agonism	
	In	Out	In	Out	In	Out	In	Out	In	Out
1 Bon Jovio♂	9	68	49	9	48	16	129	102	0	1
2 Butcho♂	47	88	78	65	90	41	168	122	0	12
3 Carmelita	11	88	1	3	7	18	51	39	2	10
4 Cary*	62	11	3	1	0	0	30	10	13	1
5 CJ	–	–	6	12	5	15	55	98	1	4
6 Cleo	42	115	4	20	11	63	92	139	0	0
7 Dusky	43	10	14	6	4	27	103	102	3	0
8 Jasper*♂	13	4	5	2	2	0	20	3	2	0
9 Jeni*	15	4	5	0	0	0	20	6	7	0
10 Mason♂	11	33	70	93	85	65	189	197	1	11
11 Marley*♂	24	3	0	0	1	0	15	3	0	0
12 Mints	17	9	4	0	2	0	102	53	10	4
13 Molly	133	21	5	0	4	11	33	92	8	0
14 Sunday♂	47	23	129	128	64	23	167	171	1	4
15 Uva♂	25	8	79	105	44	86	271	232	6	7

* denotes juvenile monkeys.

2.5 Calculation of social role

An R-Index (RI) was calculated to further characterize each monkey's role in the five social networks of embrace, face-embrace, tail-wrapping, grooming, and agonism (Liao et al., **2018**). The RI uses weighted network metrics to determine the ratio of initiating versus receiving social behaviors, and sorts individuals into categories using the following formula: $RI = W_o / (W_i + W_o)$ where W_o is weighted out-degree (initiated the social behavior) and W_i is weighted in-degree (received the social behavior). RI scores greater than 0.5 indicate that the individual initiated more than received for a given behavior, and RI scores lower than 0.5 indicate that the individual received more than initiated for a given behavior. RI was not calculated for any monkey with 0 interactions (i.e., individual did not initiate or receive a given behavior). Mean (M) and standard deviation are also reported. RI analyses expand on the social network analyses by providing statistical analyses of initiating versus receiving ratios between juveniles and adults, and also between males and females.

2.6 Statistical analyses

Nonparametric tests were used to assess the statistical significance of degree centrality and R-Index scores, as data were not normally distributed. Within network differences for degree centrality and betweenness centrality between adults and juveniles were examined using independent-samples Mann–Whitney U tests. Independent-samples Mann–Whitney U tests were also used to examine the

effect of age (juvenile or adult) and sex (male or female) on RI scores for each social behavior. All analyses were conducted in IBM SPSS Statistics 20 with an α level of .05. We provide a measure of effect size (Cohen's r) for each nonparametric test to guide interpretations (Fritz, Morris, & Richler, **2012**). We suggest following the standard interpretation of $r = .2$ as a small effect, $r = .5$ as a medium effect, and $r = .8$ as a large effect (Cohen, **1988**).

Given that social network data are inherently nonindependent and often scaled, we also tested our data against a null model as suggested by Farine (**2017**). Null models resample and simulate randomized data sets for comparison, and are particularly relevant when examining patterns in social data for hypothesis testing. Applied within primate social networks, Rimbach et al. (**2015**) used a similar method of taking network data not following a normal distribution, testing it nonparametrically, and then testing it against a resampled null model. Using this permutation method, 10,000 randomizations of each social network were generated. These randomizations yielded a distribution of U -statistics that our data were tested against. A statistical test $p < .05$ resulted in rejection of the null. All permutation tests were conducted in R (R Core Team, **2019**).

Using SOCPROG, we utilized the Multiple Regression Quadratic Assignment Procedure (MRQAP) to examine relationship between behavioral matrices (compiled version 2.8; Whitehead, **2009**). MRQAP generates partial matrix correlations of multiple predictor matrices to a dependent matrix, where each partial correlation controls for the other predictor. We ran two MRQAP tests. For the first test, we examined how embrace, face-embrace, and tail-wrap were interrelated by setting face-embrace and tail-wrap as predictor variables and embrace as the dependent variable. For the second test, we examined how embrace, grooming, and agonism were interrelated by setting groom and agonism as the predictor variables and embrace as the dependent variable.

2.7 Ethical note

The DuMond Conservancy Institutional Animal Care and Use Committee approved the study (Protocol #2014-04). The work was performed in accordance with the ASP Principles for Ethical Treatment of Non-human Primates and the laws of the United States.

3 RESULTS

A total of 111 data collection sessions were completed, yielding a total of 3,256 social interactions. Of these, 1,433 were embrace, 369 were face-embrace, 449 were tail-wrapping, 950 were grooming, and 55 were agonism. A list of raw occurrences is provided in Table S1. Figure 2 depicts network graphs across behavior types, and degree centrality values are presented in Table 1. One adult (CJ) was not included in any grooming analyses given a large wound sustained from an injury that inflated grooming scores; her individual grooming occurrences (425 instances) were approximately four times the group average (103 instances), and were focused on the injury location.

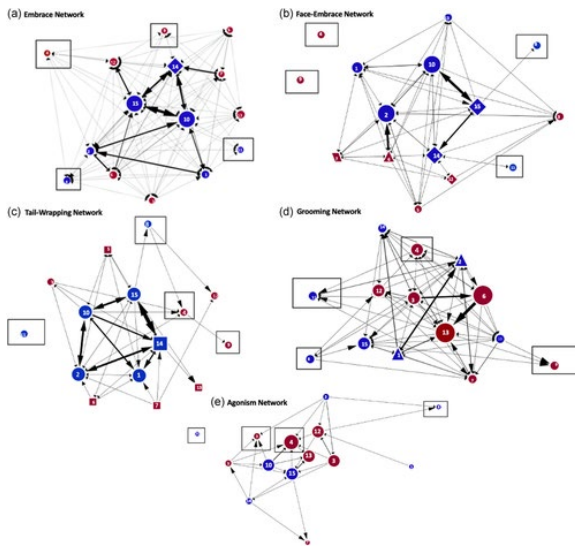


Figure 2 a-e) Social networks are presented for embrace, face-embrace, tail-wrapping grooming, and agonism. Thickness of edge denotes frequency of dyadic interactions, where thick edges are high frequencies and thin edges are low frequencies. Arrows depict if interactions occurred bi-directionally or uni-directionally. Size of arrows are small or large to indicate the balance of interactions between dyads where large indicate high directional frequency and small arrows denote smaller directional frequencies. Juvenile nodes are indicated with transparent boxes. Male nodes are blue, female nodes are red. Nodes positioned about the center of the graph are higher in degree centrality values while nodes on the periphery were low in degree centrality. Node size represents respective degree of connectedness where larger nodes achieved higher degree centrality values and smaller nodes achieved lower values. Degree centrality analyses for embrace, face-embrace, and tail-wrapping showed significant differences between adults and juveniles ($p < .05$) while grooming and agonism showed no age class differences. The degree centrality analyses showed significant differences between adults and juveniles for embrace, face-embrace, and grooming ($p < .05$) but not tail-wrapping or agonism. Nodes with the highest betweenness centrality values where there were significant differences (embrace and face-embrace) are represented with diamond shapes. Nodes with the highest closeness centrality scores where there were significant differences (face-embrace and grooming) are represented with triangles, and the highest clustering coefficient values where there were significant differences (face-embrace and tail-wrap) are represented with squares. For face-embrace, node 7 is represented as a parallelogram because they achieved the highest closeness and clustering coefficient values

3.1 Social network analysis

With regard to degree centrality, juveniles were not as highly connected within their social networks for embrace, face-embrace, and tail-wrapping as adult monkeys. Degree centrality values did not statistically differ for grooming or agonism. Mann–Whitney U tests determined the statistical significance of these within network differences such that juveniles had low degree centrality, and thus occupied peripheral network positions for embrace ($U = 0.05$; $p = .002$; $d = 0.7$; Figure **2a**), face-embrace ($U = 0$; $p = .002$; $d = 0.8$; Figure **2b**), and tail-wrapping ($U = 4$; $p = .01$; $d = 0.8$; Figure **2c**). There were no differences in degree centrality between juveniles and adults for grooming ($U = 1$; $p > .05$; Figure **2d**) or agonism ($U = 11$; $p > .05$; Figure **2e**). These findings can be visualized by inspecting the grooming and agonism network graphs. For grooming, Cary is positioned about the center of the graph, indicating high centrality. For agonism, both Cary and Jeni have centrality comparable to adults as they have similar network positions. A complete list of degree centrality values is provided in Table S1.

For betweenness centrality, Mann–Whitney U tests determined significant differences between juvenile and adults for embrace ($U = 5.5$; $p = .007$; $d = 0.8$) and face-embrace ($U = 0$; $p = .001$; $d = 0.8$). No statistical differences were detected for grooming, tail-wrapping, or agonism (all $p > .05$). For embrace, Sunday (0.09) achieved the highest betweenness score. Sunday (0.27) and Uva (0.17) achieved the highest face-embrace betweenness scores. Thus, these individuals acted as social facilitators within their respective networks, and their removal from a network would be significantly more likely to cause disconnection among nodes within a network. A complete listing of all betweenness centrality values may be found in Table S2.

For closeness centrality, Mann–Whitney U tests determined significant differences between juveniles and adults for face-embrace ($U = 2$; $p = .002$; $d = 0.8$) and grooming ($U = 3$; $p = .008$; $d = 0.8$) but not embrace, tail-wrapping, or agonism (all $p > .05$). Bon Jovi (1.0) and Butch (0.8) had the highest grooming closeness centrality scores. The juveniles ranged from 0 to 0.4. Cary (0.4) received the highest closeness score of the juveniles, with the score falling on the lower end of the score ranges for females (range 0.4–0.6). Cary is the eldest of the juveniles in the group. Cleo (0.6) and Dusky (0.7) received the highest face-embrace closeness scores. These individuals have more efficient networks due to being situated close to other nodes, requiring less interaction with peripheral nodes to achieve centrality. A complete list of all closeness centrality values may be found in Table S3.

For clustering coefficient, Mann–Whitney U tests determined significant differences between juveniles and adults for face-embrace ($U = 15.5$; $p = .04$; $d = 0.4$) and tail-wrapping ($U = 3$; $p = .003$; $d = 0.8$) but not for grooming, embrace, or agonism (all $p > .05$). Dusky (0.7) had the highest value for face-embrace. CJ, Cleo, Dusky, Molly, and Sunday all had the high values for tail-wrapping (all 0.5). Overall, adult values varied slightly but were relatively similar in range while juvenile values remained low. The results indicate that for face-embrace and tail-wrapping behaviors, adults form more interconnected cliques while the juveniles in this group do not. A complete list of all clustering coefficient values may be found in Table S4.

3.2 Social role calculation

R-Index scores by monkey, age class, and social behavior are given in Table 2. Figure 3 depicts the effects of age class on R-Index scores, and Figure 4 depicts the effects of sex on R-Index scores. $RI_{EMBRACE}$ ranged from 0.13 to 0.74 ($M = 0.42 \pm 0.17$). A Mann–Whitney U test found a significant effect of age class ($N = 15$; $U = 0$; $p = .001$) but did not find a significant effect of sex ($N = 15$; $U = 21$; $p = .463$) on embrace social role. Juveniles were receivers for the embrace behavior, whereas adults equally initiated and received. $RI_{FACE-EMBRACE}$ ranged from 0.00 to 0.87 ($M = 0.45 \pm 0.33$). Both female juveniles (Cary, Jeni) did not initiate or receive face-embrace, and therefore did not have a $RI_{FACE-EMBRACE}$ score. A Mann–Whitney U test found a marginal effect of age class ($N = 13$; $U = 1$; $p = .051$) and a significant effect of sex ($N = 13$; $U = 6$; $p = .035$) on face-embrace social role. Juveniles only received face-embrace, whereas adults ranged in the degree of receiving and initiating this behavior. With regard to sex differences, females largely initiated face-embrace, whereas males were more often receivers. $RI_{TAIL-WRAP}$ ranged from 0.00 to 0.83 ($M = 0.38 \pm 0.28$). One male juvenile (Marley) did not initiate or receive tail-wrap, and therefore did not have a $RI_{TAIL-WRAP}$ score. A Mann–Whitney U test did not find an effect of age class ($N = 14$; $U = 7$; $p = .170$) or sex ($N = 14$; $U = 27$; $p = .755$) on tail-wrap social role. RI_{GROOM} ranged from 0.11 to 0.89 ($M = 0.42 \pm 0.29$). One female adult (CJ) sustained an injury that

inflated her grooming values, and was removed from the analysis. A Mann–Whitney U test found an effect of age class on grooming ($N = 14$; $U = 5.50$; $p = .036$). Juveniles were receivers for grooming, whereas adults equally initiated and received grooming. There was no effect of sex ($N = 14$; $U = 29$; $p = .620$) on grooming social role. $RI_{AGONISM}$ ranged from 0.00 to 1.00 ($M = 0.48 \pm 0.42$). One male juvenile (Marley) and one adult female (Cleo) did not initiate or receive agonism, and therefore did not have a $RI_{AGONISM}$ score. A Mann–Whitney U test did not find an effect of age class ($N = 13$; $U = 4$; $p = .077$) or sex ($N = 13$; $U = 33$; $p = .101$) on agonism social role.

Table 2. R-Index scores by monkey, age class, and social behavior

Monkey	Age	$RI_{EMBRACE}$	$RI_{FACE-EMBRACE}$	$RI_{TAIL-WRAP}$	RI_{GROOM}	$RI_{AGONISM}$
<i>Males</i>						
1 Bon Jovi	Adult	0.44	0.25	0.16	0.88	1.00
2 Butch	Adult	0.42	0.31	0.45	0.65	1.00
10 Mason	Adult	0.51	0.43	0.57	0.75	0.92
14 Sunday	Adult	0.51	0.26	0.50	0.33	0.80
15 Uva	Adult	0.46	0.66	0.57	0.24	0.54
8 Jasper	Juvenile	0.13	0.00	0.29	0.24	0.00
11 Marley	Juvenile	0.17	0.00	–	0.11	–
<i>Females</i>						
3 Carmelita	Adult	0.43	0.72	0.75	0.89	0.83
5 CJ	Adult	0.64	0.75	0.67	–	0.80
6 Cleo	Adult	0.60	0.85	0.83	0.73	–
7 Dusky	Adult	0.50	0.87	0.30	0.19	0.00
12 Mints	Adult	0.34	0.00	0.00	0.35	0.29
13 Molly	Adult	0.74	0.73	0.00	0.14	0.00
4 Cary	Juvenile	0.25	–	0.25	0.15	0.07
9 Jeni	Juvenile	0.23	–	0.00	0.21	0.00

Note: See text for calculation of R-Index scores.

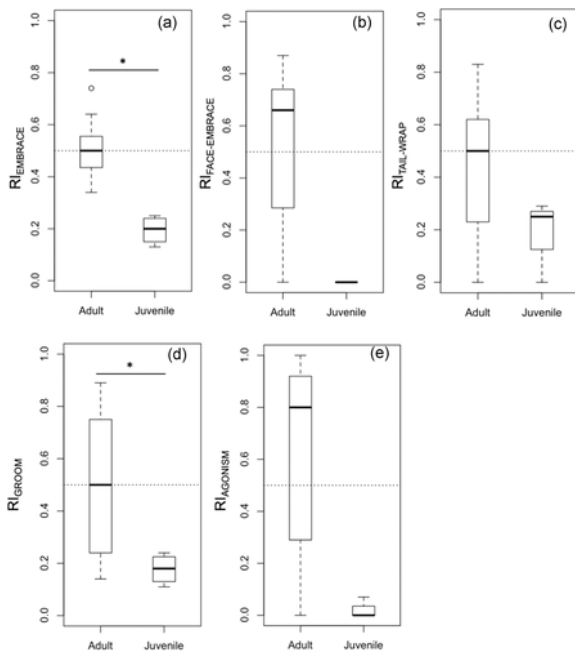


Figure 3 The effect of age class on R-Index scores for embrace, face-embrace, tail-wrap, groom, and agonism; * $p < .05$

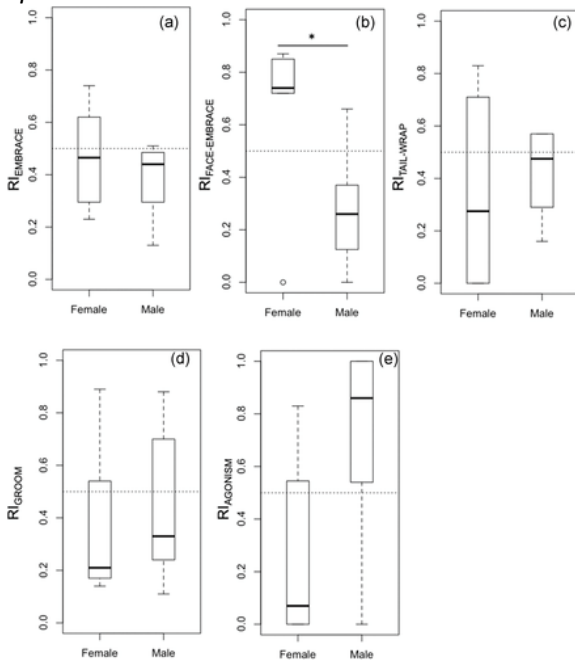


Figure 4 The effect of sex on R-Index scores for embrace, face-embrace, tail-wrap, groom, and agonism; * $p < .05$

3.3 Matrix correlations

The first MRQAP partial matrix correlation examined the relationship between embrace, face-embrace, and tail-wrap. Embraces were significantly correlated with both tail-wrap (partial $r = .374$; two-tailed $p = .002$; $N = 15$; 1,000 permutations) and face-embrace (partial $r = .547$; two-tailed $p < .001$). The second MRQAP partial matrix correlation examined the relationship between, groom, embrace, and agonism. Embrace was not significantly correlated with groom (partial $r = .153$; two-tailed $p = .096$; $N = 15$; 1,000 permutations) or agonism (partial $r = .018$; two-tailed $p = .384$).

4 DISCUSSION

The aim of this study was to apply network analytics to better understand the development of social interactions in spider monkeys. In employing a network approach, our preliminary results demonstrate that using SNA allows for examining multiple facets of the development of social processes. The use of multiple centrality metrics in conjunction with clustering coefficient and the R-Index analysis allowed us to examine the different qualities of centrality, triadic connections, and individual social roles for each behavior within juveniles and adults. Given previous literature in spider monkeys and chimpanzees, we hypothesized that juvenile and adult grooming networks would differ. We predicted that across all network metrics, adults would be more connected, achieving higher centrality and clustering coefficient values within grooming. We utilized degree centrality to test differences in social role participation and predicted that juvenile and adult network positions would differ due to juveniles receiving grooming but rarely initiating it. We also explored age-related network differences with four other behaviors (i.e., embrace, face-embrace, tail-wrapping, and agonism) across all network metrics, as well as between-behavior relationships for all behaviors to determine common and distinct behavioral functions.

Contrary to our prediction, our analyses showed that juveniles and adults generally do not occupy different network positions for grooming: juveniles and adults were similarly connected within the network. The betweenness and degree centrality analyses demonstrated adults and juveniles have similar network positions for grooming. The only exception to this pattern was for closeness centrality, in which juveniles had longer path distances than adults to other nodes for grooming. In contrast, our exploratory analyses showed differences between adults and juveniles within other behavioral networks. The degree centrality network results for embrace, face-embrace, and tail-wrapping showed clear differences in connectedness within the networks such that juveniles occupy more peripheral positions within these social networks, and adults are generally central and highly connected. The betweenness centrality network results showed that adults, but not juveniles, act as social facilitators for embrace and face-embrace. No age class betweenness centrality differences were found for tail-wrapping or agonism.

There are important distinctions that may explain the network differences for degree and betweenness centrality found between grooming and agonism compared to embrace, face-embrace, and tail-wrapping. Grooming and agonism are behaviors found in all primates (di Bitetti, **1997**; Dunbar, **1991**; Henzi & Barrett, **1999**). Grooming is the quintessential affiliative behavior that is most commonly observed to measure social bonds in primates. However, within spider monkeys, grooming follows an atypical pattern in which grooming may occur at lower rates than other species typical affiliative behaviors such as the embrace (Aureli & Schaffner, **2008**; Fedigan & Baxter, **1984**; Schaffner & Aureli, **2005**; Slater et al., **2007**). For example, it is fairly common in primates to see high grooming rates between mother and offspring dyads (Lee, Mayagoitia, Mondragón-Ceballos, & Chiappa, **2010**; Nishida, **1988**). However, this pattern was only the case for one mother–offspring dyad (i.e., Cleo–Cary) within our data set. Furthermore, the R-Index results replicated patterns found by Ahumada (**1992**) in which a wild sample of juveniles initiated less grooming than adults, and received grooming more than adult spider monkeys. However, our network results showed that both adults and juveniles were highly connected within this network. We preliminarily suggest grooming may be a behavior that juveniles

begin to integrate into at an earlier stage than the other species typical behaviors, and that grooming may begin as an extension of maternal bonding and investment. Moreover, their connectedness may be related to juveniles remaining close to mothers during grooming, which often occurs in longer time periods with multiple bouts, and would make them more likely participants in grooming. However, we did not quantify juveniles' proximity to mothers in this study.

In contrast to grooming, embrace, face-embrace, and tail-wrapping occur as interactive events, and can be considered ritualized social traditions (Santorelli et al., **2011**). They are multimodal in that they co-occur with the whinny vocalization, contact gesture, and olfaction (Liebal, Waller, Slocombe, & Burrows, **2013**). Furthermore, partial matrix correlations indicate that these three social traditions co-occur among dyads but have patterns distinct from those of grooming or agonism. Thus, these behaviors may be more complex than grooming, with juveniles needing to develop the skills to execute each component part before juveniles can fully replicate these traditions and integrate themselves into these behavioral networks. Research in other species, including humans, indicates that early interactions form the bedrock for learning the social skills necessary for adult social engagement (e.g., Branchi et al., **2013**; Suomi, **1997**). In utilizing a network approach here, we show that the structure of the early interactions for embrace, face-embrace, and tail-wrapping involves juveniles being in the role of the receiver before the ratio begins to even out in adulthood, as indicated by the social role data.

Our results yielded a common network pattern where face-embrace emerged as the behavior in which network structure between adults and juveniles consistently diverged for every network metric. Our results suggest that face-embrace is a behavior with complex structural patterns that emerge in adulthood. Overall within face-embrace, adults were both more connected and served as connectors, meaning adults brokered interactions among individuals, and had more efficient face-embrace networks. Beyond centrality, the clustering coefficient results suggested that face-embrace is a behavior where higher level triadic interactions occur in adults, but not juveniles. There may be characteristics of face-embrace that drive these overall network patterns that emerge in adulthood.

We previously described a spectrum of risk associated with affiliative behaviors in spider monkeys, with face-embrace carrying the highest risk (Boeving & Nelson, **2018**; Boeving et al., **2017**). To summarize, face-embrace requires close contact of the face and mouth to the body, which may put individuals at risk for unexpected aggression or disease transmission. However, embraces are generally considered to be a signal of benign intent and maybe an alliance-forming behavior that modulates social bonds (Aureli & Schaffner, **2007**; Schaffner & Aureli, **2005**). Considering the different patterns for adults and juveniles, the cost of the potential risk incurred by juveniles may outweigh the benefit of early participation and integration into the face-embrace network, which may be another reason for the low frequency of initiating face-embrace. Moreover, our previous work also suggested face-embrace to be more risky than the embrace, which is in line with the current findings showing differences in network patterns between juveniles and adults for face-embrace, but not embrace, for every network metric. In contrast, grooming is a low-risk behavior but one which requires more time investment. Visual inspection of the grooming network shows that the individuals central in grooming are not the same individuals who are central in the other affiliative networks. Thus, grooming may offer a low-risk opportunity for vulnerable individuals, including adult females and juveniles, to engage in social bonding without the added risk that characterizes embrace and face-embrace. Moreover, our

previous work demonstrated that embrace and face-embrace are behaviorally lateralized in adult spider monkeys (Boeving & Nelson, **2018**). Thus, there may be a brain–behavior relationship that corresponds to low frequencies for initiating these behaviors. This pattern may be related to potential neurobiological gains for juveniles involving social behaviors that require hemispheric specialization to interpret cues and execute appropriate responses.

In including the RI social role calculation, we provide a stepwise approach to parsing differences seen at the network level. We utilized degree centrality values to create the RI since degree is the most direct measurement of participation in social interactions (as opposed to an indirect measure). The RI results for embrace and face-embrace were straightforward, showing that juveniles receive but rarely initiate any of these behaviors. When initiating and receiving agonism were examined, no age difference was detected in social role ratio. While the RI results for embrace, face-embrace, and agonism were strongly in line with the network-level results for differences between adults and juveniles, the results for tail-wrap did not reach significance. However, juveniles engaged in tail-wrapping infrequently and therefore RI scores could not be computed for all juveniles. Within the tail-wrapping network, this low frequency is characterized as a disconnection within the network, and the juvenile is depicted in the network periphery, with no connecting edges. The nonsignificant betweenness centrality network result indicates that there is no real difference between juveniles and adults with social facilitation. This pattern can be attributed to the adults within this network, especially males, interacting with each other during these interactions, and this pattern can be seen upon visual inspection of the graph (Figure **2c**). There are no central nodes that serve as connectors to other more peripheral nodes. Tail-wrapping was first described by Klein and Klein (**1971**) as an alliance-forming behavior, however it is frequently grouped with other affiliative behaviors in recent spider monkey literature (Aureli, Di Fiore, Murillo-Chacon, Kawamura, & Schaffner, **2013**; Schaffner, Slater, & Aureli, **2012**). Tail-use in spider monkeys is more commonly discussed with regard to laterality (Laska, **1998**; Laska & Tutsch, **2000**; Nelson & Kendall, **2018**). Within the captive group from which we collected data, we observed two variations of tail-wrapping behavior in which two, and more rarely, three individuals will follow one behind the other with tails intertwined or locomote side-by-side with tails intertwined. In our group, it is most common for tail-wrapping to occur between males, but especially when three individuals are involved; the third is usually an established female (i.e., in this group, Cleo). It is possible that this behavior is analogous to arm-wrapping behavior documented in wild spider monkeys (Aureli et al., **2013**; Schaffner, Slater et al., **2012**). The differences in how these behaviors are expressed in captive versus wild environments may be due to positional behavior associated with arboreality. Our results suggest the exact function of tail-wrapping behavior is still not known, but future work could shed light on how it relates to other affiliative behaviors.

The between-behavior analysis using MQRAP allowed us to examine interaction patterns between individuals across behavior type. Traditionally, the test examines social bonds, and when there is a pattern of individuals interacting across behavior types, a common function is assumed (Whitehead, **2009**). The first MQRAP partial matrix correlation indicated that embrace, face-embrace, and tail-wrap are all related behaviors, which suggests that these three behaviors share a common function. Tail-wrap and face-embraces may be behavioral variants of embracing. The second MQRAP partial matrix correlation indicated that embraces were unrelated to grooming and agonism, suggesting that each of these behaviors are functionally distinct. The lack of significant partial

correlation between embraces and grooming suggests that embraces serve a different social function as grooming. Furthermore, the lack of significant partial correlation between embraces and agonism suggests that this tension-reduction behavior cannot be predicted from agonistic relationships.

A limitation of this study is that we did not include play behavior. Our aim was to broadly compare age-related network differences to inform how juvenile network connectedness and integration into adult social behavior differs over life stages. Because play is a quintessential behavior that occurs predominantly in juveniles in most primate species (Fagen, **2002**), and has been the focus on many previous developmental studies, we purposefully chose to focus on adult social interactions. Thus, play behavior was not central to our aim and was excluded. However, some research indicates that spider monkeys can continue to engage in play as adults (Fedigan & Baxter, **1984**; Pellis & Iwaniuk, **2000**). While age-related differences would be expected, including this behavior in future studies may illuminate how changes in play networks compare to age-related differences in other affiliative behavior networks. Future work should incorporate longitudinal approaches so that the dynamic change of network position of juveniles can be examined, particularly during the transition to adulthood. Furthermore, future work should investigate sex differences within juveniles, but such work requires a larger sample. There is only limited research on sex differences in wild juvenile spider monkeys, and sample sizes are frequently also limited (Rodrigues, **2014**; Vick, **2008**).

A second limitation is that we have investigated network dynamics of social interactions in captive spider monkeys, which may express behavioral patterns different from wild spider monkeys. In the wild, social dynamics are shaped by ecological constraints. These constraints result in frequent sex-segregated ranging and association patterns, where males and females may have limited time in association (Hartwell et al., **2014**; Rodrigues, **2014**). Furthermore, subgroup size varies flexibly with food availability, as large subgroups converge at large patches, whereas smaller subgroups are optimal when resources are scarce (Chapman et al., **1995**; Rodrigues, **2017**; Symington, **1990**). However, rather than constraining social behavior, captivity may intensify it. In a captive environment where animals cannot fission, there is a great potential risk of aggression (Davis, Schaffner, & Wehnelt, **2009**), which may intensify the need for tension-reduction behaviors such as embrace, face-embrace, and tail-wrapping. Furthermore, in the absence of traveling and foraging costs, animals may have more time to devote to social bonding behaviors such as grooming. We must be careful in assuming that the behavioral patterns observed in captivity are representative of behaviors in the wild; however, they represent part of a continuum of the animals' behavioral flexibility (Rodrigues & Boevig, **2019**). Captive research on spider monkeys does provide unique opportunities to adequately visualize social interactions that may be impeded in the wild. Captive research could also facilitate the use of a multisite approach, where data is collected from groups at different facilities to elucidate answers/to these sample-specific questions as well as ameliorate sample size issues. We stress the preliminary nature of our results here, and future work should include samples from multiple spider monkey groups. In this vein, small samples sizes are typical of studies of spider monkeys in both captive and wild settings (Ahumada, **1992**; Campbell, **2003**; Pastor-Nieto, **2001**; Riveros, Schaffner, & Aureli, **2017**; Rodrigues, Wittwer, & Kitchen, **2015**; Schaffner & Aureli, **2005**; Vick, **2008**). There is a paucity of published data on spider monkey social development, and previous studies were also consisted of small samples (Rodrigues et al., **2015**; Vick, **2008**). Although longitudinal data would be optimal to study developmental processes, collection of such data poses a challenge in primates with long

developmental periods. For this reason, cross-sectional comparisons of age groups are frequently used as a proxy for examining species typical developmental changes in behavior (Liao et al., **2018**; Link, Milich, & Di Fiore, **2018**; Rodrigues, **2007a**; Shimada & Sueur, **2014**). These challenges and limitations must be weighed closely, and considered in context with the bias that exists in the primate literature toward a few well-studied terrestrial catarrhines (Bezanson & McNamara, **2019**), limiting comparable literature for understudied species.

Here we show that the development of social interactions can be broken down into participation in social roles, that social roles vary for juveniles and adults across behavior types, and that the use of multiple network metrics across behaviors help to characterize complex social development patterns. Furthermore, the networks show that juvenile spider monkeys quickly integrate into grooming and agonism networks, but may need more time to integrate into embrace, face-embrace, and tail-wrapping. Disproportionately receiving these behaviors before beginning to initiate as well may allow juveniles to develop the social skills needed to participate in these multimodal social interactions. For animal researchers, the burden is on the quality of research design, computation, and interpretation to understand observed behavior. This burden is particularly difficult in social research given the need for precise measurement of social behaviors that also accurately represent a species' behavioral ecology. Relationships are not one-dimensional and do not emerge from within a single aspect of behavior, but rather develop across multiple facets of connection within behaviors that may each contain their own pattern. SNA provides the tools to quantify and visualize these patterns to better understand social development.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

REFERENCES

- Ahumada, J. A. (1992). Grooming behavior of spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. *International Journal of Primatology*, **13**(1), 33–49. <https://doi.org/10.1007/BF02547726>
- Aureli, F., Di Fiore, A., Murillo-Chacon, E., Kawamura, S., & Schaffner, C. M. (2013). Male philopatry in spider monkeys revisited. *American Journal of Physical Anthropology*, **152**(1), 86–95. <https://doi.org/10.1002/ajpa.22331>
- Aureli, F., & Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters*, **3**(2), 147–149. <https://doi.org/10.1098/rsbl.2007.0041>
- Aureli, F., & Schaffner, C. M. (2008). Social interactions, social relationships and the social system of spider monkeys. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology and evolution of the genus Ateles* (pp. 236–265). Cambridge: Cambridge University Press.
- Aureli, F., & Schaffner, C. M. (2010). Spider monkeys. *Current Biology*, **20**(15), R624–R626. <https://doi.org/10.1016/j.cub.2010.06.040>

- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., ... Henzi, S. P. (2008). Fission–fusion dynamics. *Current Anthropology*, **49**(4), 627– 654. <https://doi.org/10.1086/586708>
- Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: The structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, **367**(1599), 2108– 2118. <https://doi.org/10.1098/rstb.2012.0113>
- Beisner, B. A., Jackson, M. E., Cameron, A. N., & McCowan, B. (2011). Detecting instability in animal social networks: Genetic fragmentation is associated with social instability in rhesus macaques. *PLOS One*, **6**(1), e16365. <https://doi.org/10.1002/evan.21790>
- Bezanson, M., & McNamara, A. (2019). The what and where of primate field research may be failing primate conservation. *Evolutionary Anthropology: Issues, News, and Reviews*, **28**, 166– 178. <https://doi.org/10.1002/evan.21790>.
- Boeving, E. R., Belnap, S. C., & Nelson, E. L. (2017). Embraces are lateralized in spider monkeys (*Ateles fusciceps rufiventris*). *American Journal of Primatology*, **79**(6), e22654. <https://doi.org/10.1002/ajp.22654>
- Boeving, E. R., & Nelson, E. L. (2018). Social risk dissociates social network structure across lateralized behaviors in spider monkeys. *Symmetry*, **10**(9). <https://doi.org/10.3390/sym10090390>
- Branchi, I., Curley, J. P., D'Andrea, I., Cirulli, F., Champagne, F. A., & Alleva, E. (2013). Early interactions with mother and peers independently build adult social skills and shape BDNF and oxytocin receptor brain levels. *Psychoneuroendocrinology*, **38**(4), 522– 532. <https://doi.org/10.1016/j.psyneuen.2012.07.010>
- Brent, L. J., Lehmann, J., & Ramos-Fernández, G. (2011). Social network analysis in the study of nonhuman primates: A historical perspective. *American Journal of Primatology*, **73**(8), 720– 730. <https://doi.org/10.1002/ajp.20949>
- Campbell, C. J. (2003). Female-directed aggression in free-ranging *Ateles geoffroyi*. *International Journal of Primatology*, **24**(2), 223– 237. <https://doi.org/10.1023/A:102303683>
- Chapman, C. A. (1990). Association patterns of spider monkeys: The influence of ecology and sex on social organization. *Behavioral Ecology and Sociobiology*, **26**(6), 409– 414. <https://doi.org/10.1007/BF00170898>
- Chapman, C. A., Chapman, L. J., & Wrangham, R. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**(1), 59– 70. <https://doi.org/10.1007/BF00175729>
- Clark, F. E. (2011). Space to choose: Network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, **73**(8), 748– 757. <https://doi.org/10.1002/ajp.20903>
- Cohen, J. (1988). The effect size index: d. *Statistical Power Analysis for the Behavioral Sciences*, **2**, 284– 288. <https://doi.org/10.4324/9780203771587>
- Davis, N., Schaffner, C. M., & Wehnelt, S. (2009). Patterns of injury in zoo-housed spider monkeys: A problem with males? *Applied Animal Behaviour Science*, **116**(2–4), 250– 259. <https://doi.org/10.1016/j.applanim.2008.08.008>
- di Bitetti, M. S. (1997). Evidence for an important social role of allogrooming in a platyrrhine primate. *Animal Behaviour*, **54**(1), 199– 211. <https://doi.org/10.1006/anbe.1996.041610.1006/anbe.1996.0416>

- Di Fiore, A., & Campbell, C. J. (2007). The atelines: Variation in ecology, behavior, and social organization. In C. J. Campbell, A. Fuentes, K. MacKinnon, M. Panger & S. K. Bearder (Eds.), *Primates in perspective* (pp. 155– 185). New York, NY: Oxford University Press.
- Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two new world primates. *American Journal of Primatology*, **73**(8), 802– 811. <https://doi.org/10.1002/ajp.20943>
- Dunbar, R. I. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, **57**(3), 121– 131. <https://doi.org/10.1159/000156574>
- Eizirik, E., Murphy, W. J., Springer, M. S., & O'Brien, S. J. (2004). Molecular phylogeny and dating of early primate divergences. In C. F. Ross & R. F. Kay (Eds.), *Anthropoid origins—Developments in primatology: Progress and prospects* (pp. 45– 64). Boston, MA: Springer.
- Fagen, R. (2002). Primate juveniles and primate play. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development, and behavior* (pp. 182– 196). Chicago, IL: University of Chicago Press.
- Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, **8**(10), 1309– 1320. <https://doi.org/10.1111/2041-210X.12772>
- Fedigan, L. M., & Baxter, M. J. (1984). Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*, **25**(3), 279– 294. <https://doi.org/10.1007/BF02382267>
- Flack, J. C., Girvan, M., De Waal, F. B., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, **439**(7075), 426– 429. <https://doi.org/10.1038/nature04326>
- Fritz, C. O., Morris, P. E., & Richler, J. J. (2012). Effect size estimates: Current use, calculations, and interpretation. *Journal of Experimental Psychology: General*, **141**(1), 2– 18. <https://doi.org/10.1037/a0024338>
- Griffin, R. H., & Nunn, C. L. (2012). Community structure and the spread of infectious disease in primate social networks. *Evolutionary Ecology*, **26**(4), 779– 800.
- Gómez, J. M., Nunn, C. L., & Verdú, M. (2013). Centrality in primate–parasite networks reveals the potential for the transmission of emerging infectious diseases to humans. *Proceedings of the National Academy of Sciences of the United States of America*, **110**(19), 7738– 7741. <https://doi.org/10.1073/pnas.1220716110>
- Hartwell, K. S., Notman, H., Bonenfant, C., & Pavelka, M. S. (2014). Assessing the occurrence of sexual segregation in spider monkeys (*Ateles geoffroyi yucatanensis*), its mechanisms and function. *International Journal of Primatology*, **35**(2), 425–444. <https://doi.org/10.1007/s10764-013-9746-0>
- Hawkley, L. C., & Capitano, J. P. (2015). Perceived social isolation, evolutionary fitness and health outcomes: A lifespan approach. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, **370**(1669), 20140114. <https://doi.org/10.1098/rstb.2014.0114>
- Henzi, S. P., & Barrett, L. (1999). The value of grooming to female primates. *Primates*, **40**(1), 47– 59. <https://doi.org/10.1007/BF02557701>
- Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L., & Henzi, S. P. (2018). Network integration and limits to social inheritance in vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, **285**(1876), 20172668. <https://doi.org/10.1098/rspb.2017.2668>
- Kamada, T., & Kawai, S. (1989). An algorithm for drawing general undirected graphs. *Information Processing Letters*, **31**(1), 7– 15.
- Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, **50**(4), 343– 356. <https://doi.org/10.1007/s10329-009-0153-2>

- Klein, L., & Klein, D. (1971). Aspects of social behaviour in a colony of spider monkeys at San Francisco Zoo. *International Zoo Yearbook*, **11**(1), 175– 181.
- Laska, M. (1998). Laterality in the use of the prehensile tail in the spider monkey (*Ateles geoffroyi*). *Cortex*, **34**(1), 123– 130. [https://doi.org/10.1016/s0010-9452\(08\)70741-x](https://doi.org/10.1016/s0010-9452(08)70741-x)
- Laska, M., & Tutsch, M. (2000). Laterality of tail resting posture in three species of New World primates. *Neuropsychologia*, **38**(7), 1040– 1046. [https://doi.org/10.1016/s0028-3932\(99\)00147-5](https://doi.org/10.1016/s0028-3932(99)00147-5)
- Lee, P., Mayagoitia, L., Mondragón-Ceballos, R., & Chiappa, P. (2010). Sex differences in learning the allocation of social grooming in infant stump-tailed macaques. *Behaviour*, **147**(9), 1073– 1099.
- Lehmann, J., & Ross, C. (2011). Baboon (*Papio anubis*) social complexity—A network approach. *American Journal of Primatology*, **73**(8), 775– 789. <https://doi.org/10.1002/ajp.20967>
- Levé, M., Sueur, C., Petit, O., Matsuzawa, T., & Hirata, S. (2016). Social grooming network in captive chimpanzees: Does the wild or captive origin of group members affect sociality? *Primates*, **57**(1), 73– 82. <https://doi.org/10.1007/s10329-015-0494-y>
- Liao, Z., Sosa, S., Wu, C., & Zhang, P. (2018). The influence of age on wild rhesus macaques' affiliative social interactions. *American Journal of Primatology*, **80**(2), e22733. <https://doi.org/10.1002/ajp.22733>
- Liebal, K., Waller, B. M., Slocombe, K. E., & Burrows, A. M. (2013). *Primate communication: A multimodal approach*. Cambridge: Cambridge University Press.
- Link, A., Milich, K., & Di Fiore, A. (2018). Demography and life history of a group of white-bellied spider monkeys (*Ateles belzebuth*) in western Amazonia. *American Journal of Primatology*, **80**(8), e22899. <https://doi.org/10.1002/ajp.22899>
- MacIntosh, A. J., Jacobs, A., Garcia, C., Shimizu, K., Mouri, K., Huffman, M. A., & Hernandez, A. D. (2012). Monkeys in the middle: Parasite transmission through the social network of a wild primate. *PLOS One*, **7**(12), e51144. <https://doi.org/10.1371/journal.pone.0051144>
- Makagon, M. M., McCowan, B., & Mench, J. A. (2012). How can social network analysis contribute to social behavior research in applied ethology? *Applied Animal Behaviour Science*, **138**(3–4), 152– 161. <https://doi.org/10.1016/j.applanim.2012.02.003>
- McCowan, B., Anderson, K., Heagarty, A., & Cameron, A. (2008). Utility of social network analysis for primate behavioral management and well-being. *Applied Animal Behaviour Science*, **109**(2–4), 396– 405.
- McCowan, B., Beisner, B. A., Capitanio, J. P., Jackson, M. E., Cameron, A. N., Seil, S., ... Fushing, H. (2011). Network stability is a balancing act of personality, power, and conflict dynamics in rhesus macaque societies. *PLOS One*, **6**(8), e22350. <https://doi.org/10.1371/journal.pone.0022350>
- Milton, K., & Hopkins, M. E. (2006). Growth of a reintroduced spider monkey (*Ateles geoffroyi*) population on Barro Colorado Island, Panama. In A. Estrada, P. A. Garber, M. S. M. Pavelka & L. Lueke (Eds.), *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior and conservation* (pp. 417– 435). New York: Springer.
- Nelson, E. L., & Kendall, G. A. (2018). Goal-directed tail use in Colombian spider monkeys (*Ateles fusciceps rufiventris*) is highly lateralized. *Journal of Comparative Psychology*, **132**(1), 40– 47. <https://doi.org/10.1037/com0000094>
- Newton-Fisher, N. E. (2012). *Animal behaviour pro (Version v1)*. Canterbury, UK: Apple.
- Nishida, T. (1988). Development of social grooming between mother and offspring in wild chimpanzees. *Folia Primatologica*, **50**(1–2), 109– 123. <https://doi.org/10.1159/000156335>

- Nunn, C. L. (2012). Primate disease ecology in comparative and theoretical perspective. *American Journal of Primatology*, **74**(6), 497– 509. <https://doi.org/10.1002/ajp.21986>
- Palacios-Romo, T., Castellanos, F., & Ramos-Fernandez, G. (2019). Uncovering the decision rules behind collective foraging in spider monkeys. *Animal Behaviour*, **149**, 121– 133.
- Pastor-Nieto, R. (2001). Grooming, kinship, and co-feeding in captive spider monkeys (*Ateles geoffroyi*). *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association*, **20**(4), 293– 303. <https://doi.org/10.1002/zoo.1029>
- Pellis, S. M., & Iwaniuk, A. N. (2000). Adult–adult play in primates: Comparative analyses of its origin, distribution and evolution. *Ethology*, **106**(12), 1083– 1104. <https://doi.org/10.1046/j.1439-0310.2000.00627.x>
- Ponzi, D., Zilioli, S., Mehta, P. H., Maslov, A., & Watson, N. V. (2016). Social network centrality and hormones: The interaction of testosterone and cortisol. *Psychoneuroendocrinology*, **68**, 6– 13. <https://doi.org/10.1016/j.psyneuen.2016.02.014>
- Puga-Gonzalez, I., Sosa, S., & Sueur, C. (2019). Social networks analyses in primates, a multilevel perspective. *Primates*, **60**(3), 163– 165. <https://doi.org/10.1007/s10329-019-00720-5>
- R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ramos-Fernández, G., Boyer, D., Aureli, F., & Vick, L. G. (2009). Association networks in spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology*, **63**(7), 999– 1013. <https://doi.org/10.1007/s00265-009-0719-4>
- Ramos-Fernández, G., & Morales, J. M. (2014). Unraveling fission-fusion dynamics: How subgroup properties and dyadic interactions influence individual decisions. *Behavioral Ecology and Sociobiology*, **68**(8), 1225– 1235. <https://doi.org/10.1007/s00265-014-1733-8>
- Rebecchini, L., Schaffner, C. M., & Aureli, F. (2011). Risk is a component of social relationships in spider monkeys. *Ethology*, **117**(8), 691– 699. <https://doi.org/10.1111/j.1439-0310.2011.01923.x>
- Rimbach, R., Bisanzio, D., Galvis, N., Link, A., Di Fiore, A., & Gillespie, T. R. (2015). Brown spider monkeys (*Ateles hybridus*): A model for differentiating the role of social networks and physical contact on parasite transmission dynamics. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, **370**(1669), 20140110. <https://doi.org/10.1098/rstb.2014.0110>
- Riveros, J. C., Schaffner, C. M., & Aureli, F. (2017). You are not welcome: Social exchanges between female spider monkeys (*Ateles geoffroyi*). *International Journal of Primatology*, **38**(5), 856– 871. <https://doi.org/10.1007/s10764-017-9982-9>
- Rodrigues, M. A. (2007a). Age and sex-based differences in social interactions and spacing in mantled howling monkeys: Implications for juvenile social development. *The Journal of Developmental Processes*, **103**.
- Rodrigues, M. A. (2007b). *Sex differences in the social behavior of juvenile spider monkeys (Ateles geoffroyi)*. Iowa State University, Ames, Iowa.
- Rodrigues, M. A. (2014). Emergence of sex-segregated behavior and association patterns in juvenile spider monkeys. *Neotropical Primates*, **21**(2), 183– 189. <https://doi.org/10.1896/044.021.0204>
- Rodrigues, M. A. (2017). Female spider monkeys (*Ateles geoffroyi*) cope with anthropogenic disturbance through fission–fusion dynamics. *International Journal of Primatology*, **38**(5), 838– 855. <https://doi.org/10.1007/s10764-017-9981-x>
- Rodrigues, M. A., & Boeving, E. R. (2019). Comparative social grooming networks in captive chimpanzees and bonobos. *Primates*, **60**(3), 191– 202. <https://doi.org/10.1007/s10329-018-0670-y>

- Rodrigues, M. A., Wittwer, D., & Kitchen, D. M. (2015). Measuring stress responses in female Geoffroy's spider monkeys: Validation and the influence of reproductive state. *American Journal of Primatology*, **77**(9), 925– 935. <https://doi.org/10.1002/ajp.22421>
- Rushmore, J., Caillaud, D., Matamba, L., Stumpf, R. M., Borgatti, S. P., & Altizer, S. (2013). Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *Journal of Animal Ecology*, **82**(5), 976– 986. <https://doi.org/10.1111/1365-2656.12088>
- Sade, D. S. (1972). Sociometrics of *Macaca mulatta* I. Linkages and cliques in grooming matrices. *Folia Primatologica*, **18**(3–4), 196– 223. <https://doi.org/10.1159/000155480>
- Sade, D. S., Altmann, M., Loy, J., Hausfater, G., & Breuggeman, J. A. (1988). Sociometrics of *Macaca mulatta*: II. Decoupling centrality and dominance in rhesus monkey social networks. *American Journal of Physical Anthropology*, **77**(4), 409– 425. <https://doi.org/10.1002/ajpa.1330770403>
- Santorelli, C. J., Schaffner, C. M., Campbell, C. J., Notman, H., Pavelka, M. S., Weghorst, J. A., & Aureli, F. (2011). Traditions in spider monkeys are biased towards the social domain. *PLOS One*, **6**(2), e16863. <https://doi.org/10.1371/journal.pone.0016863>
- Schaffner, C. M., & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. *International Journal of Primatology*, **26**(5), 1093– 1106. <https://doi.org/10.1007/s10764-005-6460-6>
- Schaffner, C. M., Rebecchini, L., Ramos-Fernandez, G., Vick, L. G., & Aureli, F. (2012). Spider monkeys (*Ateles geoffroyi yucatanensis*) cope with the negative consequences of hurricanes through changes in diet, activity budget, and fission–fusion dynamics. *International Journal of Primatology*, **33**(4), 922–936. <https://doi.org/10.1007/s10764-012-9621-4>
- Schaffner, C. M., Slater, K. Y., & Aureli, F. (2012). Age related variation in male–male relationships in wild spider monkeys (*Ateles geoffroyi yucatanensis*). *Primates*, **53**(1), 49– 56. <https://doi.org/10.1007/s10329-011-0271-5>
- Schel, A. M., Rawlings, B., Claidiere, N., Wilke, C., Wathan, J., Richardson, J., ... Slocombe, K. (2013). Network analysis of social changes in a captive chimpanzee community following the successful integration of two adult groups. *American Journal of Primatology*, **75**(3), 254– 266. <https://doi.org/10.1002/ajp.22101>
- Schmitt, C. A. (2010). *Comparative behavior, development and life history of wild juvenile atelin primates (Ateles belzebuth and Lagothrix poeppigii)* (Ph.D. thesis). New York University, New York.
- Shannon, P., Markiel, A., Ozier, O., Baliga, N. S., Wang, J. T., Ramage, D., ... Ideker, T. (2003). Cytoscape: A software environment for integrated models of biomolecular interaction networks. *Genome Research*, **13**(11), 2498– 2504. <https://doi.org/10.1101/gr.1239303>
- Shimada, M., & Sueur, C. (2014). The importance of social play network for infant or juvenile wild chimpanzees at Mahale Mountains National Park, Tanzania. *American Journal of Primatology*, **76**(11), 1025– 1036.
- Shimooka, Y. (2015). Association networks and life history of female spider monkeys. In T. Furiuchi, J. Yamagiwa & F. Aureli (Eds.), *Dispersing primate females. Primatology monographs* (pp. 23– 43). Tokyo, Japan: Springer.
- Slater, K., Schaffner, C., & Aureli, F. (2007). Embraces for infant handling in spider monkeys: Evidence for a biological market? *Animal Behaviour*, **74**(3), 455– 461. <https://doi.org/10.1016/j.anbehav.2006.11.026>
- Smith-Aguilar, S. E., Aureli, F., Busia, L., Schaffner, C., & Ramos-Fernández, G. (2019). Using multiplex networks to capture the multidimensional nature of social structure. *Primates*, **60**(3), 277– 295. <https://doi.org/10.1007/s10329-018-0686-3>

- Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011). How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, **73**(8), 703– 719. <https://doi.org/10.1002/ajp.20915>
- Suomi, S. J. (1997). Early determinants of behaviour: Evidence from primate studies. *British Medical Bulletin*, **53**(1), 170– 184. <https://doi.org/10.1093/oxfordjournals.bmb.a011598>
- Symington, M. M. (1990). Fission-fusion social organization in Ateles and Pan. *International Journal of Primatology*, **11**(1), 47– 61. <https://doi.org/10.1007/BF02193695>
- Vick, L. G. (2008). Immaturity in spider monkeys: A risky business. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology and evolution of the genus Ateles* (pp. 288– 328). Cambridge: Cambridge University Press.
- Wakefield, M. L. (2013). Social dynamics among females and their influence on social structure in an East African chimpanzee community. *Animal Behaviour*, **85**(6), 1303– 1313. <https://doi.org/10.1016/j.anbehav.2013.03.019>
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications, Vol. 8*. Cambridge: Cambridge University Press.
- Whitehead, H. (2009). SOCPROG programs: Analysing animal social structures. *Behavioral Ecology and Sociobiology*, **63**(5), 765– 778. <https://doi.org/10.1007/s00265-008-0697-y>
- Wrzus, C., Hänel, M., Wagner, J., & Neyer, F. J. (2013). Social network changes and life events across the life span: A meta-analysis. *Psychological Bulletin*, **139**(1), 53– 80. <https://doi.org/10.1037/a0028601>