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Social Processes through the Lens of Network Science in Spider Monkeys

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

SOCIAL PROCESSES THROUGH THE LENS OF NETWORK SCIENCE IN SPIDER MONKEYS

A dissertation submitted in partial fulfillment of
the requirements for the degree of
DOCTOR OF PHILOSOPHY
in
PSYCHOLOGY
by
Emily R. Boeving

2020

To: Dean Michael R. Heithaus
College of Arts, Sciences, and Education

This dissertation, written by Emily R. Boeving, and entitled Social Processes through the Lens of Network Science in Spider Monkeys, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Michael Heithaus

Asia Eaton

Robert Lickliter, Co-Major Professor

Eliza Nelson, Co-Major Professor

Date of Defense: November 6, 2020.

The dissertation of Emily R. Boeving is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2020

DEDICATION

For Dr. Hani Freeman Wild, who saw me.

For my mother, Jan Pilkington, and my grandmother, Zelda Pilkington, for supporting me in every way possible throughout this entire process. When things were hard for me, I know they were hard for you, too, and in many ways I feel that the three of us have gone through this Ph.D. together. I love you and thank you so much for everything.

And, for the animals I have met along the way that inspired me to do this work.

This is for you.

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This work was made possible by the support, guidance, and opportunities created by many people I want to acknowledge and thank. The journey to this point did not begin in graduate school, but at a zoo in my hometown where at fifteen years old I had the opportunity to shadow in the primate area. I began observing, and quickly became fascinated by the diverse ecology and behavior of primates. I thought I might like to do something professional with primates, but I had no idea what that would be. My first summer as an undergraduate I signed on for a field course on primate behavioral ecology in the Atlantic lowlands of Costa Rica at El Zota Biological Field Station, a decision that changed the course of my life. This opportunity connected me with peers from around the world with similar aspirations of studying primates, and I met primatologists for the first time. When I returned to my university that fall, I designed my first experiment examining hand preference in Sulawesi macaques at the Memphis Zoo and began attending academic conferences and presenting as well. The next summer I was selected to participate in a research opportunity at Yale University's Comparative Cognition Laboratory. After graduation, I entered a master's program in evolutionary anthropology at Durham University in the UK, from which I gained a multi-disciplinary international perspective on the field of primatology. I mention these things to say that it has been a journey to this point but also that primatology itself can be approached from many topical areas and my experiences in the field, in the laboratory, as an anthropology student, and as a student of psychology have collectively led me to the perspective I bring to primatology today.

I want to thank some of my undergraduate professors, especially Dr. Chris Long and Dr. Krista Peppers. As an undergraduate, I did not realize the rarity of having so much quality one-on-one time with professors. These people gave of their time for guidance, advice, writing letters on my behalf, and much more for the duration of my time spent as an undergraduate and beyond and I thank them sincerely.

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A few years before beginning my Ph.D., I moved from Arkansas to Chicago to participate in a research program with the Lester E. Fisher Center for the Study and Conservation of Apes at the Lincoln Park Zoo. During this experience, I gained more skills and refined those I already had for measuring behavior. It was also my first time getting to work closely with chimpanzees and gorillas and was truly a thrill. I want to thank Dr. Steve Ross for the opportunity to be a part of the “hub of ape science” where I gained valuable research skills and had the opportunity to co-author a paper. As a research intern, I had the opportunity to travel with the Lincoln Park Zoo to San Juan, Puerto Rico for the annual meeting of the American Society of Primatologists where I met who would become my Ph.D. mentor, Dr. Eliza Nelson. Dr. Hani Freeman, a postdoctoral researcher at the time, connected me with Dr. Nelson. I want to thank Hani for her friendship, support, advice, and encouragement along the way, and especially for introducing me to Dr. Nelson.

I want to thank Dr. Eliza Nelson for taking me on as a Ph.D. student in 2014, and again in 2018. I had some research under my belt but I was very eager to improve those skills, learn new ones, and gain real writing experience with the goal of becoming a published author. Dr. Nelson provided me with opportunities right away to hone writing skills as we began collaborating a manuscript shortly after meeting in Puerto Rico. I’ve learned a lot about writing, the writing process, and animal research in general from Dr. Nelson. I want to thank Dr. Nelson for the trust she put in me over the years to collect data from the spider monkeys, which involved training and coordinating many research assistants to identify the monkeys, identify the behaviors and use the digital data collection system that I was eager to implement. Dr. Nelson also encouraged me to attend and present at conferences which allowed me good practice at public speaking and scientific engagement early on. I want to thank Dr. Nelson for setting a high bar and challenging me to reach it. I have enjoyed working with Dr. Nelson and learning from Dr. Nelson and will miss the coffee shop collaborations.

When I came to FIU, I had never had formal coursework in developmental theory and I want to thank Dr. Robert Lickliter for providing excellent courses to learn and discuss such topics. I also want to thank Dr. Lickliter for helping me navigate the muddy waters of academia on more than one occasion. I am very grateful Dr. Lickliter informally welcomed me into his lab space – an experience that was beneficial as I was able to begin expanding my skillset to studying bobwhite quail social networks. It was also fun to interact with his lab during lab meetings and to take part in discussions from a perspective outside of primates.

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ABSTRACT OF THE DISSERTATION

SOCIAL PROCESSES THROUGH THE LENS OF NETWORK SCIENCE IN SPIDER MONKEYS

By

Emily R. Boeving

Florida International University, 2020

Miami, Florida

Professor Eliza Nelson, Co-Major Professor

Professor Robert Lickliter, Co-Major Professor

This dissertation presents a series of empirical studies which aim to deepen and broaden what is known about social processes in spider monkeys. In recent decades, the burgeoning field of network science has brought a new perspective to many disciplines. Although network science has emerged in multiple content areas (e.g., neuroscience, economics), the application and utility of social network analysis to quantify social processes has seen great advances. Sociality and component processes have been described as mystifying and left many perplexed at the basic question, “What is social?” There is no easy answer to this question but one issue is clear – traditional tools and instruments used to measure social processes may limit our ability to fully understand them. However, social network analysis (SNA) allows for the assessment of social processes in ways that distinguish it from traditional analyses by utilizing network metrics that allow for multiple dimensions of social assessment. In the first study, we apply social network analysis to better understand the relationship between social network structure and affiliative behaviors. Through this work we delineate a spectrum of social risk across behavior types and discuss this in light of current theory. Next, we implement social network analysis to characterize age class differences in social development for the first time in a spider monkey model. Finally, we use a mixed methods approach to assess the relationships between cognition as measured by problem solving skill and social network position. Through this collection of work, we demonstrate social processes viewed through the lens of network science provides valuable insight into the ecology of spider monkeys.

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Introduction

1.1 Introduction to Social Network Analysis

Network science is uniquely capable of assessing connection in relational data. Connection is an integral part of life and in network science is mathematically represented with the network graph composed of interconnected elements (Sporns, 2010). With roots in the mathematical field of graph theory, network graphs can represent “real world” connection among individuals, or broad relationships among variables in process. Social Network Analysis (SNA) came about from multidisciplinary efforts from social psychologists, anthropologists, and sociologists aiming to implement concepts of graph theory to the study of human ties, and how information flows through those ties. Thus, SNA came about at a time when scientists were seeking new methods to quantify social processes with a similar level of rigor used in assessing other research questions but had not been previously utilized in quantifying relational data. SNA is a computational tool that can be utilized to solve non-standard analytical problems. Independence is the key assumption in standard data sets within the behavioral sciences. However, SNA is designed to measure coaction among social entities, especially the influence they may have between each other, as well as degree of connectedness. Beyond the use of the concepts of a social network in metaphorical terms, SNA methods provide mathematical statements of structural properties with operationalized definitions, thereby enabling the development of testable models (Wasserman & Faust, 1994). The development of this methodology brought with it what many consider to be a distinct perspective within the social and behavioral sciences where the focus is not solely on the individual or one-to-one relationships between an individual and multiple others. Instead, SNA harkens to the relational metatheory (Overton, 2007) for dynamic systems (Thelen & Smith, 1995) in which the emphasis is on relationships among interacting units where relations, and direction of relation, are defined by linkages. A key assumption of the network perspective is that patterns of interactions concatenate structures. SNA provides a path forward for quantifying such relationships.

Within SNA, one-mode networks are most commonly presented. These are classical networks in which nodes represent individuals and edges represent interaction types (**Fig.1.1**). Within primatology, this network approach has been utilized extensively. Primatologists' interest in implementing the one-mode network technique is grounded in the need to visualize social ties. The first published use of a network technique with primates was Sade (1965), in which a sociogram, which can be used to measure reciprocity and direct connections, was used to diagram grooming interaction in macaques. The decades that followed saw multiple sociogorams published, characterizing social ties across a variety of behaviors including agonism (Keverne 1992; Pearl & Schulman, 1983), grooming (Chepko-Sadeet et al., 1989; Fairbanks, 1980; Mitani, 1986; Nakagawa, 1992; Pearl, 1983; Seyfarth, 1976; Seyfarth, 1977; Soczka, 1974); and play (Cheney, 1978; Pearl & Schulman, 1983; Soczka, 1974). Computational advancements for

SNA in which algorithms generate network graphs from data did not appear until the year 2000 (see Borgatti, 2002), but primatologists were reluctant to waiver from established methodologies, continuing to produce sociograms created manually (i.e., by hand, researcher selects position of variables in graph) (for a review, see Brent, 2011). Not only did this manual technique create a computational limitation, it meant that researchers were selecting the position of nodes themselves, thus creating the potential of creating graphs that do not reflect the structural relationships built into a formal social network analysis where placement of nodes within a graph indicates strength of connection. The advancements in computation for SNA, now built into multiple algorithms within software packages (e.g., SOCPROG, Whitehead, 2009; Cytoscape, Shannon et al., 2003; Gephi, Bastian, Heymann, & Jacomy, 2009), have also allowed for the assessment of indirect social connections, or the bridging of connection between two nodes that do not interact directly, but are connected indirectly through the node being assessed. Importantly, indirect social connection has been suggested to be particularly important for species with complex social relationships that understand perspectives of others (Brent, 2011).

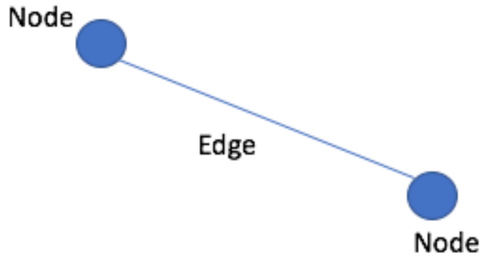

Figure 1.1 Network Components. Nodes typically represent individuals. Edges represent observed social interactions connecting the two individuals.

1.2 Spider Monkey Ecology

Spider monkeys live in societies associated with complex social relationships. Spider monkeys are a non-human primate platyrrhine monkey species belonging to the genus Ateles. Ateles phylogeny is characterized by divergence from humans 36 million years ago, making Ateles more distant relatives than chimpanzees that diverged only 8 million years ago (Eizrik Murphy, Springer, & O'Brien, 2004). Like chimpanzees and humans, spider monkeys live in the fission-fusion social dynamic, characterized by complex social relationships, and defined by individuals splitting into small sub-groups (fission) and reuniting into larger groups (fusion) (Aureli et al., 2008). Yet spider monkeys are unique in that they are the only platyrrhine primate species to live in fission-fusion (Klein & Klein, 1977; Symington, 1990). Along with the characteristic ebb and flow of social movement in fission-fusion comes greater likelihood of variation in social interaction partners and low stability in social hierarchy. Together these elements define spider monkey social groups as being low in cohesion, and places spider monkeys in stark contrast to strongly cohesive societies with stable, known hierarchies (e.g., macaques). Although spider monkeys are situated as a more distant phylogenetic species to humans compared with the more widely studied chimpanzee and catarrhine monkeys, their strong social similarity to humans make them an ideal species to investigate social processes, particularly with regard to evolutionary and developmental convergence.

The choice to study a species in the wild or captivity is one that must be addressed in animal research. Spider monkeys inhabit the canopy of Central and South American forests. Thus, collecting behavioral data for the social domain in which observation of two identifiable individuals is necessary can prove exceedingly difficult. This limitation has led to equivocal findings in general frequencies of social behaviors between wild and captive populations. Studying social behavior in the field has also led to grouping multiple social behaviors together as simply “social,” often measured by proximity of association given the visual constraints instead of breaking behaviors down into specific categories, and to a distinct lack of cognitive studies. Spider monkeys engage in distinctive multi-modal social interactions at times of fusion. These interactions generally fall into two classes of behaviors: affiliation (e.g., embrace) and agonism (e.g., contact aggression). Previous field research on these behaviors in spider monkeys suggests the embrace is considered a greeting behavior that serves as a signal for benign intent, especially during tension reduction (Schaffner & Aureli, 2005). However, captive studies have shown there are variations of the embrace involving the physical positioning of the face and partner choice that differ along the element of risk (Boeving, Belnap, & Nelson, 2017; Boeving & Nelson, 2018). Thus specificity is important since subtle differences can elucidate important information about a species social ecology. For these reasons, studying spider monkey social behavior in captivity is optimal, provided the species is socially housed. Doing so will allow for observation of multiple levels of sociality, which will allow for deepening and broadening knowledge of this species. Studying spider monkeys in captivity permits measurement across multiple levels of sociality, which would not be possible in the wild. Such multi-level measurement will provide a robust corpus of social data for a comprehensive characterization of spider monkey sociality.

1.3 Multiple Levels of Measurement

Social process is best conceived of as a multi-component complex system, encompassing the domain of sociality and all co-acting dimensions**.** Although no universal research framework exists for the study of sociality in non-human primates, social data are usually collected from one of three levels of measurement: the individual (e.g., cognition), the dyad (e.g., social interaction), and the structure within the group (i.e., sub-groupings). Acquiring cognitive data involves administration of a test instrument that requires the subject to complete a task. Among non-human primates, these instruments are administered by a human experimenter to a non-human primate subject. Social interaction consists of observable actions, or a signal and response between two individuals. Although multiple methods for acquiring social interactive data are utilized (e.g., live-coded digital data collection, video recording), the gold standard is behavioral observation using operationally defined behaviors in a species ethogram. A social subgrouping captures information about association among a larger group other than the dyad, and is best quantified by examining a social network, or a structurally defined group of connected individuals.

1.4 Statement of Objectives

The objective of this work is to apply the lens of network science to the study of primate social systems. As such, the overall goal of the study is to elucidate patterns using social network analysis in three topical areas in primatology. Specifically, the investigations presented in this work aim to 1) elucidate dissociable network structures across socially lateralized behaviors in spider monkeys, 2) implement social network analysis as a tool to characterize social development in spider monkeys, and 3) explore relationships between cognition and social network position in spider monkeys with a mixed method approach.

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Chapter 2

Social Risk Dissociates Social Network Structure across Lateralized Behaviors in Spider Monkeys

2.1 Abstract

Reports of lateralized behavior are widespread, although the majority of findings have focused on the visual or motor domains. Less is known about laterality with regards to the social domain. We previously observed a left-side bias in two social affiliative behaviors—embrace and face-embrace—in captive Colombian spider monkeys (*Ateles fusciceps rufiventris*). Here we applied social network analysis to laterality for the first time. Our findings suggest that laterality influences social structure in spider monkeys with structural differences between networks based on direction of behavioral bias and social interaction type. We attribute these network differences to a graded spectrum of social risk comprised of three dimensions.

2.2 Introduction

Reports of lateralized behavior are widespread, particularly in the visual and motor domain (Rogers & Vallortigara, 2015; MacNeilage et al., 2009). Decades of research has led to the general consensus that behavioral lateralization is subserved by asymmetric brain function. These brain-behavior asymmetries may serve to streamline neurobiological processes, thereby increasing behavioral efficiency in unpredictable or arousing situations, such as social interactions

(Rogers & Vallortigara, 2015; Vallortigara & Rogers, 2005). Thus, laterality may be particularly advantageous in gregarious species such as primates.

In a recent synthesis of prior research, Rogers & Vallortigara (2015) linked left biases in social behavior to the right hemisphere as a general pattern of lateralization in vertebrates. However, we later showed that not all social behaviors are associated with this pattern of laterality (Boeving et al., 2017). Specifically, we found that two variations of embracing, but not grooming, were lateralized in Colombian spider monkeys. We argued that the differences in lateralization in social affiliative behaviors were due to the social dynamic in which these behaviors occurred, with grooming considered a low-stakes routine state while embraces were high-stakes risky events. In this study, we focused on assessing the behavioral patterns among individuals within a group, and did not take into account the relational patterns of the group as a whole (e.g., interaction history). While consistent with other laterality investigators, this reductionist approach does not capture the true dynamics of a social system, begging the question: does laterality influence social structure?

Spider monkeys are one of a handful of primates living in fission-fusion (Aguilar-Melo et al., 2018), a social dynamic defined by separations and reunions. Embraces are a contact greeting gesture that occur at the time of reunions in spider monkeys (Schaffner & Aureli, 2005). In the standard embrace, the hands are wrapped around the body and the face is placed along the trunk (Schaffner & Aureli, 2005; Eisenburg, 1976). A variation is the face-embrace, in which faces touch (Boeving et al., 2017). Fission-fusion is characterized by marked unpredictability and low social cohesion compared with species that have a known stable hierarchy, cohesive social groups, and low variability in interactive exchanges (Aureli et al., 2008; Ramos-Fernandez et al., 2018). With these differences in mind, social interactions within species living in fission-fusion may consist of a level of risk unlike that experienced in other social dynamics, and laterality may play a role in negotiating this risk (MacNeilage et al., 2009). In general, social behavior in fission-fusion species is remarkably multi-dimensional, and can be difficult to tease apart.

One method for teasing apart complex social systems is social network analysis (Seur et al., 2011), a concept with roots in the mathematical field of graph theory. Social network analysis is a tool used to compute and visualize structural relationships in relational data. There is a long history of applying network analysis in the study of sociality in primates (for a review see Brent et al., 2011) and other species (Wey et al., 2013). Yet social network analysis has never been applied in the area of behavioral laterality. Network analysis alone has the unique ability to characterize and mathematically represent global inter-connected elements (Sporns, 2011). Within behavioral laterality, network level information may provide a more sophisticated method to examine topological patterns that represent potential advantages of laterality for behavior, and to accurately depict the multi-dimensional nature of social interaction.

As our primary objective, we leveraged social network analysis in the dataset reported by Boeving et al. (2017) to examine whether similarly lateralized behaviors (i.e., embrace and face-embrace) also have similar network structures, and we predicted that these networks would not differ. In our secondary objective, we examined social networks based on direction of laterality (i.e., left or right) regardless of behavior type by pooling embrace and face-embrace into an affiliative category. We hypothesized that laterality would influence network structure, and we predicted that global left and right affiliative networks would diverge. Finally, we examined the influence of both direction of laterality and behavior type on social network structure by creating four sub-networks of left embrace, left face-embrace, right embrace, and right face-embrace. We hypothesized that laterality, but not behavior type, would alter network structure. We predicted that the left sub-networks would differ from the right sub-networks, but that sub-networks within a behavior (i.e., embrace or face-embrace) would not differ.

2.3. Methods

2.3.1 Social Network Construction from Live-Coded Behavior

We constructed social networks from live coded behavioral observations of 15 captive Colombian spider monkeys *(Ateles fusciceps rufiventris)*. Portions of these data were previously reported in Boeving et al. (2017). To briefly summarize, 186 h of data were captured between May and August 2015 using the Animal Behaviour Pro mobile iOS application on apple iPod 5th generation (Newton-Fisher, 2012). The application was programmed with information about the individual monkeys to capture initiators and receivers of embrace and face-embrace with the modifier set as side (i.e., left or right positioning). Left or right was recorded with reference to the positioning of the faces regardless of whether there was contact or not. Directionality was not determined by any positioning of the limbs. Data were collected using the continuous sampling method, and *ad libitum* recording method (Martin & Bateson, 1993; Altmann, 1994) so that all occurrences of the target behaviors could be captured across three equally distributed time periods throughout the day to avoid disruptions due to husbandry procedures. The DuMond Conservancy Institutional Animal Care and Use Committee approved the research, and the study was conducted in accordance with the laws of the United States. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

2.3.2 Social Network Analysis

We utilized social network analysis as the computational method to investigate potential structural differences within all networks. Networks were computed and visualized in Cytoscape (http://www.cytoscape.com) (Version 3.4.0; Shannon et al., 2003), an open source software project for modeling interaction networks. The network metric of *degree centrality*, which provides a composite score from the *in-degree* value (i.e., interactions directed towards a monkey) and *out-degree* value (i.e., interactions directed by a monkey to others), was examined because this metric quantifies the number of edges (i.e., social interactions) shared between nodes (i.e., monkeys). The degree centrality of node (v) for a given graph (G) = $(\mathcal{V}, \mathrm{E})$ with $|\mathcal{V}|$ nodes and $|\mathrm{E}|$ edges defined as:

$$C_D(\nu) = deg(\nu)$$

Using the metric degree centrality, the total number of interactions for each individual was computed where monkeys with the most connected interactions (initiated or received) were positioned in the center of the graph and monkeys with fewer connected interactions were positioned along the perimeter. Within Cytoscape, we used a variant of the “Kamada-Kawai Algorithm,” a spring-embedded algorithm that forces connected nodes together while also forcing disconnected nodes away from the center (Kamada & Kawai, 1989). We constructed weighted networks because this method is best suited for graphically representing the variation in social bonds (Kerth et al., 2011; Voelkl et al., 2011). All edges were weighted based on frequency of interaction with thicker edges denoting more interactions and thinner edges denoting fewer interactions. Node size denotes variation in rank of degree centrality where larger nodes indicate higher values of degree centrality and smaller nodes indicate lower values of degree centrality.

2.3.3. Statistical Analysis

To examine whether similarly lateralized behaviors (i.e., embrace and face-embrace) have similar network structures, we first pooled frequency data from each behavior separately regardless of side to create global embrace and global face-embrace networks. To investigate the potential effect of laterality on social network structure, we then pooled affiliative frequency data according to side of positioning to create global left affiliative and global right affiliative networks.

Finally, we examined the effect of laterality within each type of embrace by constructing four direction x behavior networks: left embrace, right embrace, left face-embrace, and right face-embrace. *t*-Tests and ANOVA with post hoc comparisons were used to compare the resulting networks.

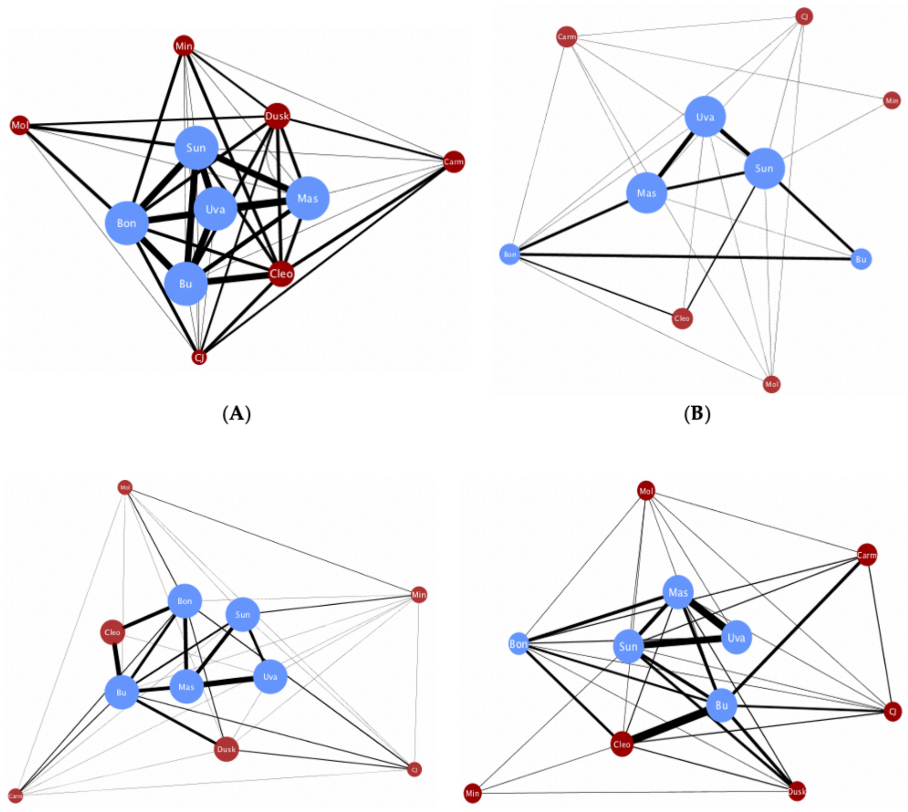
2.4. Results

A total of 1623 social interactions were examined. Of these, 1270 were embraces and 353 were face-embraces, corresponding to 1227 left affiliative and 396 right affiliative interactions. Four juveniles were excluded from further analysis due to multiple zero values for out-degree, which we suggest is age-related and would not accurately portray degree centrality in the spider monkey group. Network degree centrality values for the global comparisons can be found in **Table 2.1**. Unpaired *t*-tests found a significant difference in degree centrality between the global embrace and face-embrace networks ($t(28) = 3.43$, $p < 0.01$, $d = 1.296$; **Fig. 2.1**), and a significant difference in degree centrality between the global left and right affiliative networks ($t(20) = 3.92$, $p < 0.001$, $d = 1.753$). There was no sex difference in the global left affiliative, global right affiliative, or global embrace networks (all $p > 0.05$). However, there was a sex difference in the face-embrace network such that females initiated the face-embrace behavior more than males, and males received more of these interactions compared to females ($F(1,13) = 4.82$, $p < 0.05$, $\eta^2 = 0.270$). To further examine structural differences between embrace and face-embrace within the context of laterality, we examined the four sub-networks (left embrace, right embrace, left face-embrace, right face-embrace). ANOVA revealed a significant difference in degree centrality among the sub-networks ($F(3,40) = 20.72$, $p < 0.001$, $\eta^2 = 0.608$; **Fig. 2.2**). Post hoc analyses found that each sub-network was different from the others (all $p < 0.05$).

Table 2.1. Individual Degree Centrality Values.

Monkey	*Sex*	Left Affiliative	Right Affiliative	Embrace	Face-Embrace
Bon Jovi (Bon)	M	202	57	214	62
Butch (Bu)	M	294	82	263	128
Carmelita (Carm)	F	76	25	82	24
Cleo	F	208	62	208	73
CJ	F	108	32	123	19
Dusky (Dusk)	F	164	46	191	31
Mason (Mas)	M	372	104	342	141
Mints (Min)	F	79	38	136	4
Molly (Mol)	F	94	25	110	15
Sunday (Sun)	M	261	101	296	83
Uva	M	386	144	445	121

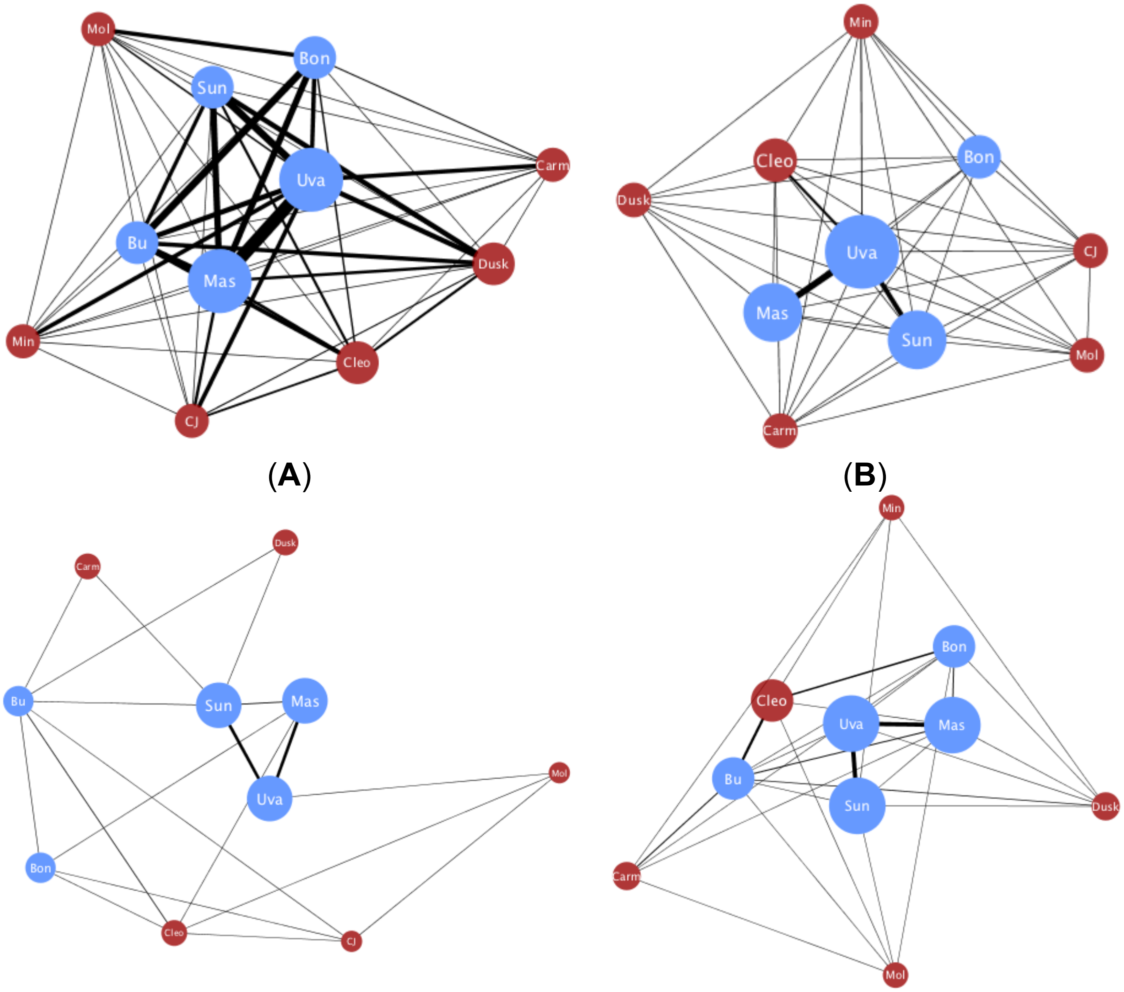
M = Male, F = Female. The higher the degree centrality value, the more highly connected a monkey is to others.



(A) (B)

(A) (B)

Figure 2.1. Global Affiliative Networks. Global left affiliative and global right affiliative networks differ. Red denotes females, and blue denotes males. Nodes are weighted such that the larger the node, the higher the degree centrality. Edges are weighted such that thickness denotes frequency of interactions.



(**A**) (**B**)

(**C**) (**D**)

Figure 2.2. Lateralized Networks for Embrace and Face-Embrace. Clockwise from top left: (**A**) Left embrace; (**B**) Right embrace; (**C**) Left face-embrace; and (**D**) Right face-embrace. Networks are ordered on social risk index (see text for details). Red denotes females, and blue denotes males. Nodes are weighted such that the larger the node, the higher the degree centrality. Edges are weighted such that thickness denotes frequency of interactions

2.5. Discussion

The primary objective of this study was to examine if behaviors with similar patterns of behavioral laterality would also have similar social network structures. We examined the social affiliative behaviors, embrace and face-embrace, which we previously have shown to be left lateralized in spider monkey behavior (Boeving et al., 2017). Contrary to our predictions, we found that the network for embrace was structurally different from that of face-embrace. We then explored our secondary objective examining whether the side with which the social affiliative behaviors were performed had an effect on network structure. Here our results confirmed our prediction that the global left affiliative network was structurally different from the global right affiliative network. Finally, our analysis of sub-networks parsing direction within each behavior partially supported our prediction. All four sub-networks were different from each other, suggesting an interaction between laterality and behavior type. We discuss these differences in social network structure in the context of three dimensions of social risk.

The concept of risk is often described in the non-human primate literature in the context of risk of aggression from neighboring groups (Wrangham et al., 2007), predation (Hill & Lee, 1998), and loss of resources (Jernvall & Wright, 1998), all of which are typical challenges for species living in the wild. Rebecchini et al., (2011) first identified embracing as a component of risk in spider monkeys, and Boeving, Belnap, & Nelson (2017) suggested that embrace risk may be graded according to the type of physical contact with face-embrace having higher risk given the close placement of the faces. By comparison, embrace is lower risk because the faces do not touch. Here, we label this type of risk *contact risk*. Although embrace and face-embrace have a similar left behavioral lateralization pattern, the finding that they do not have similar network structures supports the conclusion that these behaviors are related but distinct. The graphical representation of the embrace network conveys the robustness of this behavior (**Fig. 2.2**). Specifically, most individuals engaged in embracing, and with high frequencies, yielding a network graph with most monkeys having high values for degree centrality. Overall, this pattern indicates strong cohesion in the embrace network. In contrast, the face-embrace network depicts interactive patterns in which only a few males were strongly bonded. When in-degree and out-degree were examined, both males and females initiated and received within the embrace network, but there was a significant difference in the face-embrace network where females initiated more face-embrace and males received more of this behavior. This sex difference is notable because aggression towards females from male spider monkeys is a known pattern (Fedigan & Baxter, 1984), making the social lives of female spider monkeys especially risky. In captivity, intra-group aggression is an important consideration given that wild female spider monkeys emigrate from their natal group (Fedigan & Baxter, 1984; Link et al., 2018). We envisioned the face-embrace to be the riskier of the two embraces given the close face contact. Yet, with the known pattern of aggression towards females in mind, our social network analysis points to a second aspect of social risk within the face-embrace: *partner risk.* Social risk in relation to sex roles has been widely discussed in the human literature. For example, female sexual risk taking within certain communities is associated with greater risk of male aggression towards them (Campbell et al., 2008; Jewkes et al., 2003). Contact and partner variables have also been examined in the literature on social touch laterality in human kissing (Gunturkun, 2003; Chapelain et al., 2015; Ocklenburg & Gunturkun, 2009; Sedgwick & Elias, 2016; van der Kamp & Canal-Bruland, 2011) and embracing (Packheiser et al., 2018; Turnbull et al., 1995) although these studies have not framed their findings in the context of risk, which may be an avenue in the future to connect these two streams of research.

A third type of risk identified by our network analyses is *laterality risk.* This dimension of risk was informed by our analyses that identified a structural difference between the global left affiliative and global right affiliative networks. In the left affiliative network, several monkeys were central. In contrast, the right affiliative network had a significantly different architecture in which fewer monkeys were central to the network, and in which the behavior occurred less frequently. Previous work has suggested that the right hemisphere plays an important role in the monitoring and detection of uncertain events in the environment, while the left hemisphere is more involved in routine behavior (MacNeilage et al., 2009). This role differentiation between hemispheres is particularly relevant when considering the positioning of the body for embrace and face-embrace. Specifically, if the functional split between hemispheres is correct, then positioning others on the right side for either behavior would be risky. Moreover, face-embrace would be especially risky given the close contact of the face coupled with the hypothesized decrease in ability for social monitoring when engaging others on the right side. It would thus be advantageous to position conspecifics on the left side given the hypothesized neural processing benefit. In line with this hypothesis, the structure of the left lateralized affiliative network pattern can be characterized as a highly cohesive network where all monkeys engaged in the behavior, and engaged frequently. In contrast, the right lateralized network was lower in cohesion; engagement occurred less frequently, with only a few monkeys reaching high values of degree centrality. Although not recorded in this study, capturing the sequence of behaviors that follow these risky interactions would further test this theory, and is a goal for future work. The hypothesized spectrum of risk is presented in **Fig. 2.3.**

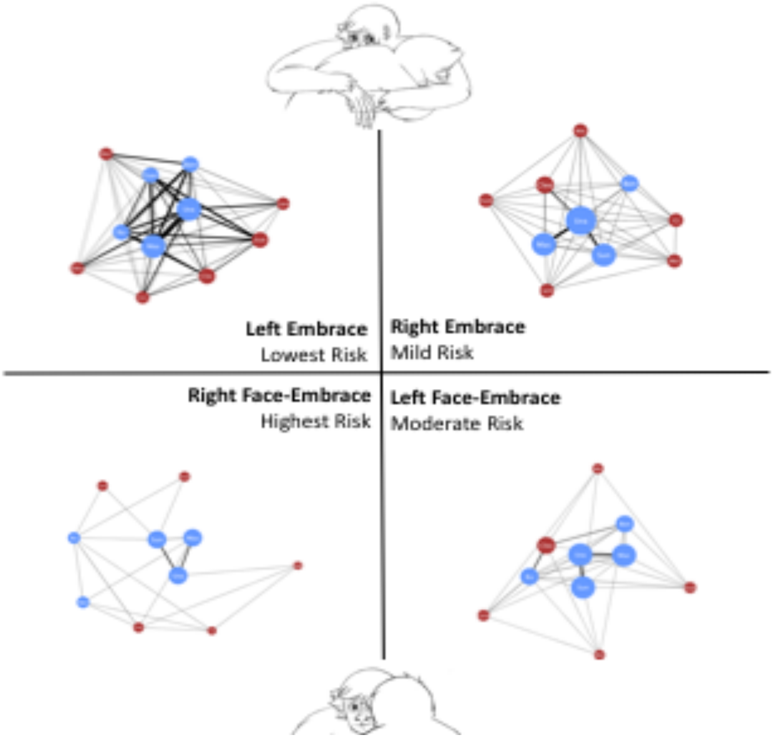


Figure 2.3. Spectrum of Risk with Associated Networks. Clockwise presentation of network dissociation associated with social risk with illustration of embrace and face-embrace.

Table 2.2 Dimensions of Social Risk.

Behavior	*Laterality*	*Contact*	*Partner*	Risk Index
Left Embrace	Low	Low	Low	**Lowest**
Right Embrace	High	Low	Low	**Mild**
Left Face-Embrace	Low	High	High	**Moderate**
Right Face-Embrace	High	High	High	**Highest**

Although we collected data over a four-month period, one limitation of this study is that we were not able to assess the stability of these networks over time. Juvenile data were excluded from analyses due to the low frequency of engagement in the behaviors we examined. However, we would expect this pattern to change as individuals mature and develop social bonds. The novel application of social network analysis could quantify this process, not only in primates, but other highly social species. Moreover, here we have utilized a between-networks approach based on our research question, but a within-networks approach across two or more timepoints could provide information about how an individual's position in a network changes as a function of development. A developmental network approach would also broaden our knowledge of the factors that contribute to the emergence of social laterality and its function.

Taken together, the structural differences between the four sub-networks confirmed a graded spectrum of social risk in spider monkeys along the three dimensions of risk: contact, partner, and laterality (Table 2). The sub-network with the lowest risk (i.e., left embrace) had the most participation and strongest cohesion, whereas the sub-network with the highest risk (i.e., right face-embrace) had the least participation and was the most disjointed of the networks indicating low cohesion (Figure 1). To answer our original question posed in the introduction, these findings suggest that laterality influences social structure. However, we acknowledge that social structure may also influence laterality, or that the relationship is bidirectional. Future work using longitudinal designs may address this point. Additional studies should also aim to include network analyses of other behavioral domains that could be related to laterality, such as cognition and motor skill. In conclusion, social network analysis is an exciting new avenue for characterizing brain-behavior relationships. In using this unique computational method to elucidate factors that drive global differences in social network topology, we advance our understanding of laterality within a social framework.

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Chapter 3

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

3.1 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 hours 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*s < .05). Network and social role differences are discussed in light of social development and aspects of the different behaviors.

3.2 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 pair-wise 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, Boyer, Aureli, & Vick, 2009; Ramos-Fernández & Morales, 2014; 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 multi-dimensional 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 social network analysis 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 sub-groups 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 multi-modal 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; Henazi & Barrett, 1999), whereas multi-modal 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 multi-modal 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.

3.3 Methods

3.3.1 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, Florida, United States. The main enclosure measured 8.84 m x 3.96 m x 4.47 m. The adjoining room measured 3.30 m x 1.92 m x 1.77 m and was connected directly to an indoor night house, which measured 3.30 m x 1.09 m x 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.

3.3.2 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 3.1**.

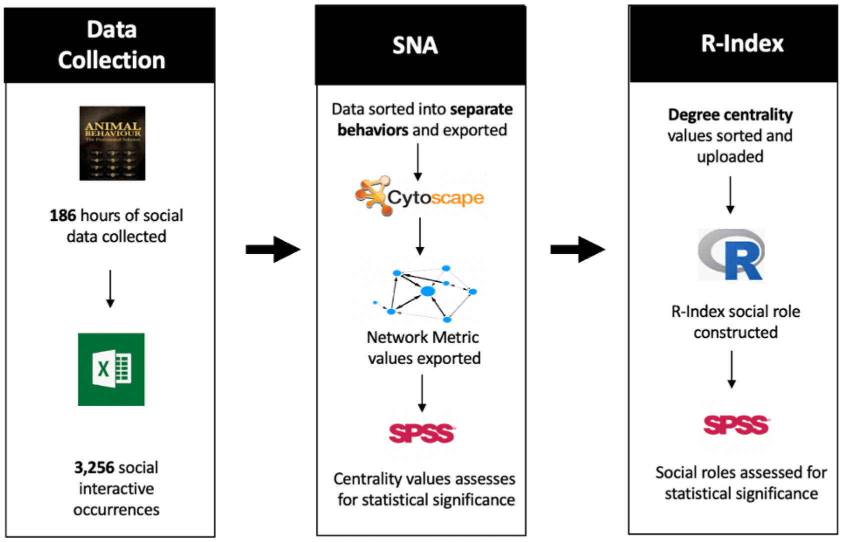

Figure 3.1. Data Pipeline.

3.3.3 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 ninety-minute sessions, across three intervals throughout the day: 9:30 AM – 11:30 AM, 12:30 PM – 2:00 PM, and 4:00PM – 5:30 PM. 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, Belnap, & Nelson, 2017; Boeving & Nelson, 2018). Embrace was recorded when individuals wrapped arms around the body, placing the head down towards 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 non-contact aggression such as chasing (Klein & Klein, 1971).

3.3.4 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 5 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 3.1**).

3.3.5 Social Role Calculation

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 outdegree (initiated the social behavior) and W_i is weighted indegree (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 vs. receiving ratios between juveniles and adults, and also between males and females.

3.3.6 Statistical Analyses

Non-parametric 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 alpha level of .05. We provide a measure of effect size (Cohen's *r*) for each non-parametric test to guide interpretations (Fritz, Morris, & Richler, 2012). We suggest following the standard interpretation of r=0.2 as a small effect, r=0.5 as a medium effect, and r=0.8 as a large effect (Cohen, 1988).

Given that social network data are inherently non-independent and often scaled, we also tested our data against a null model as suggested by Farine (2017). Null models re-sample and simulate randomized datasets 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 non-parametrically, 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 inter-related 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 inter-related by setting groom and agonism as the predictor variables and embrace as the dependent variable.

3.3.7 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.

3.4. 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. **Fig. 3.2** depicts network graphs across behavior types, and degree centrality values are presented in **Table 3.1**. 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.

3.4.1 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), face-embrace (*U* = 0, *p* = .002, d = 0.8), and tail-wrapping (*U* = 4, *p* = .01, d = 0.8). There were no differences in degree centrality between juveniles and adults for grooming (*U* = 1, *p* >.05) or agonism (*U* = 11, *p* >.05). The network graphs depicting these results is presented in **Fig. 3.2**. These finding 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 3.1.**

Table 3.1. In-Degree (In) and Out-Degree (Out) Centralities.

ID	Groom		Tail-wrap		Face-embrace		Embrace		Agonism	
	In	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**	**In**	**Out**
1 Bonjovi ♂	9	68	49	9	48	16	129	102	0	1
2 Butch ♂	47	88	78	65	90	41	168	122	0	12
3 Carm	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

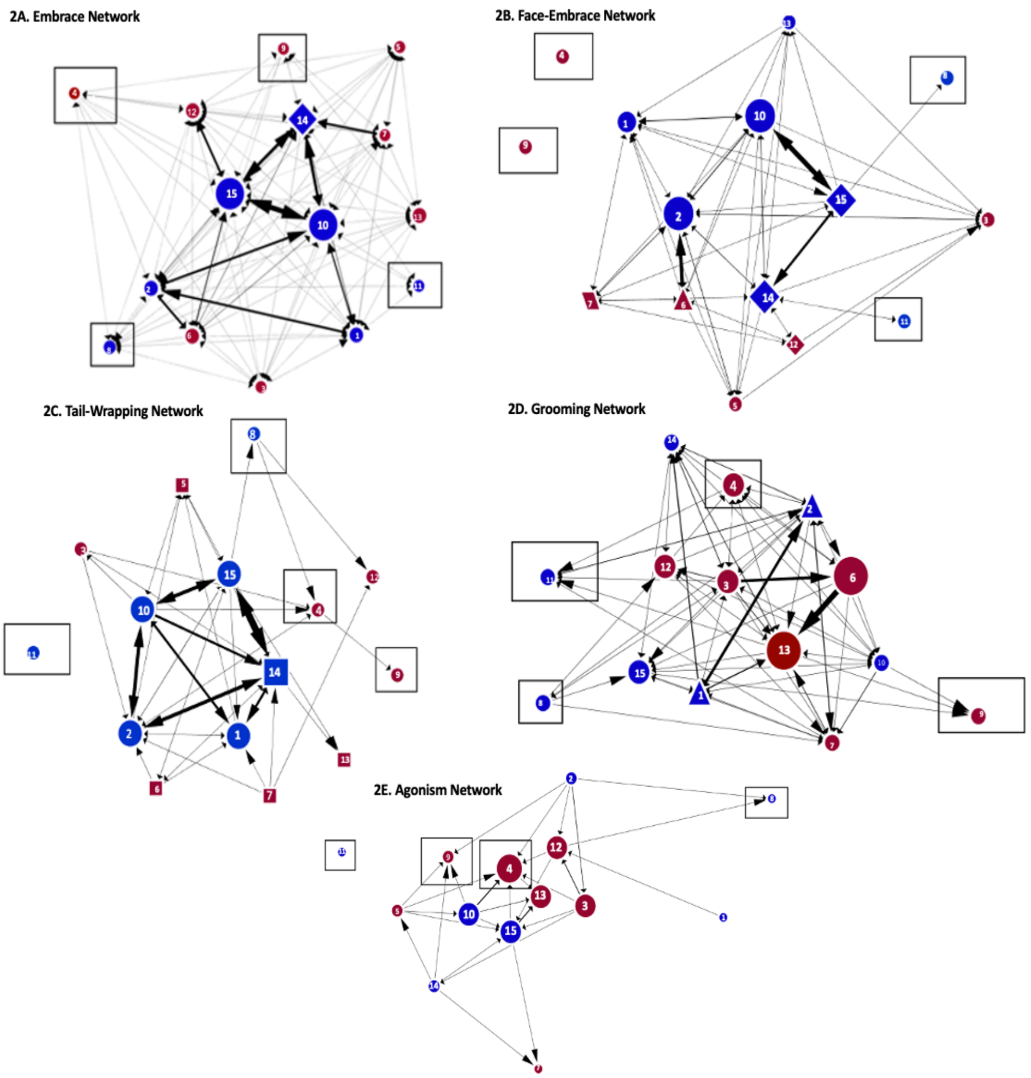

Figure 3.2. Social networks across Each Behavior Type. Social networks are presented for embrace, face-embrace. tail-wrapping, grooming, and agonism. Thickness of edge denotes frequency of dyadic interactions, where thick edges are high frequencies and thin edges are low frequencies. Arrows depict if 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.

For betweenness centrality, Mann Whitney U-tests determined significant differences between juvenile and adults for embrace (U = 5.5, p = 0.007, d = 0.8) and face-embrace (U = 0, p = 0.001, d = 0.8). No statistical differences were detected for grooming, tail-wrapping or agonism (all $p > .05$). For embrace, Sunday (.09) achieved the highest betweenness score. Sunday (.27) and Uva (.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 3.2.**

Table 3.2. Betweenness Centrality Values.

ID	Groom	Tail-wrap	Face-embrace	Embrace	Agonism
	Scaled	Scaled	Scaled	Scaled	Scaled
1♂	.03	.02	.03	.06	0
2♂	0.1	.08	.06	.07	0
3	.08	.006	.06	.09	.02
4*	.03	.06	.05	.03	0.2
5	--	0.1	0.4	.04	.03
6	.02	.01	0.1	0	0
7	.04	0.1	.02	.06	0
8*♂	.01	.06	0	.01	0
9*	.14	0	0	.02	0
10*♂	0.4	.09	0.4	.04	.003
11♂	0	0	0	.02	0
12	0.1	0	0.2	.02	.05
13	0.1	0	.0.1	0.1	0
14♂	.02	0.5	0.3	.09	.04
15♂	.08	0.2	0.2	.07	.06

For closeness centrality, Mann Whitney U-tests determined significant differences between juveniles and adults for face-embrace (U = 2, p = 0.002, d = 0.8) and grooming (U = 3, p = 0.008, d = 0.8) but not embrace, tail-wrapping, or agonism (all p > 0.05). 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, requiring less interaction with peripheral nodes to achieve centrality. A complete list of all closeness centrality values may be found in **Table 3.3**

Table 3.3 Closeness Centrality Values.

	Groom	Tail-wrap	Face-embrace	Embrace	Agonism
ID	Scaled	Scaled	Scaled	Scaled	Scaled
1♂	1.0	0.4	0.3	0.7	0.5
2♂	0.8	0.4	0.4	0.7	0.5
3	0.6	0.4	0.5	0.2	0.6
4*	0.4	1.0	0	0.6	1.0
5	--	0.5	0.5	0.5	0.8
6	0.6	0.5	0.6	0.6	0
7	0.4	0.5	0.7	0.7	0
8*♂	0.5	0.8	0	0.5	0
9	0	0	0	0.7	0
10♂	0.7	0.6	0.5	0.5	0.8
11*♂	0	0	0.4	0.7	0
12	0.5	0	0.5	0.5	0.7
13	0.5	0	0.5	0.2	0
14♂	0.6	0.5	0.6	0.5	1.0
15♂	0.5	0.6	0.4	0.5	0.9

For clustering coefficient, Mann Whitney U-tests determined significant differences between juveniles and adults for face-embrace (U = 15.5, p = 0.04, d = 0.4) and tail-wrapping (U = 3, p = 0.003, d = 0.8) but not for grooming, embrace, or agonism (all p > 0.05). 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 3. 4.**

Table 3. 4. Clustering Coefficient Values.

ID	Groom	Tail-wrap	Face-embrace	Embrace	Agonism
	Scaled	Scaled	Scaled	Scaled	Scaled
1♂	0.5	0.4	0.4	0.4	0
2♂	0.3	0.3	0.4	0.4	0.5
3	0.3	0.4	0.3	0.5	0.3
4*	0.4	0.2	0	0.5	0.2
5	--	0.5	0.4	0.5	0.3
6	0.4	0.5	0.3	0.5	0
7	0.4	0.5	0.7	0.4	0.5
8*♂	0.5	0	0	0.5	0.5
9*	0.5	0	0	0.5	0.2
10♂	0.4	0.3	0.4	0.4	0.2
11*♂	0.5	0	0.4	0.5	0
12	0.4	0	0.3	0.4	0.2
13	0.4	0.5	0.4	0.5	0.5
14♂	0.4	0.5	0.2	0.5	0.2
15♂	0.3	0.3	0.4	0.4	0.2

3.4.2 Social Role Calculation

Figure 3.3 depicts the effects of age class on R-Index scores, and **Figure 3.4** depicts the effects of sex on R-Index scores. $RI_{EMBRACE}$ ranged from 0.13 to 0.74 (*M* = 0.42 ± 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. $RI_{FACE\text{-}EMBRACE}$ ranged from 0.00 to 0.87 (*M* = 0.45 ± 0.33). Both female juveniles (Cary, Jeni) did not initiate or receive face-embrace, and therefore did not have a $RI_{FACE\text{-}EMBRACE}$ 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. $\mathrm{RI}_{\text{TAIL-WRAP}}$ ranged from 0.00 to 0.83 (*M* = 0.38 ± 0.28). One male juvenile (Marley) did not initiate or receive tail-wrap, and therefore did not have a $\mathrm{RI}_{\text{TAIL-WRAP}}$ 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. $\mathrm{RI}_{\text{GROOM}}$ ranged from 0.11 to 0.89 (*M* = 0.42 ± 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. $\mathrm{RI}_{\text{AGONISM}}$ ranged from 0.00 to 1.00 (*M* = 0.48 ± 0.42). One male juvenile (Marley) and one adult female (Cleo) did not initiate or receive agonism, and therefore did not have a $\mathrm{RI}_{\text{AGONISM}}$ 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.

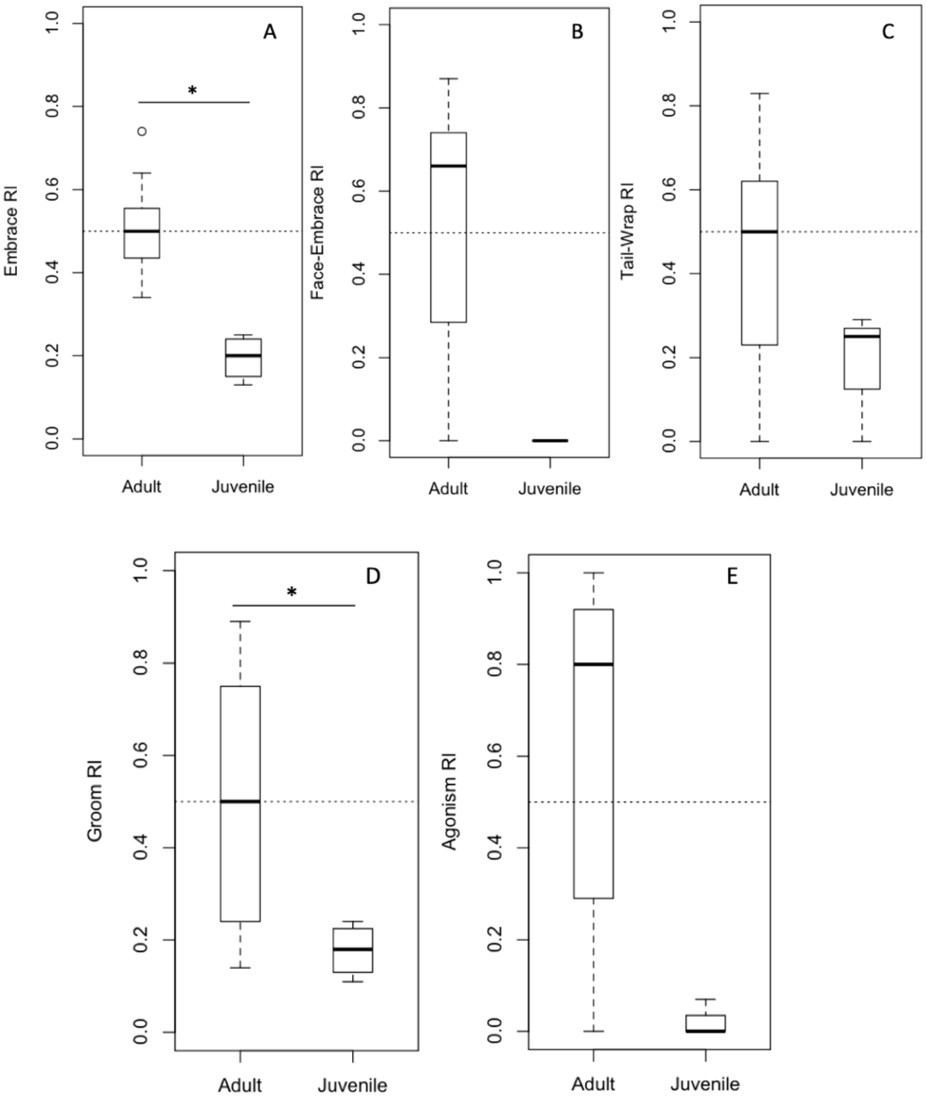

Figure 3.3. The Effect of Age Class on R-Index Scores. (A) embrace, (B) face-embrace, (C) tail-wrap, (D) groom, and (E) agonism. **p* < .05.

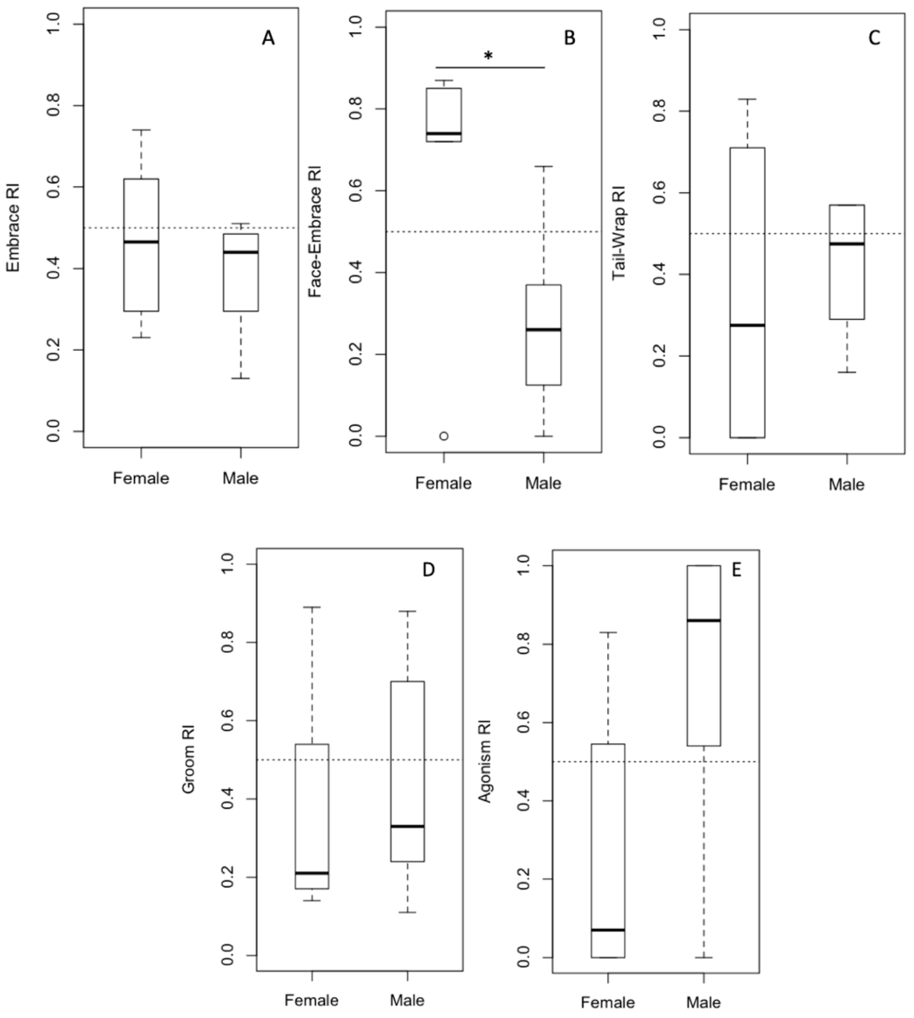

Figure. 3.4. The Effect of Sex on R-Index Scores. (A) embrace, (B) face-embrace, (C) tail-wrap, (D) groom, and (E) agonism. **p* < .05.

3.4.3 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).

3.5 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 adult 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; Henazi & Barrett, 1999). Grooming is the quintessential affiliative behavior that is most commonly observed in order 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-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 multi-modal in that 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 et al., 2017; Boeving & Nelson, 2018). 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 may be 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 non-significant 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 (**Fig. 3.2**). 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 inter-twined 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 Multiple Regression Quadratic Assignment (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 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 & Boeving, 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 multi-site 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 a 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 multi-modal 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. Social network analysis provides the tools to quantify and visualize these patterns in order to better understand social development.

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Chapter 4

Innovators broker social interactions in spider monkeys

4.1 Abstract

In the last decade, the burgeoning fields of network science and cognitive science have contributed significantly to the study of animal behavior. However, these two fields are considered disparate, with the methods subserving each discipline traditionally applied separately to study social organization and animal cognition. Thus, the degree to which these dimensions intersect is not understood. Here we implement multi-modal methods to examine the relationship between problem solving skill, specifically innovation, and social network position in spider monkeys. We captured social interaction data for three behaviors: grooming, embracing, and tail-wrapping. We administered a cognitive paradigm, requiring problem solving to assess cognitive flexibility, and performed social network analytics to characterize the underlying social structure across the three behaviors. We predicted that problem solvers would be central in embrace networks given the socioecology of spider monkeys. However, our results showed that problem solvers were central in the tail-wrapping network, in which they play key social brokering roles. We attribute this pattern to differences in social decision making, where innovators invest in interactions requiring less effort with more gains in social capital.

4.2 Introduction

In recent decades, the fields of network science and cognitive science, two disparate yet burgeoning disciplines, have contributed significantly to the study of animal behavior (Wey et al., 2008; Hurley & Nudds, 2006). However, the methods subserving these fields have traditionally been applied separately to study social organization and animal cognition. Thus, the degree to which these dimensions intersect is not understood. Animals, including humans, self-organize into structural components known as social networks that are maintained through affiliative interactions (c.f., Pinter-Wollman et al., 2014). Across taxa, primates spend more time socially engaged than any other behavior and can be characterized with complex behavioral repertoires (Sussman et al., 2005). Thus, identifying the underlying patterns of social organization, and how phenomena may influence these patterns, is essential for fully elucidating the socio-behavioral ecology of primates.

Observation studies have dominated the field of primatology, leading to large assortments of studies identifying social patterns for many primate species. These studies have increased the overall knowledge of behavioral dynamics and how these vary within and across primate groups. However, behavior alone is only one domain of functional processes. Characterizing complex phenomena, such as social processes and the relationship of these processes to other variables, may necessitate the use of mixed methods of measurement and analysis that crosses domains in order to comprehensively identify ecological patterns. With the advanced computation of network analytics, researchers can now go beyond behavioral frequencies and quantify social processes using multidimensional network graphs. The nature of these graphs allows for examination of network metrics, which convey unique aspects of social information that can only be gleaned using network analytics. Specifically, the ability to characterize both direct social interaction (i.e., degree centrality) and indirect social connection (i.e., betweenness centrality) allows for the unique examination of actual participation in behavior as well as the relative control of a network based on the prominence of the entities an individual interact with. Moreover, individualized phenotypic information that may be especially relevant to understanding social decision making, such as cognitive skill, can be depicted in the context of the individual in relation to others if social network analysis is utilized. Such detailed information may be necessary to fully understand how the social roles individuals play within networks converge with other processes to ultimately form social systems with underlying structures.

Broadly conceived, cognition is a multi-component process that enables animals to acquire, process, and store information (Shettleworth, 2010). Thus, cognition is an integral element of animal life that is necessary for many behavioral functions, and together behavioral and cognitive processes determine how individuals interact with their environment (Chow et al., 2018). As cognition is thought to sub-serve intelligence, individuals with certain cognitive skills may glean fitness benefits. Problem solving ability, for example, may enable individuals to innovate and exploit resources in novel ways, thus conferring ecological advantages. Moreover, having a close social tie to individuals with problem solving skills may indirectly convey these fitness benefits as well. Cognitive flexibility is particularly important in problem solving as it is the process that subserves the innovation of novel, adaptable solutions to a changing environment (Ionescu, 2012). Cognitive flexibility is a construct that is an emergent property of execution function, and neurological studies in humans have suggested that cognitive flexibility is the product of several cognitive processes working coherently to generate responses (Dajani & Uddin, 2015). The advanced computation of network analytics may provide unique opportunities to explore the complex relationship between cognitive flexibility and social decision making by elucidating how skilled problem solvers structure their social networks.

While no studies have specifically investigated the relationship between cognitive flexibility and social network structure in primates, previous investigations of primate cognition in the context of social network organization have included studies with diverse methods that can be divided into two topical categories: information transmission and fitness benefits. With regard to information transmission, studies have been designed in wild contexts to examine the information flow of tool use skills. For example, Hobatier et al., (2014) created a novel network algorithm to determine the order of learning a task in the wild (i.e., moss sponging) built from co-presence of chimpanzees at a watering hole. Studies in a captive context typically include the introduction of an apparatus and paradigm. For example, Claidiere et al., (2014) used co-presence of individual squirrel monkeys at the site of a foraging apparatus to build social learning networks. The authors suggest that the common method for building social networks, through observed social interactions, may not be appropriate (especially for social learning experiments) given that these interactions are out of the context of the cognitive paradigm or task. With regard to fitness benefits, for example, Kulachi et al. (2018) introduced a novel foraging task to a group of lemurs, and found that individuals that solved the task sooner, and more frequently, were approached and groomed more than non-solvers such that they became central in their networks. Stammback et al. (1988) introduced a foraging task in crab eating macaques and identified specialist within the group that could successfully operate the apparatus to dispense food. The authors showed there was an increase in grooming and spatial affiliation between multiple specialist and non-specialist dyads, which correlated with the overall benefit (food) gained by the non-specialists. One meta-analysis conducted by Pasquaretta et al., (2014) found that primate species with high neocortex ratio, considered an indirect measure for cognitive capacity, had high frequencies of positive affiliative interactions reported in their studies and were more likely to have efficient networks.

Taken together, the methods for studying cognition in the context of social networks are extremely diverse. There is a tendency to introduce foraging tasks as the method for assessing problem solving in order to keep the task ecologically valid. Yet this may not provide necessary information for a specific cognitive construct. Moreover, social networks are traditionally built from dyad associations (i.e., occupying the same general physical space), or dyadic social interactions. Yet, the differences between association and interaction are vast. Association may provide more specific information for social learning experiments, but interaction data could provide more detailed information regarding individualized patterns. As grooming is considered the quintessential behavior for maintaining social bonds in primates, it is the social interaction most often utilized to construct social networks. Lehmann et al., 2007; MacIntonsh et al., 2012). However, grooming is not used to maintain social bonds in all primates, and focusing on a single behavior does not provide a comprehensive examination of the relationship between cognition and sociality (Schaffner & Aureli, 2005).

Spider monkeys follow what is described as an atypical social pattern in that embraces, but not grooming, are utilized for maintaining social bonds (Schaffner & Aureli, 2005). Spider monkeys are characterized by a complex behavioral repertoire with multiple social interaction types (Boeving et al., 2017, 2018, 2020). Spider monkeys may be an ideal species to further investigate potential relationships between cognitive flexibility and sociality given their socio-ecology. Moreover, there is a lack of studies investigating cognition as a whole in plattyrhines. To address this gap, we investigated the potential relationship between cognition as measured by problem solving, and social networks in spider monkeys across three behavior types: grooming, embracing, and tail-wrapping. We hypothesized that there is a relationship between problem solving skill and social network organization. Given that embraces are known to maintain social bonds in spider monkeys, we predicted that problem solvers would be central in the embracing network and not in the grooming network or tail-wrapping network.

4.3 Methods

4.3.1 Subjects

Behavioral 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, Florida, United States. The main enclosure measured 8.84 m x 3.96 m x 4.47 m. The adjoining room measured 3.30 m x 1.92 m x 1.77 m and was connected directly to an indoor night house, which measured 3.30 m x 1.09 m x 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. 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.

4.3.2 Ethical Note

The DuMond Conservancy and Florida International University Institutional Animal Care and Use Committee approved the study (FIU protocol 13-069, DC 2012-03). The work was performed in accordance with the American Society of Primatologists Principles for Ethical Treatment of Non-Human Primates and the laws of the United States.

4.3.3 Cognitive Testing Procedure

Data from the elevated task (adapted from Zander & Judge, 2015) was previously reported as a component of a test battery assessing laterality of the spider monkey tail (Nelson & Kendall, 2018). To summarize, the elevated task required monkeys to obtain an out-of-reach food item from a PVC tube placed on top of two book ends. A PVC bar (1.5 cm in diameter X 20.3 cm in length) baited with a food item (e.g., marshmallow or peanut butter and jelly mix) was placed on top of elevated bookends (8.9 X 26.7 cm^2 base). The bar was elevated to 17.1 cm. A successful trial consisted of a monkey obtaining the out-of-reach baited bar with the tail, without dropping or having it taken by another monkey before it reached them. Ten trials were collected for each monkey, with trials divided by monkeys locomoting between them, and were recorded on nonconsecutive days.

4.3.4 Behavioral Data Collection

Behavioral data were collected as part of large project investigating social processes in Colombian spider monkeys, with subsets previously reported (Boeving et al., 2017; Boeving et al., 2018). All 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 ninety-minute sessions, across three intervals throughout the day: 9:30 AM – 11:30 AM, 12:30 PM – 2:00 PM, and 4:00PM – 5:30 PM. The All-Occurrence recording method was utilized given the interest in recording targeted dyadic social behaviors across match-to-time samples. Embrace was recorded when individuals wrapped arms around the body, placing the head down towards the shoulder or trunk of the body, and was often accompanied with the whinny vocalization. Grooming was recorded when individuals used the hands or mouth to pick or mouth the fur of another individual. Tail-wrapping was recorded when individuals locomoted side-by-side or one behind the other with tails entwined

4.3.5 Social Network Construction and Analysis

The network metrics of *degree centrality* and *betweenness centrality* were chosen in order to assess both direct and indirect social connection. Degree centrality is a direct measure of social connection, most accurately representing actual participation in a social behavior. Contrastingly, 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 focused on this network metric to help determine within network differences of social facilitation between flexible problem solvers and non-problem solvers across the three behaviors. Data files were uploaded to Cytoscape (http://www.cytoscape.com) (Shannon et al., 2003) an open source software project for modeling networks. 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

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.

4.3.6 Statistical Analyses

Non-parametric tests were used to assess the statistical significance of betweenness centrality scores, as data were not normally distributed. Within network differences betweenness centrality between problem solvers and non-problem solvers were examined using independent-samples Mann-Whitney U tests. As social network data are not independent, a boot-strapping method was utilized to resample data against a null model for 10,000 iterations (Farine, 2017). Results that remained significant after this procedure were retained.

4.4 Results

4.4.1 Behavior and Cognitive Testing

A total of 111 data collection sessions were completed, yielding a total of 3,256 social interactions. Of these, 1,433 were embrace, 449 were tail-wrapping, and 950 were grooming. Seven monkeys participated in the experimental task, with each monkey solving all thirty trials.

4.4.2 Social Network Analysis

For betweenness centrality, problem solvers were found to be social brokers in tail-wrapping networks. Mann Whitney U tests determined the statistical significance of these within-network differences such that problem solvers were significantly more likely to control tail-wrapping networks ($U = 11$, $p < 0.05$) but not grooming or embrace networks (both $p > 0.05$) (**Fig. 4.1**) The degree centrality analysis yielded no significant results when comparing network position for problem solvers and non-solvers across embrace, grooming, and tail-wrapping (all $p > 0.05$). The individual scores for betweenness centrality are presented in **Table 4.1** and scores for degree centrality are presented in **Table 4.2.**

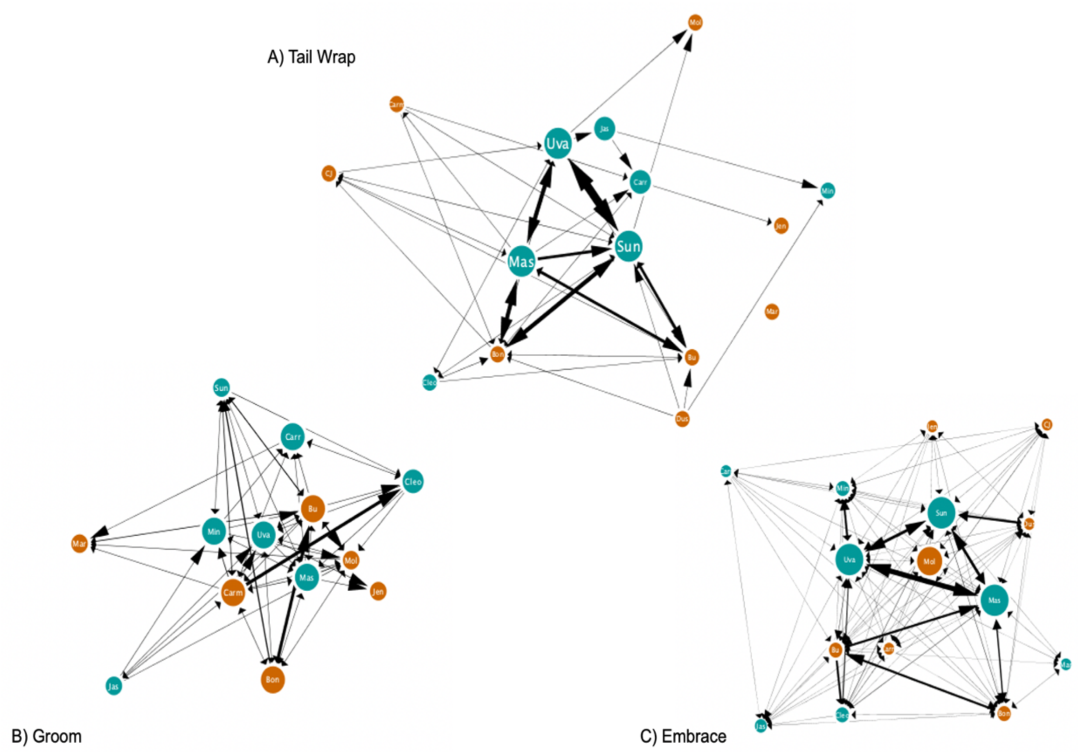

Figure 4.1 Social Networks for Each Behavior Type. Males are represented with teal colored nodes and females are represented by orange colored nodes. Thickness of lines denotes edge weights. Arrows represent direction of interaction.

Table 4.1. Betweenness Centrality Values.

ID	Name	Groom	Embrace	Tail - Wrap
		Scaled	**Scaled**	**Scaled**
1	Bon Jovi ♂	.03	.06	.02
2	Butch ♂	0.1	.07	.08
3	Carmelita	.08	.09	.006
4	Cary	.03	.03	.06
5	CJ	--	.04	0.1
6	Cleo	.02	0	.01
7	Dusky	.04	.06	0.1
8	Jasper ♂	.01	.01	.06
9	Jeni	.14	.02	0
10	Mason ♂	0.4	.04	.09
11	Marley ♂	0	.02	0
12	Mints	0.1	.02	0
13	Molly	0.1	0.1	0
14	Sunday ♂	.02	.09	0.5
15	Uva ♂	.08	.07	0.2

Table 4.2. Degree Centrality Values.

ID	Name	Groom	Embrace	Tail - Wrap
		Scaled	Scaled	Scaled
1	Bon Jovi ♂	167	231	58
2	Butch ♂	135	290	145
3	Carmelita	99	90	4
4	Cary	73	40	4
5	CJ	--	153	18
6	Cleo	157	231	24
7	Dusky	53	205	20
8	Jasper ♂	17	23	7
9	Jeni	19	26	5
10	Mason ♂	44	386	163
11	Marley ♂	27	18	0
12	Mints	26	155	4
13	Molly	133	125	5
14	Sunday ♂	70	338	257
15	Uva ♂	33	558	149

4.5 Discussion

The goal of this study was to assess the potential relationship between problem solving skill and social network organization. We administered a problem solving task to assess cognitive flexibility. Social networks were constructed from three social behaviors: grooming, embracing, and tail-wrapping. We hypothesized that there is a relationship between cognitive flexibility and social network organization. We predicted that individuals with problem solving skills would be central in the embracing network but not the grooming network. We then explored the relationship between problem-solving skill and social network organization using tail wrapping behavior, a less described interaction thought to be an affiliative alliance-forming behavior. Contrary to our prediction, individuals who solved the problem-solving task were central in the tail-wrapping network, but not the grooming or embracing networks. Below we offer potential explanations for these patterns.

There are important differences between the social metrics of degree and betweenness centrality that should be considered in the context of spider monkey social behavior. Betweenness centrality is an indirect measure of centrality that stands out among other social network metrics. Beyond direct connections, it allows for the examination of control and social brokerage within a network. An individual high in betweenness centrality typically connects more peripheral individuals to highly connected individuals, and if removed the network fractionates. Across behaviors, we found that the only differences in betweenness centrality when comparing the network positions of problem solvers to non-solvers occurred within tail-wrapping; those individuals with high betweenness centrality were innovators in the problem solving task. In contrast, degree centrality is a direct measurement of social interactions, where those with centrality incur the most direct participation in interactions. The degree centrality analysis yielded no significant results when comparing problem solvers to non-solvers. Another way to characterize betweenness centrality is as a measure of social brokerage, where those high in betweenness employ a strategy of interaction involving connecting peripheral individuals to highly connected individuals. As we found significant results for the comparison of problem solvers to non-solvers for betweenness centrality, it can be interpreted that who monkeys interact with is related to problem solving such that there is a difference in network position between problem solvers and non-solvers. Furthermore, we suggest problem solvers invest in a social dynamic in which there is less effort for more gain in social capital. In contrast, degree centrality can be interpreted as a measure of social effort where those high in degree centrality are engaged in significantly more social interactions than those low in degree centrality; degree is high because of actual participation in a behavior, not from interacting with specific individuals. As we found no significant results for this comparison, it is interpreted that the degree of participation in these behaviors is not related to problem solving skill. Although understanding the mechanisms underlying this behavioral dynamic is beyond the scope of this paper, it should be noted that social decision making such as what we have described is often described as advanced, strategic, and especially relevant to the development of culture in work with apes and humans (Hermann et al., 2010). Future work expanding on different dimensions of problem solving could help elucidate more about why cognitive flexibility seems to be particularly relevant for social behavior.

We predicted that problem solvers would be central in embrace network given the atypical social pattern for spider monkeys in which embracing, not grooming, is used to maintain social bonds. The tail-wrapping behavior was included for exploratory purposes given the paucity of knowledge about this behavior. Tail-wrapping has not been characterized functionally beyond that of a potentially alliance-forming and communicative behavior (Eisenburg, 1976). We have previously noted noticeable anecdotal differences both in the physical display of this behavior, and among engagement patterns (Boeving et al., 2020). Tail-wrapping involves use of the tail in a manner that separates the behavior from other affiliative interactions. Unlike embracing and grooming, tail-wrapping occurs in motion. The behavior begins at the time the tails inter-twine and continues with two monkeys locomoting side-by-side or one-behind-the-other. At least within the captive setting, the monkeys locomote about the perimeter of the enclosure or from one side to another with tails intertwined, and on rare occasions this may involve a third monkey attempting to intertwine the tail with the two. Although territorial behavior is often described with regard to inter-group behaviors, in the captive environment most social influences are within a group, or intra-group. Thus, this interaction may be an ecological behavior that occurs in the wild at the perimeter of territories. However, in the captive environment it is possible the behavior may develop as an intra-group alliance-forming behavior. However, as there is so little information about this behavior, considering social tail use in other species is particularly important.

Other primates have been noted to use their tails in a social context. To summarize, tail use among mammals can be divided into two social communication categories: tactile (contact) and visual (non-contact). Bolivian Titi Monkeys, for example, form monogamous pairs that engage in tactile communication by tail twining while resting on branches (Moynihan, 1966). Ring-tailed lemurs engage in both visual and olfactory communication in *stink fights* that involve waving their tails back and forth, emitting a pungent aroma from glands (Jolly, 1966). Fat-tail dwarf lemurs store fat in their tails for hibernation, thus signaling their health to potential mates (Fietz & Dausmann, 2006). Beyond primates, many animal species have been documented to use the tail as a social cue. For example, wood bison exhibit different tail postures across behavior types (Komers et al., 1992). Wolves are known to advertise their dominance status with the position of their tail (Mech, 1970). Marine mammals, such as bottle nose dolphins engage in tail slaps during conflict (Weaver, 2003). In comparison to these species known to use the tail in a social context, spider monkey tail-wrapping is much more interactive, involving tactile social communication and coordinated locomotion. For this reason, it is possible that other species may not develop a complex social network organization for tail behavior in the social context as is seen with spider monkeys, however this possibility has not yet been tested.

Traditional studies examining relationships between cognition and social network organization have examined these elements with a foraging task in relation to grooming or association. Our task involved use of the tail to solve a novel problem, and the differences in network position for problem solvers was only significant for the tail-wrapping network. Thus, both the task and the social behavior involved use of the tail. One possibility is that problem solvers were central in this tail-wrapping network because they were specifically skilled at using the tail flexibly in different situations. However, if this were the case we would expect direct connection, or degree centrality, to be high for problem solvers. Instead, the results suggest problem solvers may engage in this behavior strategically, netting them control of this behavioral network.

The methods of network science and cognitive science can be leveraged to elucidate complex patterns in the study of animal behavior. Social network analysis and the study of cognition converge with the acquisition, measurement, and interpretation of behavior. One limitation to our study is that our task is not replicable for many primate species given the requirement of fully prehensile tails. Replicability is a concern in cognitive science in general, and steps have been taken to amend this issue. For example, the Primate Cognition Test Battery (PCTB) was designed with replicability and species comparisons in mind (Hermann et al., 2010). However, limitations also exist within this battery as many tasks require modification for comparisons outside of apes and catarhine monkeys. Much cognitive work has also begun to shift toward the use of touch screens, which has special promise for captive environments where separation of individuals may not always be possible (Cronin et al., 2017). Although sample size is often an issue with primate models, this could be amended by large scale coordination of multiple study sites in the future.

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Conclusion

The work presented here offers a network science perspective to spider monkeys sociality and demonstrates that when different phenomena are examined through the lens of network science, patterns emerge that would otherwise not be possible to examine with traditional methods. Study one demonstrated that social risk influences network structure in socially lateralized behaviors. Our second study showed that complex network structure emerges as a feature of adulthood in spider monkeys. Our final study characterizes the relationship between problem solving skill and social network structure as one in which innovators broker social interactions.

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