

RESEARCH ARTICLE

Aggression, Grooming and Group-Level Cooperation in White-Faced Capuchins (*Cebus capucinus*): Insights From Social NetworksMARGARET C. CROFOOT^{1–3}, DANIEL I. RUBENSTEIN^{3*}, ARUN S. MAIYA⁴, AND TANYA Y. BERGER-WOLF⁴¹*Division of Migration and Immuno-ecology, Max Planck Institute for Ornithology, Radolfzell, Germany*²*Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panamá*³*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey*⁴*Department of Computer Science, University of Illinois at Chicago, Chicago, Illinois*

The form of animal social systems depends on the nature of agonistic and affiliative interactions. Social network theory provides tools for characterizing social structure that go beyond simple dyadic interactions and consider the group as a whole. We show three groups of capuchin monkeys from Barro Colorado Island, Panama, where there are strong connections between key aspects of aggression, grooming, and proximity networks, and, at least among females, those who incur risk to defend their group have particular “social personalities.” Although there is no significant correlation for any of the network measures between giving and receiving aggression, suggesting that dominance relationships do not follow a simple hierarchy, strong correlations emerge for many measures between the aggression and grooming networks. At the local, but not global, scale, receiving aggression and giving grooming are strongly linked in all groups. Proximity shows no correlation with aggression at either the local or the global scale, suggesting that individuals neither seek out nor avoid aggressors. Yet, grooming has a global but not local connection to proximity. Extensive groomers who tend to direct their efforts at other extensive groomers also spend time in close proximity to many other individuals. These results indicate the important role that prosociality plays in shaping female social relationships. We also show that females who receive the least aggression, and thus pay low costs for group living, are most likely to participate in group defense. No consistent “social personality” traits characterize the males who invest in group defense. *Am. J. Primatol.* 73:821–833, 2011. © 2011 Wiley-Liss, Inc.

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INTRODUCTION

Social animals, including most primates, collaborate to achieve collective goals, such as territorial defense [e.g. Bonanni et al., 2010; Heinsohn & Packer, 1995; Kitchen & Beehner, 2007; Radford & Du Plessis, 2004] and predator detection and dissuasion [Cowlshaw, 1994; Eberle & Kappeler, 2008; Lloyd et al., 2006], and many also exchange services, such as grooming and coalitional support with their group mates [Barrett et al., 1999; Cheney et al., 2010; Gilby & Wrangham, 2008; Perry et al., 2004]. Although numerous factors, including kinship, dominance relationships, previous interactions, and reproductive state, influence whether or not individuals will help one another [Perry et al., 2008; Silk et al., 2004], spatial proximity is a prerequisite for most types of cooperation. Individuals cannot cooperate if they are not close enough to perceive that their assistance is needed or desired and to provide said service within an appropriate timeframe. Thus, the cooperative partners who are potentially available to an animal will be shaped, in large part, by with whom it chooses to spend time.

In most primate social groups, patterns of association and interaction among individuals are neither random nor homogenous [Hinde, 1983]. Although some individuals spend large amounts of time in close proximity to their group mates, others tend to be socially peripheral, maintaining weaker social links to the rest of their group [e.g. Granovetter, 1973; Ramos-Fernandez et al., 2009]. How a group's association network is organized may have important effects on the levels of cooperative behavior it can maintain [Allen et al., 2010; Voelkl & Kasper, 2009;

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*Correspondence to: Daniel I. Rubenstein, Department of Ecology and Evolutionary Biology, 106A Guyot Hall, Princeton University, Princeton, NJ 08544-2016. E-mail: dir@princeton.edu

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Wu et al., 2010]; so, understanding the factors that shape these networks may yield insight into why group cooperation succeeds in some instances and fails in others.

Various forces, including ecology, demography, and kinship, shape patterns of individual association within social groups [e.g. Silk et al., 1999; Wey & Blumstein, 2010], but at a proximate level, it is the interactions both positive and negative between individuals that determine who spends time with whom. Aggression and affiliation are conspicuous features of life in most primate social groups [Carpenter, 1942]. Formal dominance relationships reflecting individual differences in competitive ability are a major organizer of social interactions in many primate species [Bernstein, 1976], whereas grooming not only serves to cement and strengthen affiliative relationships, but can also be exchanged for social goods and services [Barrett et al., 1999]. Patterns of cooperation within primate social groups often reflect the affiliative and aggressive relationships between group mates. For example, in chimpanzee groups, close associates exchange grooming at high rates and are also more likely to provide coalitional support to one another during within-group disputes [Gilby & Wrangham, 2008]. Similarly, capuchins in need of coalitional support preferentially solicit help from high-ranking group mates with whom they have strong affiliative relationships [Perry et al., 2004]. Relationships between pairs of individuals are critical for understanding patterns of cooperative behaviors, such as grooming and coalitional support that are, by their very nature, dyadic. However, many important behaviors are not dyadic, but instead involve collective action and collaboration among many group mates (e.g. territorial defense and predator mobbing). To understand why individuals choose to cooperate (or defect) in these contexts, relationships between pairs of individuals may be less important than how individuals are connected within the group as a whole.

Social network theory offers new tools for characterizing social structures, which allow us to explore an individual's relationship to his (or her) group as a whole, and offers a new perspective on the complex connections among group mates, which complements the analysis of relationships between pairs of individuals that has been the focus of traditional dyadic analyses of social relationships [Wasserman & Faust, 1994]. Studies on many species, ranging from fish [Croft et al., 2004, 2006], to marine mammals [Lusseau & Newman, 2004] and ungulates [Cross et al., 2005; Fischhoff et al., 2007; Rubenstein et al., 2007], have relied on networks of proximity to gain insights into how social networks form and function, how an individual's position within their social network shapes their behavior, and how the structure of social networks influence the emergence of collective group behaviors. Social

network theory and analysis can provide new insight into these group-level phenomena, because they allow the social structure of a group to be more than the sum of its parts; network analyses can distinguish emergent properties of the social relationships between individuals, which would not necessarily be observable in their pair-wise interactions [Croft et al., 2006]. In social species, many interactions are not dyadic, but instead involve multiple individuals acting either as participants or observers. Network analysis can help understand these complex patterns of behavioral exchange, which go beyond simple reciprocation, because they take into account not only the pattern of an individual's behavior, but also how that pattern relates to behavior of other individuals and connections among behaviors of those other individuals. It shows the breadth and diversity of individual actions, and hence the nature and strength of an individual's connectedness to all others in its social sphere. By quantitatively examining group structure in terms of key metrics, such as an individual's connectivity to others in his or her group, the connections among his or her neighbors or how central an individual is within a group and by comparing the networks of different types of relationships, network theory can offer insights into the patterns of interactions among group members and the way social phenotypic features affect the cooperative tendencies that help groups persist [Flack et al., 2006]. Network analysis provides a way to quantify the relationships among a group of individuals, which may be useful for understanding the mechanisms of exchange of social goods and the emergence of collective behaviors. It has, however, rarely been used in studies of cooperation in non-human primates [but see Voelkl & Kasper, 2009].

Here, we use social network analyses to investigate how the patterning of aggressive and affiliative interactions among individuals are related and, in turn, shape patterns of association among three neighboring white-faced capuchin monkey (*Cebus capucinus*) social groups. We look at the relations between these types of interactions both from an individual and a network-wide perspective. We use the tools of social network analysis to determine how individual activities in one social dimension relate to activities in other social dimensions. We then test whether location within these social networks predicts participation in defending the group during simulated territorial intrusions. In effect, we assess whether there are "social personalities" that emerge from networks of proximity, aggression, and grooming that characterize individuals who assume risk during collective group defense. Capuchins, which live in multimale, multifemale groups organized by female philopatry and male dispersal, are a highly collaborative species, known for their impressive social intelligence and strategic use of coalitional alliances during competitive interactions

[Fragaszy et al., 2004; Perry et al., 2004, 2008]. Neighboring groups are mutually intolerant and regularly engage in intensely aggressive territorial fights [Crofoot, 2007; Perry, 1996b]. Although high-ranking males and females are the primary antagonists in these interactions [Perry, 1996b], participation is highly variable and why some individuals respond to territorial intrusions by calling, approaching, or fighting while others flee remains poorly understood. We address this question by determining if “social phenotypes” of males and females responding to simulated territorial intrusion differ from those not investing in territorial defense.

METHODS

We studied the social behavior of white-faced capuchin monkeys (*C. capucinus*) living in three neighboring social groups on Barro Colorado Island (BCI), Panama, from January 2009 through to April 2010. All research described in this article received clearance from the Smithsonian Tropical Research Institute Institutional Animal Care and Use Committee (assurance number 2008-03-12-08), complied with the laws of the Republic of Panama and the United States of America, and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

Study Site

BCI (9°9'N, 79°51'W) is a 15.6-km² island of semi-deciduous lowland tropical forest that was isolated from mainland Panama in 1914 when the Chagres River was dammed to form Lake Gatun and the Panama Canal. Designated a reserve in 1923, BCI has been administered by the Smithsonian Institute since 1948. Half of BCI is covered by relatively young forest (at least 100 years old) that is still growing back from clearing that occurred during the French attempt to build the canal in the late-1800s. The remainder of the forest is older and is not thought to have undergone substantial anthropogenic disturbance in the last 200–400 years [Leigh, 1999]. This older forest is quite diverse, containing 299 tree species in a 50 ha plot [Hubbell et al., 1999]. A stable population of between 250 and 300 capuchins in 15–20 social groups is thought to live on BCI [Crofoot, unpublished data; Mitchell, 1989; Oppenheimer, 1968].

Study Groups and Behavioral Data Collection

Three of the six habituated capuchin social groups on BCI that have been studied since 2004 were selected as the focus of this study. One individual in each of these groups has been fitted with a radio collar [see Crofoot et al., 2009, for details related to animal capture], allowing us to track their movements using the Automated Radio Telemetry

TABLE I. Composition of Three *Cebus capucinus* Study Groups

Group	All adults	Males	Females
BLT	10	2	8
FC	9	3	6
Top	14	6	8

System on BCI [Crofoot et al., 2008]. All adults and subadults are individually recognized based on physical characteristics. The study groups ranged in size from 9 to 14 adults (Table I), and their composition remained relatively stable over the course of this study. Only interactions among adults were used in constructing networks in our study. In the first 2 months of the study, an adult female in one of the study groups (Top) disappeared and a young adult male switched study groups (from BLT to Top) and then died. These individuals were excluded from our analyses owing to insufficient behavioral data. However, we included an adult female from the Top group who died and an adult male from FC group who disappeared in the last month of the study.

MCC and three assistants collected focal animal behavioral data, using an instantaneous scan sampling methodology [Altmann, 1974]. Focal individuals were observed for 10 min periods, during which we recorded their behavior and the identity of all their associates (group mates located within five body lengths of the focal individual) every minute. During focal follows, data on grooming and aggression were recorded on an all-events basis, including the identity of the initiator and the recipient. To ensure that focal follows were independent, no individual was sampled twice with a 2 hr period and we attempted to sample all adults in the group before resampling any individual. We collected >250 hr of focal animal data, with an average of 7 hr of data per individual. We calculated dyadic association rates (the percentage of time two individuals, A and B, spent within five body lengths of each other) as a ratio: the total number of scans where A and B were observed together divided by the total number of behavioral scans of animal A plus the total number of behavioral scans of animal B. Because aggressive interactions and grooming are so rare in this population (capuchins in these social groups spent <3% of their time grooming and <1% of their time in aggressive social interactions), we supplemented the focal data with ad libitum data on these behaviors.

For our analyses, we were primarily interested in the initiation of prosocial and agonistic contact among group mates; thus, during all aggressive interactions and grooming bouts, we recorded the identities of the individual who initiated the behavior and the recipient. In aggressive interactions that involved coalitionary

support by a third party, we only included the original participants in our analyses. We excluded cases where coalitionary support was solicited and secured before the start of the aggressive interaction. Capuchins often changed roles during grooming bouts, with the groomer becoming the groomee and vice versa. The frequency of role changing, as well as the overall duration of such grooming bouts, provides important information about the quality of dyadic relationships [Manson et al., 1999, 2004]. In this set of analyses, we chose to focus on the initiation of these affiliative interactions, rather than other measures of grooming behavior, for two main reasons. First, initiation of a grooming bout reflects the prosocial intent of an individual, whereas measures, such as time spent grooming, are the outcome of an interaction between two individuals. Second, we felt that as a behavioral event (as opposed to a behavioral state), grooming initiation was most directly comparable to our data on aggressive interactions. Thus, in our analyses, we considered only the initial grooming interaction: the capuchin who started the bout grooming was the groomer and the individual who first received grooming was the groomee. Because *ad libitum* data can be biased toward the more visible members of a social group, we compared the total grooming data set (*ad libitum* plus focal) to the more limited dataset based only on the focal individual data. In all cases, there was a strong positive correlation between the network metrics calculated from the two data sets, and network correlations between the matrices were strongly and positively related for all three social groups.

For each study group, we created interaction matrices for each of the three types of interaction: aggression, grooming, and proximity. Aggression and grooming are directional relationships and the matrix entry (A, B) represents the number of times individual A has initiated aggression (or grooming) toward individual B. The proximity matrix is symmetric, so both entries (A, B) and (B, A) reflect the number of times the individuals A and B were observed within five body lengths of each other. We also attempted to elucidate dominance relationships based on dyadic aggression and approach/avoid interactions, and tested for the presence of a linear hierarchy for the males and females in each group using MatMan (Noldus Information Technologies, Wageningen, Netherlands). In all groups, the alpha male could be easily identified, and we thus classified adult males as either alpha or subordinate. However, none of the female dominance hierarchies were significantly linear; so, rather than assigning each individual a rank, we instead classified them as either high- or low-ranking depending on the proportion of group mates they defeated.

Playback Experiments

To investigate individual variation in responses to territorial intrusions, we broadcast vocalizations

from neighboring capuchin social groups within the range of each of our study groups. Vocalizations were recorded using a Marantz PMD-660 portable recorder (Marantz America, Inc., Mahwah, NJ) and a Sennheiser ME66 shotgun microphone (Sennheiser Electronic Corp., Old Lyme, CT). The auditory stimuli were meant to simulate the presence of another group and consisted of 1 min of group-feeding noises, including food-associated calls [“huh” vocalizations; Gros-Louis et al., 2008; Oppenheimer, 1973], and the sounds of falling fruits and moving monkeys, punctuated halfway through by screams associated with a within-group fight. All stimuli were made using Raven Lite 1.0 [Charif et al., 2006] and were broadcast from an iPod (Apple Inc., Cupertino, CA) using a MiniVox Lite speaker (Anchor Audio, Inc., Torrence, CA). Stimuli were not broadcast more than once to any of the study groups, and experiments were not conducted if the focal group had had an aggressive encounter with any of their neighbors that day. During playback experiments, the speaker was placed ~80 m from the focal individual (measured using a Garmin GPSmap 60csx, Garmin Inc., Olathe, KS) in the direction of the home range of the group whose vocalizations were being broadcast, controlling the distance from the boundary of the focal group’s home range. We selected a different adult as the focal individual for each experiment and recorded their reaction to the simulated territorial intrusion, including whether they approached the speaker or emitted threat vocalizations. Females with offspring that were too young to travel independently were not selected as focal individuals for these experiments, because the presence of a vulnerable infant might reasonably be expected to influence whether a female chooses to participate in potentially dangerous intergroup interactions.

Network Measures and Statistics

We calculated network metrics from data on spatial associations, grooming, and aggression in each of the three study groups at two scales. First, we computed group-wide network properties that measure the overall connectivity of a network, such as the size and number of strongly connected components and cliques [Scott, 2000]. A path in a network between two individuals is a sequence of (directed) links that connects those two individuals. In an undirected network, a connected component is a set of individuals where every two are connected by a path. In a directed network, a strongly connected component is a set of individuals, each of which has a directed path to every other individual in the set. In a (strongly) connected component, all the individuals are reachable from all others and all are connected in a cyclic manner. In network terminology, a clique is a set of nodes (in our case, individuals), in which each

dyad is connected not by a path but by a link. Thus, in a clique, everybody is directly interacting with everybody else. We look at *maximal* cliques, which are defined as cliques of individuals where no other individual can be added to make a larger clique.

Second, we computed individual-level network metrics that we felt had clear biologically relevant interpretations: those that measured the number of connections to other group members and whether or not those individuals were themselves important actors in the network. Accordingly, we computed out- and in-degrees, weighted out- and in-degrees, and both weighted and unweighted PageRank for each individual. An individual's degree is the number of other individuals in the network to whom he or she is connected. Out-degree is the number of group mates the individual directs a given action toward, whereas in-degree is the number of group mates from whom an action is received. In a symmetric network, such as the network of proximity relationships, in- and out-degree are the same. In the interaction matrix, in-degree of individual A is the *number* of nonzero entries in the column of A, whereas the out-degree is the *number* of nonzero entries in the row of A. Weighted degree of an individual tracks the number of *connections*, rather than the number of other individuals the individual is connected to. The weighted out-degree is the number of outgoing connections of an individual. For example, in an aggression network, out-degree of an individual would be the total number of aggressive interactions the individual has initiated toward others. Weighted in-degree is the number of incoming connections of an individual and for the aggression network that would be the total number of aggressive interactions directed toward that individual. In the interaction matrix, weighted in-degree of an individual A is the *sum* of nonzero entries in the column of A, whereas the out-degree is the *sum* of nonzero entries in the row of A. All degrees are in essence local measures: a degree of an individual, weighted or unweighted, does not change even if the interactions among all the other individuals change completely. In essence, it is a measure of direct

connectedness. Thus, we choose another measure, PageRank [Brin & Page, 1998], to measure the broader reach of an individual's interactions. PageRank belongs to the class of methods ranking individuals in a social network that define the most important individuals as those who have connections from other most important individuals [Bonacich, 1972, 2007]. In a network of asymmetric dyadic interactions, such as grooming or aggression, these types of ranking methods measures the "value" of each individual in the total supply-demand system created by the directed interactions [Hubbell, 1965; Leontief, 1941]. Who is the most valuable groomee? PageRank views it as the individual who gets most grooming not just from anybody, but from other valuable groomees. So, the PageRank of an individual who is groomed by others (who also receives a lot of grooming) is higher than the PageRank of an individual who receives the same amount of grooming from those who are not groomed by anybody. This recursive definition of PageRank takes the structure of the entire network into consideration, not just the local neighborhood of an individual, when evaluating an individual's rank. For symmetric dyadic relations, such as proximity, there is no equivalent of a PageRank measure, and thus we relied on degree as the measure of an individual's gregariousness. We used the implementation of PageRank algorithm provided with the igraph software [Csardi & Nepusz, 2006]. In the aggression (or grooming) network, PageRank ranks individuals by how much aggression (or grooming) they *receive* and the reverse PageRank ranks individuals by how much aggression (or grooming) they *give*. The undirected PageRank ranks individuals by the total amount of aggression (or grooming) in which they are involved. We used both weighted and unweighted versions of PageRank. The weighted version takes into account not only the presence or absence of an interaction between individuals, but also the number of interactions between those individuals.

The network measures are summarized in Table II. We investigated sex- and rank-based differences in these metrics using Student's *t*-tests,

TABLE II. Summary of Network Measures Used in the Analysis

Measure	Definition
<i>Network level</i>	
(Strongly) connected component	Set of nodes where every two are connected by a path
Clique	Set of nodes where every two are connected by a link
<i>Individual level</i>	
Degree	Number of other nodes to which a given node is connected
Weighted degree	Number of links to other nodes which a given node has
Out (in) degree	Number of other nodes to (from) which a given node has direct links
PageRank	Rank of a node is (recursively) a function of the ranks of the incoming nodes
Weighted PageRank	Rank of a node is (recursively) a function of the ranks of the nodes connected by all incoming links

and relationships between the network metrics using nonparametric correlations (Kendall's τ). Differences in the response to simulated territorial intrusions by males and female and by high and low ranking individuals were explored using chi-square tests, and the relationship between individuals' network metrics and their responses to playbacks were tested using logistic regression. All statistical analyses were conducted in JMP (SAS Institute, Inc., Carey, NC).

RESULTS

Structure of Capuchin Social Networks

For all three study groups, networks corresponding to aggression, grooming, and proximity relationships exhibit complex nonlinear patterns of interactions (Fig. 1). Inspection of the graphs and comparisons of the group-wide metrics show that there is more

similarity among the networks within each relationship type across groups than among the networks of the same group. All aggression networks had seven strongly connected components (Table III), most of those singleton individuals. The presence of strongly connected components with more than one individual means the existence of a cycle of relationship. In BLT and FC, those are indeed simple cycles, whereas in Top the cyclic pattern is more complicated, involving half the group (Fig. 1). For example, in FC troop's aggression network, Mimi is aggressive to Chevelu, who in turn is aggressive to Beverly, who is aggressive to Mimi. Few of these cycles are dyadic (less than 10% of aggressive relationships are bidirectional) and some involve more than triads. This suggests that aggressive relationships have a group-wide structure that are not immediately obvious in a dyadic analysis and would be better

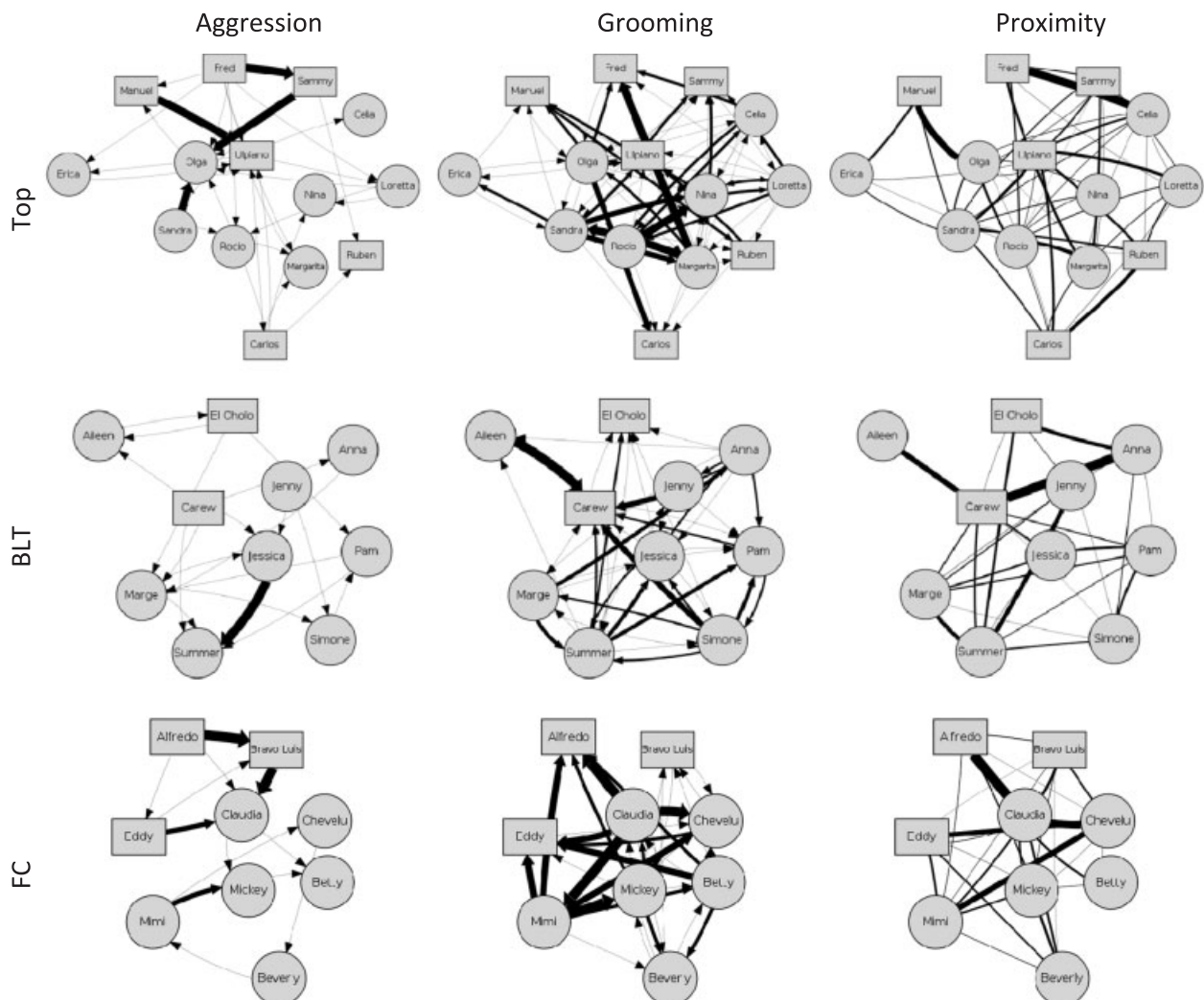


Fig. 1. Networks of aggression, grooming, and proximity by group. Each row in the table of networks below corresponds to all the networks of a group and each column corresponds to the three group networks of the same relation. Within the networks of the same group, individuals have the same position for easy comparison across relations. Males are represented by rectangles and circles represent females; the individuals are labeled by their names. The thickness of a link represents the relative number of interactions between the corresponding pair of individuals.

TABLE III. Network Characteristics of Aggression, Grooming, and Proximity Networks

Table 2	Aggression		Grooming		Proximity	
	Number of strongly connected components	Nonsingleton components and their size	Number of strongly connected components	Nonsingleton components	Number of maximal cliques	Size maximal cliques (minimum/maximum)
Top	7	(8) Carlos-Erica-Loretta-Manuel-Margarita-Olga-Rocio-Ulpiano	1	All individuals	15	Minimum = 3, maximum = 6
BLT	7	(2) Aileen-El Cholo (3) Marge-Pam-Simone	1	All individuals	7	Minimum = 4, maximum = 5
FC	7	(3) Beverly-Chevelu-Mimi	2	All but Alfredo	4	Minimum = 4, maximum = 6

The nonsingleton strongly connected components are components that have more than one individual. The membership of these is listed explicitly for each network and their size is given in parentheses. For the proximity networks, the range of the sizes of the maximal cliques is listed.

captured using analytical tools that take the entire network structure into consideration. Comparing the Kendall’s τ rank correlations of network measures in the aggression network (Table IV) indeed shows that aggression is a global relationship. In all networks, there are highly significant correlations between in-degree (the number of those who are aggressive toward an individual) and weighted PageRank (much aggression is received from those who themselves receive much aggression). That is, *how many* others are aggressive toward a given individual is highly correlated with *how much* aggression those others receive and, more importantly, *from whom*. By contrast, at the local level of simple comparison of the aggression received and given by any individual, there are no significant correlations between either weighted degrees (total amount of aggression) or unweighted degrees (number of aggression partners) for either giving or receiving aggression (out- or in-degree, respectively).

In the grooming networks, which reflect the initiation of grooming events, virtually the entire group is one strongly connected component where every individual has a “grooming path” to everyone else. The proximity network in all three groups is also one large connected component. To get information on how tightly connected individuals are in this network, we look for maximal cliques in proximity networks. The size of the cliques (the number of individuals in them) is similar across the three groups, ranging between three and six individuals (Table III).

At the individual level, Kendall’s τ rank correlations of various network measures between aggression and grooming networks show that receiving aggression and giving grooming were strongly linked in all troops (Table IV). Both aggression weighted in-degree (total amount of aggression received) and aggression in-degree (the number of those who are aggressive toward an individual) are strongly positively correlated with grooming weighted out-degree (total amount of grooming given). This relationship, however, is extremely local and direct. At the global network scale, there is no

consistent significant relationship across all troops between giving grooming and receiving aggression. Only in the FC troop is there a significant Kendall’s τ rank correlation coefficient between aggression weighted PageRank (those who receive much aggression from others who receive much aggression) and grooming weighted reverse PageRank (those who initiate grooming with group mates, who themselves initiate grooming with many others).

Interestingly, aggression is not correlated with proximity at either the local or global scale (Table IV). This suggests that while capuchins do not seek out associations with aggressive individuals, they do not avoid them either. Grooming, on the other hand, is connected to patterns of spatial association (Table IV). Reverse PageRank (those who initiate grooming with group mates, who themselves initiate grooming with many others) is correlated with degree (number of others in close proximity). That is, the number of an individual’s neighbors is correlated not just with how many others an individual grooms, but how many others they groom and so on. In addition, among the females of two of the three troops (BLT and Top), grooming out-degree (the number of others an individual grooms) is correlated with weighted proximity degree (the amount of time an individual spends with others), although this trend does not reach statistical significance. Note that, here again, the global relationship between grooming and proximity, as measured by PageRank, is more significant than the local relationships measured by degrees (and through dyadic analysis).

Individual Responses to Simulated Territorial Intrusions

Focal individuals responded to simulated territorial intrusions in 11 of the 27 experiments (41%). In six cases (22%), they rapidly moved toward the speaker broadcasting the vocalizations of a neighboring social group, and in nine cases (33%) they emitted aggressive threat vocalizations. Males were

TABLE IV. Correlations by a Group of Various Network Metrics Both Within and Between Networks of Aggression, Grooming, and Proximity

	Top				BLT				FC			
	All		Female		All		Female		All		Female	
	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value	Coefficient	P-value
<i>Aggression vs. aggression</i>												
In-degree vs. out-degree *L	-0.13	0.51	0.22	0.45	-0.42	0.09	-0.18	0.54	-0.41	0.13	0.00	1.00
In-degree (wt.) vs. out-degree (wt.) *L	-0.14	0.48	0.13	0.65	-0.31	0.22	0.00	1.00	-0.27	0.32	0.00	1.00
In-degree vs. PageRank (wt.)	0.62	0.001	<i>0.51</i>	<i>0.07</i>	0.83	0.001	0.85	0.003	0.54	0.04	0.54	0.12
Out-degree vs. PageRank	0.00	1.00	0.16	0.58	-0.27	0.28	-0.04	0.9	-0.54	0.04	-0.39	0.27
<i>Aggression vs. grooming</i>												
In-degree vs. out-degree (wt.) *L	0.47	0.02	0.37	0.20	0.49	0.05	0.37	0.20	0.55	0.04	0.54	0.12
In-degree (wt.) vs. out-degree (wt.) *L	0.42	0.04	0.37	0.20	0.51	0.04	0.40	0.17	0.43	0.11	0.45	0.21
PageRank (wt.) vs. reverse PageRank (wt.)	0.12	0.55	0.00	1.00	0.38	0.13	0.21	0.46	0.67	0.01	0.33	0.35
Out-degree (wt.) vs. reverse PageRank	-0.23	0.23	0.20	0.49	-0.10	0.70	0.08	0.78	-0.36	0.17	0.30	0.40
<i>Aggression vs. proximity</i>												
Out-degree vs. degree *L	0.07	0.71	0.08	0.77	0.18	0.46	0.14	0.64	0.10	0.70	0.59	0.10
Out-degree (wt.) vs. degree *L	0.06	0.76	0.17	0.56	0.15	0.54	0.09	0.76	0.00	1.00	0.48	0.18
In-degree (wt.) vs. degree (wt.) *L	0.07	0.71	0.04	0.89	-0.14	0.57	0.11	0.69	0.00	1.00	0.15	0.67
Reverse PageRank vs. degree	0.00	1.00	-0.11	0.69	-0.09	0.70	-0.20	0.49	0.09	0.73	-0.07	0.84
<i>Grooming vs. proximity</i>												
Out-degree vs. degree (wt.) *L	0.14	0.49	<i>0.52</i>	<i>0.07</i>	0.33	0.18	<i>0.49</i>	<i>0.09</i>	-0.06	0.82	-0.15	0.67
In-degree (wt.) vs. degree (wt.) *L	-0.14	0.48	0.13	0.65	-0.31	0.22	0.00	1.00	-0.27	0.32	0.00	1.00
Reverse PageRank (wt.) vs. degree	0.27	0.17	0.41	0.15	0.28	0.25	0.35	0.22	0.51	0.06	0.64	0.07
Reverse PageRank vs. degree	0.32	0.11	0.34	0.24	0.52	0.04	0.59	0.04	<i>0.45</i>	<i>0.09</i>	0.50	0.16
PageRank (wt.) vs. degree	0.18	0.36	0.04	0.90	0.52	0.04	0.67	0.02	0.21	0.43	0.36	0.31

Local metrics are indicated by “*L.” Bold values are statistically significant at $P < 0.05$. Italicized and underlined values depict strong trends at $P < 0.10$.

more likely to approach the speaker than females, although this trend does not reach statistical significance (4 of 10 males approached compared with 2 of 17 females; $\chi^2 = 2.904$, $P = 0.088$). There was no sex difference in the likelihood that an individual emitted vocal threats (3 of 10 males vs. 6 of 17 females; $\chi^2 = 0.079$, $P = 0.778$). Surprisingly, however, high-ranking individuals were not more likely to respond aggressively to the simulated territorial intrusions than their low-ranking counterparts; 27% of high-ranking individuals approached the speaker compared with 19% of low-ranking individuals ($\chi^2 = 0.274$, $P = 0.60$), whereas 36% of high- and 31% of low-ranking individuals gave vocal threats ($\chi^2 = 0.077$, $P = 0.7818$).

For males, there were no network characteristics that distinguished those who responded aggressively to playbacks. For females, only location within the aggression network has a significant effect on the odds that an individual responded aggressively to playbacks. The relationship to aggression is somewhat surprising: the odds of an individual giving threat vocalizations are *negatively* related to the number of individuals in their group who direct aggression against them (aggression in-degree; $\chi^2 = 5.23$, $df = 1$, $P = 0.02$; see Table III). In effect, individuals who receive aggression from few of their group mates are more likely to incur moderate risk by performing threat vocalizations in response to territorial threats.

DISCUSSION

The structuring of capuchin social groups involves both agonistic and affiliative interactions. At the scale of entire groups, each network type is more strongly similar across groups than it is to different network types within groups. Aggression networks in each group consist of many small connected components, whereas grooming networks for each group consists of one large component that connects virtually every member of each group (Table III). Although the sparseness of the aggression network reflects, at least in part, the relative infrequency of these interactions, the existence of nonsingleton, especially triad or larger, connected components suggests complex substructuring of agonistic relationships which traditional dyadic measures would be unable to capture. That, at the local level of the individual, no correlations exist between giving and receiving aggression for any measure of degree or PageRank, also underscores the cyclicity and nonlinearity of aggressive relationships in our study population. Based on reports of strong linear dominance hierarchies in this species at other research sites [Bergstrom & Fedigan, 2010; Perry et al., 2008], we would have expected to find a negative relationship between giving and receiving aggression at both the local (i.e. in- vs. out-degree) and global (PageRank vs. reverse PageRank) scale.

In all three groups, circular triads and more complex patterns of aggressive challenges are common, explaining why we were unable to produce a linear dominance hierarchy, and suggesting that in this population aggressive relationships among individuals require an understanding of group-wide structure of agonistic interactions that only an analysis of entire networks can provide. Capuchin groups are characterized by a complex set of alliances among group mates, with individuals regularly providing coalitional support for their allies during aggressive interactions [Perry et al., 2004]. The dynamics of these nondyadic relationships may account for the complex structuring of the aggression networks of our study groups. Unfortunately, we did not have enough data on patterns of coalitional support to include them in our analyses, but we feel that a comparison of aggressive and coalitional networks may yield valuable insight into the structuring of capuchin social groups.

At the group-wide level, the existence of one large strongly connected component that encompasses virtually every member of each group suggests grooming is a more inclusive and egalitarian activity than aggression. Similarly, the three proximity networks consist of only one connected component. What is interesting, however, is that despite differences in the size of our study groups, the size of maximal cliques across the groups is very similar. Because cliques are subgroups in which every individual is connected by a direct link, perhaps only a limited range of sizes (3–4 at the lower end and 5–6 at the upper end) provide social stability and offer a set of potential associates that will be engaged when needed in important social settings. Alternately, it is possible that these cliques reflect patterns of relatedness among the group mates. In this case, the limited range of sizes of capuchin cliques that we observe might be owing to constraints that demographic processes place on matriline size.

For some types of social interactions, the network graphs and analyses are similar for all three capuchin groups, whereas for others they are not. In our study, the structure of aggression networks shows that agonistic interactions play a major role in shaping capuchin sociality, but the relationships that develop among individuals are nonlinear. Aggression networks within capuchin groups are tightly connected to those of grooming. Capuchins that are aggressively challenged by many individuals initiate many grooming bouts. This is the pattern that we would expect to observe if capuchins followed a “grooming up the hierarchy” strategy, wherein low-ranking individuals curried favor with dominant group mates by grooming them [Seyfarth, 1977]. Previous studies on the relationship between grooming effort and rank in capuchins have yielded conflicting results. Although some studies have found evidence that capuchins groom up the hierarchy [Perry, 1996a], others have found no relationship between

rank and grooming [Manson et al., 1999; Schino et al., 2009], and some have even found evidence that capuchins groom down the hierarchy [O'Brien, 1993; Parr et al., 1997]. Although our data are not directly comparable with these previous studies, as we focused on the initiation of grooming bouts rather than the total amount of time spent grooming, they do demonstrate strong local connections between grooming and aggression networks in this capuchin population. A careful inspection of the graphs, however, shows that the patterns are not consistent with a "grooming up the hierarchy" strategy; the recipients of aggression do not groom their aggressors. The relationship emerges more as a matter of "social personality": those who get beat up by many groom many. We found no global, network-wide relationship between the patterns of grooming and aggression. Because giving grooming is not negatively correlated with receiving aggression, if it is a strategy for currying favor and avoiding aggression, it does not seem to be particularly successful.

Because proximity—a measure of which individuals choose to associate with—is a precursor to social interactions, it is interesting that the number and strength of close spatial associations is related to the structure of grooming but not aggression networks. This suggests that aggressive challenges do not require proximity, do not lead to negative relationships (i.e. individuals that are attacked do not avoid their aggressors), and do not influence an individual's association preferences. However, giving and receiving grooming does have a positive relationship with proximity.

Contrary to what one might expect, in our study, high levels of social integration do not increase the odds of a female choosing to respond aggressively to simulated territorial intrusions. If close affiliative relationships are beneficial to capuchins, as has been found in other primate species [Silk et al., 2009], the females that have the most to gain from group living seem not to invest more in group defense than their socially peripheral group mates. Instead, patterns of aggression, but not dominance, seem to influence patterns of female participation in group territorial defense. The negative relationship between a female's aggression in-degree and her odds of reacting negatively to the simulated territorial intrusions might, at first glance, seem to indicate that high-ranking females (who receive little aggression owing to their dominant social status) are most involved in group defense. However, in contrast to previous studies [Perry, 1996b], we found that high-ranking females were no more likely than their low-ranking counterparts to participate in aggressive territorial defense. Our results may instead indicate that females who pay the lowest costs for group living are most likely to participate in group defense.

Individuals live in groups because the benefits they receive exceed the costs that accrue from associating

with others [Alexander, 1974; Rubenstein, 1978]. Conflict with neighboring groups over limited resources is a regular occurrence in many primate species [Cheney, 1987], and this competition can impose serious costs, up to and including group extinction [Jolly & Pride, 1999], if not successfully countered. However, participating in aggressive encounters with neighboring groups can be dangerous; why some individuals incur this risk while others hang back remains unclear. Our results show that both males and females call (33%) in response to playbacks of simulated calls of neighboring groups or even rush forward (22%) toward the group's boundary. What is interesting is that there are no consistent "social personality" traits characterizing males that call or approach the boundary in response to simulated calls. Even though females respond only slightly (35%), but not significantly, less than males (50%) to intruder calls, females that receive *little* aggression are those that call. This suggests that protecting the group does not necessarily require high levels of aggressivity or centrality in any social network. The genetic relatedness of the population is not yet known, but it is possible that participation in intergroup conflicts may be related to kinship. Alternately, the proximate context of each interaction, including which group mates an individual is close to and whether they respond aggressively to the territorial threat, may have a larger influence on the likelihood that an individual joins in group defense than his or her position within the social network of the group. If participation in territorial defense is contingent on the behavior of group mates, simultaneous data on the reactions of all group members would be needed to understand why some individuals respond aggressively to the simulated territorial intrusions while others do not. We were unable to obtain this level of behavioral detail owing to the constrained visibility in the forest where we work, but feel that a focus on social contingency in future studies will be important.

Many of the relationships that influence the structure of primate societies create complex patterns that involve many individuals, necessitating analytical tools that take the entire pattern of interactions into consideration. Previously, studies have aggregated dyadic interaction indices to create a measure of the overall pattern of interaction between an individual and his or her group [e.g. Foster et al., 2009]; social network analysis provides a more elegant mathematical framework for achieving exactly this without the assumption of independence of dyads which is implicit in dyadic analysis [Buckley, 1967; Lewin, 1951]. The strength of network analysis is its ability to summarize complex relationships among a group of individuals. It can take both a global, group-level view of such relationships (using measures, such as average path length [Scott, 2000], density [Scott, 2000], betweenness [Freeman, 1979], PageRank, reverse PageRank, and kernel [Borgwardt, 2007], or pattern mining techniques [Chakrabarti & Faloutsos,

2006; Getoor & Diehl, 2005]) or a very local view, focused on the relationships of a particular individual [using degrees and clustering coefficient; Scott, 2000]. The greatest insight will likely be gained from network metrics that take the connectivity of the entire network into consideration (such as PageRank in our study), as they can reflect aspects of an individual's "social personality" that would not necessarily be captured by examining one-on-one relationships with group mates. They also provide a group-level measure of social relationships that could be compared across groups, to better understand how patterns of interaction within a group shape the collective behaviors of the group as a whole. For example, one might predict that the strength and overall connectivity of a group's affiliative networks might be related to the performance of the group in collective activities, such as territorial defense. With data on only three capuchin groups, we were unable to test this hypothesis. In fact, few studies have obtained the necessary data on a sufficient number of groups to undertake such a comparison, but we hope that as network analyses become more widely adopted and as their ability to quantify differences in the social organization of groups becomes better understood, studies that attempt to answer such questions by taking the social group as the unit of analysis will become more common.

To take full advantage of the network analysis tools, we need to understand not only their potential applications, but also their limitations. Network measures often do not belong to the standard space of traditional probability distributions, they do not normalize in intuitive ways, and significance of results is nontrivial to estimate. Many modern network analysis methods [Brandes & Erlebach, 2005] require large numbers of individuals to have statistical power, especially when comparing across network of different relationships. Yet, collecting data about social behavior of animals is an extremely time-consuming task and many data sets are small. However, with the advancement of automated data collection techniques (such as video surveillance, GPS, and other tracking methods), animal social network data are also growing in size and the power of social network analysis, as well as the depth of the insights it provides, will only increase.

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