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A Social Network Analysis Of Hamadryas Baboons

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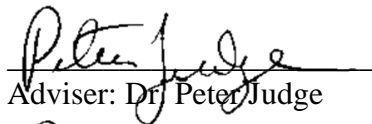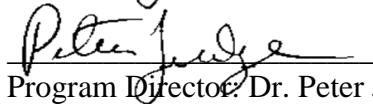A SOCIAL NETWORK ANALYSIS OF HAMADRYAS BABOONS

by

Christian A. Treat

A Thesis

Presented to the Faculty of Bucknell University
In Partial Fulfillment of the Requirements for the Degree of
Bachelor of Science with Honors in Animal Behavior

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ABSTRACT

The study of animal sociality investigates the immediate and long-term consequences that a social structure has on its group members. Typically, social behavior is observed from interactions between two individuals at the dyadic level. However, a new framework for studying social behavior has emerged that allows the researcher to assess social complexity at multiple scales. Social Network Analysis has been recently applied in the field of ethology, and this novel tool enables an approach of focusing on social behavior in context of the global network rather than limited to dyadic interactions. This new technique was applied to a group of captive hamadryas baboons (*Papio hamadryas hamadryas*) in order to assess how overall network topology of the social group changes over time with the decline of an aging leader male. Observations on aggressive, grooming, and proximity spatial interactions were collected from three separate years in order to serve as 'snapshots' of the current state of the group. Data on social behavior were collected from the group when the male was in prime health, when the male was at an old age, and after the male's death. A set of metrics was obtained from each time period for each type of social behavior and quantified a change in the patterns of interactions. The results suggest that baboon social behavior varies across context, and changes with the attributes of its individual members. Possible mechanisms for adapting to a changing social environment were also explored.

INTRODUCTION

Animal species that live in groups interact with one another using a range of social behaviors. The relationships formed between group members not only serve to sustain the coherence of the group, but also to mitigate competition caused by group living (Cords, 1997). Social interactions are not random (Hinde, 1983; Koyama, 2003; Silk et al., 2004), but are the result of individuals sharing a collective sense of behavior, whether it is influenced by dominance, threat response, or survival motives. As a result, interactions between individuals in the same social structure form unique patterns of associations.

The social structure of the animal group has both ultimate and proximate significance. Group organization has been found to be related to the cognitive ability of a species. The Social Brain Hypothesis suggests that the group size of social animals is strongly correlated to the size of the neocortex (Dunbar, 1998). The size of the neocortex is suspected to contribute to the level of social intelligence in the animal. For example, neocortex volume has been correlated to the extent of male mating strategies and the frequency of primate play behavior (Pawlowiski et al., 1997; Lewis, 2001). Research suggests that some aspect of this brain structure places an upper threshold on the number of relationships that an animal can sustain (Dunbar, 1992). An analysis of 31 primate species found that the neocortex size correlated to the size of small grooming cliques within the larger social group (Kudo and Dunbar, 2001). Dunbar (2003) maintains that individual investment in these smaller cliques are crucial for maintaining alliances, which protect the individual from intergroup competition and other costs of group living. Thus,

forming relationships is not only essential in animal social groups, but the level of investment in partners suggests some degree of social cognition.

Animal social structures also influence more immediate biological phenomenon, including disease transmission, social learning, predator-prey interactions, and mating behavior (Sih et al, 2009). For example, disease transmission and the increasing level of gregariousness in animals is expected to contribute to a higher parasite prevalence and intensity (Moller et al, 1993). This cost of group living is due to close proximity and interaction among members in the social group. Nunn et al. (2003) demonstrated that in wild primates, host density had the greatest effect on parasite species richness. Thus, increased exposure to disease may be a cost of group living, but how the animal's social group is structured influences how this drawback is transmitted throughout the group.

Traditional methods of observing and analyzing social groups rely on a piecemeal manner of observing interactions among dyads. Hinde (1976) suggested a framework of social organization in order to guide the studies for primatologists and social psychologists (Figure 1). The social structure of an animal group is first comprised of interactions between individuals. This basic unit consists of behaviors, which typically contain temporal information of the interaction as well as the context and quality. The suite of behavioral interactions among a pair describes the relationship of that particular dyad.
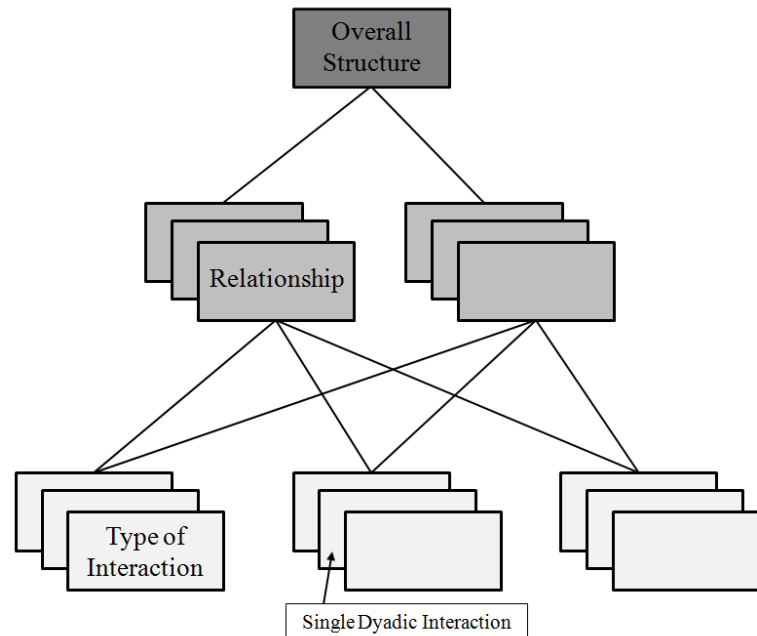
Figure 1. Schematic of Hinde's framework of social structure, adapted from Brent et al. (2011).

By investigating dyadic relationships, the larger level of animal sociality can be analyzed. Pair-wise interactions allude to everyday encounters among individuals. Whitehead and Dufault (1999) identify two classes of information that form the building blocks for a social network. First, dyadic interactions can be identified based on spatial proximity. The scale to which constitutes a pair-wise association varies on the research question, but in general, what constitutes an interaction can be defined as the potential to exchange information socially (Bradbury & Vehrencamp, 1998). Uses of spatial data to analyze animal social structures include distance to nearest neighbors and food patch occupancy (Sibbald et al., 2005; King et al., 2011). Dyadic interactions can also be identified by social behaviors. This includes a wide range of behaviors including affiliative, competitive, cooperative, and sexual interactions. Sade (1972), for instance, constructed a social network of macaques (*Macaca mulatta*) based on grooming behaviors among actors and recipients of the groom.

What defines an interaction has a wide range of interpretations to ethologists, but the basic template of an encounter is characterized—in Hinde's (1976) words—as when, "A does X to B." Furthermore, the longitudinal interactions of individuals over time describe the relationship of the particular dyad. Relationships can be generalized from a suite of observable behavior and named according to the types of interaction, such as mother-infant interactions or male-male aggression (Simpson, 1973). However, relationships do not have to be thought of in terms of kinship or dominance interactions. In primatology, King et al. (2011) found that short-term foraging partnerships in desert baboons (*Papio ursinus*) are determined by grooming interactions and tolerance to be in proximity of the other individual. Relationships, however they are defined, are useful because they can reliably predict the future behavior of the dyad.

Hinde (1976) asserts that the patterns of relationships among all members of the group ultimately determine the overall social structure. As mentioned previously, this has important fitness consequences. Guppies (*Poecilia reticulata*) have been a model organism in studies of cooperative behavior and tit-for-tat predator inspection (Dugatkin, 1991). Croft et al. (2004) found that persistent partner associations among female guppies existed in a wild population, which is the basic requirement for reciprocal altruism. In socially grazing animals such as the sheep (*Ovis aries*), the social structure has been observed through distribution of individuals across a landscape. Proximity to other grazing neighbors was found to be influenced by the perceived threat of predation, and how this social structure changes as a function of predation has important survival value (Krause, 1994; Sibbald et al., 2004).

Understanding the social structure also reveals the role of individuals in the group. Recognizing the presence of an 'alpha male' is a colloquial example of how individual behavior emerges at the group level. However, analyzing the presence of the individual in a global context reveals the importance of particular members. Lusseau and Newman (2004) analyzed a community of bottlenose dolphins (*Tursiops truncatus*) that was assorted into subgroups of similar sex and age classes. The authors found that in each subgroup, particular members acted as outside links to the members of other subgroups. The authors suggested that by serving as "social brokers" between communities, certain individuals play a crucial role of maintaining the cohesiveness of the entire community. Key individuals have been found to have a profound impact on the entire group. Flack et al. (2005; 2006) investigated the significance of policing behavior in high-ranking male pigtail macaques (*Macaca nemestrina*). Experimental removal of these individuals led to an increase of agonistic interactions in the group, and simulated removals under this same scenario revealed a decrease of affiliative behaviors such as grooming and play among group members. These findings suggest that certain individuals are important for maintaining the cohesion of the group. Simulated removals of individuals in other animal species have been demonstrated to change the original network structure. In wild Columbian ground squirrels (*Urocitellus columbianus*), the removal of individuals that were connected to a large number of other group members created fragmented networks while random removal of individuals kept the original group structure intact (Manno, 2008). The cohesion of chimpanzee (*Pan troglodytes*) grooming networks was also drastically altered after targeted removal of individuals and led to isolated clusters compared to random removal (Kannglesser et al, 2011).

On one level, sociality can be understood in terms of the network position of the individual and their respective influence on the group. However, the social interactions beyond the individual level, yet not at the global level, are also of importance. As mentioned previously, with Lusseau and Newman's (2004) example in bottlenose dolphins, subgroups exist in animal populations. The mechanisms of association among particular individuals are suggested to be caused by preferential interaction among similar members. Homophily arises due to similarities such as phenotype, geographical range, and genetic relatedness (Newman, 2002). These subgroups, or 'cliques,' are of biological relevance because they can predict which individuals will interact with whom under different scenarios. Sueur et al. (2008) found that rhesus macaques (*Macaca mulatta*) exhibited modularity in the group by associating with other kin during collective movements. In guppies (*Poecilia reticulata*), assortativity was predicted by individuals with similar body length and their tendency to shoal (Croft et al., 2005). Furthermore, the presence of subgroups is an important characteristic of the social structure as a whole because it can reveal the social style in an animal species. Different species of primate groups can be characterized by a continuum of social tolerance, classified at one end by a strong dominance hierarchy and strong kin preference and at the other end, a looser dominance hierarchy and low levels of nepotism (Sterck et al., 1997). Sueur et al. (2011) compared two species of macaques (*Macaca mulatta, Macaca fuscata*), one with a tolerant and the other with an intolerant social style, and found that higher levels of subgrouping existed in the despotic, nepotistic species. Thus, this behavioral bias toward interacting with preferred members is important in understanding the evolution in social behavior.

The previous discussions of the effects of the individual and subgroups on the social structure as a whole have alluded to the fact that sociality can also be understood by analyzing the group globally. This global approach is important for analyzing the network in order to reveal the cohesion of the group. Cohesion is based on the extent to which the group is connected and the ability for transmission in the network throughout group members (Wey et al., 2008). This structure can influence the spread of information or diseases among the population of the group (Lautora & Marchion, 2001; Cross et al., 2004). In primate social networks, measuring the cohesion through rates of affiliative behaviors such as grooming and proximity are determinants of group stability (Kanngiesser et al, 2011; Clark, 2011). Ultimately, maintaining group stability is essential because social networks with diverse partner integration benefit from increased cooperation and positive social contagion (Flack, 2006).

Studying animal sociality is not limited to a single animal network. Comparative analyses have examined multiple networks across context, behaviors, time, and even among different species in order to bring a fuller understanding of social behavior (Harvey & Pagel, 1991; Krebs & Davies, 1996). For example, Lehman and Ross (2011) compared the different social behaviors of baboons (*Papio anubis*), and analyzed social networks based on aggressive, displacement, grooming, mounting, and presenting behavior. They found structural differences among the networks, and the authors suggested that in order to fully understand social relationships, a variety of behaviors must be investigated. This approach is useful because generalizations can be made of the overall structure of a particular animal network (Sade & Dow, 1994). Brent et al. (2013) compared the social structure of macaques during the mating season and birth season.

They found that seasonal changes existed in the associative behavior between females, and during the mating season, the group was more defined by subgroups and stronger dyadic bonds between individuals. The authors predicted that this social variability in reproductive seasonality is a result of increased investment in individual alliances, which is necessary during times of increased male-female consortships and female-female aggression. Thus, the structure of a particular animal group is not always a static entity, and the topology can change as a function of the context.

What is Social Network Analysis?

The study of sociality in animals has advanced in recent years through the use of social network analysis (SNA). SNA refers to a suite of computing tools that mathematically model social interactions to identify and quantify patterns in social networks as well as visualize these patterns through sociograms (Freeman, 2004; Brent et al., 2011). SNA originated in mathematical graph theory in the 1930s (Croft et al., 2008; Brent et al., 2011), yet application of SNA to animal groups has emerged in recent years (Krause et al., 2009). Traditionally, observations have focused on the pair-wise interactions between primates (Couzin & Krause, 2003). However, patterns of sociality rarely occur in dyads, and it is difficult to conduct accurate observational studies on the group as a whole (Wey et al., 2008). SNA rebuilds the entire network by linking the associations between all individuals, enabling group-level dynamics to be observed as well as the sum of all inter-individual relationships. Thus, SNA allows behavior to be studied in the context of the social network (Kasper & Voelkl, 2009). Permutation-based tests are necessary for analyzing network-based information due to the non-independent nature of social interactions (Hanneman & Riddle, 2005).

In order to build a social network, social information collected at the dyadic scale is represented by a sociomatrix, which represents all possible combinations of pair-wise interactions between each individual of the group. These matrices represent the social interaction at the population level. The most simple of these matrices is an unweighted, undirected matrix, that either shows if the two individuals are or are not connected. At the other spectrum of complexity is a weighted, directional matrix, which shows not only if the interaction occurred, but the frequency (or strength) as well as the actor and the recipient for the behavior (Figure 2). Both matrix types have their own benefits and drawbacks, but for the scope of this discussion, a "matrix" will refer to one that is weighted and directed (See Croft et al, 2008 for a detailed discussion of the different types of matrices in SNA).
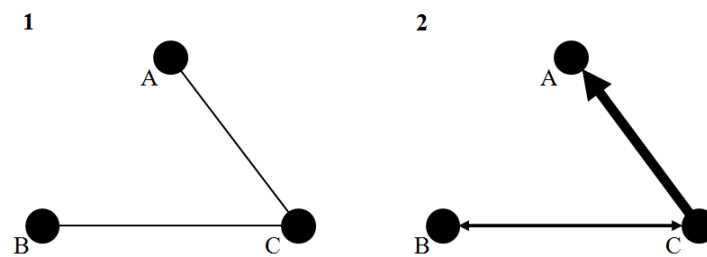
Figure 2. **(1)** An undirected and unweighted 3-node network, and **(2)** a directed and weighted 3-node network. **(2)** Gives information about the direction and the strength of the interactions between individuals while **(1)** does not.

Social networks are modeled as sociograms. These visual diagrams consist of individual actors as nodes that are connected to each other with edges representing the frequency and direction of the social interaction. SNA enables visual exploration of relational data, but several statistical techniques are available for more complex testing.

To this point, analyzing sociality in the context of the group has revealed the importance of the role of the individual, the presence of subgroups, and consequences of

the global structure of the network. Ultimately, understanding and analyzing this social

phenomenon is only possible through network statistics of SNA.

Purpose of Research

The main purpose of this study was to perform a longitudinal analysis on the social

structure of a captive group of hamadryas baboons (*Papio hamadryas*) using SNA. The

typical hamadryas baboon society is described as a four-tiered social system (Kummer,

1984; Stammbach, 1987). At the core of this social structure is the one male unit, which

is composed of a leader male, females, and related offspring (Kummer, 1968a). This is

the most stable social grouping, however, temporary affiliations due to spatial and social

associations can create larger levels of social organization (Abegglen, 1984).

The captive group at Bucknell was classified as a one male unit, and has been subject

to some especially drastic changes. In 2001, Doug (Dg) was a young alpha male of the

group. As Dg aged and declined in health, subordinate males that challenged Dg for

dominance were separated from the group to prevent possible infanticide and to eliminate

further aggression of the subordinate male toward the younger juveniles and infants. By

2011 Dg was at an old age, yet maintained his alpha status. In 2012, Dg died of old age,

and no male was present to assume an alpha position. A social environment fluidly

changes as a result of its membership and the roles that its members play. So, in order to

fully encompass how the topology of the network changes over time, behaviors were

collected from the group when Dg was at his prime (2001), at old age (2011), and after

his death (2012) and serve as 'snapshots' of the topology of the group at each of these

time periods. The behaviors that were observed include grooming, spatial proximity, and

agonistic behaviors. The social significance of each of these three behaviors and how they pertain to primate groups will be explained in turn.

The formation of grooming dyads serves as an important social function in primate societies, and has been studied extensively as an altruistic behavior (Dunbar, 1991). Grooming serves a hygienic function because ectoparasites and debris are removed from the body surface during grooming bouts. This fits the criterion for altruism because the actor (groomer) is investing time in the behavior while the recipient incurs hygienic benefits (Kurland, 1977; Barton, 1985). In addition, grooming is an affiliative behavior that strengthens social bonds (Spruijt et al., 1992), and has many functions from forming coalitions for support during agonistic events (Henzi-Barrett, 1999) to repairing relationships after conflicts (Judge et al., 2006). Grooming in this context is also considered to be an altruistic behavior because individuals that invest in grooming risk injury if agonistic events were to occur (Silk, 1982). Furthermore, grooming can be preferentially directed, such as biased toward kin that are philopatric (Sterch et al., 1997), or directed toward dominant individuals for increased tolerance (Smith et al., 2007). Therefore, SNA would be especially useful in measuring the differences in strengths of grooming partnerships in the baboon networks.

Spatial patterns such as proximity may not constitute as a physical interaction among group members, but these patterns of association should not be overlooked. Similar to grooming, proximity to other individuals is an affiliative measure because it reveals social tolerance, even in the presence of a monopolizable resource (Ventura et al., 2007; King et al., 2011). In fact, some studies have labeled affiliative associations as 'friendships,' which are characterized by frequent spatial proximity and grooming bouts

(Palombit et al., 1997). Closer spatial proximity is also important for maintaining the cohesion of the group because social information is mediated at closer distances (Pitcher & Parrish, 1993; Fernandez-Juricic & Kacelnic, 2004). This influences the level of behavioral synchrocity and group coordination of behavior (King & Cowlishaw, 2009).

Relationship quality can also be measured by observing agonistic interactions that arise from intergroup competition, such as competing over food and access to social partners (Aureli & Smucny, 1998). Agonistic behavior typically arises in the form of a ritualized threat, from chest-beating displays in male gorillas (*Gorilla gorilla*; Hall, 1964) to conspicuous facial expressions in rhesus macaques (Altmann, 1962). Correlates between increasing levels of aggression and cortisol levels within individuals have also been found (Bergman et al., 2005), indicating the physiological impacts of agonistic interactions. Furthermore, immediate social impacts of agonistic interactions include increased aggression, threat of injury, and a decrease in the cohesion of the social group (de Waal, 2000; Flack et al., 2006).

At each of the three different time periods, networks of affiliative, spatial and agonistic behaviors were created in order to assess how the captive group changed over time. Analyses were conducted at different resolutions in order to more fully capture network topology. Node-based measures determined how the network was structured around focal individuals, such as the leader male Dg. Sub-group measures determined how social interactions are patterned within the group. Finally, group level measurements described the overall topology of the social network, and enabled multiple networks to be assessed among each of the time periods.

In summary, the objectives of the project were:

1. Measure multiple social networks at each of the three time periods.

2. At each time period, collect individual, subgroup, and group measures.

3. Use this information to show how the network topology changes over time.

This work will contribute to the growing field of SNA in primatology, where literature explaining social relationships is limited. By completing the objectives, this project will address several knowledge gaps in the current literature because the study takes into account a variety of behaviors and employs a longitudinal analysis of these behaviors. SNA is also a valuable tool for observational studies of social groups. Furthermore, characterizing social systems in a statistical manner allows for a finer description of a social group, and enables a standardized method of comparison of social structures between different primate species. Ultimately, this project investigates social behavior and will contribute to the burgeoning field of SNA in animal behavior.

METHODS

Subjects & Housing

The subjects for the study were a captive group of hamadryas baboons (*Papio hamadryas*) socially-housed at Bucknell University's Animal Behavior Laboratories in Lewisburg, Pennsylvania. Table 1 describes the demographics of the captive population and the attributes of its group members in 2001, 2011, and 2012. Housing remained constant in each of the three time periods.

Table 1
Demographics of baboon populations from each study year

2001			2011			2012		
Code	Gender	Age Class	Code	Gender	Age Class	Code	Gender	Age Class
Am	female	adult	Ac	female	adult	Ac	female	adult
Ct	female	adult	Al	female	adult	Al	female	adult
Dg	**male**	**adult**	Ct	female	adult	Ct	female	adult
Kw	female	adult	**Dg**	**male**	**adult**	Ks	female	adult
Rt	female	adult	Ks	female	adult	Ky	female	sub-adult
Al	female	sub-adult	Av	male	sub-adult	Ad	female	juvenile
Kd	male	sub-adult	Ae	male	juvenile	Az	female	juvenile
Kf	male	sub-adult	Cp	male	juvenile	Cp	male	juvenile
Rm	male	sub-adult	Ky	female	juvenile	Kx	male	infant
Cl	male	juvenile						
Kb	male	juvenile						
Kr	male	juvenile						
Ks	female	juvenile						
Re	male	juvenile						
Rp	male	juvenile						
Ro	male	infant						

Grey background indicates females present in all three time periods. Leader male is in bold.

Subjects were housed in an enclosure consisting of four interconnected compartments, one of which was outdoors and three that were indoors. The largest of these areas was the outdoor compartment, measured 9 x 11 x 4.5m. It contained gravel substrate and permanent fixtures such as a tire swing and a metal climbing structure that

were used for animal enrichment. Primate feed and water were available *ad libitum*. The outdoor observation post was adjacent to this area and was separated by a chain-link fence, which allowed visual access to the entire outdoor enclosure. When the temperature dropped below 40˚F, subjects were locked indoors in the three temperature-controlled enclosures each measuring 9 x 6 x 2.5m. Subjects were able to move freely between these three areas.

Behavioral Observation

Subjects were identified based on physical appearance. Data were collected during May 2011 to August 2011 and from August 2012 to January 2013 using focal sampling techniques (Altmann, 1974). Data from 2001 was collected from September 2001 to November 2002 (DeBolt, 2003). All observation sessions occurred at times between 0930 and 1930 hours, and sessions typically lasted one to two hours. Data collection consisted of ten minute focal observations on a randomly selected baboon. The duration of the social behavior and the individual behavior was recorded as well as the actor and recipient of the dyad when relevant. Behavior on this ethogram included affiliative interactions, such as grooming and the formation of grooming partners, acts of aggression such as threats and bites, and spatial associations such as proximity to other individuals (Appendix 1). This was consistent with past studies employing SNA (Lehmann and Ross, 2011; Croft et al., 2011; Kanngiesser et al., 2011), and the behavioral definitions used were consistent throughout each of the three time periods. Observations were spoken into a digital voice recorder and later compiled, coded in a standard form, and entered into Microsoft Excel for creating social matrices.

Analyses

For each behavior category of interest, the software program UCINET was used for analyzing the matrices. UCINET is a software package for analyzing social networks (Borgatti et al., 2002). It offered a range of network analysis procedures, which will be described below. Matrices were normalized to make quantitative comparisons between networks (Kasper & Voelkl, 2009). Integrated in this program is Netdraw, which allows the user to create two-dimensional visualizations of the network in order to graphically represent the social network and its respective social behavior. UCINET and Netdraw are one of the most frequently used software packages for SNA.

Individual-based measures take an egocentric approach to describe the role of the individual in the network. Interpreting these node-based measures reveals the position of the individual in the network, as well as the effect the individual has on other members. *Node degree* measured the total number of edges, or partners, connected to a single node and indicated the relative position of the individual in the network because more edges connected to a node indicated an individual with a more centralized position. This was further broken down into the *in-degree*, which is the number of edges directed to the node, and the *out-degree*, which is the number of edges emitted from the node (Newman, 2003). These values represented the sum of social interactions in which the individual was an actor or a recipient, and higher values indicated the relative centrality of the individual through increased levels of social interaction (Wasserman & Faust, 1994).

The presence of subgroups in a network was also revealed through SNA. The *clustering coefficient* describes the extent to which the network is concentrated around the focal animal. This was derived from the number of neighbors to the focal node that were also connected to each other (Newman, 2003). Higher values of this metric

indicated that all individuals connected to the focal node are also completely connected to all other individuals.

In order to compare individual and subgroup network metrics, these values were averaged within the respective matrix to illustrate the cumulative distribution of these measurements within the group. *Mean node degree* and *mean clustering coefficient* allowed for changes in the network topology to be assessed. This also enabled social interactions to be studied in the context of the entire network rather than a 'bottom-up' approach. Calculating the descriptive statistics for individual measures and group-level measures were also necessary for direct comparisons among the different networks (Kasper & Voelkl, 2009).

Furthermore, group-measures addressed the overall network structure, and were used to determine the level of cohesion in the group. Network *density* measures the proportion of all present ties between nodes to the maximum number of possible ties. This value represents the quantity of dyads in a population. *Degree centrality* describes the extent to which a network is structured around a single individual. This value ranged from 0 to 1, where a value of 1 indicates a network where all nodes are centered around a single individual and 0 indicates that all group members have equal prominence (Wasserman & Faust, 1994). *Reciprocity* of interactions also revealed the cohesion of the group because mutual relationships allows for equal flow of information throughout the network (Mahagon et al, 2012; Wey et al., 2008).

Due to the non-independent nature of social interactions, permutation-based approaches were used to test the statistical significance of these measured network values. Statistical analyses were conducted in the UCINET program for comparing mean

degree, network density, and matrix correlation. Comparing network statistics of degree

centrality and clustering coefficient required statistical algorithms to be written in

additional programs such as R (Lehmann & Ross, 2011), which was beyond the scope of

this project. Therefore, degree centrality and clustering coefficient values were reported

and compared qualitatively based on their relative values.

In UCINET, permutation-based equivalents of the t-test, one way ANOVA, and

Pearson's correlation were available. Generally speaking, each of these tests randomly

shuffled the values between the observed groups, and then generated a test statistic. For

this set of analyses, this process was repeated 10,000 times, and the measured network

statistics were considered significant if the observed value was in the top 5% of all

randomized values. The Pearson correlation was calculated in a similar permutation-

based manner, but rather than randomly shuffling values between groups, matrices were

tested for correlation via a "Quadratic Assignment Procedure" (QAP) (Krackhardt, 1987).

The QAP first calculates the Pearson correlation across corresponding cells of each

matrix and then randomly permutes these matrices. The Pearson correlation was

calculated for this randomized matrix, and this process was repeated 10,000 times to

generate a distribution of all possible correlations. The Pearson correlation was

considered significant if it was greater than 95% of all possible values.

Networks were visualized using Netdraw within UCINET (Borgatti et al., 2002).

These sociograms included the attribute information of the node (shape represented

gender, and color represented age) as well as the frequency and direction of the social

behavior. Edges were weighted by line thickness to symbolize the relative frequency of

the interaction between a dyad.

Finally, the baboon network was compared to documented primate networks. Kasper

and Voelkl (2009) conducted a global analysis of interaction data of 70 different primate

species. Primate social organization was compared by creating networks of socio-

positive behaviors, which included grooming and proximity data. Consistent with their

procedure, a sociopositive matrix was created by pooling the grooming and proximity

networks of the observed species. The matrix was then symmetrized by combining

actor/recipient interaction frequencies into one unidirected matrix in the form:

$M_{sym} = M + M'$. Network density of this new sociopositive graph was then calculated,

and compared to current literature on primate social networks.

RESULTS

During the 2012 study period, 45 hours of focal observation data were collected by the author. In 2011, 36 hours of focal observations were collected by the author. Data from 2001 included 154.5 hours of focal observations collected by Nicola Debolt Robertson.

Network Measures

Across all three time periods, networks describing agonistic and grooming interactions were not fully connected, which indicated that some members were not involved in an agonistic or grooming dyad. The only exception was the grooming network in 2001 (Appendix 2). Proximity networks were fully connected in all three time periods, indicating that all group members were directly associated with other individuals, or indirectly connected to other members via their direction connections (Appendix 2).

Network density was calculated for all behavioral networks in each time period (Table 2). To determine if the observed network density was a function of the network's unique topology rather than a result of random variation in the network, each network was compared to a randomized network of shuffled edges. All network densities were significantly different from their respective theoretical network (Bootstrap test: z-values between -3.26 and -18.23, all $p<0.05$).

Table 2

Network statistics for three observed behaviors for a baboon group with a prime alpha male (2001), old alpha male (2011), and no male (2012)

	Agonistic			Grooming			Proximity		
	2001	2011	2012	2001	2011	2012	2001	2011	2012
Network Density	0.063	0.056	**0.125**	**0.142**	0.139	0.139	**0.408**	0.306	0.389
Degree Centrality	10.180	6.429	**11.533**	16.659	**21.056**	16.071	16.266	14.877	**28.212**
Clustering Coefficient	0.310	0.000	**0.917**	0.391	0.000	**1.188**	2.779	3.353	**5.190**
Reciprocity	na	na	na	10.530	14.290	**42.860**	**38.980**	11.110	23.810

Bold indicates the greatest value of each network statistic across the three time periods. Network statistics were weighted to allow comparisons across multiple networks

Degree centrality was standardized so comparisons of each network across the three time periods could be made independent of group size. In the agonistic network, the highest degree centrality was observed in 2012 (C_D=11.533). The highest degree centrality measured in all grooming matrices was in 2011 (C_D=21.056). The proximity network had the highest degree centrality in 2012 (C_D=28.212). Table 2 compares this statistic across all networks.

In each network, individual measures of in-degree and out-degree were averaged and compared across time (Figure 3). The proximity network differed significantly in mean in-degree (Permutation one-way ANOVA with 10,000 permutations: F=8.29, N=3, p<0.01). Post-hoc comparisons of each time period were made by using a permutation-based two-tailed T-test with a Bonferroni correction of p=0.05/3=0.016. This method does not provide a test statistic but after using this permutation-based approach of 10,000 permutations, it was found that the mean difference of in-degrees between 2001 and 2011 of 10.03 happens 99.7% of the time in random trials (p=0.005). The mean difference of in-degrees between 2012 and 2011 of 13.88 occurs 99.8% of the time in random trials (p=0.003). There was no significant difference in means between 2001 and 2012 (p=0.2). Therefore, the mean in-degree measured in 2011 is significantly smaller than the mean in-degrees measured in 2001 and 2012, indicating that initiated spatial proximities occurred less frequently in 2011. The agonistic network and the grooming network did not show a significant difference in their mean out-degree or their mean in-degree.
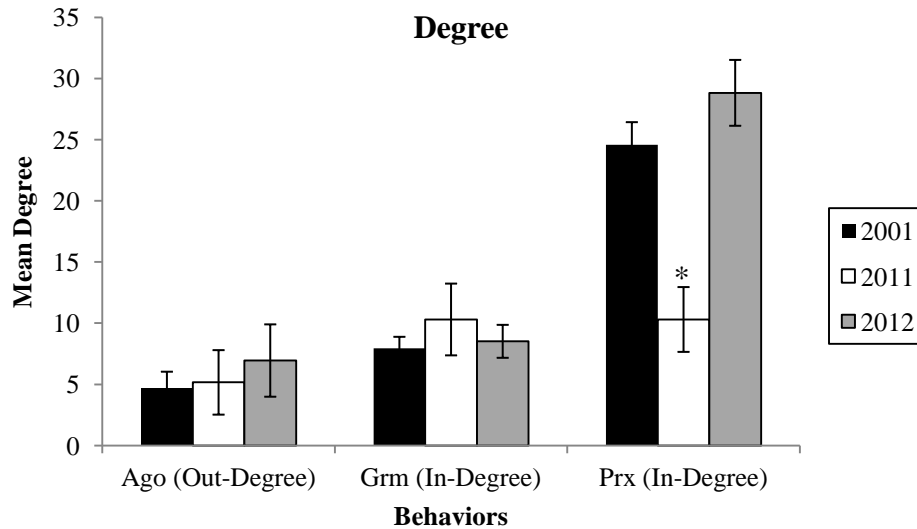
Figure 3. Comparison of mean in-degree and mean out-degree across different behaviors. Bars represent mean (and standard error) of mean network degree in each time period; significant differences are indicated by an asterisk ($p<0.016$).

Mean clustering coefficients measured the extent of overall clique organization in the group, and provided a method of comparison of each network across the three time periods. Higher values indicated the tendency of the network to be clustered around a single individual. The highest mean clustering coefficient in the agonistic network was measured in 2012 ($C_C=0.917$). The highest mean clustering coefficient in the grooming network was measured in 2012 ($C_C=1.188$). The highest mean clustering coefficient in the proximity network was measured in 2012 ($C_C=5.190$). Table 2 compares this statistic across all networks.

Reciprocity measured the proportion of interactions that were reciprocated relative to the number of dyads with any interaction existing between them. This ratio was only calculated for affiliative behaviors because the agonistic networks consisted of asymmetrical interactions and thus did not produce a ratio. For grooming, the greatest amount of reciprocity occurred in 2012, where 42.86% of all grooming interactions were

reciprocated. The greatest amount of reciprocation in proximity interactions occurred in 2001, where 38.98% of all ties were reciprocated.

At each time interval, agonistic, grooming, and proximity networks were tested to measure the extent of correlation between behaviors (Table 3). There was a significant negative correlation in 2012 between agonistic and grooming networks (QAP Pearson's correlation with 10,000 permutations: r= -0.624, p<0.05). There was no significant correlation between behaviors in any other time period, although it is worth noting that in 2011 there was a strong positive correlation between the agonistic and grooming networks (r=0.739, p=0.372).

Table 3
Correlation Coefficients of Behavior Networks Across Time

2001	Agonistic	Grooming	Proximity
Agonistic	--	-0.052 (0.476)	-0.002 (0.536)
Grooming		--	-0.013 (0.483)
Proximity			--
2011	Agonistic	Grooming	Proximity
Agonistic	--	0.739 (0.372)	-0.123 (0.406)
Grooming		--	-0.041 (0.496)
Proximity			--
2012	Agonistic	Grooming	Proximity
Agonistic	--	**-0.624 (0.015)**	0.307 (0.060)
Grooming		--	-0.168 (0.177)
Proximity			--

Probability levels appear in parentheses after correlation coefficients. Bold indicates p-values with p<0.05

Grooming and proximity networks were combined into a pooled matrix representing all sociopositive interactions in order to be compared with Kasper and Voelkl's (2009) procedure. Densities were measured for these sociopositive matrices. The respective

densities in 2001, 2011, and 2012 were 0.508, 0.361, and 0.528. Compared to Kasper

and Voelkl's (2009) findings, the median density was 0.75 and ranged from 0.49-0.93.

DISCUSSION

A comprehensive understanding of an animal social group requires long-term data on social interactions. Through the use of naturalistic behavioral coding, this project revealed the topological changes in the social structure of a captive group of hamadryas baboons. By using directed relational data, behaviors were assessed at the dyadic and polyadic scale and compared temporally.

The three behavioral networks across the three time periods showed unique network structures, indicating that baboon social networks are differentiated across time and between behaviors. The changes in social networks are not a result of a change in the overall frequency of social dyads, as would be expected as the network population changes over time. On average, there was no significant difference in the mean degree in the agonistic network (out-degree) or the grooming network (in-degree) across 2001, 2011, and 2012. Thus, the frequency at which these social behaviors were observed did not change. However, network-wide measures revealed differences in the overall topology of the agonistic and grooming networks, as indicated by the differences in network density, degree centrality, clustering coefficient, and reciprocity.

The asymmetrical proportion of directed social dyads in the agonistic network reflected the hierarchal structure in baboon populations. Although aggressive interactions were observed equally as frequently in each time period, the distribution of agonistic occurrences varied. The network density was highest in 2012, indicating that more agonistic interactions were directed to a larger number of individuals than observed in 2001 or 2011. Furthermore, these outgoing interactions were relatively centered from

one individual, as reflected by the high degree centrality measured in 2012. During this time period, a high ranking adult female was observed to initiate the majority of aggressive interactions directed to both kin and non-kin. Taken together, these two values that are characteristic of the 2012 agonistic network revealed the tendency of aggressive interactions to originate from one focal individual and be directed to a proportionally larger percentage of other group members than compared in 2001 or 2011. Comparing to the 2011 agonistic network with the lowest measured network density and degree centrality, far more aggressive interactions were initiated by more individuals and directed to a smaller proportion of group members.

The clustering coefficient in the agonistic network was highest in 2012. This value represents the greater extent to which aggressive interactions occurred within the group. Rather than isolated agonistic events between single dyads, multiple parties were involved in these interactions. For this directed network, this indicates the linearity of aggressive behavior. Another key feature of the 2012 agonistic network is that recipients of aggression were more likely to be an aggressor to another group member. In comparison, the 2011 agonistic network typically included single dyads.

The network topologies observed in the agonistic networks demonstrated the changes of intergroup aggression over time, and highlighted the difference of dominance style in male-female aggression versus female-female aggression in hamadyras baboons. Hamadryas social structures are considered despotic because the leader male plays a controlling role by keeping females in close proximity through neck bites, facial threats, and other forms of aggressive herding behavior (Gore, 1994). The low clustering coefficients observed in 2001 and 2011 are characteristic of this form of male aggression

in the one male unit because aggression in this manner is dispersed to all group members.

Leader males play a centralized role with adult females, and the 2012 agonistic network

reflected a possible change in the social structure with the absence of Dg. In this

network, agonistic interactions were largely shaped by female aggression patterns.

Typically, hamadryas females have no clear hierarchal structure compared to more

nepotistic species such as rhesus macaques (Sterch et al., 2011). However, in this

observed group, aggressive interactions occurred throughout more members, and were

directed toward select individuals. Leader males have the tendency to intervene in

female-female conflicts (Colmenares & Rivero, 1984), therefore, the absence of

individuals with such roles will lead to the increased frequency of such aggressive

interactions. Similar findings by Flack et al. (2005) showed that the removal of

individuals that acted as third-party interveners caused an increase of the intensity and

frequency of intergroup aggression in pigtail macaques.

The grooming network topology had structural characteristics that differed in the

three time periods. Network density, though not markedly greater, was highest in 2001.

This suggests that the proportion of grooming dyads was observed in a greater percentage

of the group during this time period. In 2011, the highest degree centrality was

measured, and indicated that a single individual received a proportionally greater number

of directed grooms than in 2001 or 2012. The clustering coefficient was highest in 2012.

A higher value indicated that individuals involved in grooming dyads also formed dyads

with additional partners. Therefore, grooms were more likely amongst individuals in

cliques rather than dispersed amongst all available group members. Reciprocity was also

observed to be highest in 2012, indicating that when grooming did occur, it was more likely to be a symmetrical interaction than grooms observed in 2001 or 2011.

The high clustering coefficient and percentage of reciprocity was a key characteristic in the 2012 grooming network. Not only did individuals tend to associate with select individuals more frequently, but also played relatively equal roles as actor or recipient of the grooming bout. In comparison, Dg played a prominent role in the 2001 and 2011 grooming networks as the greatest recipient of grooming interactions, yet the leader male seldom reciprocated grooms. Therefore, this change of grooming network topology demonstrated that the distribution of grooming interactions was contextually-based and changed over time.

One explanation for this change of grooming interactions between individual across time may relate to the distribution of agonistic interactions in each respective network. Grooming has numerous functions in primate societies, and the patterns of grooming dyads may be indicative of the social significance of the groom. In 2012, grooming and agonistic networks were found to have a significant negative correlation. Dyads that engaged in aggression were less likely to form grooming partnerships. This has important social consequences because grooming serves an important social function of reconciliation and decreasing stress in individuals that were involved in agonistic interactions. An absence of direct conflict resolution between the involved individuals also impacts the overall cohesion of the group because the recipient of the aggression faces further aggression, injury, and damaged relationships (de Waal, 2000). This can lead to the overall instability of the group because social interactions become fragmented and formation of dyads become less diversified (Flack, 2006). The baboon group in 2012

showed instability in its social structure because agonistic interactions were more pronounced throughout the whole group while grooming interactions were restricted amongst groups of preferred individuals.

Alternatively, the observed social structure in 2012 may not indicate instability, but rather, demonstrate a flexible social regime for mitigating the cost of group-wide aggression. Although direct reconciliation was not observed between agonistic dyads, a high percentage of reciprocity in grooming was observed. This high degree of reciprocity as well as the tendency of grooming to occur in cliques suggested the role of third-party reconciliation.

Individuals not involved in the original aggressive interaction may interact with either the aggressor or victim after such behavior occurs (de Waal & van Roosmalen, 1979; Das et al., 1997). These "bystanders" function to reduce tension among the combatants and reduce the risk of continued aggression (Call et al., 2002; Das, 2000). This also suggests an advanced level of social cognition present in primates. Recognizing participants in a social interaction that does not include the individual is a cognitively complex process. Furthermore, acting in an altruistic manner, such as by initiating grooms to the combatants, is a form of "consolation" in primates (Watts et al., 2000). This higher level of cognitive ability may reveal an increased level of social cognition, and demonstrate a mechanism for unstable social networks to cope with increased group aggression.

Theirry (2008) states that current classification schemes for primate social groups are over-simplified because they include only verbal definitions. SNA can mollify this problem by providing quantitative metrics in addition to describing a primate social group as "egalitarian" or "nepotistic" (Croft et al., 2007; Kasper & Voelkl, 2009).

Network structures have been found to vary across species (Kasper & Voelkl, 2009; Seur et al., 2011). However, there is a disparity on what network metrics should be collected and how they should be interpreted (see Wey et al., 2008 and Kasper & Voelkl, 2009 for a comparison). I used the density measurement of the pooled sociopositive matrices to illustrate this issue in the emerging field of SNA in primatology. Compared to other primate species, the network densities in this baboon population were consistent with established values in the literature (Kasper & Voelkl, 2009). The lowest observed density in this studied group was in 2011, but this value is within a range of densities that were collected in a later study from the behavioral networks of olive baboons [Lehmann & Ross, 2011; Median density 0.358, Range 0.305-0.445]. In this study, the authors concluded that the reported network density suggested that this population showed an, "intermediate to high level of social complexity" (Lehmann & Ross, 2011). However, reconciling social network metrics with social cognition is still in its infancy. The Social Brain Hypothesis suggests a link between neocortex size and network complexity in an animal species (Dunbar, 2008). Determining which network metric to be used as a predictor for social complexity is under progress. Alternatively, Lehmann and Dunbar (2009) found a negative correlation between neocortex size and network density in Old World primates. They suggest that the result of an increasingly structured social system requires social interactions to be concentrated among core social partners, causing a decrease in network density. Wey et al. (2008) suggest that the use of multiple network metrics is essential for assessing social behavior. Thus, more understanding is needed to bridge SNA methodologies with theories of animal sociality.

Nevertheless, the application of SNA to an animal framework provides a deeper understanding of social behavior. This set of analytical tools assesses the overall structure of the network above the dyadic level and enables analysis of social interactions in context of the group (Sueur et al., 2011). This complements Hinde's (1976) framework of social organization because multiple scales of animal social structures are considered. This project utilized a fraction of the computing power of SNA, yet even in this limited application, it revealed the wealth of information that is available to researchers interested in questions of social behavior. Ultimately, the intricate patterns of animal social relationship require integrative analyses that can be realized with this new emerging analytical technique.

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APPENDIX 1

Ethogram of Hamadryas Social Behavior

Aggressive and Agonistic Behavior

Submissive Interactions
Avoid (Avo): Moving more than one limb's length away from other animal within 3
    seconds of approach. Note both the focal animal and the avoided animal.

Flee (Fle): Rapid withdraw from other animal in response to aggressive behavior or an
    approach. (Onset 0s, Offset 3s) Note both the focal animal and the animal
    causing the flee.

Crouch (Crh): Lowering chest and/or head to position close to ground by bending
    forelimbs and/or hind limbs. Scored as an event. Note both the focal animal and
    the context of the crouch.

Dominant Interactions
Threat (Thr): Agonistic interaction targeting another individual (Onset 0s, Offset 3s)
    Note both the focal animal and the recipient.

    Threat-mouth (Thrm): Mouth is open but teeth are not exposed, usually
    accompanied by the thrusting of the head toward the target.

    Threat-brows (Thrb): Eyebrows raise so that white portion of the skin superior
    to the eyes and inferior to the browline is exposed.

    Threat-lunge (Thrl): Charges toward the target that do not go past the location
    of the recipient.

Chase (Chs): Rapid advance toward another animal that exceeds the recipient's
    location at the time the action begins that is not in a play context. (Onset 0s,
    Offset 3s) Note both the fleeing and pursuing animal.

Bite (Bit): Strong unrestrained grip of the skin/limb of another with the teeth, almost
    always accompanied by a scream from the recipient. Scored as an event. Note
    the initiator and the recipient.

Teeth-bare (Tbr): Upper lip raises and lower mandible opens to expose teeth toward a
    target.   Scored as an event. Note both the focal animal and the target.

Rough behavior (Rbh): Physical contact with no accompaniment of a "play face",
    where mouth is held open and facial expressions are relaxed. (Onset 3s, Offset
    3s) Note the focal animal and the recipient of the interaction.

Push (Psh): Brief physical contact where individual uses limbs or elbow to swat at or shove the recipient from the initiator. Includes interactions that do not fit the 3s rough behavior criterion. Scored as an event.

Interfere (Int): Focal subject advances quickly toward a mounting pair and ends the interaction with a threat. Scored as an event. Note the focal animal and the mounting pair.

Affiliative Behavior

Passing Proximity (Ppr): Being within one meter of another animal for less than 3s. Note both the focal subject and the other animal. Scored as an event.

Proximity (Prx): Being within one meter of another animal (Onset 3s, Offset 3s) Note both the focal subject and the other animal.

Groom (Grm): Separating hair with fingers and picking at coat or skin of another animal and occasionally putting loose particles into the mouth. (Onset 3s, Offset 3s) Note both the focal animal and the recipient of the groom.
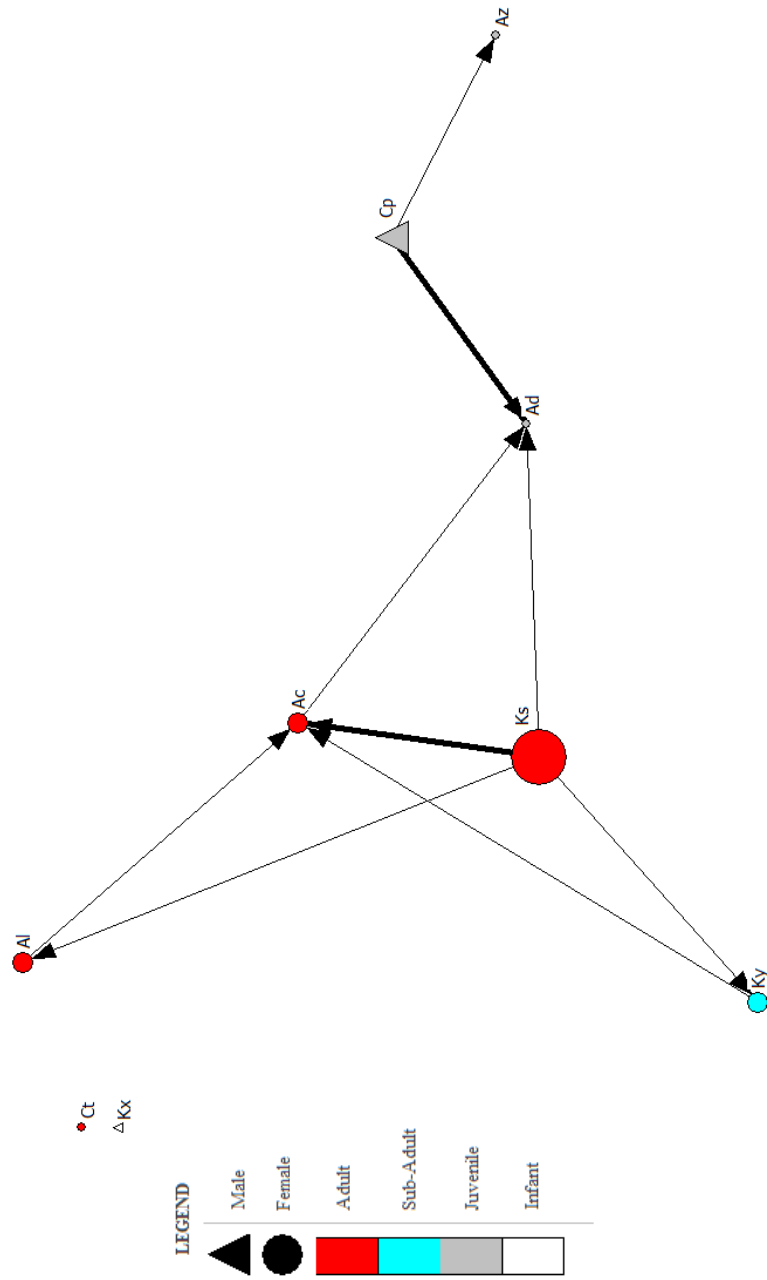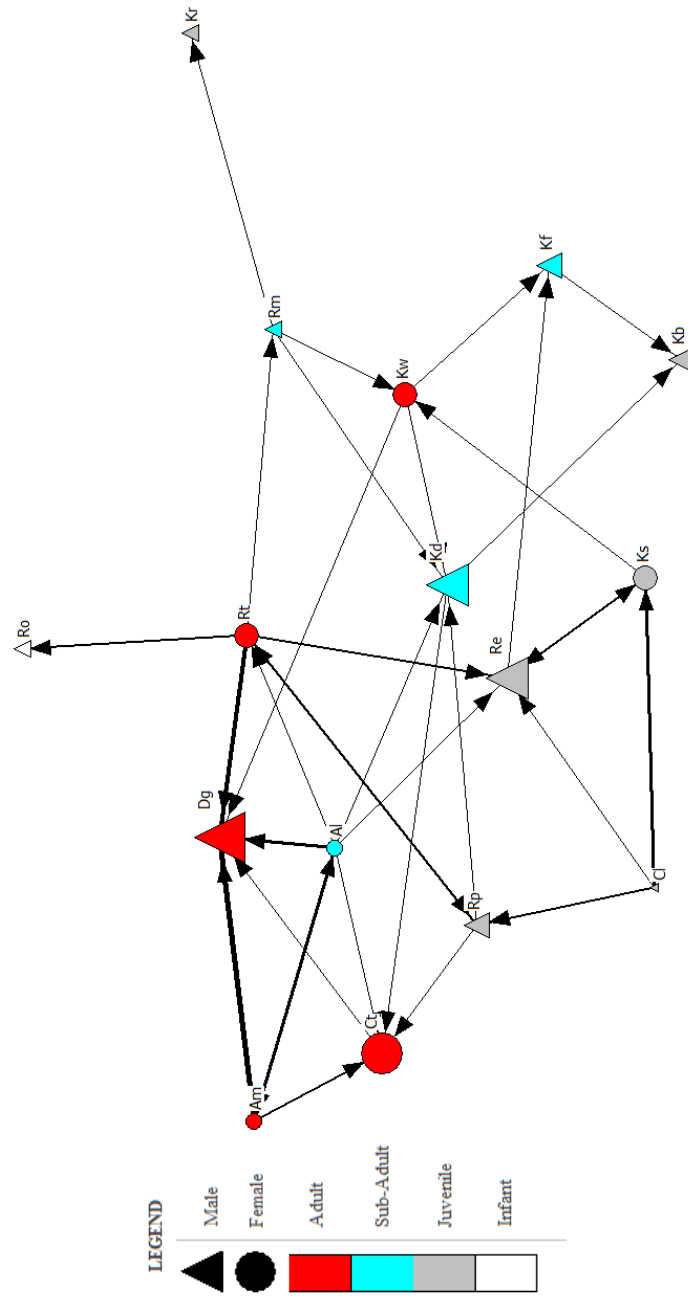
APPENDIX 2
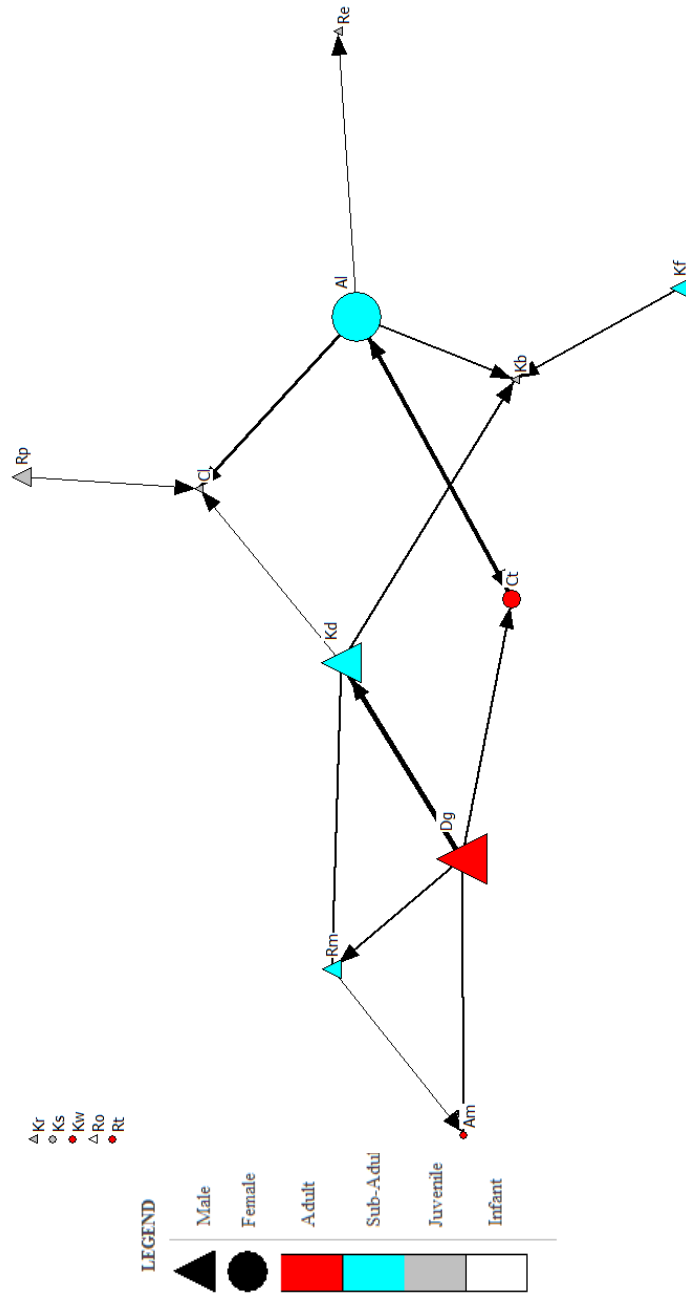
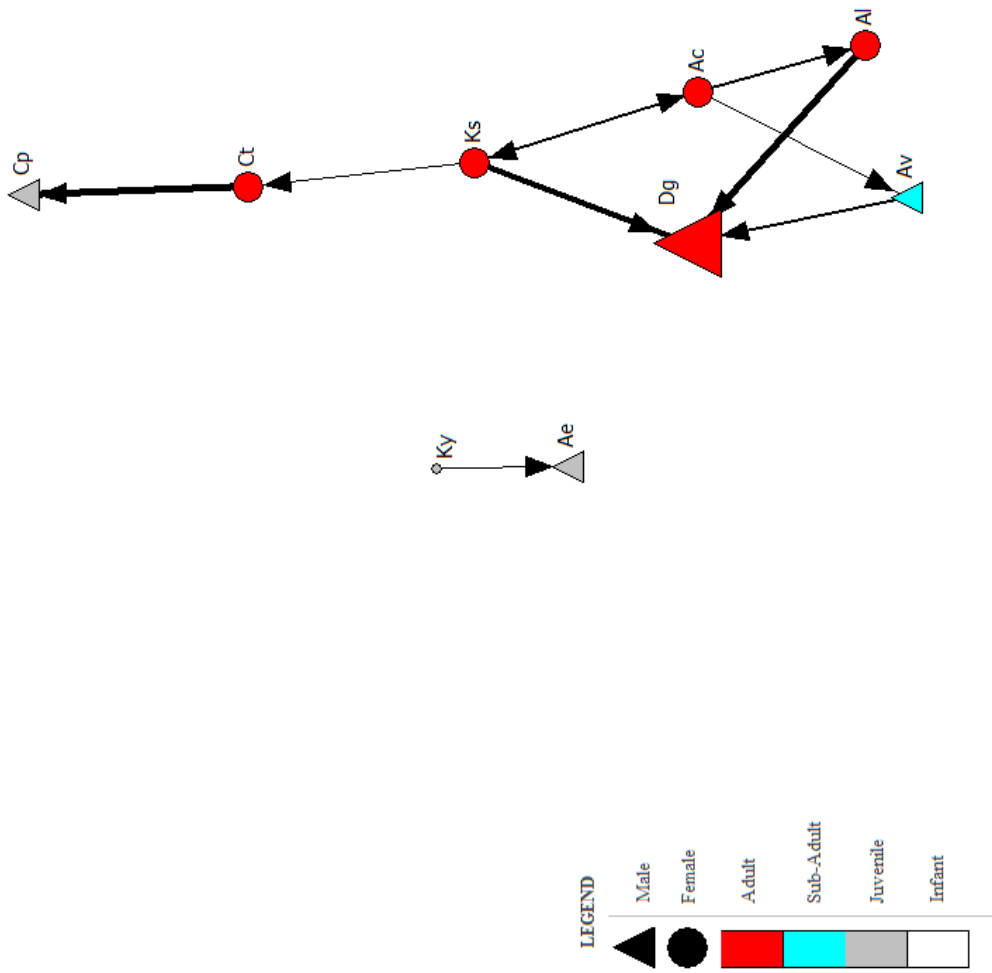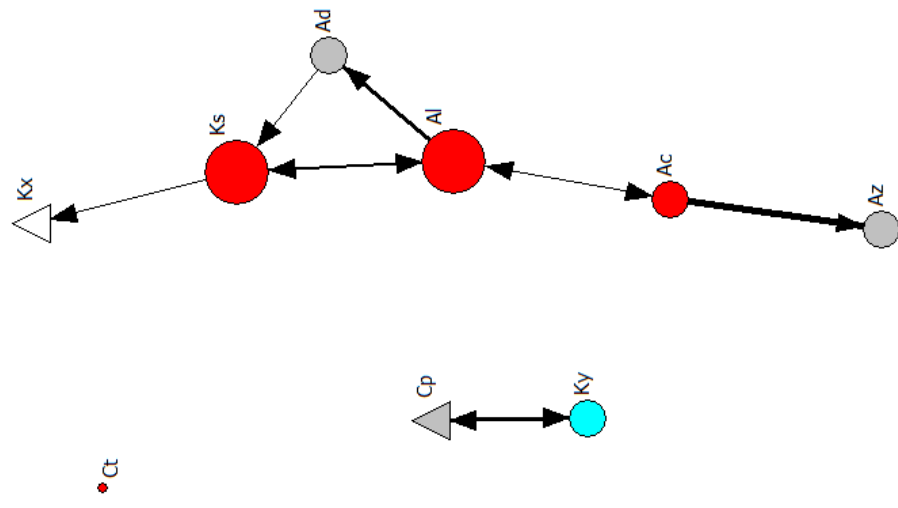
Appendix 2a. Agonistic network in 2001
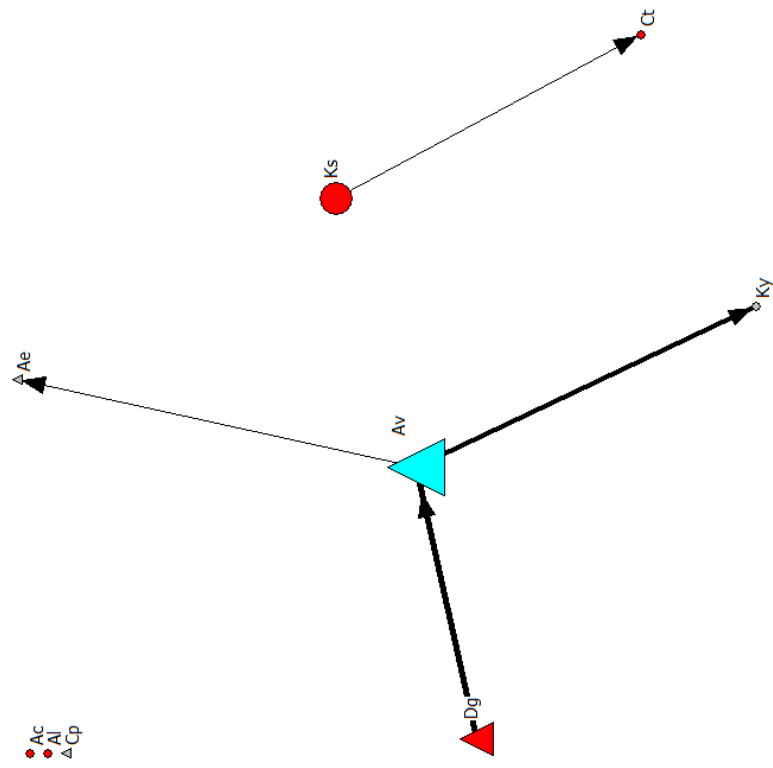
Appendix 2b. Agonistic network in 2011
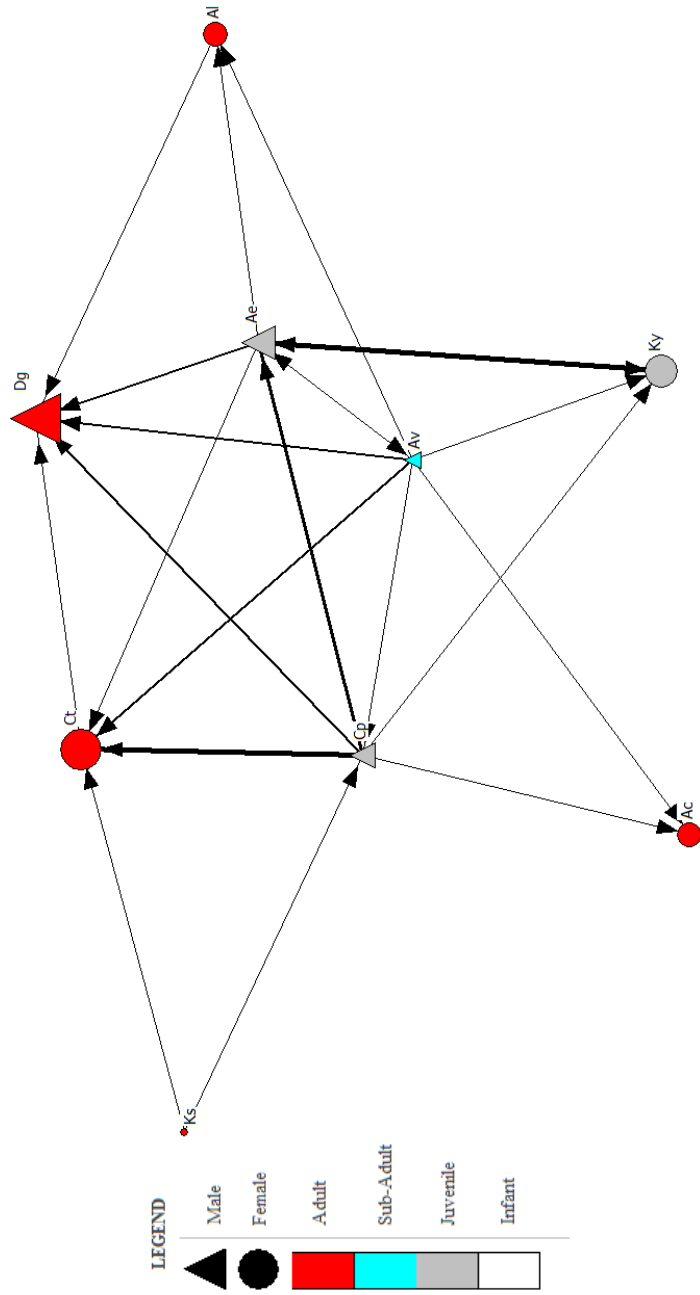
Appendix 2c. Agonistic network in 2012

Appendix 2d. Grooming network in 2001

Appendix 2e. Grooming network in 2011
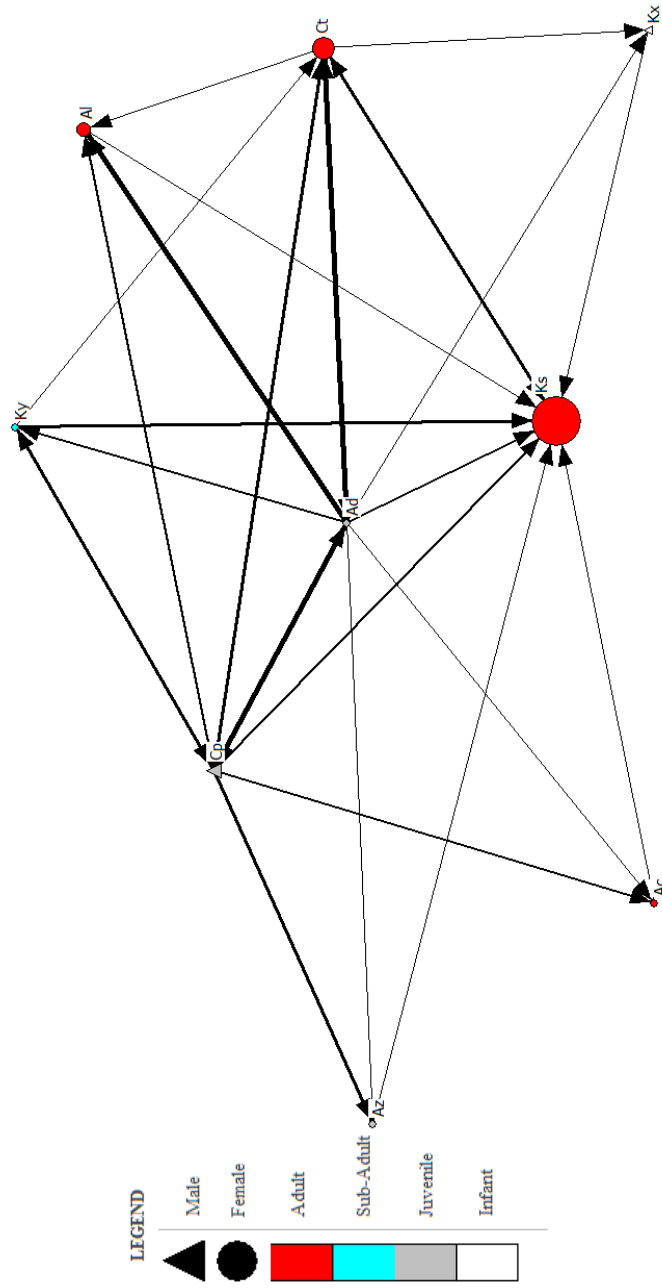
LEGEND

Male
Female

Adult
Sub-Adult
Juvenile
Infant

Appendix 2f. Grooming network in 2012

Appendix 2g. Proximity network in 2001

LEGEND

Male
Female

Adult
Sub-Adult
Juvenile
Infant

Appendix 2h. Proximity network in 2011

Appendix 2i. Proximity network in 2012

LEGEND

Male
Female

Adult
Sub-Adult
Juvenile
Infant