Effects of a social introduction on group structure: utilizing a network approach to examine changes in social structure and stability in a zoo-housed group of hamadryas baboons (*Papio hamadryas*)

by

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A thesis submitted to
Sonoma State University
In partial fulfilment of the requirements for the degree of

MASTER OF SCIENCE
in
Biology

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ABSTRACT

Comprehensive knowledge of social groups within zoos allows for better understanding of the issues surrounding group stability and how to best provide these species with optimal care. A developing area of sociality research is social network analysis (SNA), which is the analysis of social systems utilizing the construction of a network and allows scientists to utilize quantitative measures of group systems to represent social structure. In December 2015, Oakland Zoo introduced two new males to the hamadryas baboon (*Papio hamadryas*) exhibit. I examined the group structure of these baboons over the course of six months on three levels: group cohesion, subgroup structure and individual centrality. This study found that the introduction of two juvenile males decreased overall group connectedness and that the new males did not increase their individual centrality relative to the group. However, knowing that the group is less well-connected is important for zoo-staff in making further decisions that may affect to social structure of the baboon group. Further research on the social networks of hamadryas baboons could provide more information about the societal structure of this primate species. The group structure may also continue to change as the new males mature and form harems of their own. Therefore, Oakland Zoo may choose to conduct longitudinal studies to fully comprehend the structure of the baboon group. Utilizing a network approach to quantify social cohesion will allow for a better understanding of social cohesion of many species in captivity and upholding good animal welfare and care of these species.

MS Program: Biology
Sonoma State University Date: 1 May 2017

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Introduction

Many species of animals have evolved to live in groups, which provide individuals with opportunities for increased fitness. Group living individuals obtain advantages such as better access to food resources and food sharing, increased access to sexual partners, and decreased predation risk (Sueur et al, 2011; Sussman & Garber, 2011). Cooperation and sociality are behavioral tactics that allow group members to have better access to resources, maintain or enhance social position, or increase mating opportunities (Sussman & Garber, 2011). Although sociality provides many benefits, intrinsic conflict may arise due to constant interaction and competition with many individuals for food and mating opportunities (McCowan et al., 2011; Sussman & Garber, 2011). Characteristics of social groups and relationships are thought to be a result of food resources, mating opportunities, and predation; and studying social behavior provides information about how individuals maximize benefits and minimize costs of living in social groups (Enstam, 2002; Shulke & Ostner, 2012).

Group living requires that individuals form social relationships and affiliative bonds to maintain group stability (Sussman & Garber, 2011). Affiliative and aggressive behaviors have both been interpreted as tools of negotiation to establish and maintain valuable social relationships within a group (Aureli et al., 2012). Understanding how group-living individuals utilize these types of behaviors to maintain group stability is valuable in providing the best care for zoo-living species. Animals living in zoos are especially exposed to the disadvantages of group living because of space limitations which make it more difficult for individuals to escape from group conflict and also unable to migrate out of a group. Due to these limitations, captive animals may be more prone to higher rates of aggression and more bouts of deleterious aggression (aggression leading to serious injuries) (Beisner et al., 2015; McCowan et al., 2008). Since most primate species live in groups with complex social systems, it is especially important to understand the details of primate society. Studying intragroup interactions may provide insights into issues surrounding social stability and group cohesion and how to best understand the sociality of group-living species in captivity in order to provide them with optimal care (Rose & Croft, 2015).

Social stability and social cohesion are two measures of sociality that can provide insight into how intragroup interactions affect a group. Social stability is the robustness of a social group; the ability of a group to persist through time despite major changes that may occur in group structure (Beisner et al., 2011; McCowan et al., 2008). Cohesion is another factor of social structure; a cohesive group is one that is well-connected and can sustain in spite of group conflict and change (McCowan et al., 2011). The ability to quantify or measure group cohesion and stability in primate societies would improve our understanding of the health and welfare of primates in captivity because these measures are valuable predictors of deleterious aggression and can be used to prevent injuries in captive primates (McCowan et al., 2008). A study of rhesus macaque (*Macaca mulatta*) sociality by Beisner et al. in 2015 was conducted to utilize a network approach to identify patterns of interdependence between networks that could serve to distinguish stable groups from unstable groups. These researchers examined aggression and status behaviors to examine differences in stable and unstable groups, where stable groups were ones that remained intact and experienced no major changes in group membership, while unstable groups showed high levels of aggression, major changes in group hierarchy, or social collapse. Findings of this study indicated that stable groups showed a higher level of dyadic aggression-status signaling interactions and that in unstable groups, this interdependence between aggression and status changed just before social collapse (Beisner, 2015). Most sociality research has been focused on the mechanisms of maintaining social relationships *after* a group conflict, but more effort is needed to understand these same mechanisms *before* a conflict occurs (Aureli et al., 2012). Many social groups can be deemed "unstable" following a group conflict or social collapse, but it would be valuable to be able to detect group instability before such an event so that social collapse or conflict may be avoided.

A developing area of sociality research that has proven useful in this regard is Social Network Analysis (SNA), which is the analysis of social systems utilizing the construction of a network. This network is based on nodes, which are the individuals in the network, and edges, which are what connects those individuals (interactions or associations between individuals) (Borgatti et al., 2009). Social network analysis allows scientists to utilize quantitative measures of group systems to represent how social interactions influence group structure beyond what may be apparent when using simple group hierarchal or attribute data (McCowan et al., 2011).

Social network analysis originated as a tool in sociological research to examine the complex interactions between individuals and communities, specifically, the link between human relationships and social processes, including the spread of disease in social groups (Borgatti et al., 2009; Croft et al., 2010; Farine & Whitehead, 2015; Hawe et al., 2004). In the past 15 years, the utility of SNA for studying animals has come to prominence and the methodology has been applied to various aspects of animal societies

(Brent et al., 2011; Croft et al., 2010; Farine & Whitehead, 2015). SNA has been used to study a diversity of taxa: the "social cliquishness" of wild guppies (*Peocilia reticulate*), the social power of key individuals in pigtailed macaques (*Macaca nemistrina*), group affiliation in bottle-nosed dolphins (*Tursiops truncatus*), effects of habitat changes on the group structure of North American river otters (*Lontra canadensis*), and a number of other studies (Croft et al., 2005; Flack et al., 2005; Lusseau, 2003; Wey et al, 2008; Hansen et al., 2009).

The utility of SNA has even more recently been applied to animals living in captive environments, where research has focused on mechanisms maintaining social stability and variables affecting social collapse. Specifically, social network analysis is becoming a more popular form of studying primate social stability and is increasingly enhancing our understanding of the sociality of many primate systems. Recent studies have examined how individual and group characteristics and mechanisms influence social networks and stability. McCowan et al. (2011) examined how certain group and individual characteristics impacted network structure and stability. They employed network analysis to examine the effects of personality, social power, and conflict intervention on social stability, which was measured by rates of wounding. In this study, social power was defined as a measure of the extent which other group members agree on the social status of an individual; where an individual with high social power is one who other group members perceive as having the ability to get involved in the relationships of other group members. These researchers found that third-party intervention is a mechanism of maintaining group stability in rhesus macaques (*Macaca mulatta*) and also discovered that personality and social power are factors that assist in determining which individuals are key interveners in group conflicts. This provides evidence that individual and group characteristics have a profound effect on group networks and stability and useful tools in predicting social stability and assessing animal welfare (McCowan, 2011).

Social network measures have been found to be predictors of deleterious aggression (aggression leading to serious injuries) and studies have shown that manipulating group composition to improve social stability can reduce levels of aggression and mortality (McCowan et al., 2008). Beisner et al. (2015) examined captive primate groups before social collapse in order to understand the basis for group instability. They found a clear interdependence between aggression and status signaling and that this pattern of interdependence changed just before social collapse. Social stability arises from the symbiotic relationship between different behavioral networks, and an imbalance of the interdependence of behaviors is one reason for social collapse. Being able to detect any change in patterns of interdependence of behaviors would provide staff at zoos and other facilities the ability to prevent social collapse and deleterious aggression. Thus, the use of social network analysis may prove beneficial as a mechanism for use in zoos to provide the best animal care and management possible.

Studies have shown that social network analysis is a useful approach for understanding group cohesion and how it is maintained. However, this methodology has only recently been used as a tool for zoo management, which could benefit greatly from this type of study. Social network analysis has proven useful in determining how variables of sociality impact the welfare of animals in zoos. This method has provided zoos with valuable information about the importance and benefits of social bonds, which could improve our understanding of reproductive success, enclosure design, animal health, and management decisions (Rose & Croft, 2015). An SNA study by Less et al. (2010) revealed that the death or removal of an individual from a long-established group of western lowland gorillas (*Gorilla gorilla gorilla*) had negative effects on the welfare of the remaining group members. In this study, the death of a male in a stable multi-male group caused a disruption of social dynamics marked by increased agonism and dominance behaviors. A recent study examining the social group changes of a group of hamadryas baboons with declining age of the leader male found that baboon social behavior varied across context and that social networks differentiate across time and between behaviors (Treat, 2013). Also, research on animal personality in captive groups has suggested that measuring animal personalities is likely a helpful strategy for assessing zoo management decisions and animal welfare (Watters & Powell, 2012). Additional research and application of SNA to zoo management will broaden our knowledge of the impact of husbandry decisions on the social lives and health of these animals.

Animal societies can be complex and difficult to decipher and primate sociality is especially intricate due to the complicated and varied social structures of primates. In January 2016, Oakland Zoo introduced two juvenile males at two years of age (Milo and Kusa) to the hamadryas baboon (*Papio hamadryas*) exhibit, which consisted of one harem, with one alpha male and multiple females and juveniles. Hamadryas baboons are unique among primates because of their complex, multi-tiered social structure, consisting of 3-4 levels, the smallest and most stable being the One-Male-Unit or OMU. They are one of few primate species that exhibit this OMU, consisting of one male, multiple females, dependent offspring, and occasionally one or two follower males (Kummer, 1968; Swedell & Leigh, 2006). Upon first joining a one-male-unit, follower males generally first form relationships with the females of the group, but seldom copulate with them. These follower males may also eventually form social bonds with the OMU leader male as they go from juveniles to subadults. However, as follower males sexually mature and form harems of their own, they commonly acquire females from their previous OMU (Swedell et al., 2011). In the one-male-unit, the alpha male has sole access to all females and uses physical coercion or threats to maintain proximity to females (Swedell et al., 2011). The females in an OMU are essentially conditioned by this coercive behavior to remain within their unit and near the alpha male (Swedell, 2011). The cohesion of a one-male-unit is primarily due to the aggressive "herding" behavior exhibited by the alpha male (Swedell, 2011). The same herding and neckbiting behavior utilized to maintain females within is also used to move individual females from one OMU to the next. Therefore, males utilize aggression as the proximate mechanism for female transfer and the initiation of a new OMU (Swedell et al., 2011).

Due to the distinctive sociality of hamadryas baboons and the coercion behaviors exhibited by males, the addition of two new males to the exhibit may have had adverse effects on the social cohesion of the group. Therefore, studying the change in social structure that occurs provides information to zoo management about the group cohesion and welfare, possibly preventing high rates of aggression and social collapse. Specifically, since hamadryas baboons normally live in one-male units, utilizing SNA in this study gives a more comprehensive and quantifiable understanding of the change in group structure and cohesion with the introduction of two males.

I examined the group structure of these baboons, utilizing social network analysis, over the course of six months as the two males were integrated into the group. Much of the social network analysis research involving captive animals has been conducted concerning the effect of environmental changes and the removal of individuals on the social behaviors of primates; however, little research has examined the impacts of the addition of new individuals to an established group (Beisner et al., 2011; Beisner et al., 2015; Brent et al., 2011; Flack et al, 2005, 2006; Hansen et al., 2009, Less et al., 2010). This research will specifically examine how a social introduction in a group of hamadryas baboons may impact the social structure and welfare of these animals in a zoo setting.

Since social network analysis examines the sociality of a group based on a network, rather than a hierarchy, I was able to study multiple measures of group structure and cohesion. The social structure of these baboons was assessed on three levels: the cohesion at the group level, relationships within subgroups, and social power of individuals based on their centrality in the network. The expected results of this study were that as the new males had been in the group longer and therefore had more time to form social bonds and relationships with other group members, the group cohesion would increase and there would be less appearance of subgroups, as overall group connectedness increased. I also hypothesized that the centrality of the new males would increase with time due to more social connections as they had been in the group longer. Observing the network on these three different levels allowed me to fully grasp the change in social structure and cohesion with the addition of the two new males.

Group-level measures address the overall group structure and are especially useful for questions about the level of cohesion in the group. Group-level measures examined were group density and path length. Density is the number of observed edges of the network divided by the number of possible edges. Generally, a higher group density represents a greater social cohesion in a group (Beisner et al., 2015; McCowan et al., 2008). Therefore, I expected that over time, through interactions with individuals in the group, the new individuals would gain a social placement in the group and the overall density of the group would increase. Path length for an individual is the distance between two nodes using the shortest possible path. The average path length of a group gives a general idea of the network's overall connectedness, where a shorter average path length suggests a potential for quick transfer among group members (Sih et al., 2009). I predicted that the average path length would decrease as the males were integrated.

Subgroup measures may indicate how a network can be partitioned and the structure of groupings within the OMU can give a clear picture of the cohesion of the group (Hawe et al., 2004). The subgroup measure analyzed in this study was the clustering coefficient, which gives an indication of how individuals are connected. Clustering coefficient describes how densely or sparsely the network is clustered around a node and thus captures the level of cohesion of a network (Sueur et al., 2011; Wey et al., 2008). A high clustering coefficient indicates a high level of connectedness of individuals within the group and therefore I predicted that the clustering coefficient would increase the longer the males had been in the group due to more overall social interaction between group members. I had expected that as new individuals were added to a group and interacted more with the individuals of the group, the clustering coefficient of the group would increase.

The individual centrality measure examines the importance of individuals in the network, i.e., those individuals that are influential on the group structure and cohesion.

Individual centrality is the concept that individuals may play an important role in maintaining group stability that may not be captured when assessing dominance hierarchy or group attribute data (Hawe, Webster, & Shiell, 2004b; Sueur et al., 2011; Wey et al., 2008). There are multiple indicators that may be used to describe an individual's social influence. Four measures of centrality were examined in this study: closeness centrality, degree centrality or node degree, eigenvector centrality and betweenness centrality. All measures of centrality capture different aspects of an individual's placement and importance in the group structure (Lehmann & Ross, 2011). Closeness centrality describes how well-connected an individual is to all others in the network and reflects both direct and indirect relationships. Closeness is based on the shortest path length between focal individuals and other individuals and reflects a group member's potential influence on the entire group (Hawe et al., 2004b; Kasper & Voelkl, 2009; Scott, 1987; Sih et al., 2009; Streeter & Gillespie, 1992). Degree centrality is simply the number of edges connected to a node and indicates the number of relationships an individual has with all others in the network as a measure of relative popularity (Scott, 1987; Streeter & Gillespie, 1992; Treat, 2013). Eigenvector centrality represents the connectivity of an individual within its network according to the number and strength of connections and considering the centrality of the individuals with whom the individual is connected. This is a measure of social influence in that by connecting with more popular nodes, an individual's node prominence also rises (Kasper & Voelkl, 2009; Wey et al., 2008). Betweenness centrality is the total number of shortest paths between pairs of nodes that pass through an individual. This measure indicates how important an individual is as a point of social connection (Krause et al., 2007; Scott, 1987). All these measures of centrality capture different aspects of an individual's status in the group structure (Lehmann & Ross, 2011). Therefore, as the new males form more social relationships over time, I expected to note an increase in these centrality measures as they are integrated into the group.

The objectives of this research were to examine the change in social structure of zoo-living hamadryas baboons following a social introduction; as well as to assess the utility of a network approach to examining sociality of animals in a zoo-setting. This study provides information about the social structure and cohesion of this species in a zoo environment, in addition to the impact of animal introductions on social structure and individual and population welfare. This research could serve as a precedent for Oakland Zoo and other zoos in utilizing SNA for upholding good animal welfare and care.

Methods

Study site and animals

This study was conducted at Oakland Zoo, which is located within Knowland Park in Oakland, California. Oakland Zoo is an Association of Zoos and Aquariums-accredited institution that houses more than 660 animals. The baboon group consists of one mature male, five mature females, three juvenile males (including the two new males), four juvenile females, one infant female and one infant male. The study subjects include all adult and juvenile baboons. The infant female was included in behavioral observations after age 9 months. No changes to care or husbandry routines were made prior to or during the period of observation.

This project was non-invasive and was approved by Sonoma State's Institutional Animal Care and Use Committee (IACUC approval #2016-54).

Behavioral interaction data

Data collection

One-hundred-and-thirteen hours of behavioral interaction data were collected over the course of six months (July-December 2016) using all-occurrences event sampling. All-occurrences event sampling is a form of behavioral data collection where all dyadic social interactions (interactions occurring between two group members) are recorded as instantaneous events rather than a state, which indicates the duration of an activity (Altmann, 1974). This method of data collection has been employed in previous SNA studies to obtain a large amount of information on social interactions (Beisner et al., 2011; Beisner et al., 2015; McCowan et al., 2011, 2008). In this study, this method was utilized because it allows for a maximum amount of behavioral data collection. This is more useful in the construction of a group network, because it provides more data on dyadic interactions between individuals. Event sampling data were collected on all affiliative, aggressive, and dominant/submissive behaviors of the adults and juveniles in the group (N=14 individuals) (Altmann, 1974). Observational data collected included (1) the identity of the actor (2) the identity of the recipient, and (3) the behavior being performed (Table 1). If more than one event occurred at the same time (and the observer was unable to note both events), the event that began first was recorded. Observations were distributed across morning (10am-12pm), early afternoon (12pm-2pm), and late afternoon (2pm-4pm) time periods. Data were collected during one or more of these time periods on each observation day. All observational data were collected using HanDBase software (DDH Software, Inc.) loaded on an IPad Mini 2 (Apple Inc.)

Network construction

Social networks were constructed using Ucinet 6.624 (Borgatti, 2002) based on all behavioral interactions for each week. Behavioral observations noted the actors and recipients of all behaviors, thus all networks are directional, with edges indicating the directionality of the dyadic interaction. Due to the directionality of these networks, some measures are further broken down into in-measures and out-measures. In-measures are based on dyadic interactions during which the individual was the recipient of a behavior and out-measures are based on interactions in which the individual was the actor of the behavior. Measures that have in and out values are path length, closeness centrality, and degree centrality. For each week of data collection, three networks were constructed: an overall network based on all behavioral interactions, an affiliative network, and an agonistic network, each based on dyadic interactions of that behavioral category. Examining the network based on a sum total of behavioral interactions allows for a comprehensive understanding of how the compilation and balance of various behaviors corresponds to overall group structure. Affiliative behaviors are valuable in group-living species to build and strengthen social bonds. Agonistic behaviors are also important in maintaining group stability, as a tool of negotiation to maintain clear social structure within the group and to prevent bouts of deleterious aggression (Treat, 2013). Breaking the network up by these behavioral types gives more detailed information about the changing social relationships of the group. Networks were visualized using Netdraw, a software program within Ucinet, which creates a two-dimensional representation of the social network (Figures 1-3).

Association data

Data collection

One-hundred-and-eight hours of proximity data were collected over the course of five months (August-December 2016). Proximity between individuals was examined with affiliation scan samples conducted every ten minutes by two trained undergraduate biology research assistants (WC and KG). Subjects included all adult males and females and the two new juvenile males (N=8). During each scan, the assistant indicated whether individuals were associated or not, wherein association was defined as individuals being within five meters of one another. These scan samples provide valuable information about the associations between individuals and therefore the social cohesion of the group (Altmann, 1974; Campbell et al., 2011).

Network construction

Association networks were constructed using Ucinet 6.624 (Borgatti, 2002). However, rather than examining the network changes by week, networks were constructed for each month (August-December 2016); which gives an overall depiction of the changes in the group structure over time (Figure 4). Frequent and close social proximity between individuals may indicate social tolerance or bonds and is also important in the spread of information and the coordination of group movement. Therefore, association among individuals based on close physical proximity is a useful measure of social stability (Treat, 2013). Social networks were weighted based on frequencies of spatial proximity, but since spatial proximity is not directional, association networks were undirected. Also, spatial proximity is not based on behavioral interactions, and therefore only one network is constructed for each month. Networks were again visualized using Netdraw (Figure 4).

Statistical analyses

JMP Pro 13.1.00 (SAS Institute Inc., Cary, NC, USA) was used to carry out all statistical analyses. Changes of group and subgroup network measures over time were analyzed using linear mixed models, which is an important approach to modeling with a repeated measures design. Interaction data analyzed changes by week and therefore, week was indicated as a fixed effect and a repeated measure. Association data examined changes from month to month, thus month was indicated as a fixed effect and repeated measure. Model residuals were visually assessed for approximate normality and homoscedasticity. When necessary, response variables were log transformed. Changes of centrality over time were examined for the two new males to assess their change in social power. Also, effects of sex and age of all group members were examined to understand which groups showed changes in centrality over time. Regression analysis was utilized to examine changes in centrality measures of the new males (Milo and Kusa) by week. The effects of overall group sex and age on changes in individual centrality were assessed using linear mixed models with sex and age indicated as fixed effects. This was done to assess whether certain groups of individuals changed differently over time. If significantly different, linear regression models were run to visualize the changes with time.

Results

Group cohesion

Group Density

The group density of the overall interaction network did not change significantly with time, but visual analysis noted a decreasing trend (Figure 5a). The group density of affiliative and agonistic interaction networks did not change significantly with time.

Density of the association network did not change significantly with time, but visual assessment noted a trend showing decreasing group density over time (Figure 5b).

Path Length

In-path lengths of the overall interaction network significantly increased by week ($F_{1,299}$=32.51, p<.0001) as did out-path lengths of the same network ($F_{1,299}$=32.51, p<.0001) (Figure 6a). Affiliative interaction network in-path lengths ($F_{1,300}$=14.38, p=0.0002) and out-path lengths ($F_{1,300}$=10.24, p=0.0015) (Figure 6b) also significantly increased with time. Neither in-path lengths nor out-path lengths for the agonistic interaction network changed with time. Path-lengths of the association network significantly increased with time ($F_{1,38}$=6.05, p=0.0186) (Figure 6c).

Subgroup structure

Clustering Coefficient

The clustering coefficient of the network of all behavioral interactions significantly decreased with time ($F_{1,301}$=8.46, p=0.0039) (Figure 7a). However, neither the affiliative nor agonistic interaction networks showed a change of clustering coefficient with time. Clustering coefficient of the association network did not change significantly by week; however, visual analysis shows a decreasing trend of clustering coefficient over time (Figure 7b).

Individual Centrality

Closeness Centrality

Both Milo (y= -0.0056*Week + 0.682, r^2=0.23, $F_{1,20}$=5.95, p=0.024) and Kusa (y= -0.008*Week + 0.821, r^2= 0.26, $F_{1,20}$= 7.0082, p=0.0155) showed a significant decrease of overall interaction in-closeness over time. Both new males also showed significant decreases in overall interaction out-closeness over time (y= -0.011*Week + 0.805, r^2= 0.47, $F_{1,20}$= 17.42, p=0.0005; y= -0.013*Week + 0.882, r^2= 0.49, $F_{1,20}$= 19.86, p=0.0002) (Figures 8a and 8b).

There was a significant effect of age on the change in overall interaction in-closeness, where juveniles showed a significant decrease in overall in-closeness ($F_{1,299}$=4.11, p=0.0434) and adults did not. There was also a significant effect of age on the change in overall interaction out-closeness over time ($F_{1,299}$=7.28, p=0.0074). Juvenile overall out-closeness decreased more than adult overall out-closeness. Also, a significant effect of sex on the overall change in interaction out-closeness over time ($F_{1,299}$=9.45, p=0.0023) was noted, where male overall out-closeness decreased more over time than female overall out-closeness.

Neither new male showed a significant change in affiliative in-closeness, but both males did show a decreasing trend of affiliative in-closeness over time based on visual assessment (Figures 8c and 8d). However, both Kusa (y= -0.01*Week + 0.658, r^2= 0.23, $F_{1,20}$= 6.11, p=0.0226) and Milo (y= -0.015*Week + 0.667, r^2= 0.42, $F_{1,20}$= 14.21, p=0.0012) showed a significant decrease in affiliative out-closeness over time (Figures 8e and 8f).

There was also a significant effect of sex on the change of affiliative out-closeness over time, where all group males showed a larger decrease in affiliative out-closeness than all group females ($F_{1,299}$=8.49, p=0.0038).

Neither new male showed a significant change in agonistic in-closeness; however, Kusa showed a significant decrease in agonistic out-closeness over time (y= -0.008*Week + 0.432, r^2= 0.28, $F_{1,19}$= 7.55, p=0.0128) (Figure 8g). Milo did not show a significant change of agonistic out-closeness over time, but visual assessment did show a decreasing trend (Figure 8h).

The association network did not show a significant change of closeness for either of the new males over time, but visual analysis indicates that both males did show a decreasing trend of closeness by month (Figures 8i and 8j).

Degree Centrality

Neither Milo nor Kusa showed a significant change in overall in-degree over time, but Kusa did show a decreasing trend based on visual assessment (Figure 9a). Kusa showed a significant decrease in overall out-degree over time ($y= -0.059*Week + 3.96$, $r^2= 0.37$, $F_{1,20}=11.86$, $p=0.0026$) (Figure 9b). Milo did not show a change in overall out-degree by week, but visual assessment did show a decreasing trend (Figure 9c).

Sex had a significant effect on the change of overall out-degree, where males showed a significantly higher out-degree than females ($F_{1,302}=7.15$, $p=0.0079$).

Milo did not show a change in affiliative in-degree over time, but Kusa did show a decreasing trend based on visual analysis (Figure 9d). Kusa ($y= -1.04*Week + 25.89$, $r^2= 0.49$, $F_{1,20}=18.87$, $p=0.0003$) and Milo ($y= -0.54*Week + 16$, $r^2= 0.36$, $F_{1,20}=11.48$, $p=0.0029$) both showed a significant decrease in affiliative out-degree over time (Figure 9e and 9f).

There was an effect of sex on the change of affiliative out-degree over time, where male affiliative out-degree decreased significantly over time ($F_{1,296}=922$, $p=0.0026$), while female affiliative out-degree did not change.

Kusa did not show a significant change in agonistic in-degree over time, but Milo did show a visible decline (Figure 9g). Milo did not show a significant change in agonistic out-degree over time, while Kusa showed a significant decrease ($y= -0.32*Week + 9.94$, $r^2= 0.20$, $F_{1,19}=4.86$, $p=0.040$) (Figure 9h). Neither new male showed a significant change in degree centrality over time based on associations; however, both males did show a decreasing trend (Figures 9i and 9j).

Eigenvector Centrality

Both Kusa ($y= -0.013*Week + 0.482$, $r^2= 0.45$, $F_{1,20}= 16.16$, $p=0.0007$) and Milo ($y= -0.008*Week + 0.353$, $r^2= 0.35$, $F_{1,20}= 10.65$, $p=0.0039$) showed a significant decrease in overall eigenvector centrality over time (Figures 10a and 10b).

There was an effect of sex on the change in overall eigenvector centrality, where males showed a significant decrease in centrality while females showed no change ($F_{1,299}=8.76$, $p=0.0033$).

Both males showed a significant decrease of affiliative eigenvector centrality over time (Kusa: $y= -0.016*Week + 0.393$, $r^2= 0.60$, $F_{1,20}= 30.21$, $p<0.0001$, Figure 10c; Milo: $y= -0.008*Week + 0.22$, $r^2= 0.23$, $F_{1,20}= 5.83$, $p=0.0255$, Figure 10d).

There was an effect of sex on the change of affiliative eigenvector centrality over time, where males showed a significant decrease in affiliative eigenvector centrality, while females showed no significant change ($F_{1,297}=5.08$, $p=0.0249$).

Neither male showed a significant change of agonistic eigenvector centrality over time. Milo and Kusa both showed decreasing trends in eigenvector centrality over time for the association network based on visual analysis (Figures 10e and 10f).

Betweenness Centrality

Neither Kusa nor Milo showed a significant change in betweenness over time, but both males did show a visual decreasing trend of betweenness over time (Figures 11a and 11b).

There was an effect of sex on the change of overall betweenness over time, where females showed a significant increase in betweenness while males showed no significant change ($F_{1,296}$=18.33, p<0.0001). Further analysis indicated that two adult females showed significant increases in overall betweenness over time (y= 0.07*Week + 0.60, r^2= 0.29, $F_{1,20}$= 8.02, p=0.0103) (y= 0.10*Week + 0.91, r^2= 0.45, $F_{1,20}$= 16.67, p=0.0006). There was also an effect of age on the change of overall betweenness over time, where adults showed a larger increase in overall betweenness than juveniles ($F_{1,295}$=5.83, p=0.0164).

Again, neither new male showed a significant change in affiliative betweenness, but visual assessment did show decreasing trends for both males (Figures 11c and 11d).

There was an effect of sex on the change of affiliative betweenness over time, where females showed a significant increase in betweenness while males showed no significant change ($F_{1,299}$=10.33, p=0.0085). Further analysis also indicated that three females showed significant increases in affiliative betweenness with time (y= 0.59*Week + 1.36, r^2= 0.18, $F_{1,20}$= 4.51, p=0.0464; y= 0.78*Week + 0.49, r^2= 0.25, $F_{1,20}$= 6.56, p=0.0186; y= 1.19*Week + 11.96, r^2= 0.30, $F_{1,20}$= 8.58, p=0.0083). There was also a significant effect of age on the change of affiliative betweenness over time, where adults showed a significant increase in betweenness while juveniles showed no significant change ($F_{1,298}$=6.42, p=0.0118).

Milo did not show a significant change in agonistic betweenness over time, but visual analysis did indicate that Kusa showed a decreasing trend (Figure 11e). The association network showed no significant change in betweenness over time for either of the new males.

Discussion

Comprehensive knowledge of social groups within zoos allows for greater understanding of the impacts of environment, social interactions, and changes to habitats on the sociality of zoo-housed species. Through the use of social network analysis, this study found that the introduction and integration of two juvenile males into an existing hamadryas baboon one-male unit had an effect on social structure and cohesion, but not in the way I had anticipated. The three levels of analysis—group cohesion, subgroup structure, and individual centrality—revealed that the addition of the two new males may have decreased, rather than increased, overall group connectedness and that the new males did not increase their centrality relative to the group, as was expected.

Group-level measures examined in this study were group density and path length. Density is the number of observed edges of the network divided by the number of possible edges and generally, a higher group density represents a greater social cohesion in a group (Beisner et al., 2015; McCowan et al., 2008). The group density based on all social interactions did not change over time, but did show a trend of decreasing group density by week (Figure 5a). The association network also indicated a decreasing trend in group density by week (Figure 5b). This trend contradicts the prediction that overall group density would increase with time and indicates that the group is actually becoming less cohesive and more spread out. The average path length of a group gives a general idea of the network's overall connectedness, where a shorter average path length suggests a higher level of connectedness between group members (Sih et al., 2009). The expected decrease in path lengths was not observed: overall interaction in and out-path lengths both significantly increased with time (Figure 6a). Affiliative interaction in and out-path lengths also increased with time (Figure 6b), while agonistic interaction path lengths did not change. This indicates that there is less overall and affiliative interaction among all individuals of the group and the group is becoming less connected overall with time. Although this decrease in path length may be indicative of a decreasing social cohesion, the lack of change in agonistic density and path length suggests that there has been no increase in frequency of agonistic or aggressive interactions. Since such interactions are important in maintaining group stability, this lack of change may in fact indicate that the group is remaining stable, despite the decrease in other social interactions.

The subgroup measure analyzed was the clustering coefficient, which describes how densely or sparsely the network is clustered around a node and thus captures the level of cohesion of a network (Sueur et al., 2011; Wey et al., 2008). I had expected that as new individuals were added to a group and interacted more with the individuals of the group, the clustering coefficient of the group would increase. A high clustering coefficient indicates a high level of connectedness of individuals within the group. One would expect the clustering coefficient to increase the longer the males have been in the group because dyadic interactions between the males and other group members will increase, resulting in more overall social interaction. However, the clustering coefficient of the group based on overall interaction decreased significantly the longer the juveniles had been in the group (Figure 7a). This indicates that the group is becoming less clustered and well-connected overall. The affiliative and agonistic interaction networks did not show a change in clustering coefficient with time; however, post-hoc visual analysis of the dataset indicated that the clustering coefficient for the agonistic network was larger than that for the affiliative network. Therefore, although the *changes* for the affiliation and agonistic networks were not significant, there may have been a difference in how the group was structured for behaviors noted as agonistic versus those noted as affiliative. A higher overall clustering coefficient for agonism may be an indication of group stability because agonistic interaction is more spread out among group members and there is less directed agonistic behavior or agonism occurring only for certain members of the group. Agonistic behaviors are important in primate social groups because they establish and maintain a clear social status for group members; which allows the group to maintain cohesive (Beisner et al., 2015). Therefore, the lack of change in agonism with time and the overall higher clustering coefficient for the agonistic network may indicate that, although the overall clustering coefficient is decreasing and the group is becoming more spread out, there is less directed aggression and, therefore, the group is cohesive. The differences between the agonistic and affiliative network clustering coefficients and their interpretations are further evidence of how assessing a network through different behavioral interactions is beneficial in fully comprehending the structure and cohesion of the group.

The four measures of individual centrality examined in this study included closeness centrality, degree centrality, eigenvector centrality, and betweenness centrality. These measures examine the importance of individuals in the network and capture different aspects of an individual's placement and importance in the group structure

(Lehmann & Ross, 2011). Closeness centrality describes how well-connected an individual is to all others in the network and reflects both direct and indirect relationships (Hawe et al., 2004b; Kasper & Voelkl, 2009; Scott, 1987; Sih et al., 2009; Streeter & Gillespie, 1992). Both males' decreases for in and out-closeness of the overall interaction network (Figures 8a and 8b) indicate a decrease in their direct individual centrality and influence on the overall group. The decreasing trends of association closeness over time for both males (Figures 8i and 8j) also support this interpretation, showing a decreasing centrality for the two new males. Affiliative interaction closeness also decreased for both males over time, with the change in affiliative out-closeness being significant (Figures 8c-8f).

The analyses testing for the effect of sex on these changes indicate that the decreases in overall and affiliative interaction in and out-closeness were much larger for males than females, which indicate that males showed a more dramatic change over time. Since the decreases in overall and affiliative in- and out-closeness for males were much larger than those for females, this may suggest that males of the group were more impacted by the introduction than group females. However, since Milo and Kusa comprise 50% of the males in the group and were the only group members to show a significant change in affiliative out-closeness, these results may simply be the changes accrued by the two new males.

There was also a significant effect of age on the changes in overall in and out-closeness, which indicate that juvenile closeness decreased more than adult closeness. Therefore, the addition of the two males may have had a larger impact on the centrality of the juveniles of the group than that of the adults.

Milo did not show any significant changes in agonistic closeness, while Kusa did have a decrease in agonistic-out closeness with time (Figure 8g). I had expected that over time the males would interact more with all members of the group and that their overall centrality would thus increase; however, this was not observed. The influence of these two males overall decreased with time, and the decrease in affiliative closeness indicates that the amount of affiliation interactions between the males and other members of the group decreased. However, the lack of change in agonistic closeness for Milo indicates that there was no change in the amount of aggressive interactions involved between Milo and other group members. Kusa's decrease in agonistic out-closeness indicates that the amount of aggressive interactions Kusa directed towards others decreased and therefore that his influence based on agonistic behaviors decreased. Overall, these data suggest that the direct influence and centrality of the new males decreased and that the new males are actually becoming more peripheral members of the group, rather than more central as expected. However, the lack of changes in agonistic closeness, and Kusa's decrease in agonistic out-closeness suggest that, despite the males' decreases in centrality, there was no spike in aggressive interactions and therefore the group is remaining stable.

Degree centrality is the number of edges connected to a node and therefore describes the amount of social interactions of an individual and the extent to which a network is centered around an individual (Scott, 1987; Streeter & Gillespie, 1992; Treat, 2013). Overall interaction and affiliative interaction in-degree centrality did not change significantly for either of the new males, with the exception of Kusa showing decreasing trends. However, there were decreases in overall and affiliative interaction out-degree centrality for both males. This indicates that for all behaviors and for those coded as affiliative, there was no significant change in the amount of interaction directed at the two new males, but that Kusa and Milo decreased the amount which they directed affiliative behaviors at other group members. Kusa's significant decrease in agonistic interaction out-degree also indicates that he directed less agonistic behavior toward other group members over time. In addition, the association network showed a decreasing trend in degree centrality for both males (Figures 9i and 9j), which supports the findings that the two new males decreased their overall interactions with group members.

Eigenvector centrality takes into account neighbors when calculating an individual's centrality and describes a group member's indirect social power, based on the centrality of the individuals that that member is connected to. Therefore, the decreases in overall and affiliative interaction eigenvector centrality shown by the new males (10a-10d) indicate that the new males are becoming less connected with highly central individuals. Eigenvector centrality based on association between individuals also showed a decreasing trend (Figures 10e and 10f), corroborating these findings. This is also apparent based on social proximity, as the association network displayed a decreasing trend in eigenvector centrality for the new males. The effects of sex on overall and affiliative interaction eigenvector centrality further illustrate that the two males' eigenvector centrality changed differently from the other group members, as they (in addition to one other juvenile male) were the only individuals to show a change in eigenvector centrality.

Betweenness centrality indicates how important an individual is as a point of social connection based on the total number of shortest paths between pairs of nodes that pass through an individual (Krause et al., 2007; Scott, 1987). The males did not show any significant changes in interaction betweenness over time, but there were decreasing trends for overall, affiliative, and agonistic betweenness (Figures 11a-11e). Betweenness describes an individual's intermediary role in the network as a point of social connection. I had expected that as the new males were integrated into the group, their betweenness centrality would increase; however, the opposite was observed. Rather than the males becoming more locally central, their social power in terms of connectedness decreased. However, while the betweenness for group males did not change with time, the effects of sex and age indicate that females and adults had significant increases in betweenness. Although the integration of the new males did not affect the betweenness of the new males themselves, the betweenness of other group members did change. For instance, post-hoc analysis indicated that two adult females showed significant increases in overall and affiliative betweenness and another female also showed a significant increase in affiliative betweenness.

The results suggest that the new males are actually interacting less with all members of the group and are therefore decreasing their overall centrality. In turn, the group as a whole was becoming less connected and more spread out during the study period. I had originally hypothesized that the new males would increase their interactions with the group as a whole; however, the results seem to suggest that rather than increasing overall interactions, the males may be forming relationships with only certain individuals of the group. Free-ranging one-male-units of hamadryas baboons generally consist of one "leader" male, multiple females and their offspring and sometimes one or more follower males (Kummer, 1968; Swedell, 2011). These follower males generally first form relationships with the females of the group, but seldom copulate with them

(Swedell et al., 2011). They may also eventually form social bonds with the OMU leader male (Swedell et al., 2011). It is possible that the new males have formed social bonds with specific females of the group and have not yet formed a relationship with most other group members or with the leader male. Therefore, rather than the group becoming more connected and cohesive with time, the males have become more peripheral to the group and therefore the social structure has become less connected, which is indicated in the decreases in group density and path length. The decrease in clustering coefficient indicates that the group is becoming less egocentric, which also may also suggest that the group is becoming more spread out.

The decreases of the new males in individual centrality perhaps provide the best evidence to suggest that the males are interacting less with the group as a whole and are instead becoming more peripheral. The decreases of the males in closeness and degree indicate that the direct centrality of Milo and Kusa has lessened and that these two males are interacting less with the other group members overall. Eigenvector centrality also decreased for the new males, suggesting that the neighborhood of the males is getting smaller. Finally, the betweenness of the males decreased; however, the betweenness of other individuals showed significant increases. This may suggest that since the males are becoming more peripheral to the group, other group members are serving as connecting points between those males and the rest of the group and therefore the betweenness of those individuals increased.

Although the overall group connectedness and the new males' centrality both decreased, this may not necessarily indicate that the group is unstable. Generally, high group density and low average path length indicate a more cohesive group, but because hamadryas baboon social structure is different than most other primates, this generalization may not be true of this particular group of primates. In another social network analysis study, Beisner et al. (2015) described how among wild primate groups, reduced group stability or cohesion may lead to group fission; however, group fission may not be possible for captive primates and instability may result in outbreaks of serious aggression. In my study, although the group has become less connected according to the results of group density and path length, there were few significant changes seen in the agonistic network, which indicates that there has not been an increase in aggression and therefore that the group is not in danger of collapse. In addition, visual analysis of the agonistic networks and the edges of Kusa and Milo seem to indicate that there are less agonistic interactions between the two new males and other members of the group and that overall agonistic interaction are decreasing and becoming more spread out rather than showing a large amount of directed aggression towards specific individuals (Figure 3). Therefore, the group is becoming less well-connected, but since the levels of agonistic interactions appears to be constant and evenly dispersed among group members, the group seems to be stable and not in danger of social collapse. However, knowing that the group is less well-connected is important for zoo-staff in making further decisions that may affect the social structure of the baboon group. In addition, management may choose to conduct further analysis of the group sociality to detect group instability and prevent social collapse in the future. Hamadryas societies are driven by leader males and male takeover of females from one OMU to another. This takeover usually occurs when subadult males (age 2-7 years) acquire juvenile females to create new "initial units" (Kummer, 1968; Swedell et al., 2011). As the new juvenile males mature, it may be interesting and important to examine how the group structure changes and whether those males begin to form units of their own.

This study may have been improved if behavioral data could have been collected before and after the addition of the new males, rather than only after the introduction, to gain a better understanding of the change before and after an introduction of new individuals to a group. The high levels of interactions among group members, and especially between Milo and Kusa and the other individuals, during the first few months of data collection may be simply due to the novelty of the new males. The decreases in such measures as density and degree centrality may be more of a return to normalcy for the network as the novelty of the introduction decreases. Therefore, a more longitudinal study may have been more useful in understanding the changes in the network.

I had also noted through simple visual analysis of the data that some SNA measures had different values depending on the behavioral type. For instance, degree for affiliative behaviors for most individuals was much higher than that for agonistic behaviors. Therefore, although the change over time may not have been significant, the networks overall still may have been differentiated depending on the type of behavior coded for. Further research might examine the effect of behavior on different SNA measures. In addition, since this was a study of progression over time, there was no baseline to compare the networks to, which may have been useful in understanding the changes in group structure. Other factors may have contributed to these findings, such as weather or number of interactions per week, and these factors may have been better accounted for with baseline data. This was a relatively short-term study and was only able to provide a snapshot of the overall group structure. A longitudinal study of this group of baboons may have provided a better depiction of how the group structure changes, especially as the new juvenile males mature.

Conclusion

Animal societies can be complex and difficult to decipher; scientists are constantly working to understand the basis for many behaviors and social structures. Primate behavior and sociality are especially intricate due to their complicated and varied social structures as well as their high level of intelligence. Therefore, the ability to comprehend aspects of social cohesion through the use of a new methodology like SNA may be important as another tool that can be used in combination with other aspects of animal behavior research to understand the sociality of intelligent organisms.

This study was developed to serve as a model for how Oakland Zoo and others may be able to use social network analysis to examine the behavior of their animals. Providing zoo staff with another tool and method for quantifying the social lives of their animals will give management a better understanding of the social and behavioral impacts of their decisions. Data from network comparisons and quantitative measures is useful for care staff in understanding the stability and therefore the welfare of their animals. The results of this study indicate that the integration of the new males into the group resulted in a decrease in overall group connectedness and in individual centrality for the new males. Understanding the current state of the hamadryas group structure will better enable zoo management to understand signs of group instability as the juvenile males mature and attempt to form their own OMUs so that they can prevent social collapse and deleterious aggression and, in turn, better the welfare of their animals.

The focus of this study was to better understand the nature of social relationships in zoos and the factors that may affect them. This research has had direct impacts on the species and staff of Oakland Zoo, by providing a framework for employing research on animal social networks. However, this study only touched the surface; social network analysis may have implications for a variety of zoo-living species and zoo management decisions. Utilizing a network approach and being able to quantify social cohesion will allow for a better understanding of social structure and cohesion of many species in captivity and upholding good animal welfare and care of these species.

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Tables

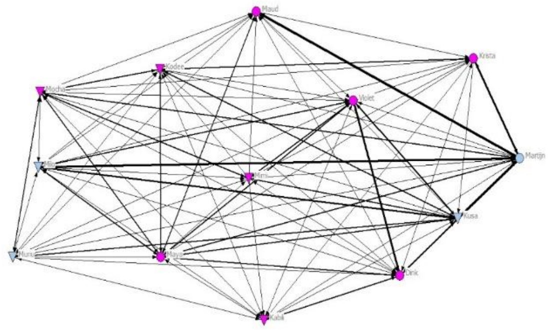
Table 1. Ethogram describing behaviors observed.

Type of Interaction	Behavior	Description
Affiliative	Approach	Individual walks towards another individual
	Displacement	Displacement of one individual by another
	Genital touch	A male touches genitals or genital area of another male
	Groom	Individual picks debris out of another individual's fur
	Groom present	Individual presents body part to another individual to be groomed
	Lip smack	Audible, rapid opening and closing of the lips, the tongue touching the lips
	Notifying present	A male will present his anogenital region to another male while passing him, often accompanied with lip-smacking
	Reach out	Individual reaches out to raise arms towards another individual
	Touch	Bodily contact with another in a non-sexual or aggressive context
Agonistic	Aggressive hold	Physical attachment to another individual in a potentially rough or harmful manner
	Bite	Individual uses teeth to make contact with another individual
	Brow raise	Individual stares at and raises eyebrows at another individual
	Chase	Individual runs or trots after an avoiding animal
	Ground beat	Individual stares at another individual and slaps palms against the ground
	Head bob	Individual moves head up and down quickly, often accompanied with brow-raising or ground beating
	Interposition	Individual places themselves between two or more other individuals in such a way as to disrupt an already occurring behavior between two other individuals
	Lunge	An individual displays a rapid aggressive movement towards another individual
	Neck bite	Individual pinches another individual's neck between incisors usually from behind
	Protected threat	A female does aggressive behavior whilst hiding or running to male.
Dominance	Crouching	Manipulation or lowering of one's body to cover another individual's body (usually male to female)
	Mount	Individual approaches another individual from behind, places hands on hips of the other and stands bipedal on legs, often touching genitals to anal area of the individual being mounted
	Possession grip	A male holds a female from behind by her sides or back

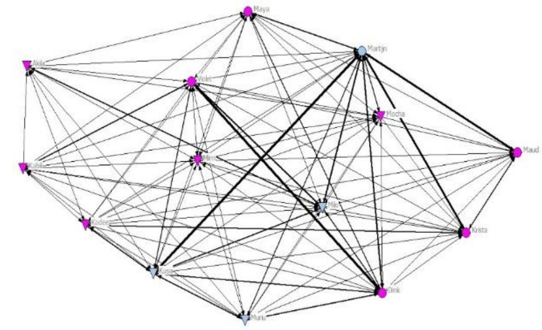
Submissive	Avoid	Individual actively keeps distance from another individual
	Fear grin	Individual bares teeth and pulls back corners of mouth into open mouthed grin
	Submissive present	With knees bent, individual will turn anogenital region to threatening individual
Not Visible	Behavior not visible	Animal's body is turned so that behavior cannot be noted
	Out of sight	Animal is not visible
Other	Other behavior	Individual displays other behavior not specified in ethogram

Figures

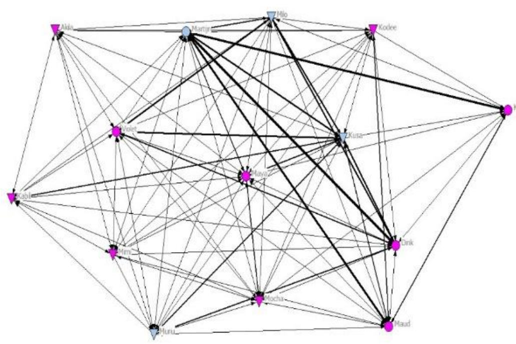
Figure 1: Networks for each month based on all behavioral interactions, with attribute data noted with node symbol and color.



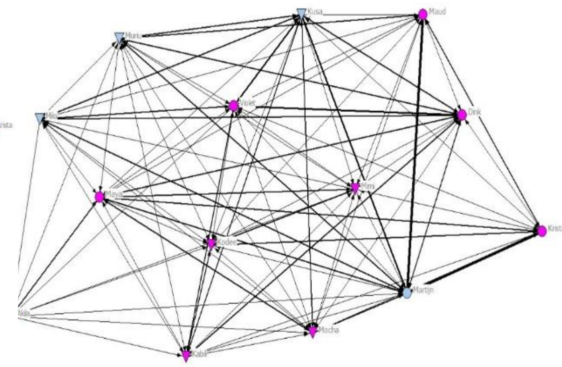
July Overall Network



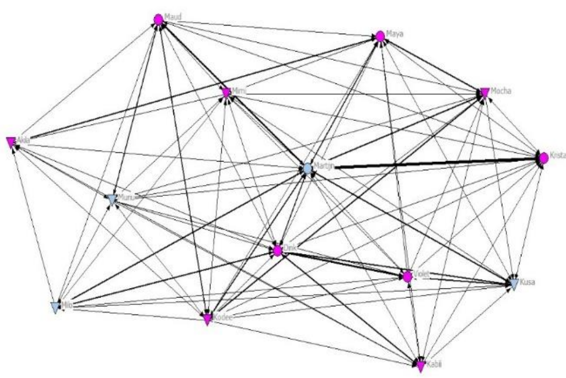
August Overall Network



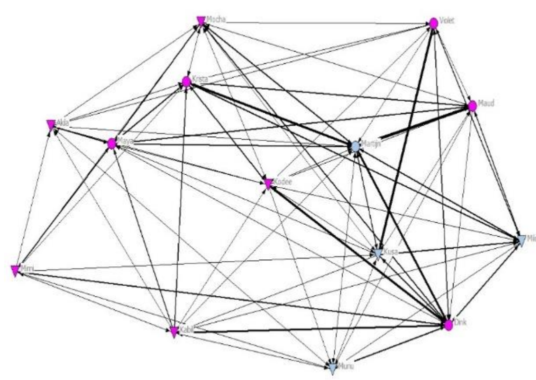
September Overall Network



October Overall Network



November Overall Network



December Overall Network

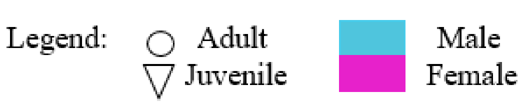


Figure 1a: Network for July based on all behavioral interactions, with attribute data noted with node symbol and color.

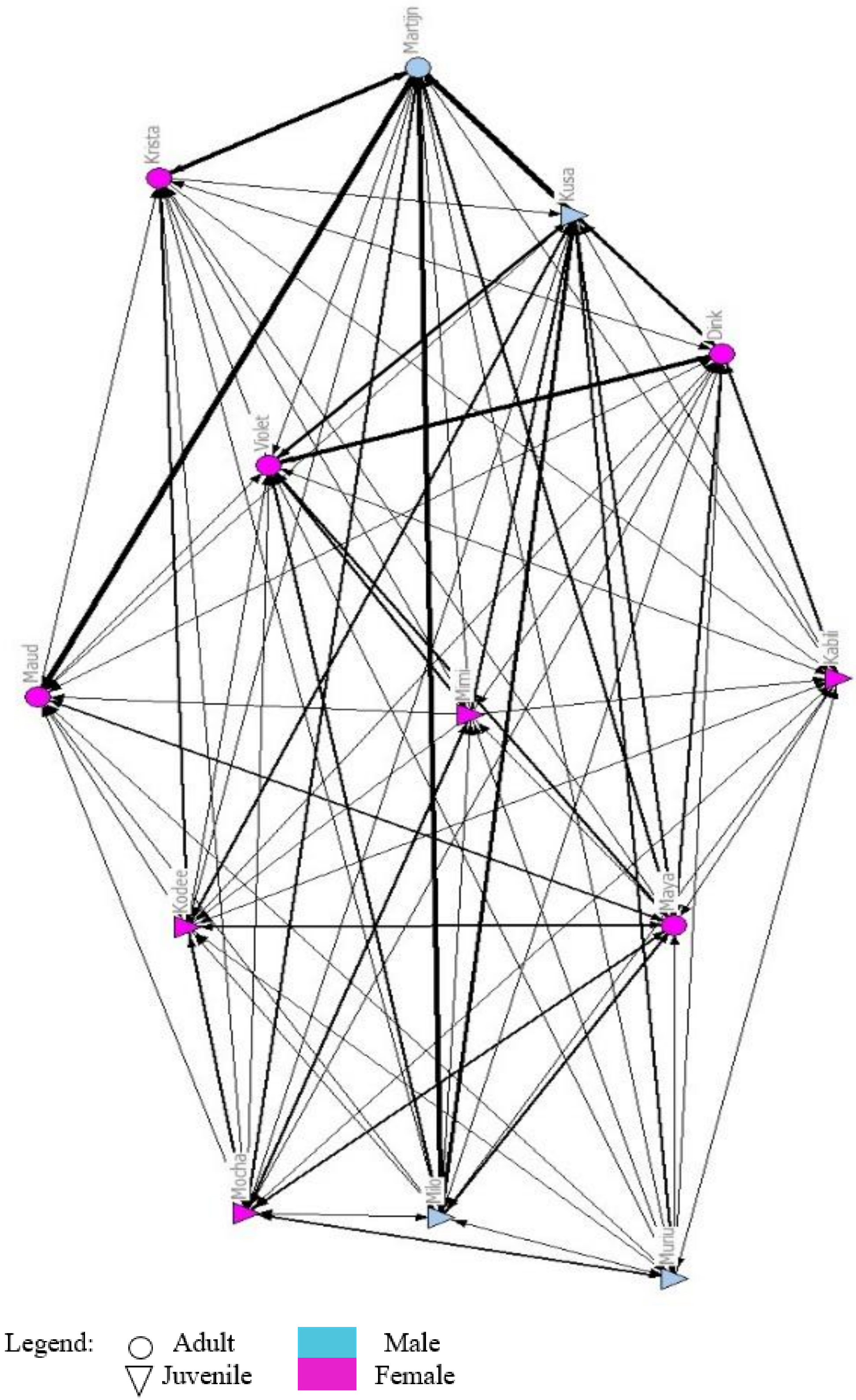


Figure 1b: Network for August based on all behavioral interactions, with attribute data noted with node symbol and color.

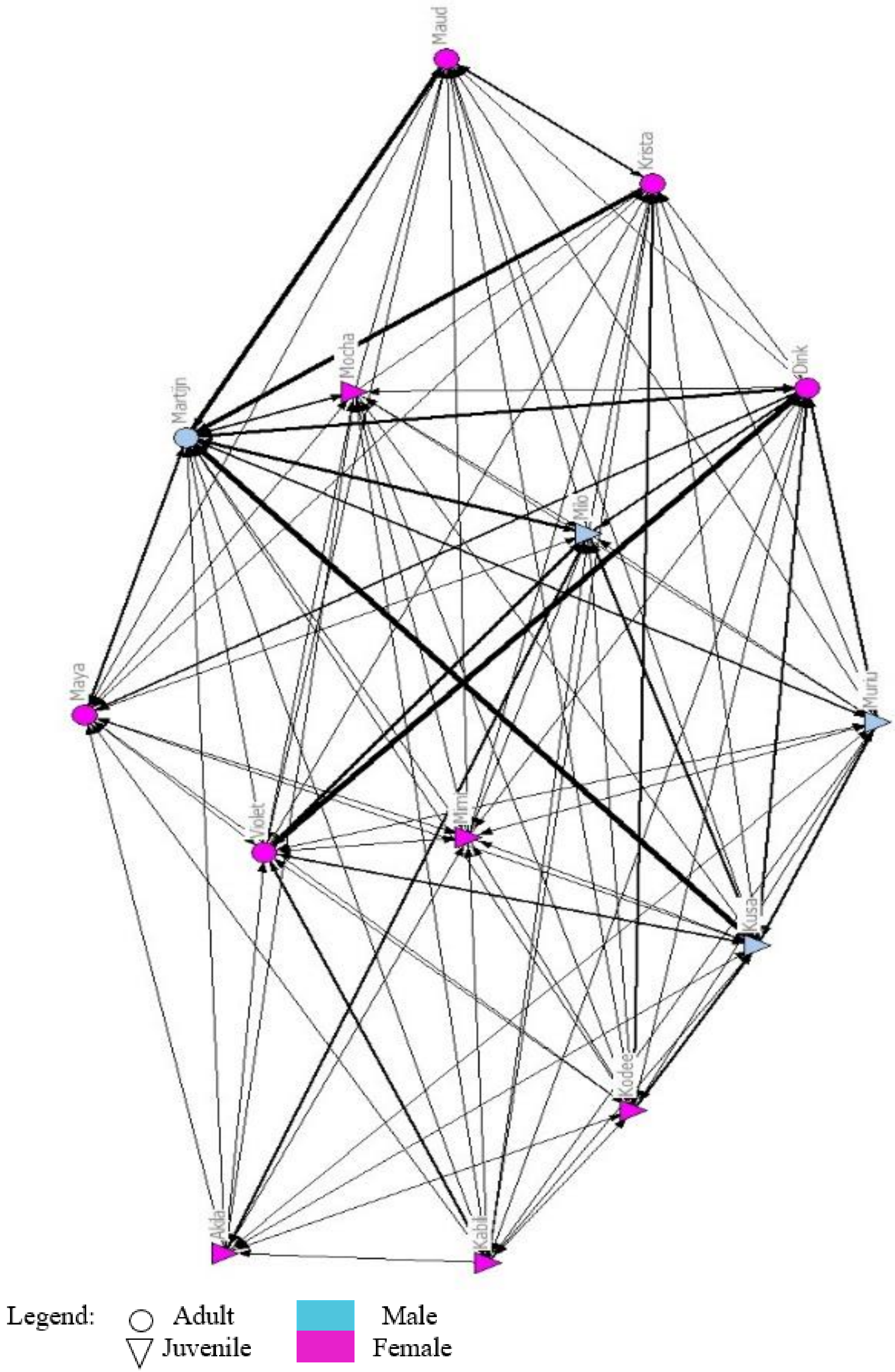


Figure 1c: Network for September based on all behavioral interactions, with attribute data noted with node symbol and color.

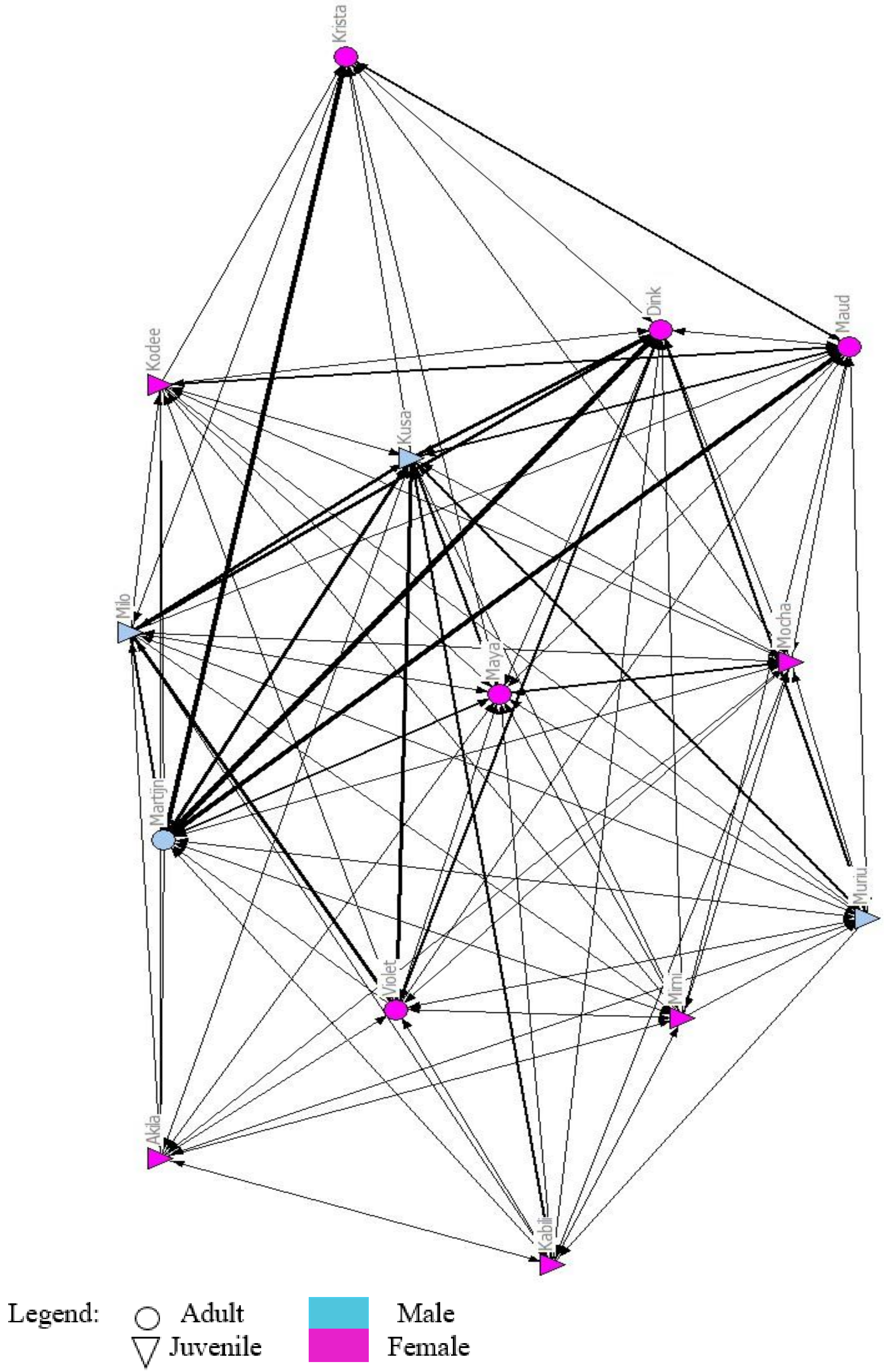


Figure 1d: Network for October based on all behavioral interactions, with attribute data noted with node symbol and color.

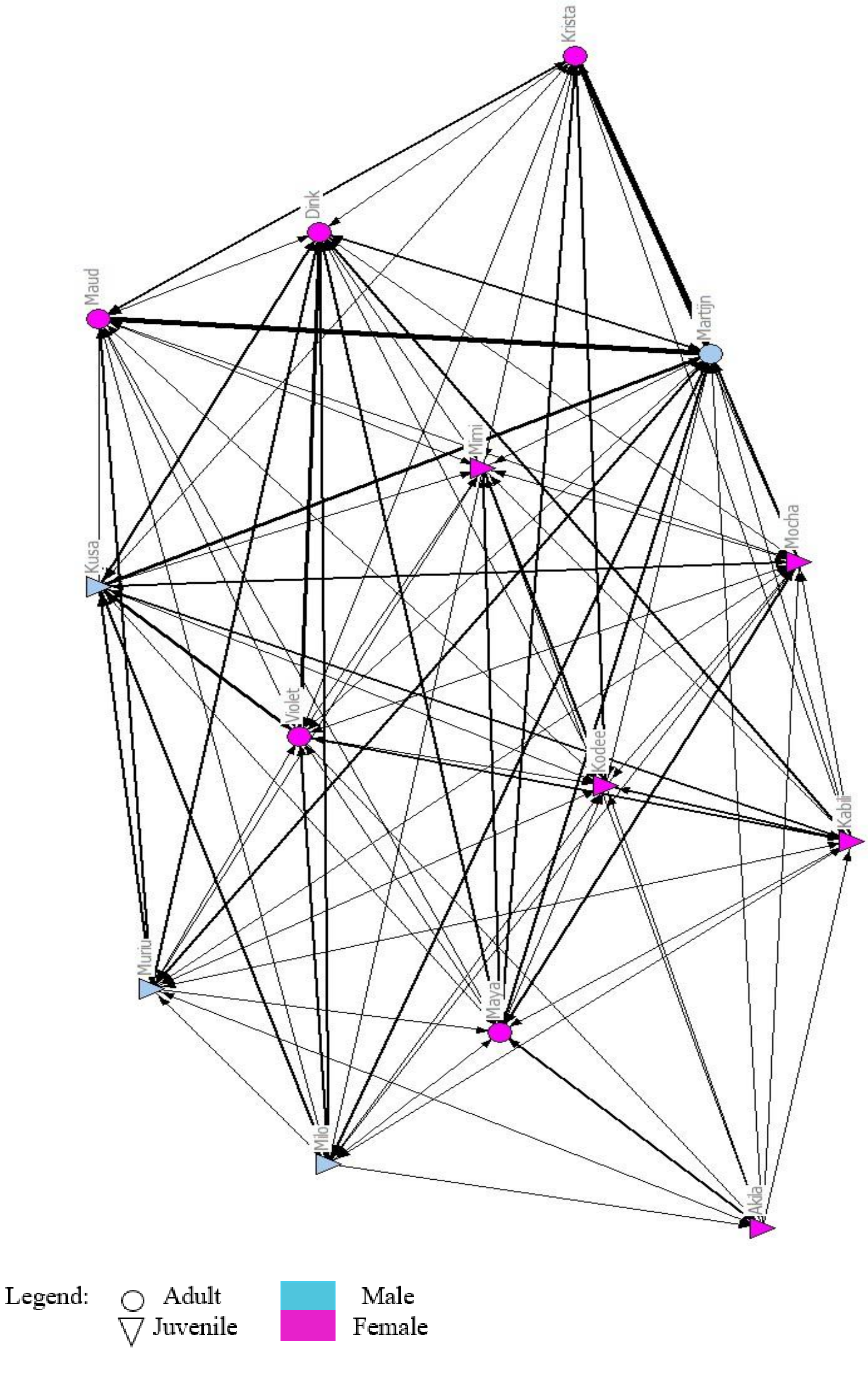


Figure 1e: Network for November based on all behavioral interactions, with attribute data noted with node symbol and color.

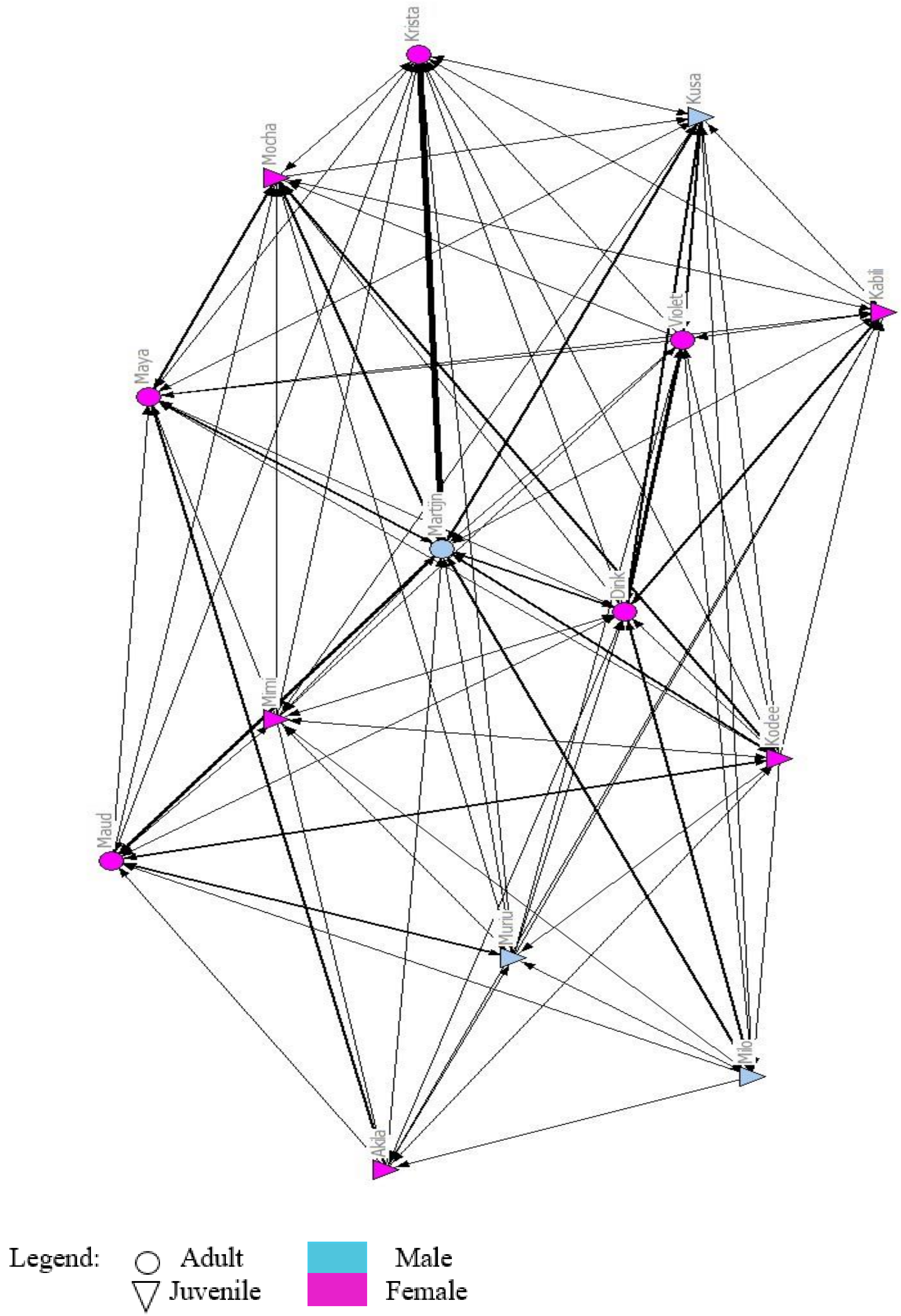


Figure 1f: Network for December based on all behavioral interactions, with attribute data noted with node symbol and color.

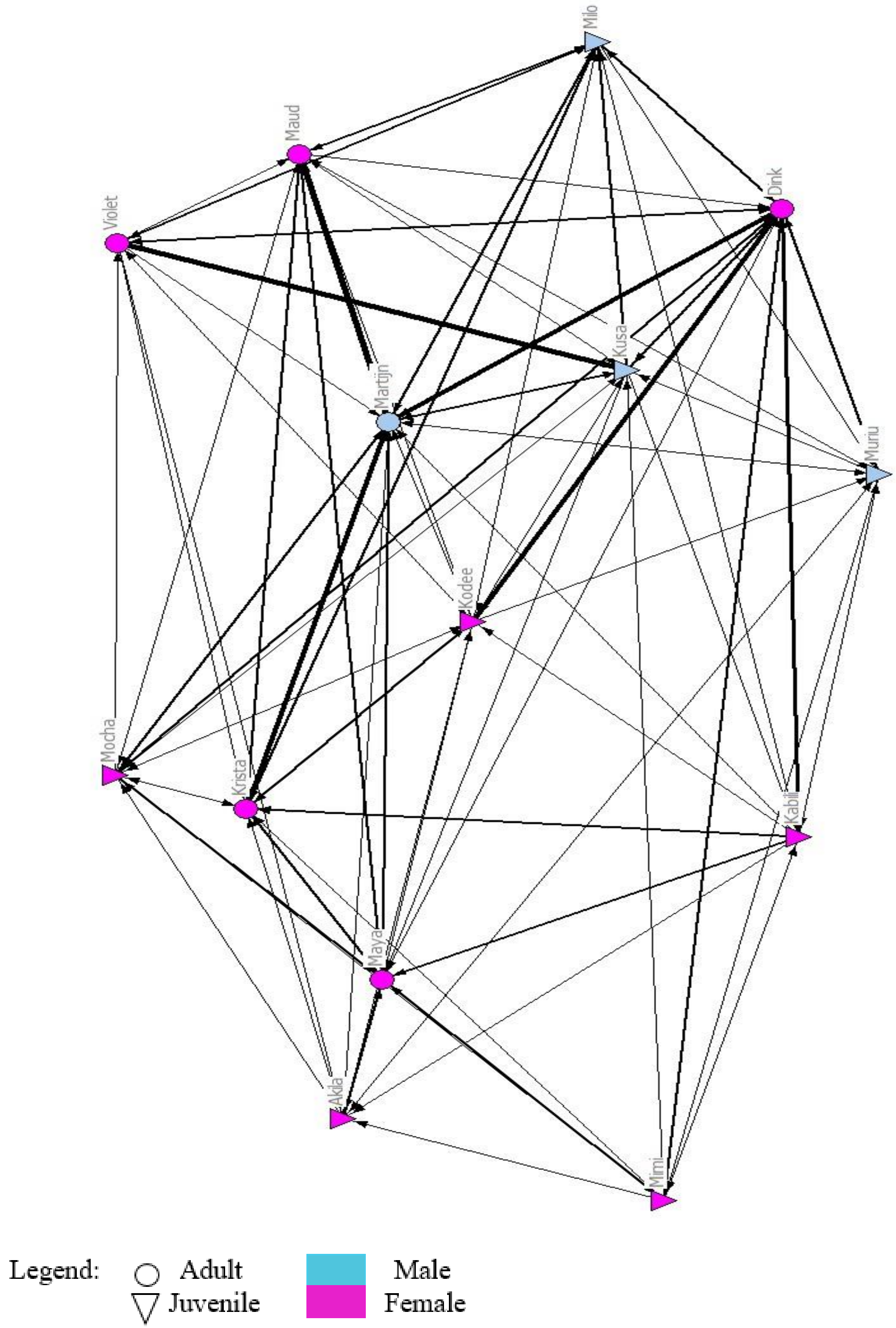
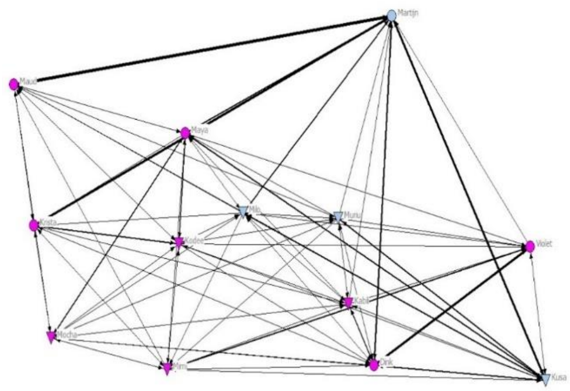
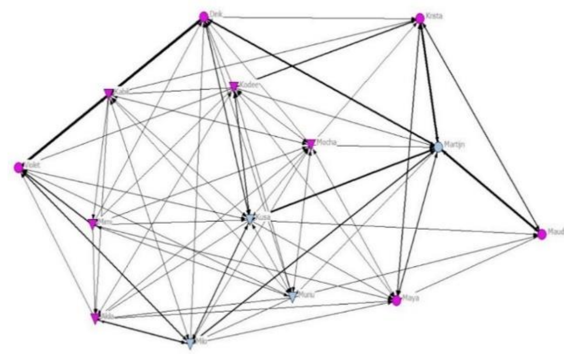


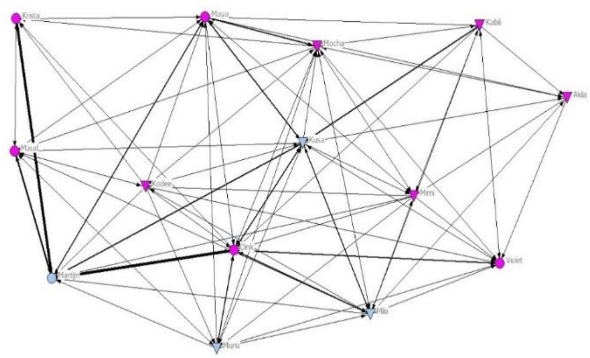
Figure 2: Networks for each month based on affiliative behaviors, with attribute data noted with node symbol and color.



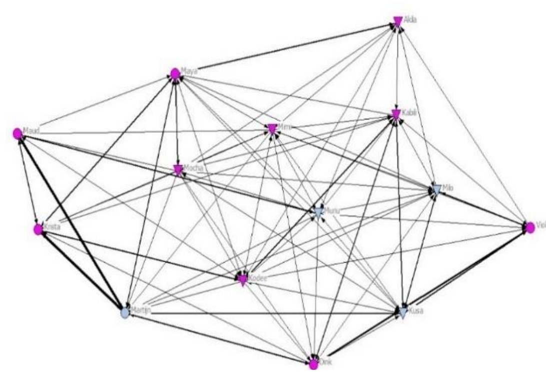
July Affiliative Network



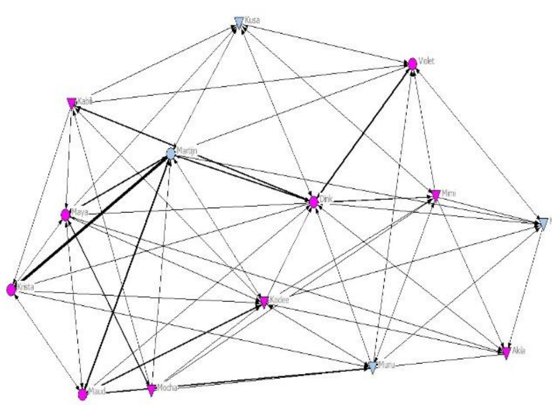
August Affiliative Network



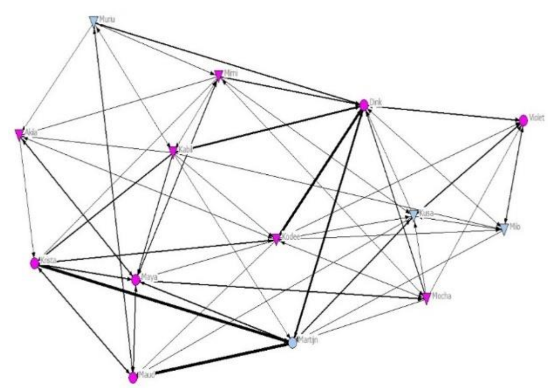
September Affiliative Network



October Affiliative Network



November Affiliative Network



December Affiliative Network

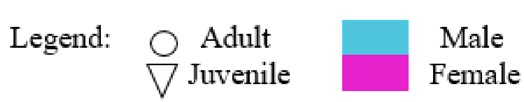


Figure 2a: Network for July based on all affiliative interactions, with attribute data noted with node symbol and color.

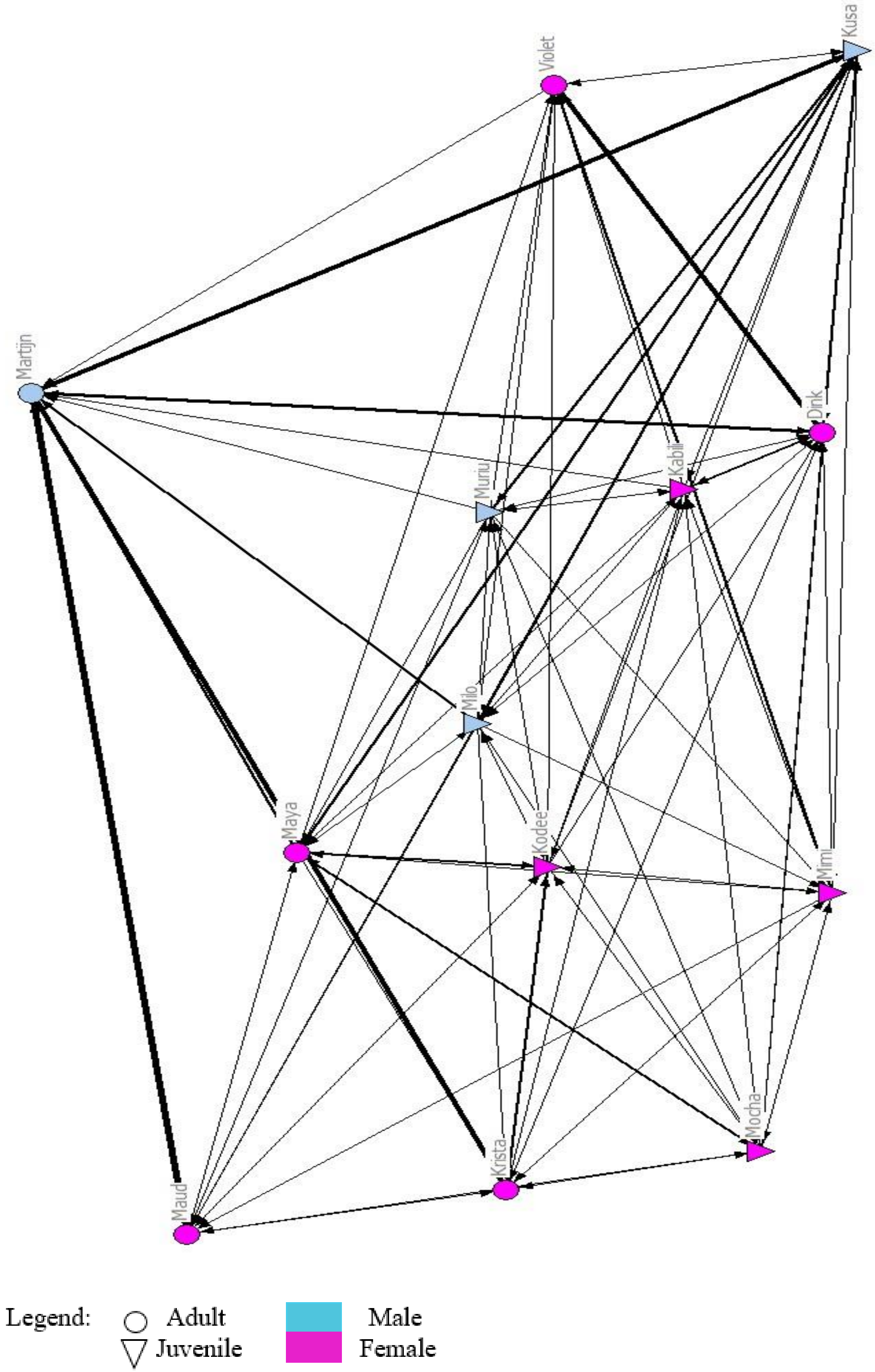


Figure 2b: Network for August based on all affiliative interactions, with attribute data noted with node symbol and color.

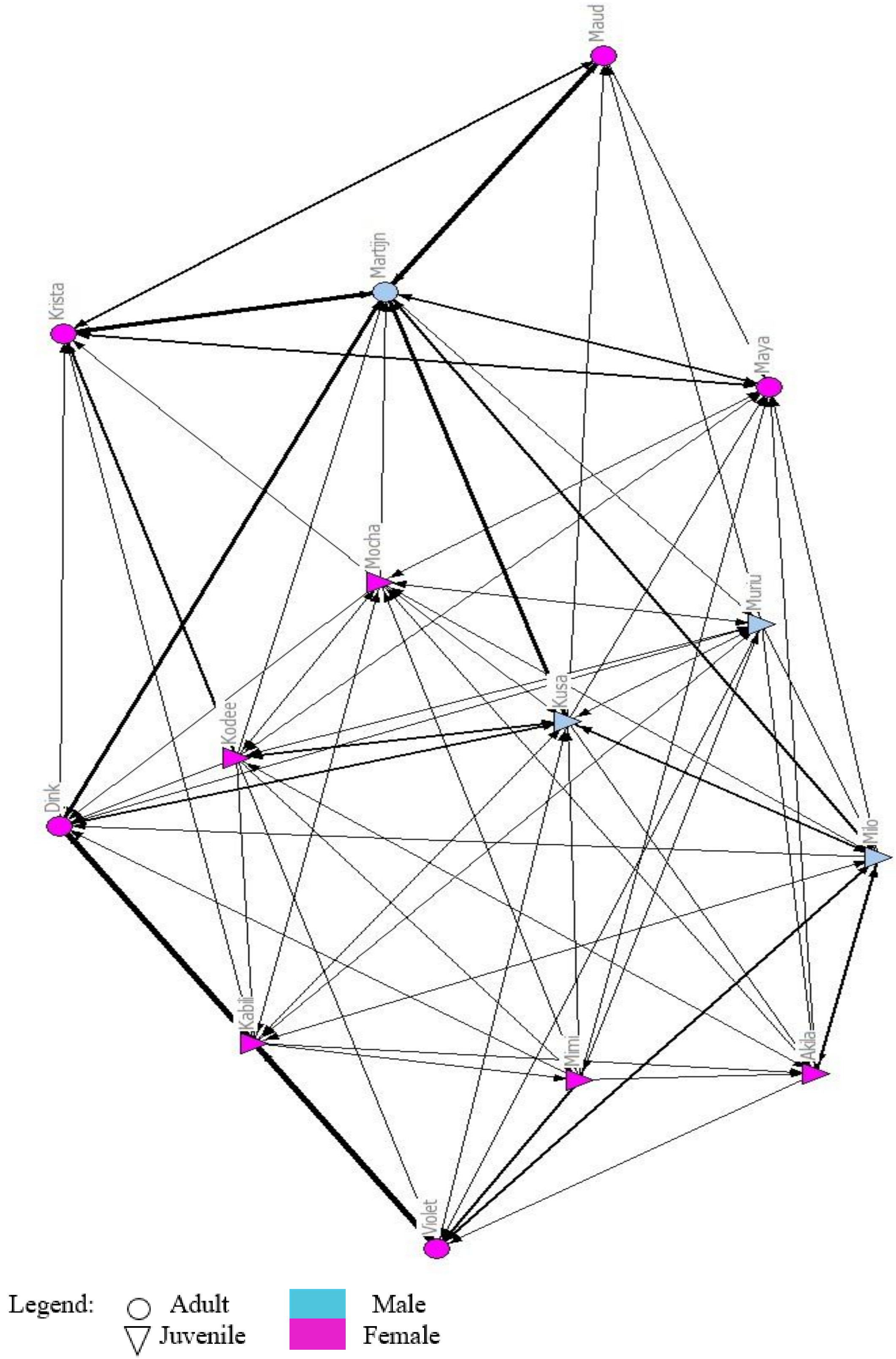


Figure 2c: Network for September based on all affiliative interactions, with attribute data noted with node symbol and color.

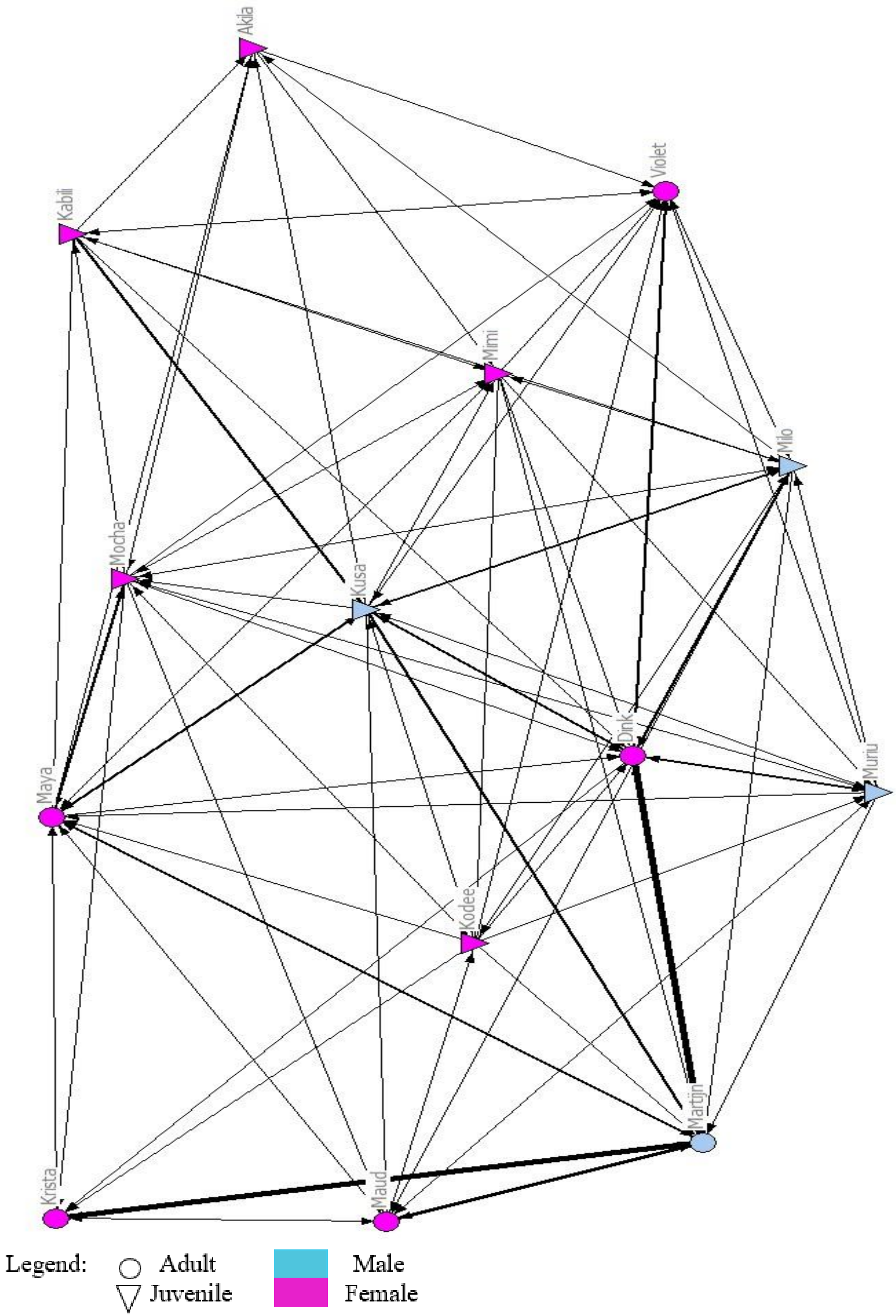


Figure 2d: Network for October based on all affiliative interactions, with attribute data noted with node symbol and color.

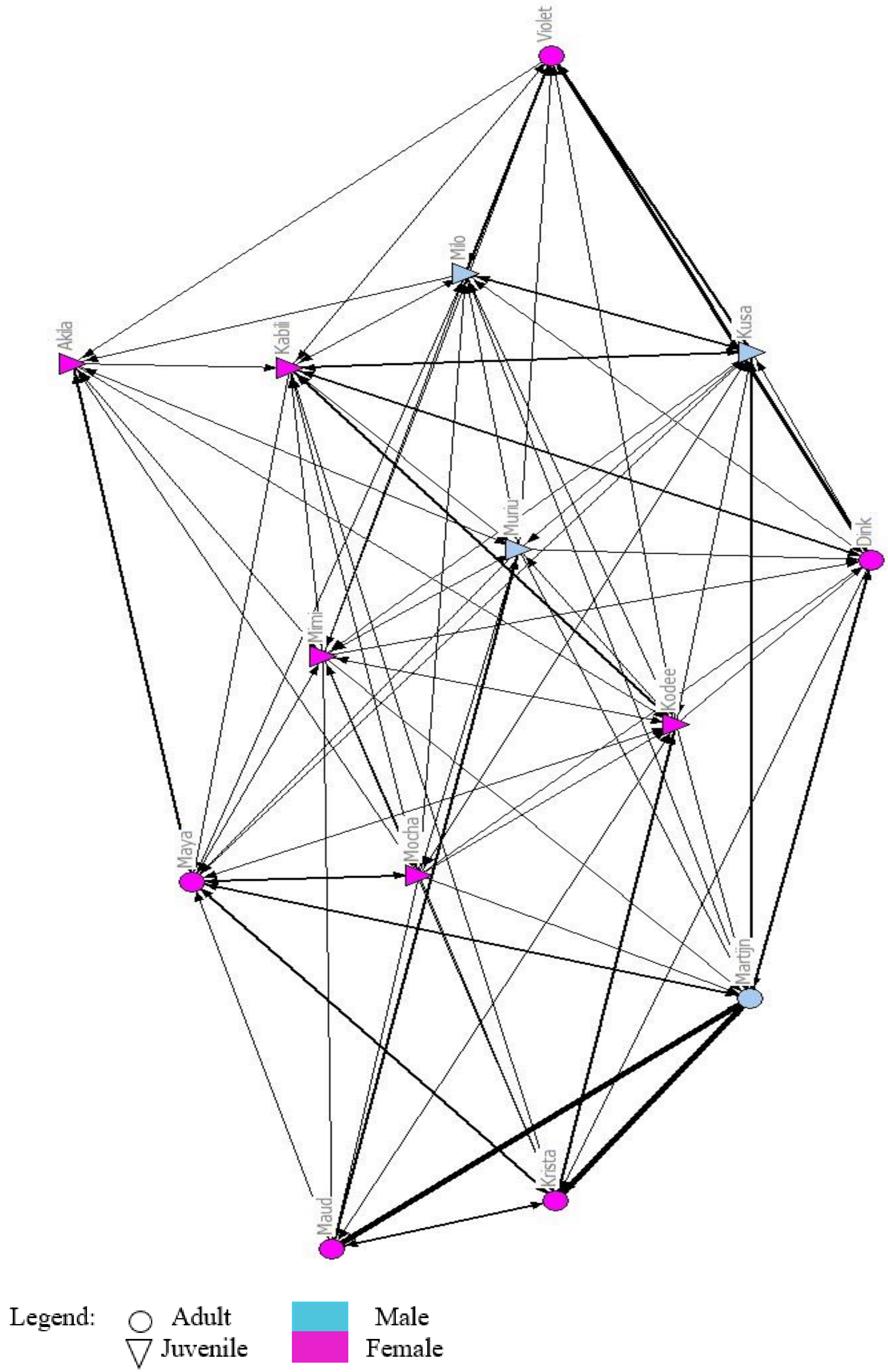


Figure 2e: Network for November based on all affiliative interactions, with attribute data noted with node symbol and color.

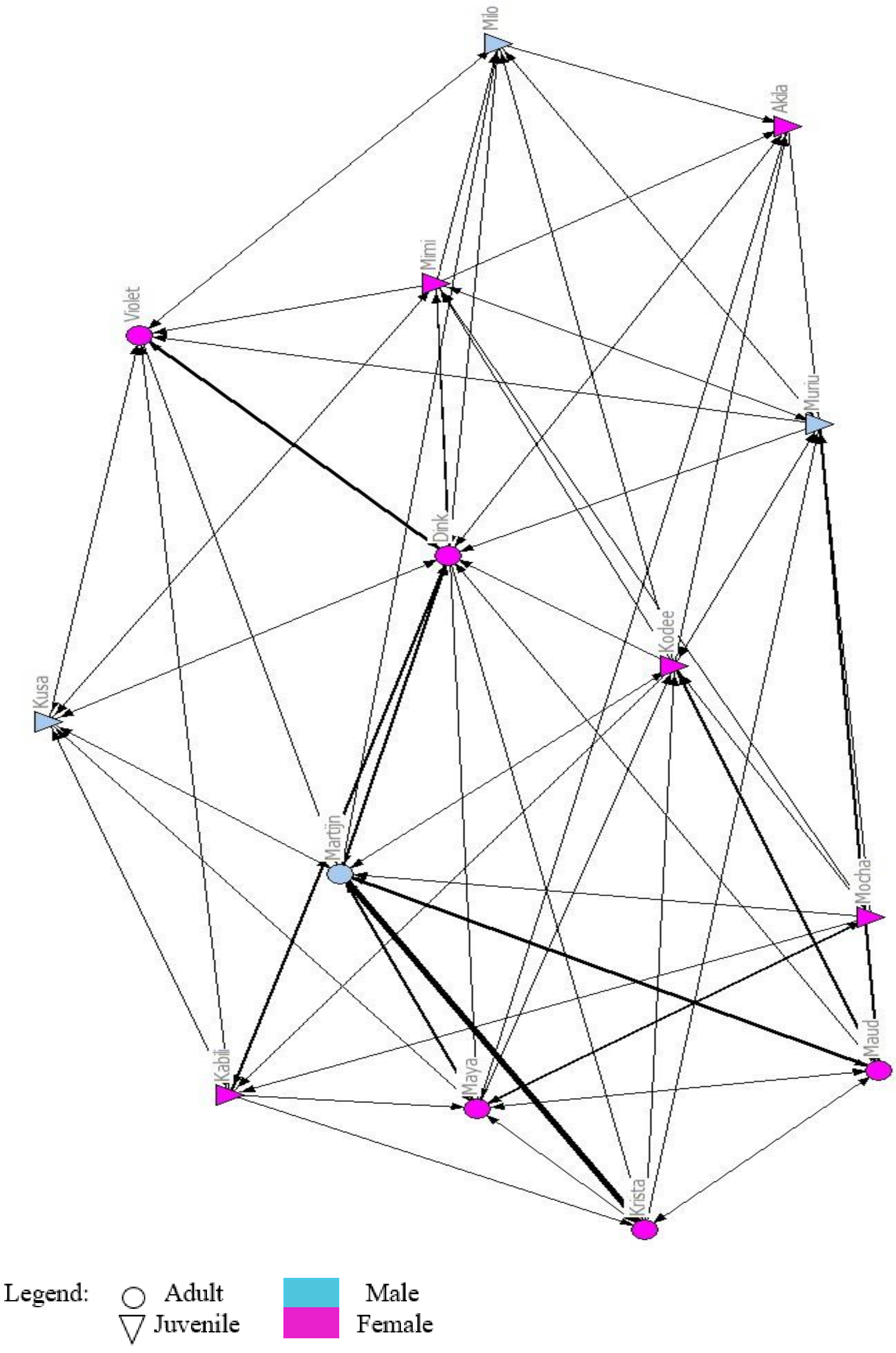


Figure 2f: Network for December based on all affiliative interactions, with attribute data noted with node symbol and color.

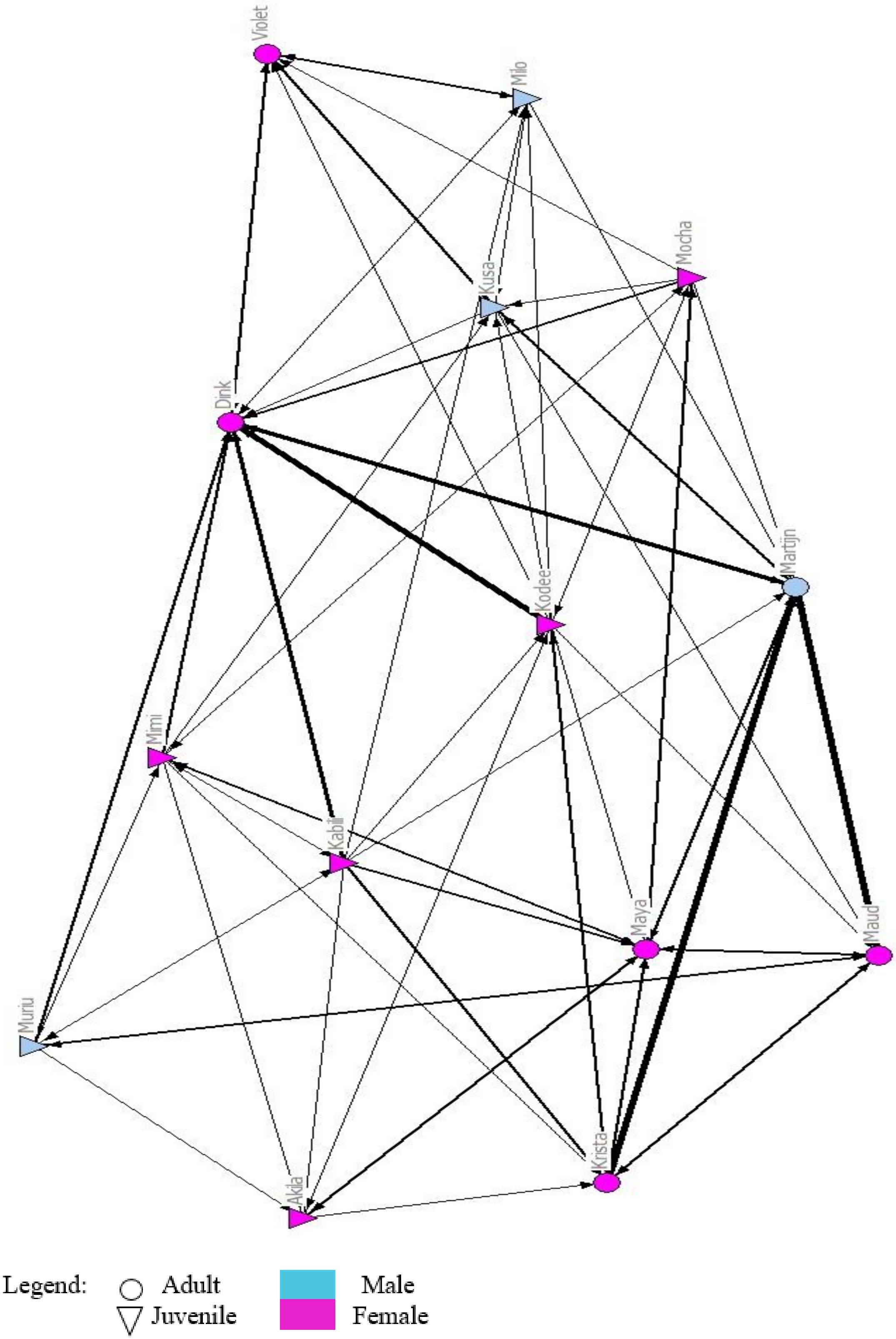
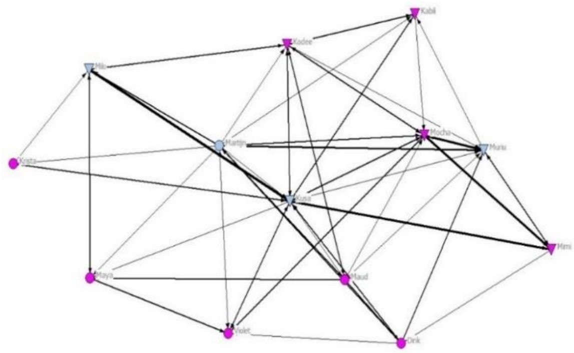
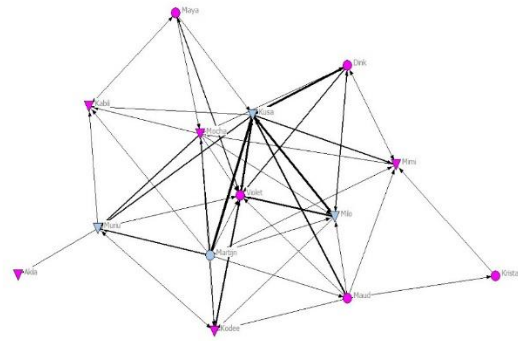


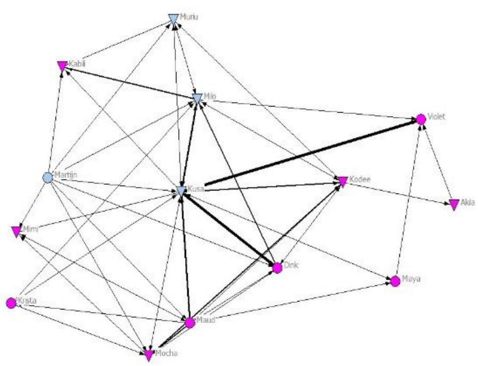
Figure 3: Networks for each month based on agonistic behaviors, with attribute data noted with node symbol and color.



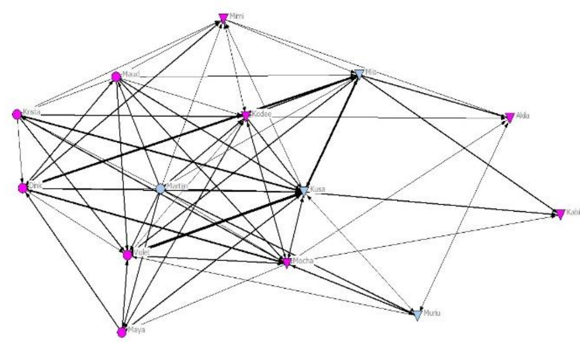
July Agonistic Network



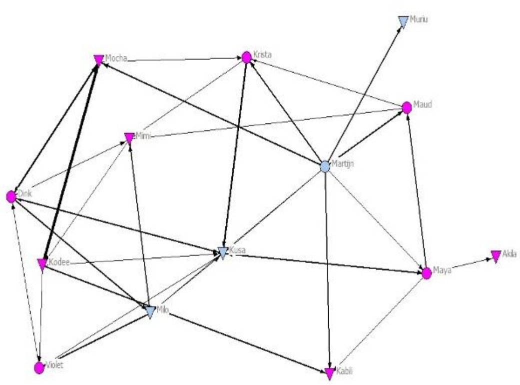
August Agonistic Network



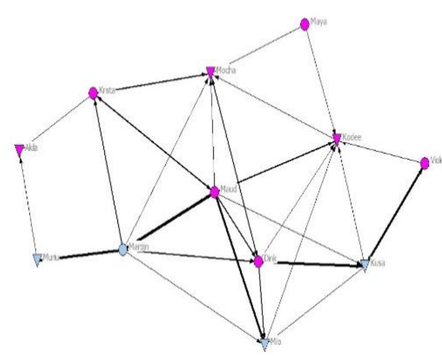
September Agonistic Network



October Agonistic Network



November Agonistic Network



December Agonistic Network

Legend: ○ Adult ▽ Juvenile | Male | Female

Figure 3a: Network for July based on all agonistic interactions, with attribute data noted with node symbol and color.

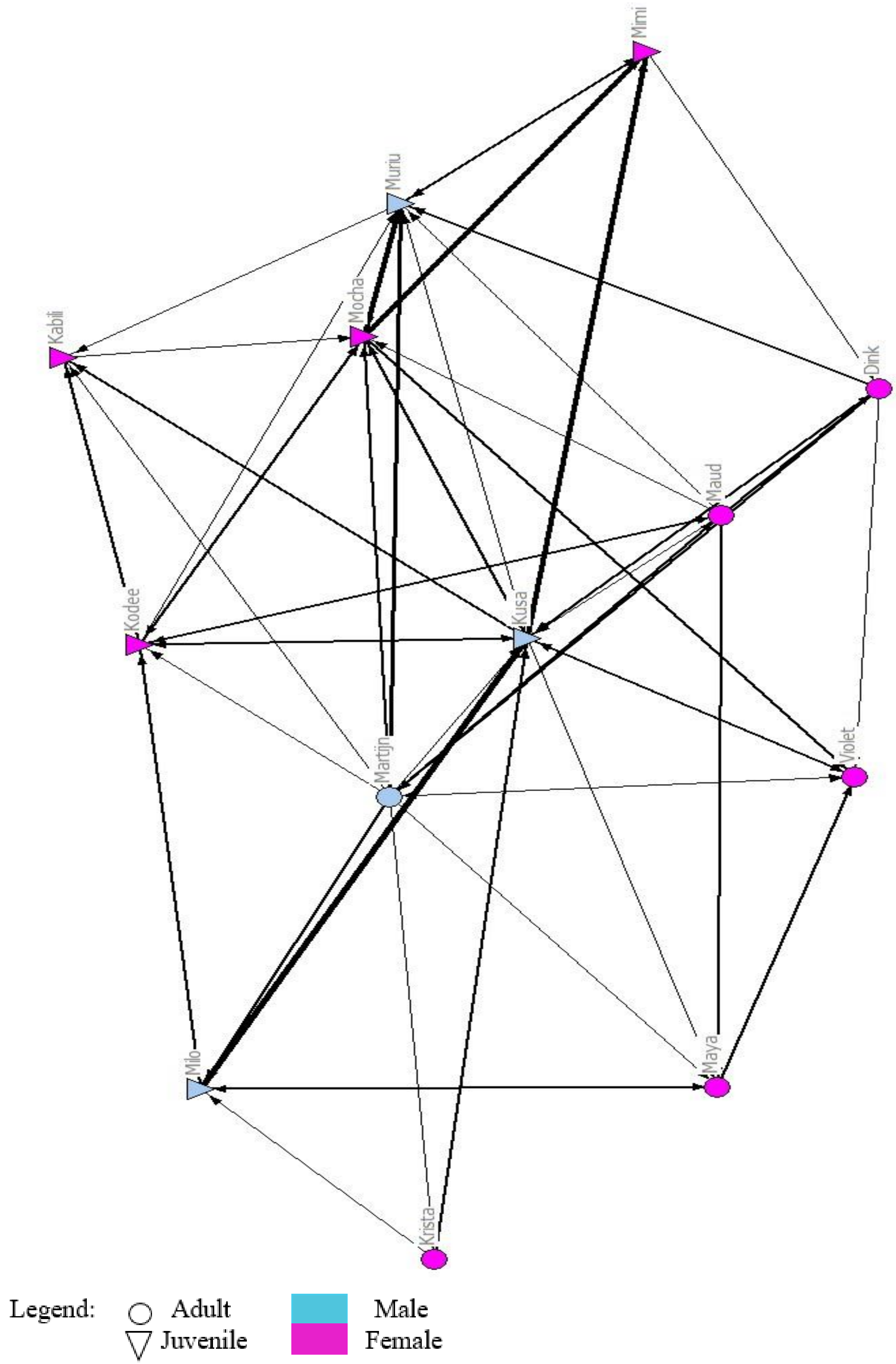


Figure 3b: Network for August based on all agonistic interactions, with attribute data noted with node symbol and color.

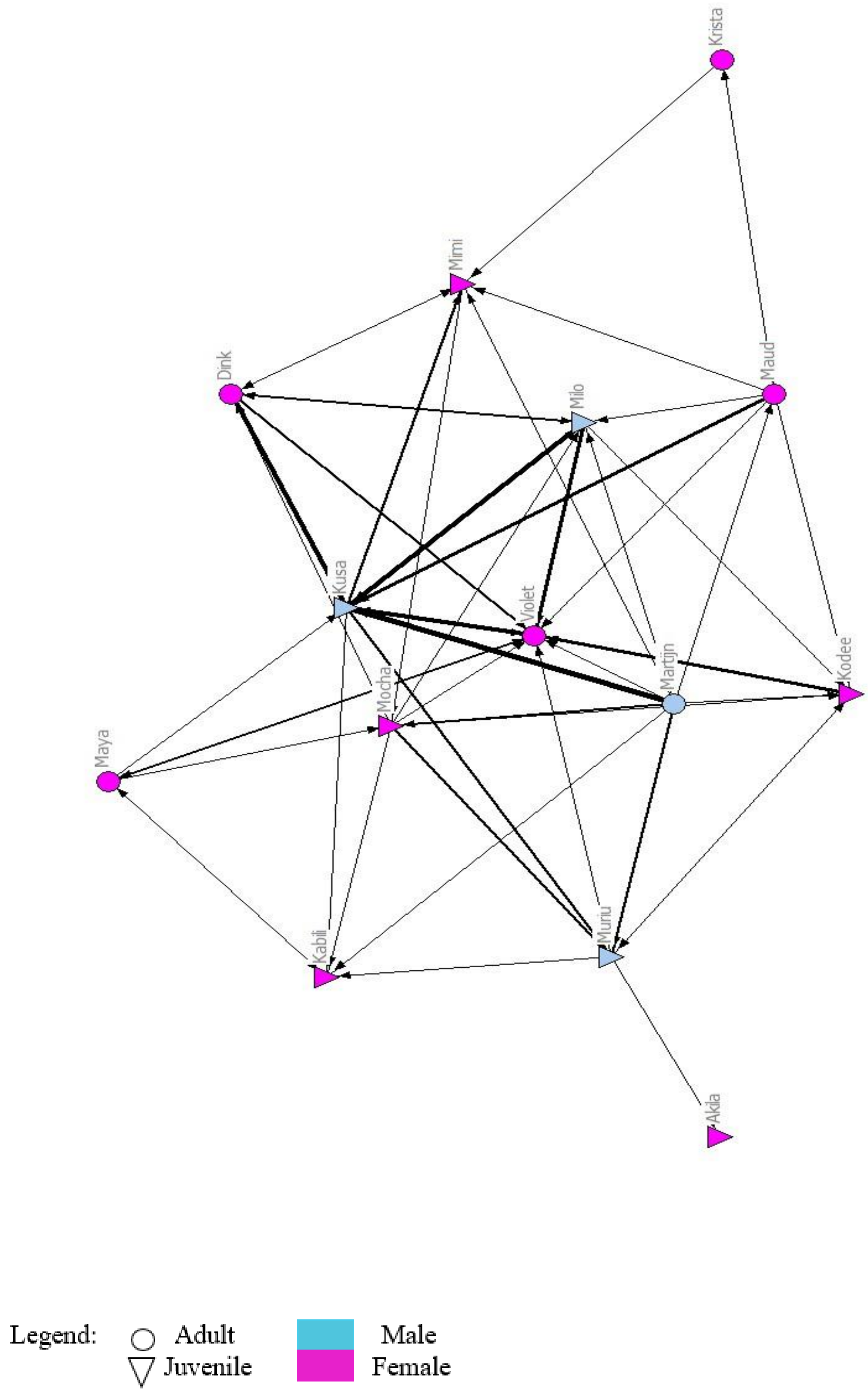


Figure 3c: Network for September based on all agonistic interactions, with attribute data noted with node symbol and color.

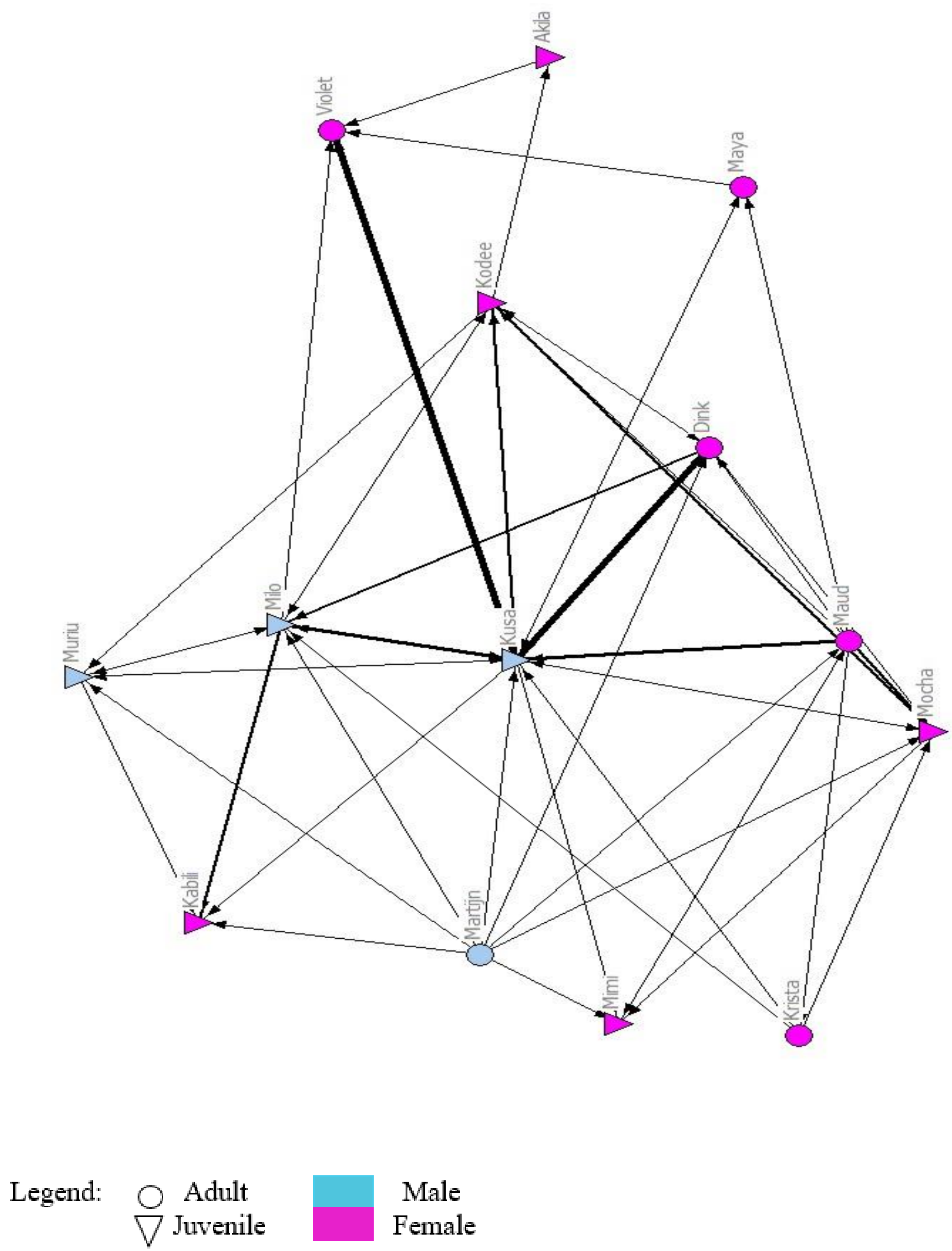


Figure 3d: Network for October based on all agonistic interactions, with attribute data noted with node symbol and color.

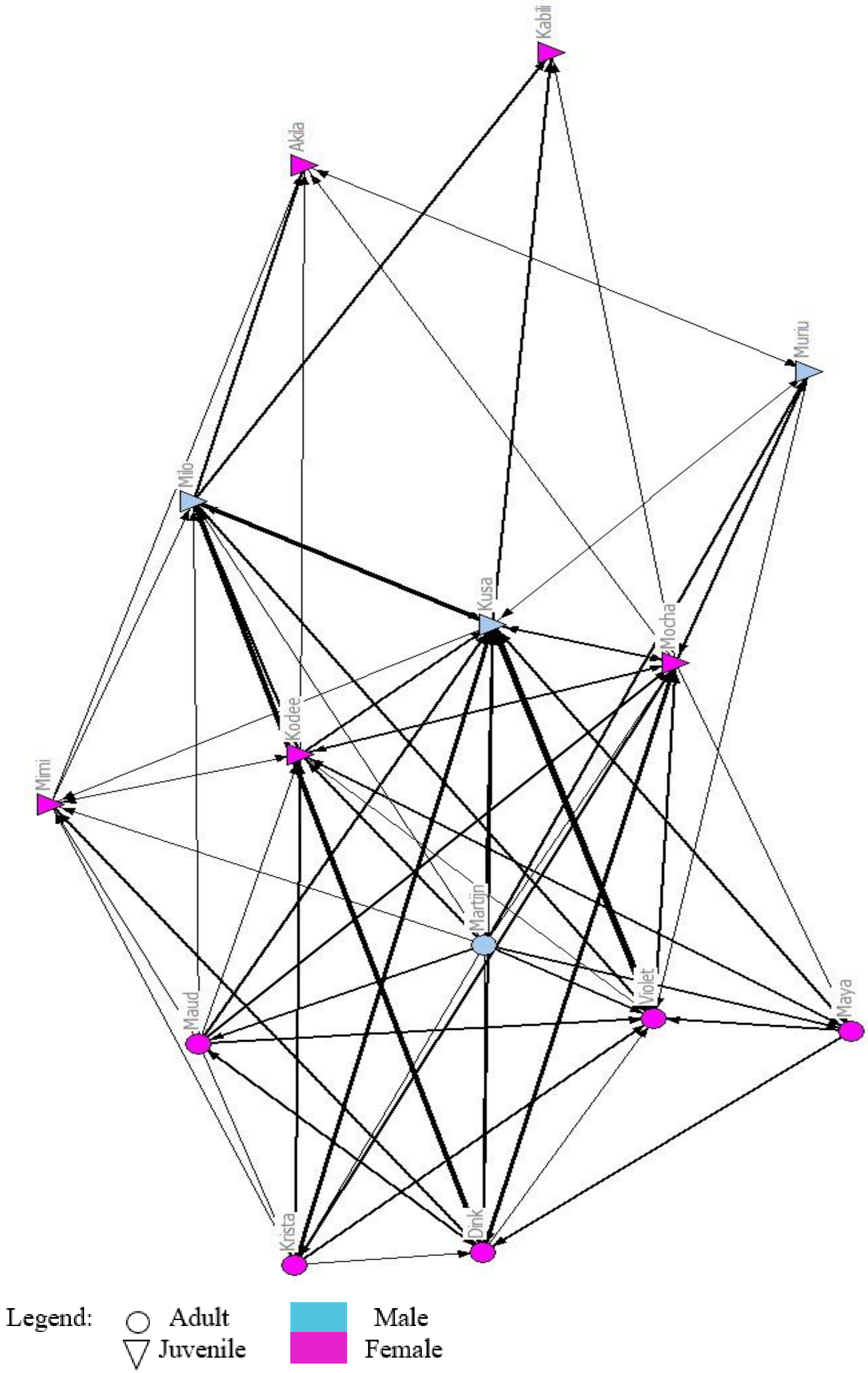


Figure 3e: Network for November based on all agonistic interactions, with attribute data noted with node symbol and color.

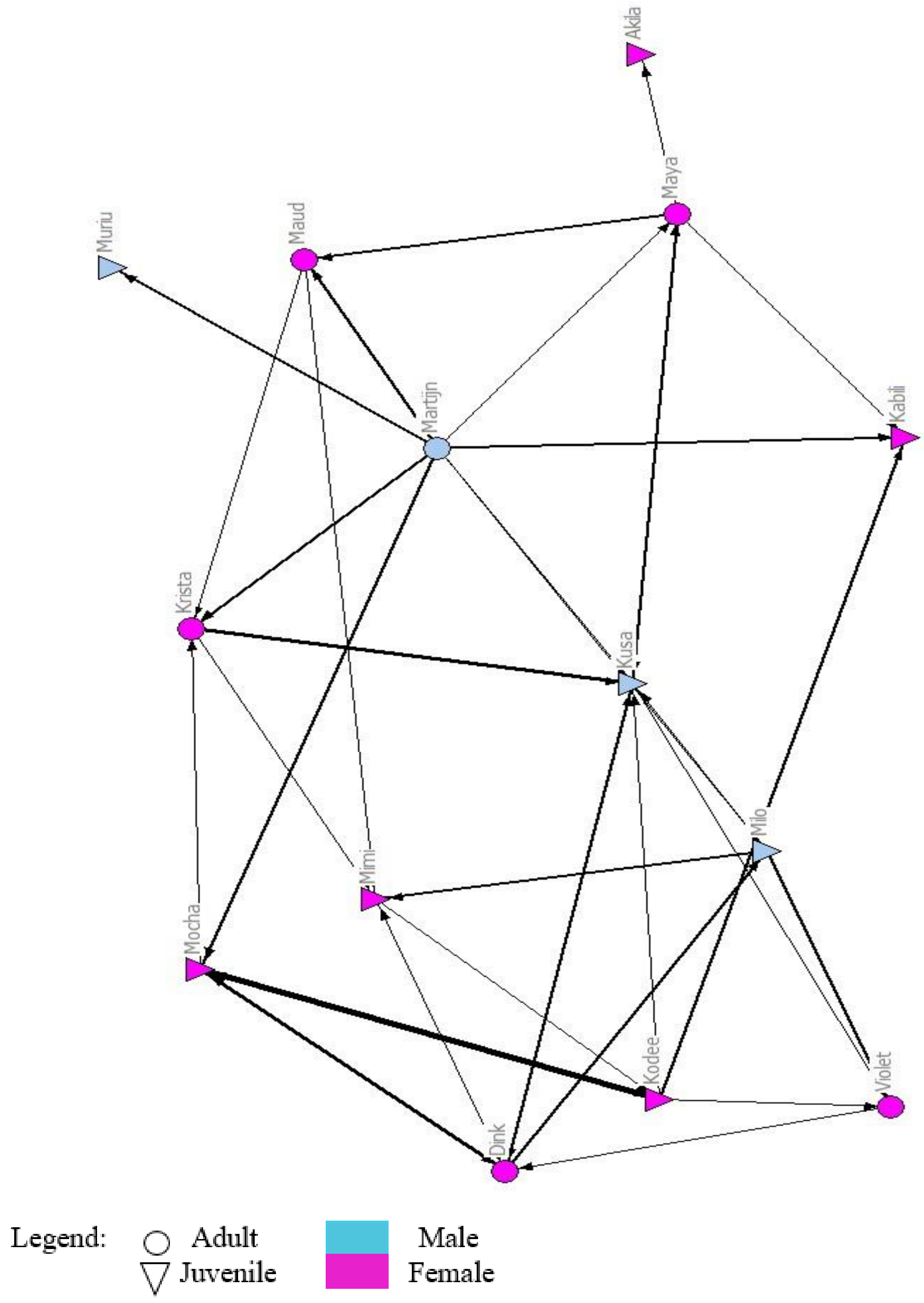


Figure 3f: Network for December based on all agonistic interactions, with attribute data noted with node symbol and color.

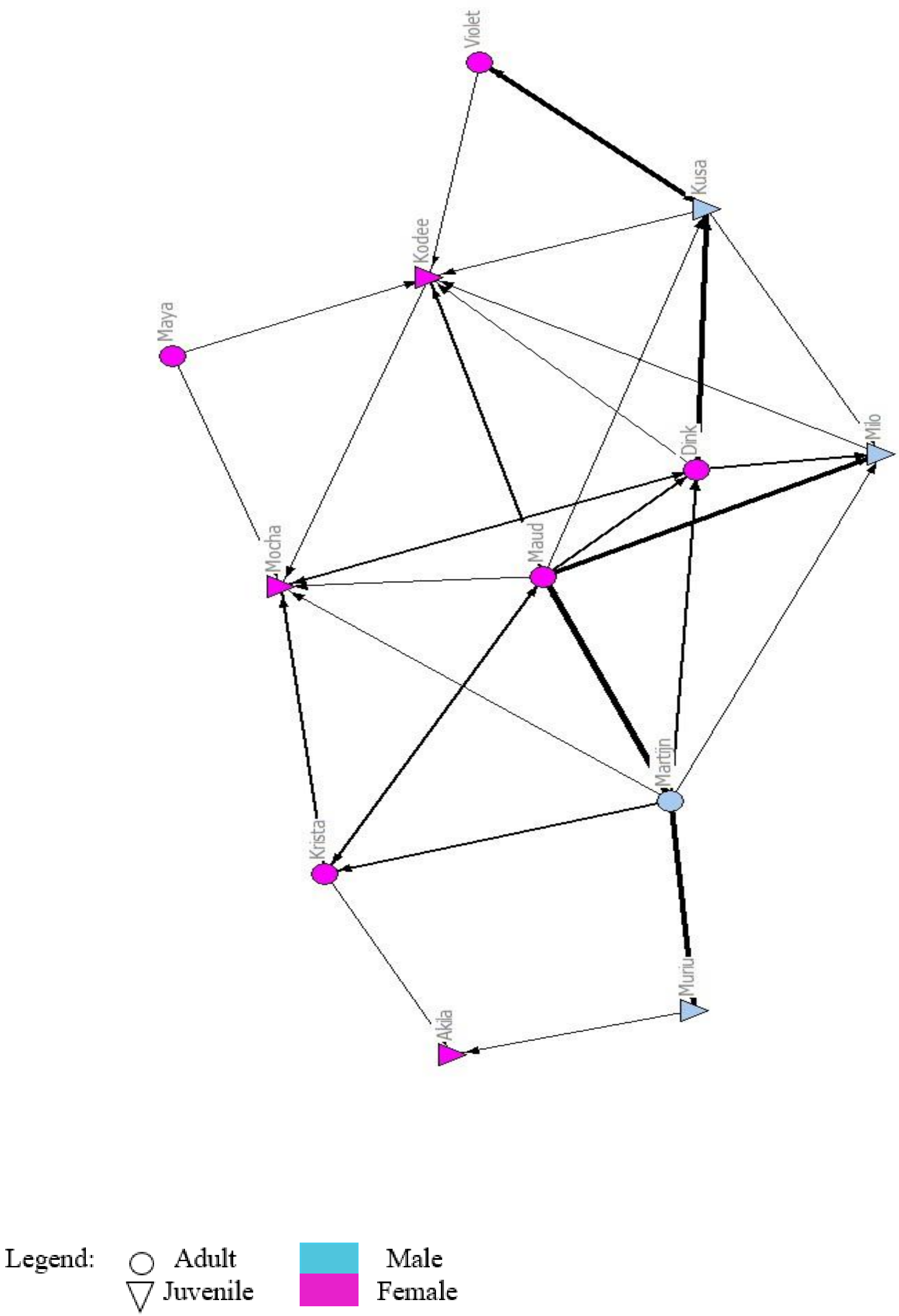
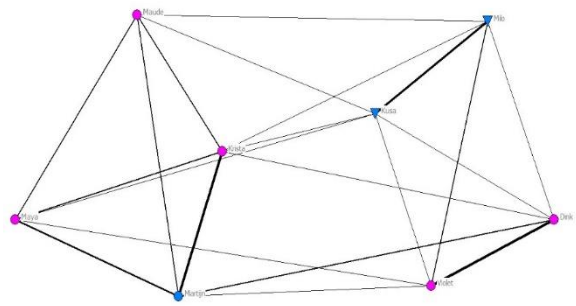
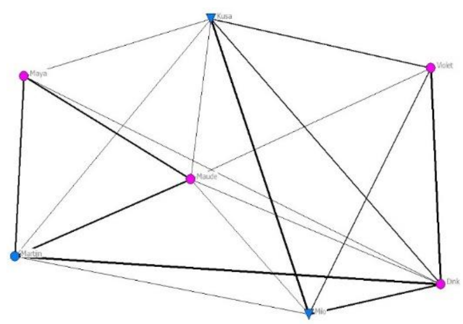


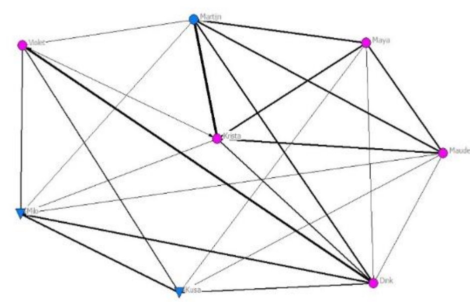
Figure 4: Networks for each month based on associations, with attribute data noted with node symbol and color.



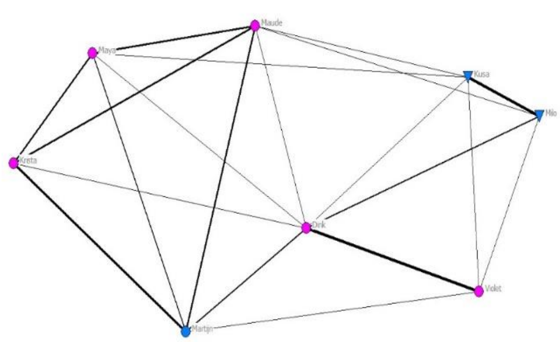
August Association Network



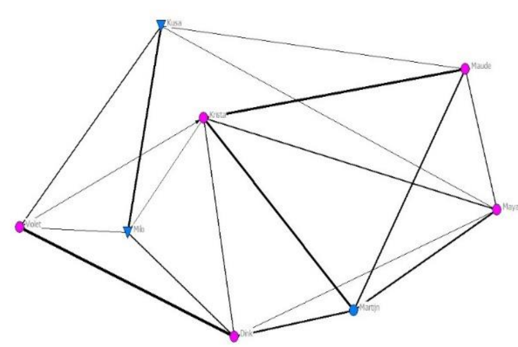
September Association Network



October Association Network



November Association Network



December Association Network

Legend: ○ Adult ▽ Juvenile Male Female

Figure 4a: Network for August based on associations, with attribute data noted with node symbol and color.

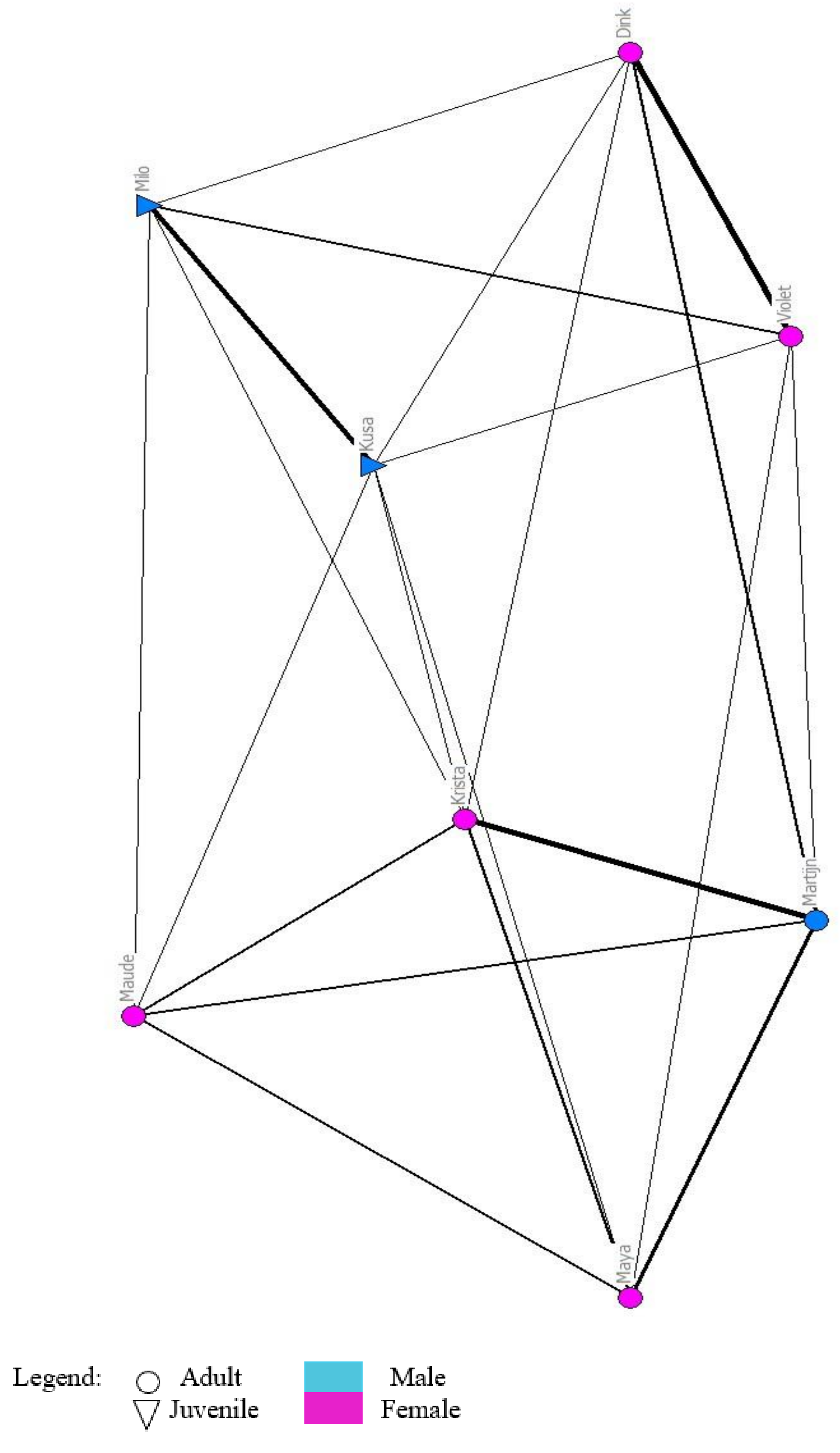


Figure 4b: Network for September based on associations, with attribute data noted with node symbol and color.

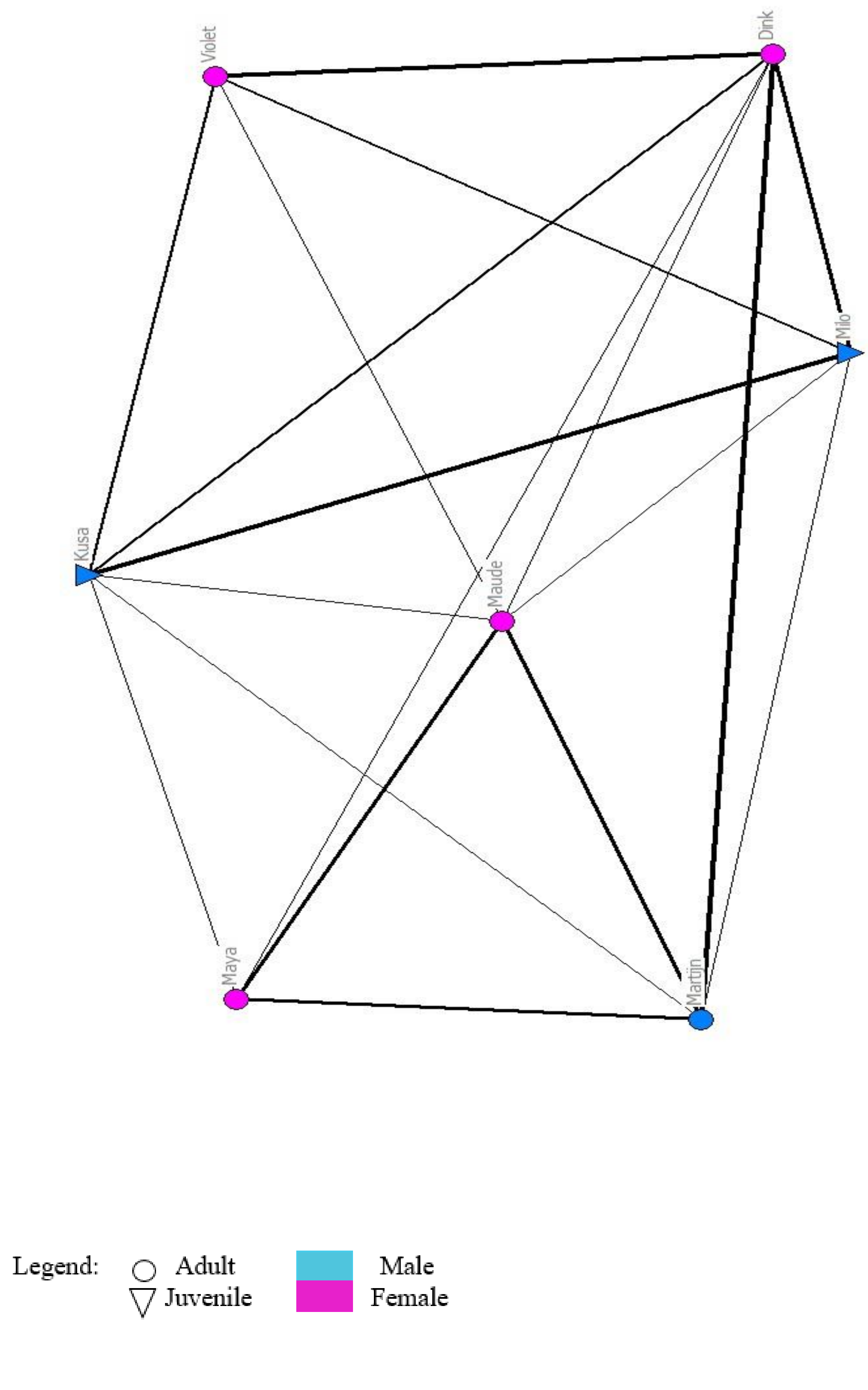


Figure 4c: Network for October based on associations, with attribute data noted with node symbol and color.

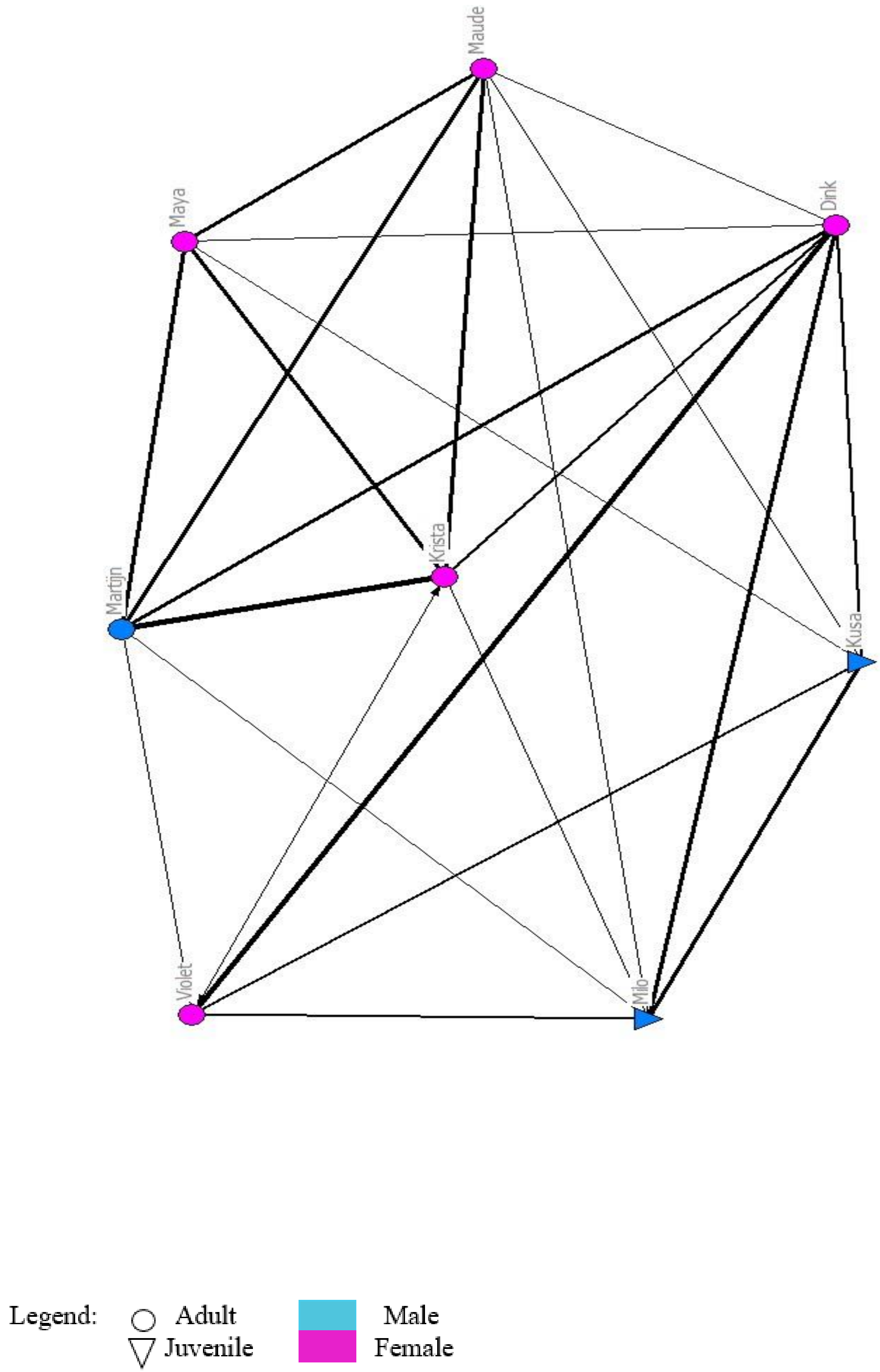


Figure 4d: Network for November based on associations, with attribute data noted with node symbol and color.

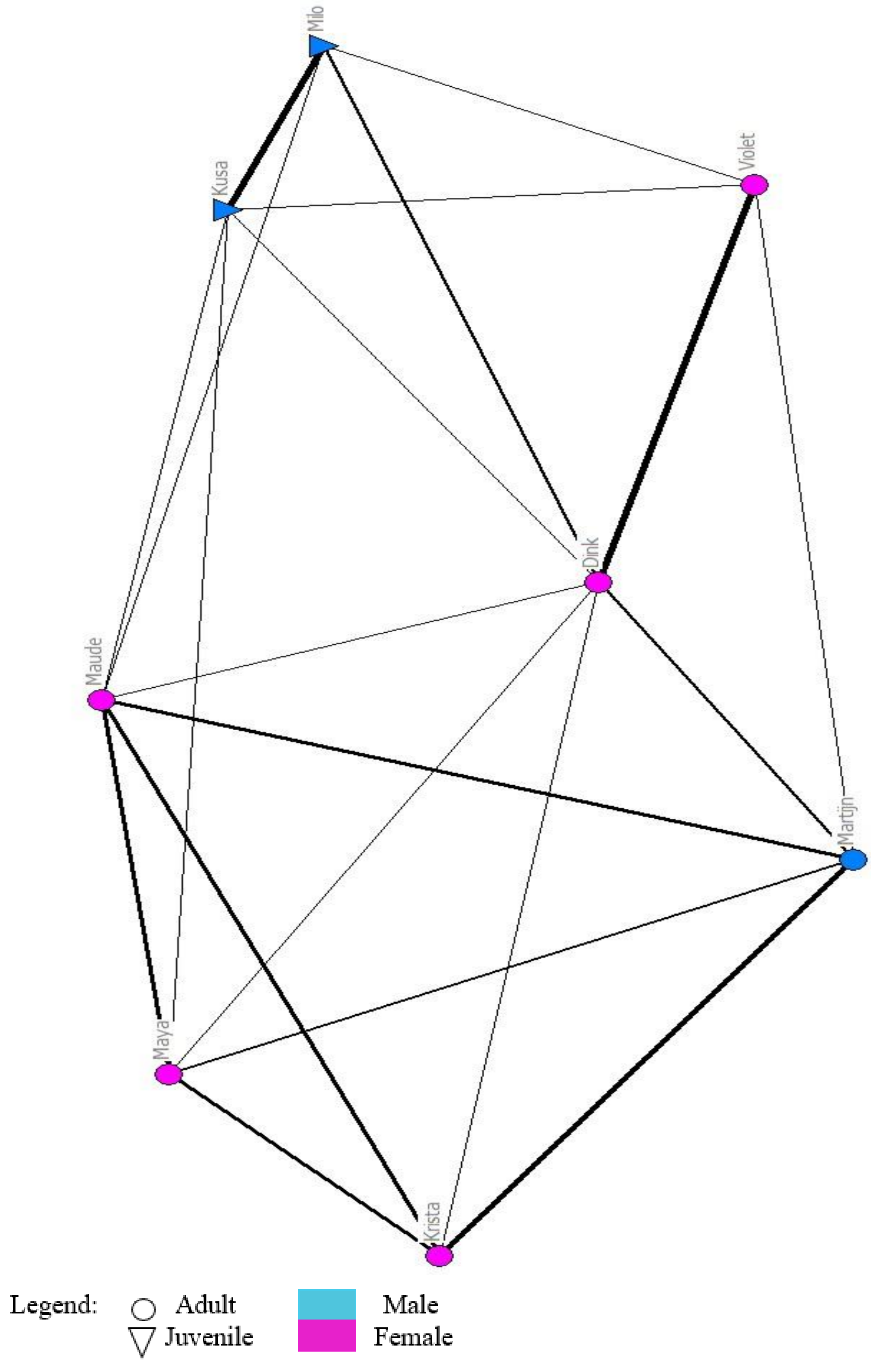
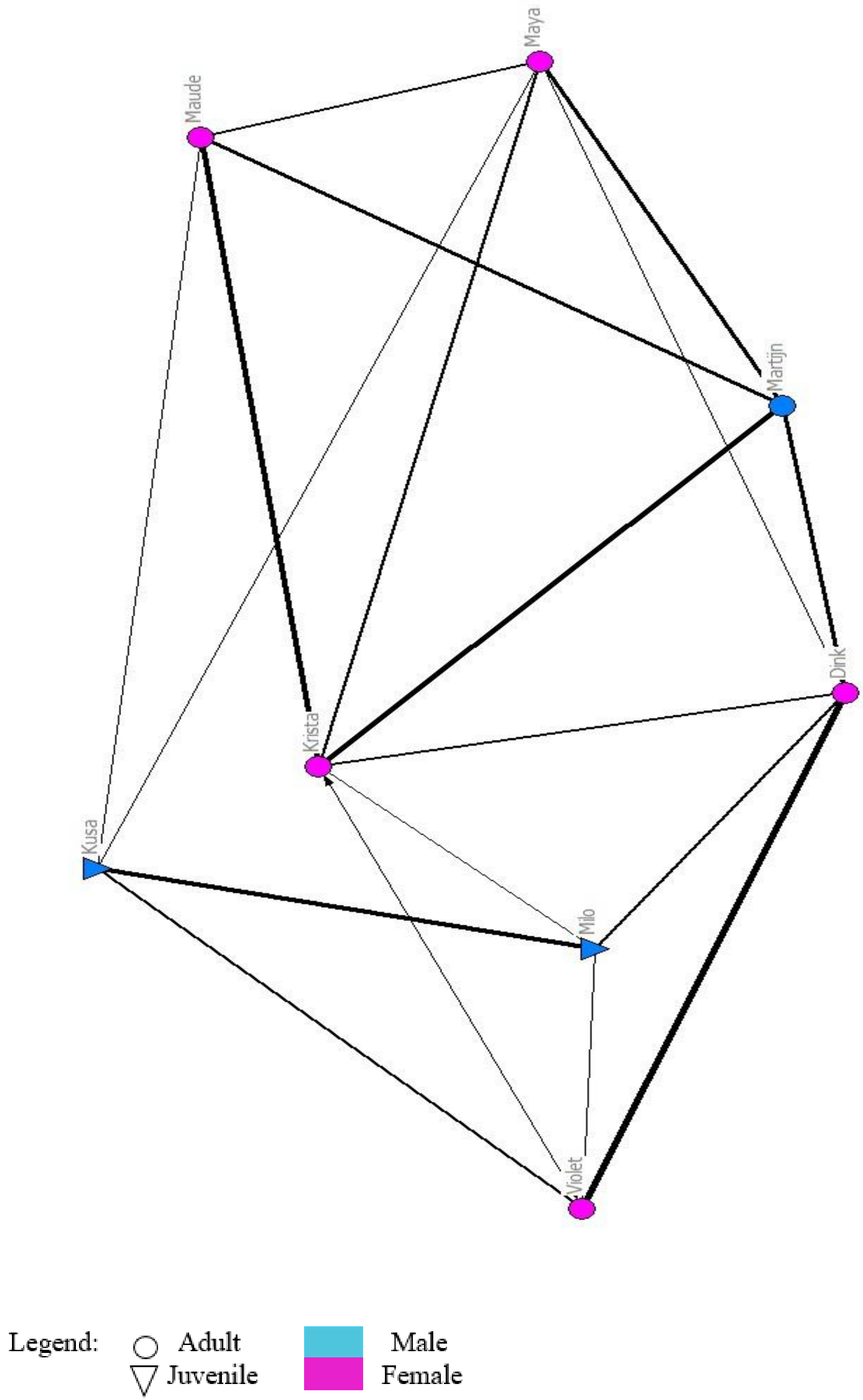


Figure 4e: Network for December based on associations, with attribute data noted with node symbol and color.



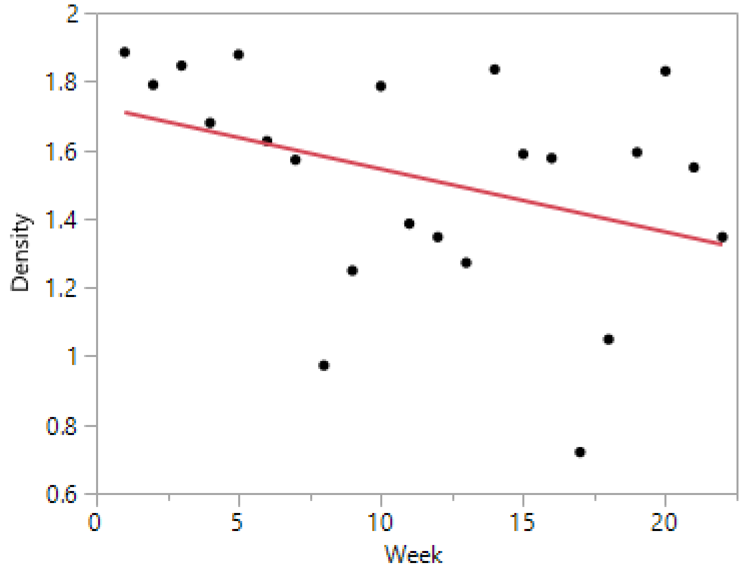


Figure 5a: Linear regression from the statistical analyses showing a decreasing trend of overall interaction group density over time.

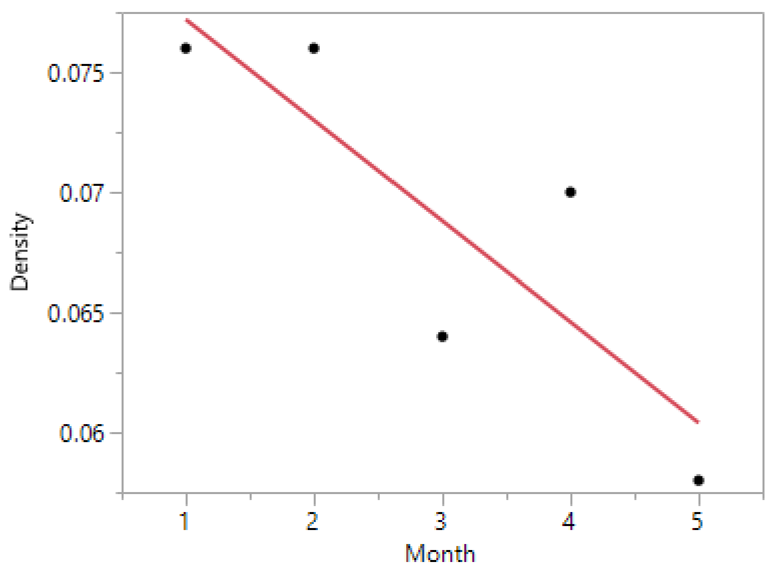


Figure 5b: Linear regression from the statistical analyses showing a decreasing trend of group density over time based on social proximity.

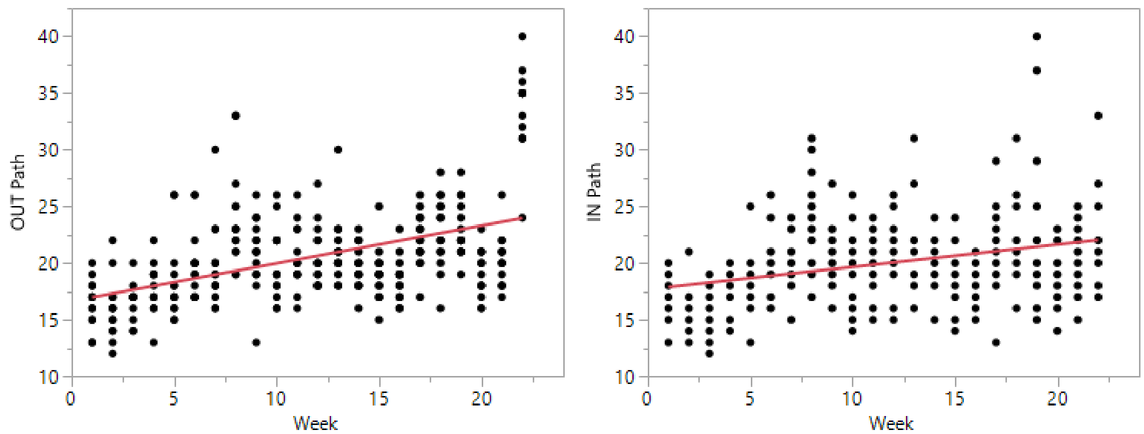


Figure 6a: Model showing that significant increases occurred in overall interaction in and out-path length over time.

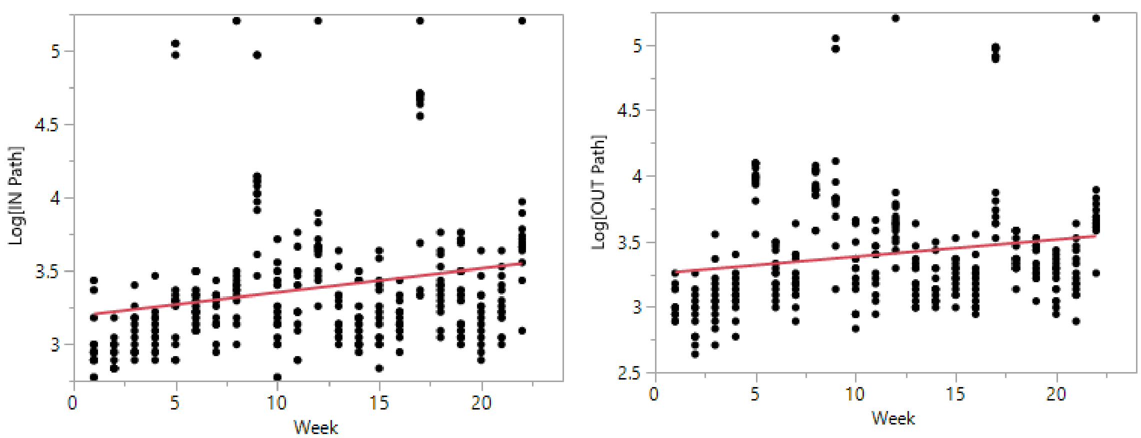


Figure 6b: Linear regression from the statistical analyses showing that affiliative interaction in and out-path length increased with time.

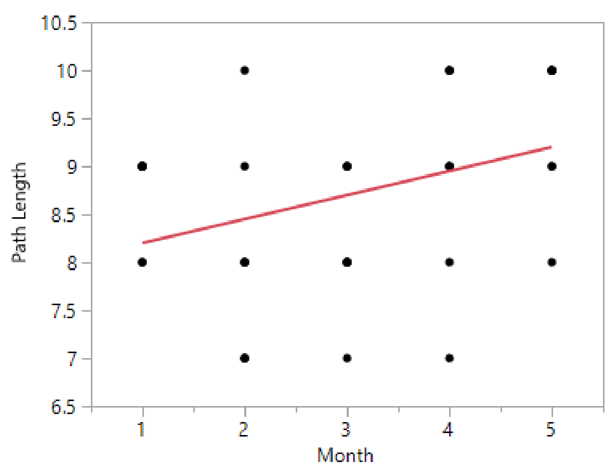


Figure 6c: Model showing a significant increase in association path length with time.

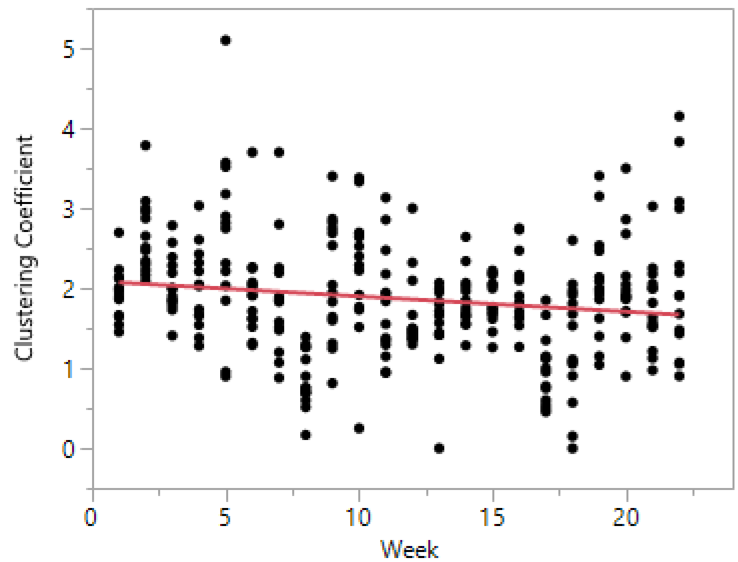


Figure 7a: Linear regression showing the significant decrease in overall interaction clustering coefficient with time.

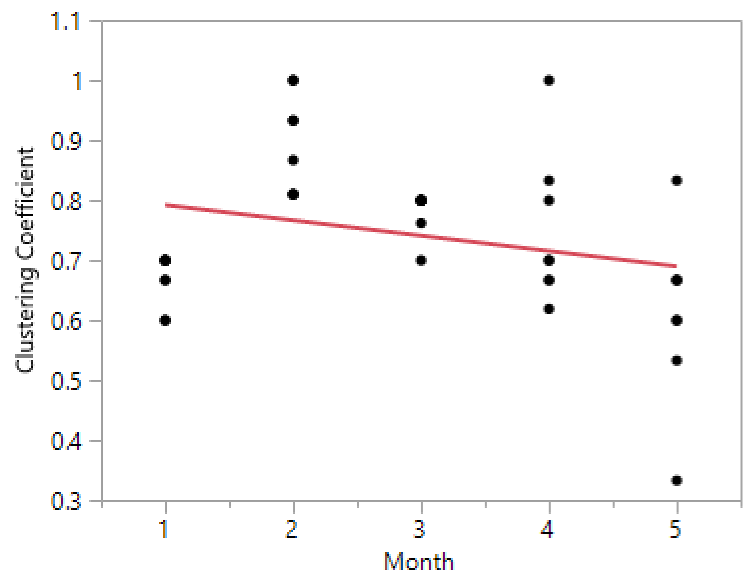


Figure 7b: Linear regression depicting a decreasing trend in clustering coefficient with time based on the association network.

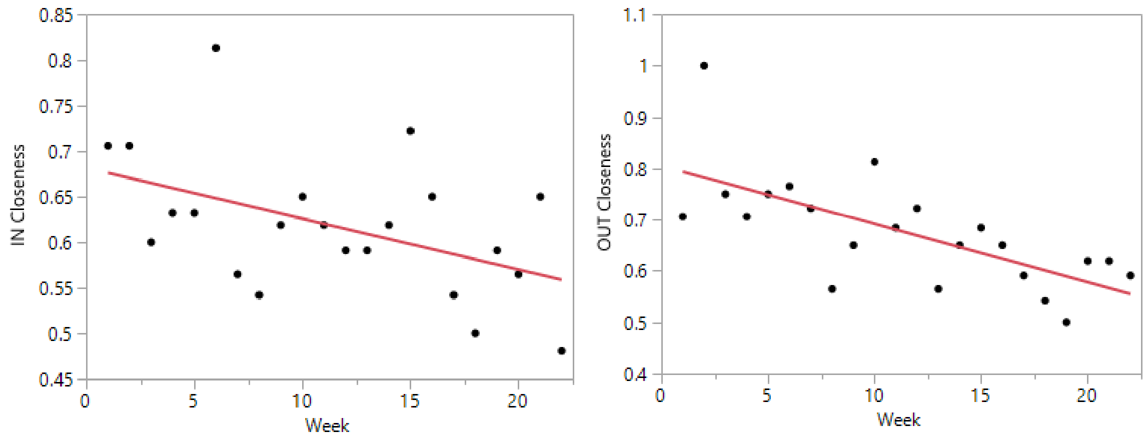


Figure 8a: Linear regression models showing the significant decreases in overall interaction in and out-closeness for Milo over time.

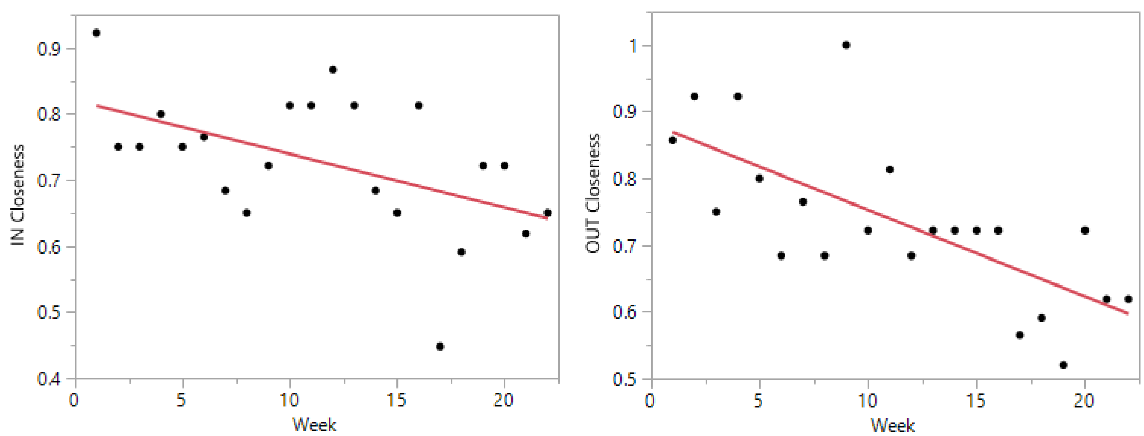


Figure 8b: Linear regression models showing the significant decreases in overall interaction in and out-closeness for Kusa over time.

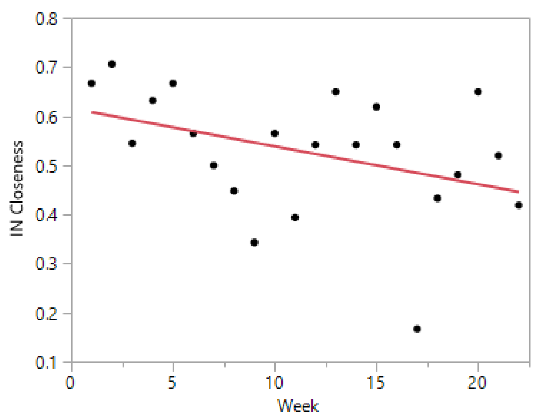


Figure 8c: Linear regression model showing the decreasing trend in affiliative interaction in-closeness over time for Kusa.

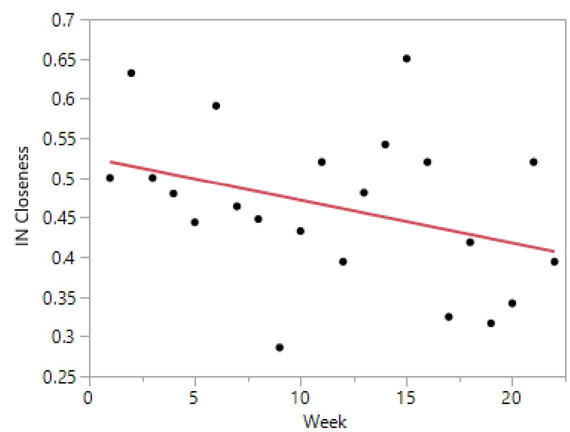


Figure 8d: Linear regression model showing the decreasing trend in affiliative interaction in-closeness over time for Milo.

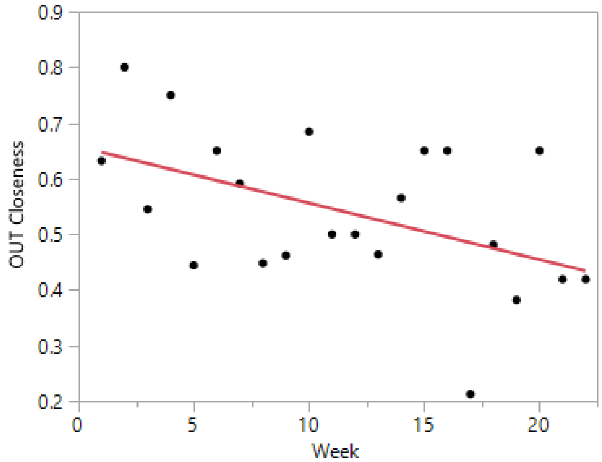


Figure 8e: Linear regression showing the significant decrease in affiliative out-closeness over time for Kusa.

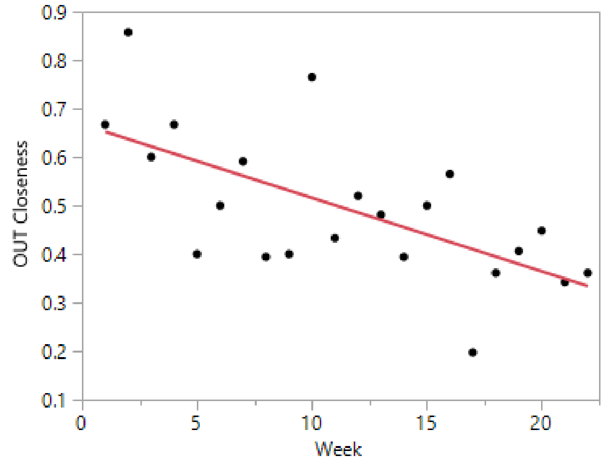


Figure 8f: Linear regression showing the significant decrease in affiliative out-closeness over time for Milo.

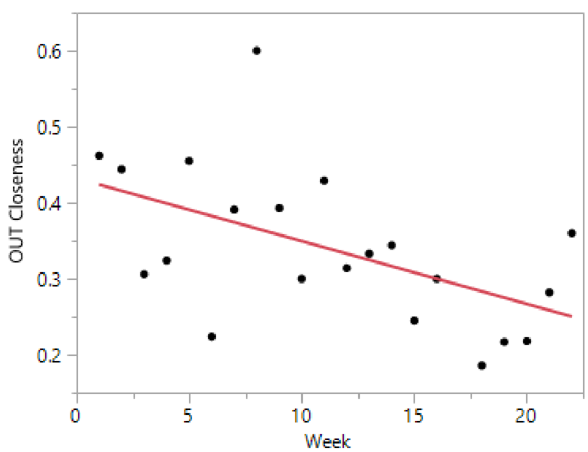


Figure 8g: Model showing a significant decrease in agonistic out-closeness with time for Kusa.

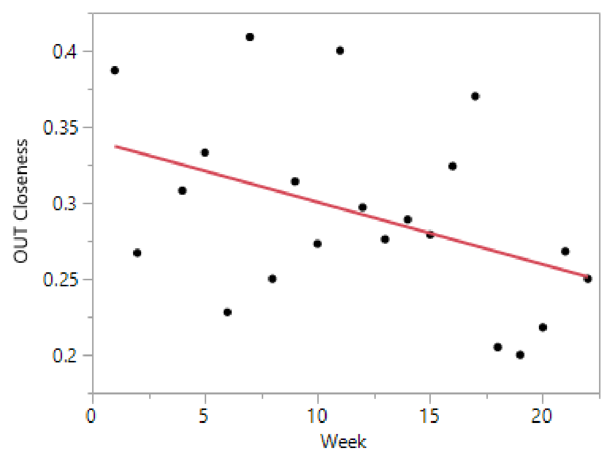


Figure 8h: Model showing a decreasing trend in agonistic out-closeness with time for Milo.

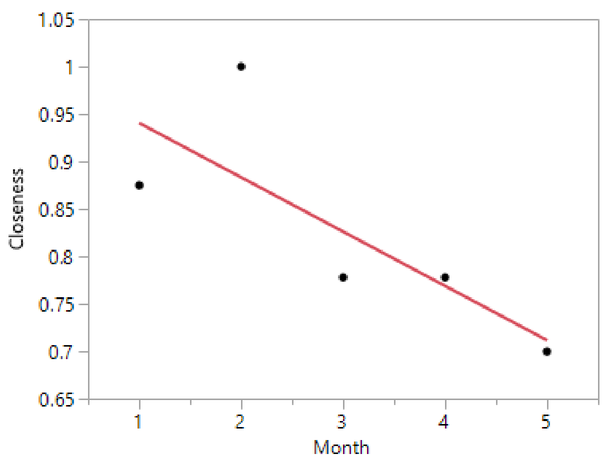


Figure 8i: Linear regression showing a decreasing trend for Kusa in closeness over time for the association network.

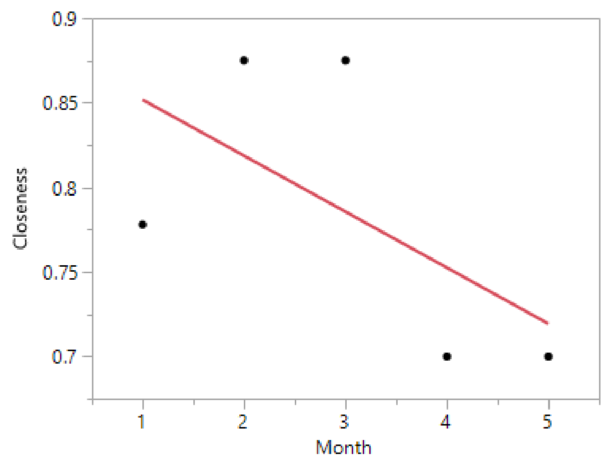


Figure 8j: Linear regression showing a decreasing trend for Milo in closeness over time for the association network.

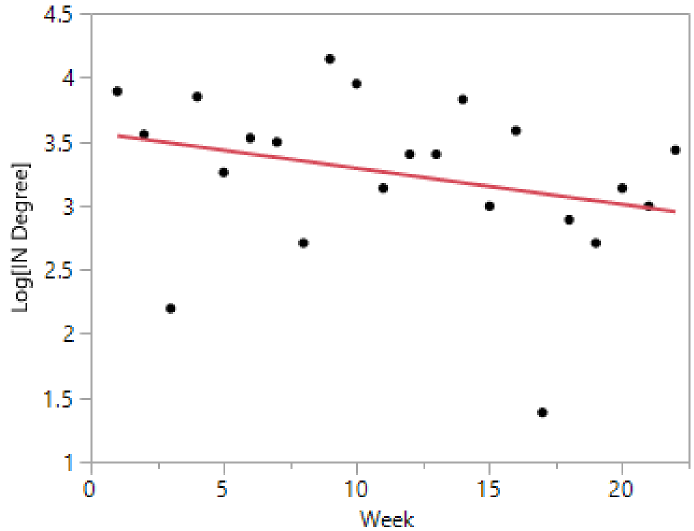


Figure 9a: Model showing a decreasing trend in overall interaction in-degree for Kusa.

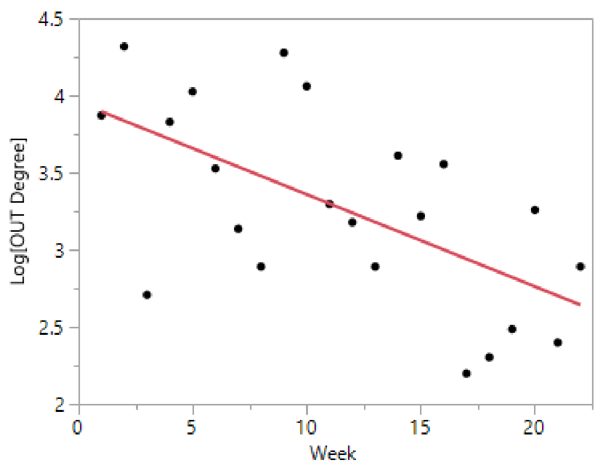


Figure 9b: Model showing a significant decrease in overall interaction out-degree for Kusa.

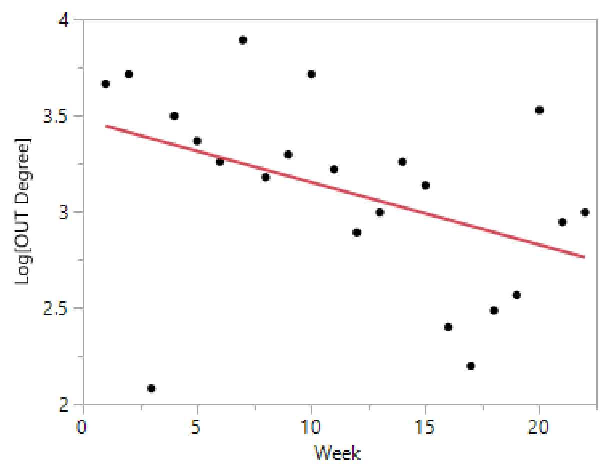


Figure 9c: Model showing a decreasing trend in overall interaction out-degree for Milo.

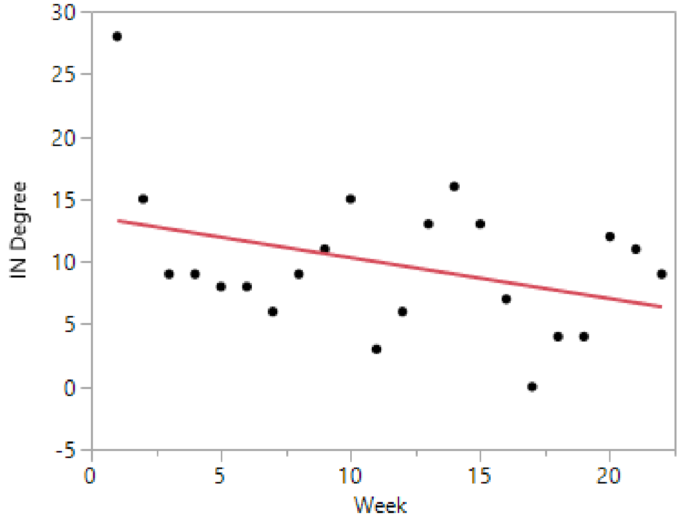


Figure 9d: Linear regression model showing the decreasing trend in affiliative interaction in-degree with time for Kusa.

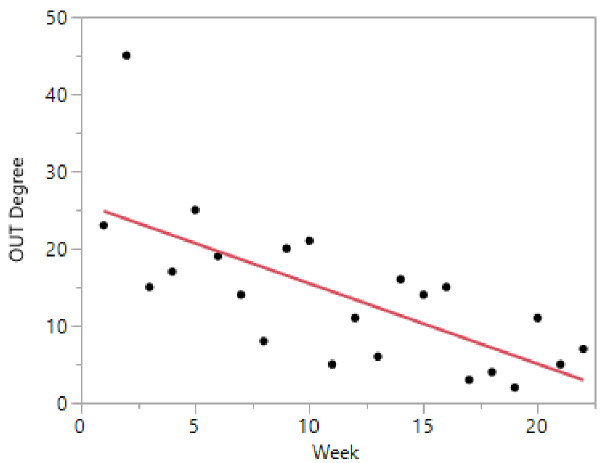


Figure 9e: Model showing a significant decrease in affiliative interaction out-degree with time for Kusa

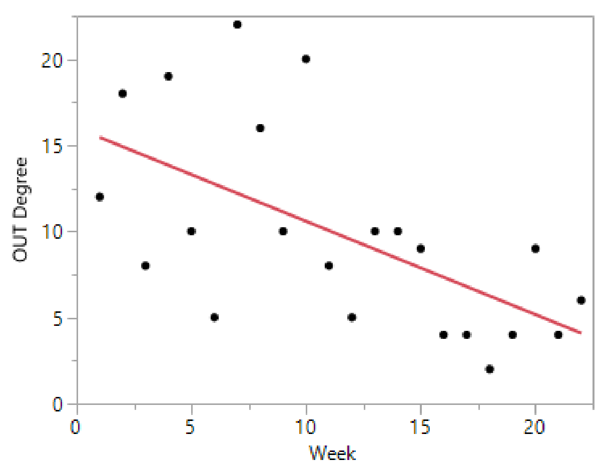


Figure 9f: Model showing the significant decrease in affiliative interaction out-degree with time for Milo.

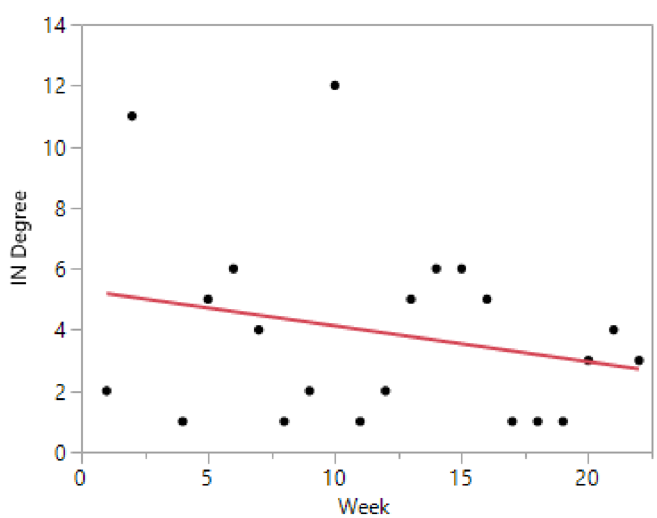


Figure 9g: Linear regression model showing a decreasing trend in agonistic interaction in-degree for Milo.

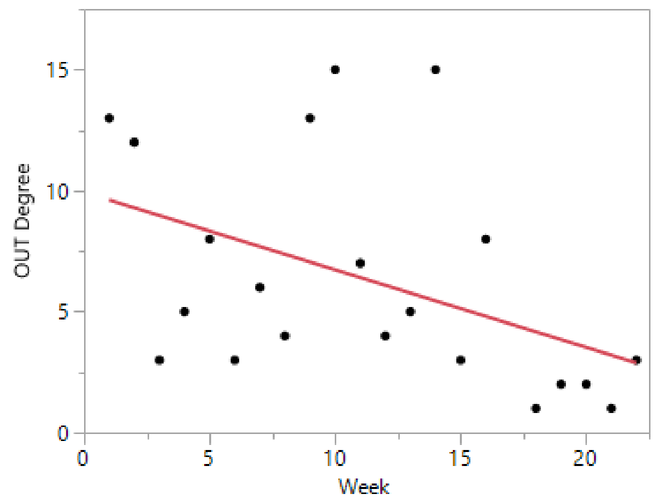


Figure 9h: Linear regression model showing a significant decrease in agonistic interaction out-degree for Kusa.

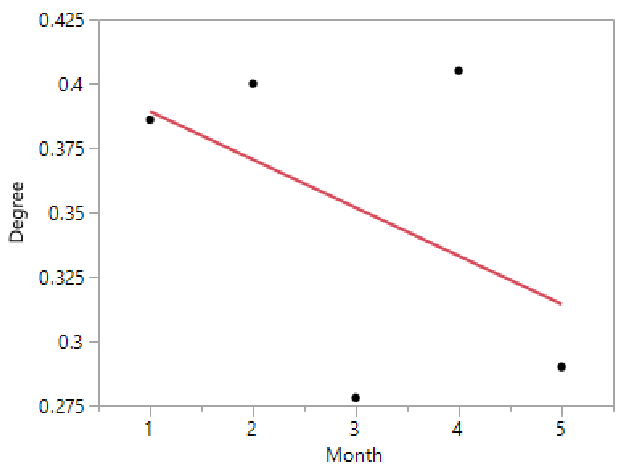


Figure 9i: Model showing the decreasing trend in association degree for Kusa.

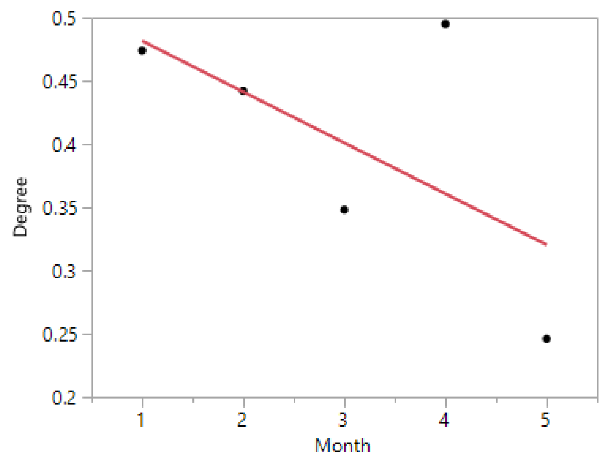


Figure 9j: Model showing the decreasing trend in association degree for Milo.

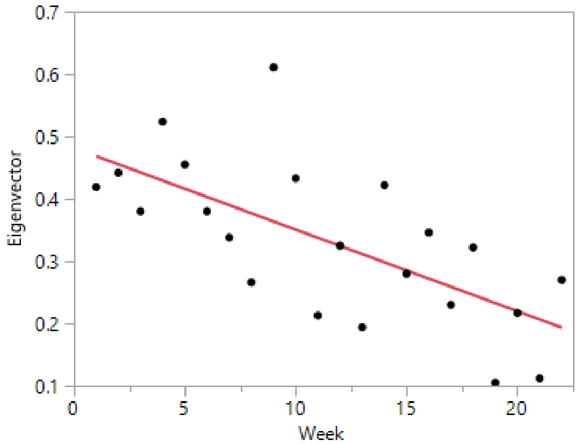


Figure 10a: Linear regression model from the statistical analyses indicating the significant decrease in overall interaction eigenvector centrality with time for Kusa.

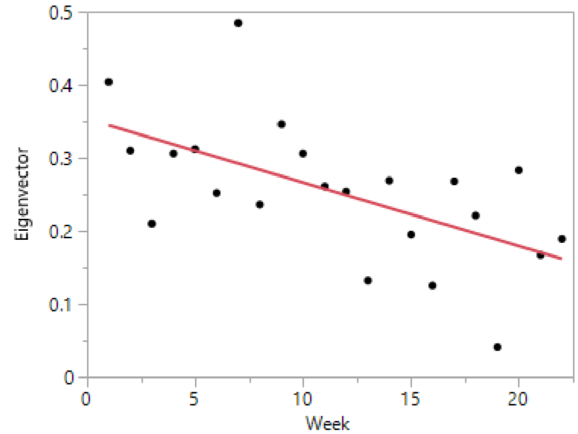


Figure 10b: Linear regression model from the statistical analyses indicating the significant decrease in overall interaction eigenvector centrality with time for Milo.

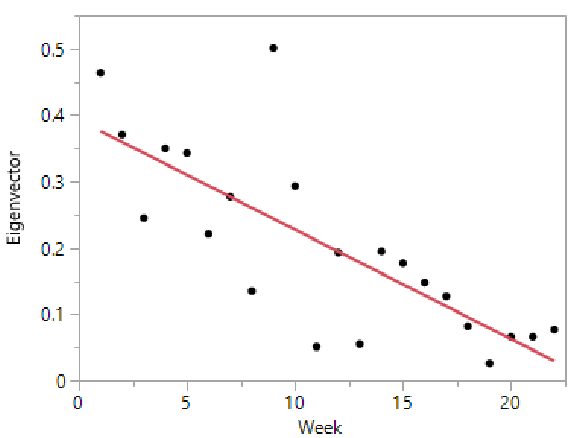


Figure 10c: Model showing the significant decrease in affiliative interaction eigenvector centrality for Kusa with time.

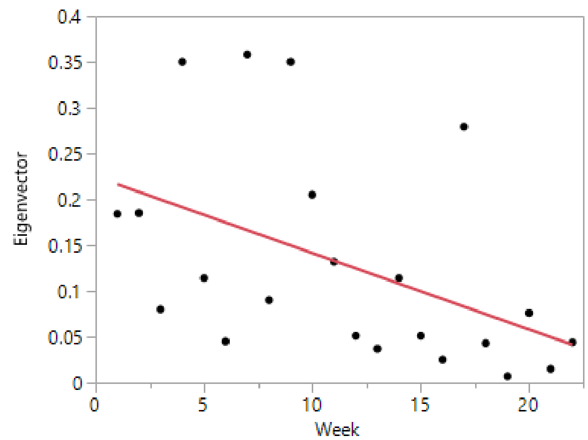


Figure 10d: Model showing the significant decrease in affiliative interaction eigenvector centrality for Milo with time.

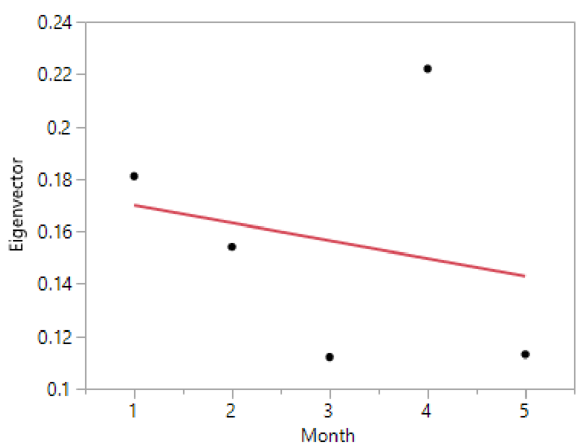


Figure 10e: Model showing the decreasing trend in association eigenvector centrality for Kusa.

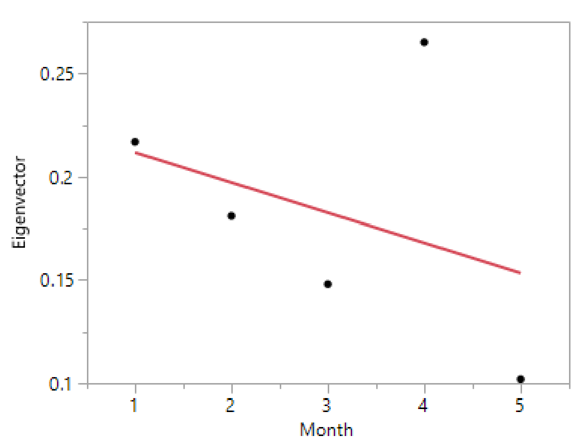


Figure 10f: Model showing the decreasing trend in association eigenvector centrality for Milo.

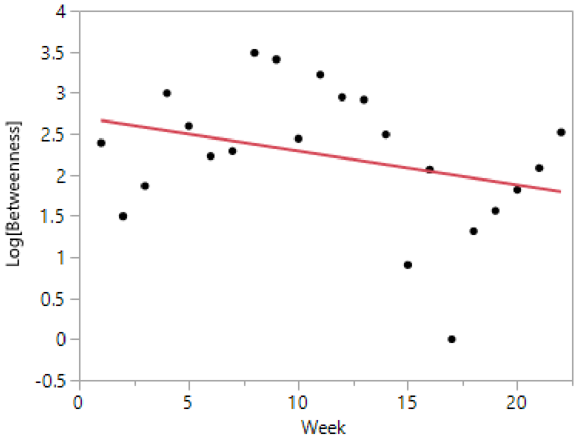


Figure 11a: Linear regression depicting the decreasing trend in overall interaction betweenness over time for Kusa.

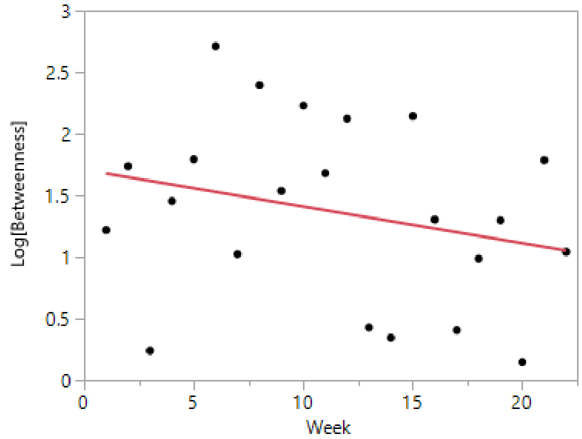


Figure 11b: Linear regression depicting the decreasing trend in overall interaction betweenness over time for Milo.

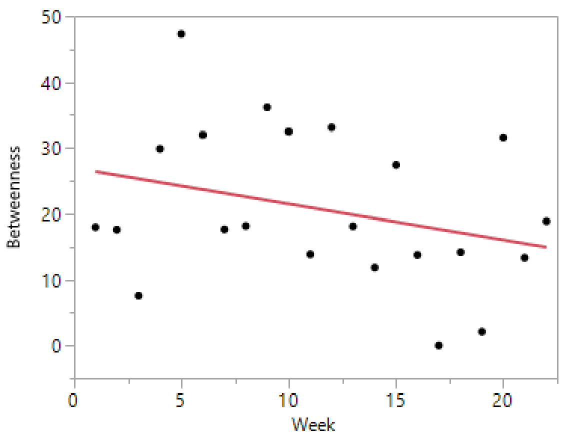


Figure 11c: Regression model showing the decreasing trend in affiliative interaction betweenness with time for Kusa.

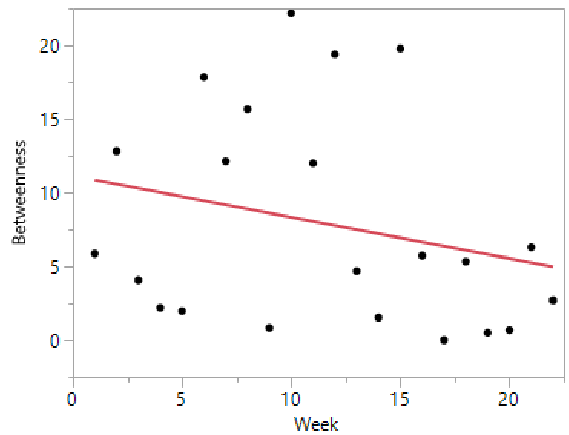


Figure 11d: Regression model showing the decreasing trend in affiliative interaction betweenness with time for Milo.

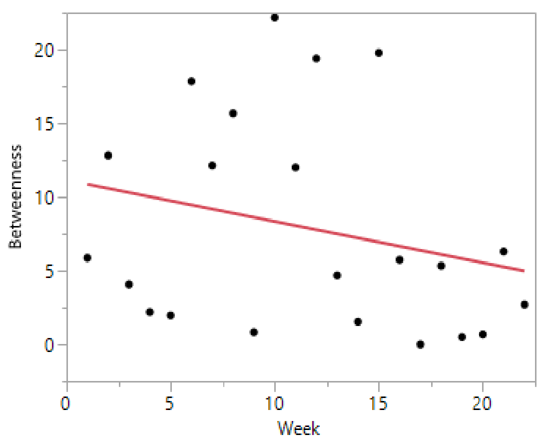


Figure 11e: Linear regression model showing a decreasing trend in agonistic interaction betweenness with time for Kusa.