Social Network Analysis of female reindeer (*Rangifer tarandus*):

Do females assort based on relatedness and age during the rut?

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A Thesis

In the Department of

Biology

Presented in Partial Fulfillment of the Requirements

For the Degree of

Master of Science (Biology) at

Concordia University

Montreal, Québec, Canada

September 2020

CONCORDIA UNIVERSITY

SCHOOL OF GRADUATE STUDIES

This is to certify that the thesis prepared

By: **Julienne Therese R. Bonoan**

Entitled: **Social Network Analysis of female reindeer (*Rangifer tarandus*): Do females**

assort based on relatedness and age during the rut?

and submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE (Biology)

complies with the regulations of the University and meets the accepted standards with respect to

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ABSTRACT

Social Network of female reindeer (*Rangifer tarandus*):

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Concordia University, 2020

Understanding the drivers of how animals socialize and associate with each other in a population has insights into the ecology, biology, and behaviour of its members. Social Network Analysis (SNA) has been growing in popularity as a tool to understand the social patterns of animal populations, where multiple factors such as age and relatedness affect social patterns. The effect of genetic relatedness and age on the social patterns of an animal population exhibiting fission-fusion group dynamics (i.e. frequent changes in group membership) was assessed using a semi-domestic herd of female reindeer (*Rangifer tarandus*), situated in Kaamanen, Finland. Analyses were done using SNA in 2009 and 2011 during the breeding season (or rut), using GPS data. We found that females had distinct social groups (or communities) and associated non-randomly in both years; however, females did not spatially assort into communities based on genetic relatedness and age. Although age did not influence community structure, age affected association levels, where females socialized with others significantly less after the age of 7. We concluded that although genetic relatedness and age may not explain the non-random spatial associations between female reindeer during the rut, there may be other factors yet to be discovered that could play a role in their social organizations. Overall, our results provided insights into the social patterns of a population exhibiting fission-fusion group dynamics.

Acknowledgement

Contribution of Authors

Dr. Robert Weladji was the principal investigator of this research with the collaboration of Dr. Guillaume Body, Dr. Øystein Holand, and Dr. Knut Røed. This work was based on the data collected by Dr. Guillaume Body, and the genetic relatedness analysis was provided by Dr. Knut Røed. For publication, the authors will be credited in the following order: Bonoan JTR, Weladji RB, Body G, Holand Ø, and Røed K.

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INTRODUCTION

Understanding the drivers of how animals in a population socialize and associate with each other to form a social system (or network) is of great importance in understanding the ecology, biology, and behaviour of its constituent members (Krause et al., 2015). The interactions between animals in which patterns describe the relationship between them forms the animal social system (Farine and Whitehead, 2015). Therefore, a social network can be defined as the social interconnectedness of different individuals based on their relationships and visualizes these interaction patterns (Krause et al., 2015). Analysis of social networks can provide insights into a multitude of processes that occur in the population, such as migration patterns (Guttal and Couzin, 2010), cooperation (Croft et al., 2006), and transmission of information (Aplin et al., 2012; Couzin et al., 2005) due to the visualization of the animal population's social patterns. Social network analysis thus has many practical applications, for example in disease management (Cross et al., 2004; Krause et al., 2007; Proffitt et al., 2012; Wey et al., 2008) or in assessing the success of conservation programs (Haydon et al., 2008).

Describing the social network of populations, however, has its fair share of limitations and challenges. One challenge is describing the social network of populations that exhibit fission-fusion group dynamics. The difficulty lies in the fact that fission-fusion groups are characterized by individuals temporarily associating and frequently changing associates as groups form and disintegrate (Aureli et al., 2008; Chapman et al., 1993; Whitehead, 1997; Whitehead and Dufault, 1999). Therefore, fission-fusion groups pose a problem as researchers describing the social network must now consider that groups may not always have the same group members to base social patterns on. Another challenge in describing the social network of

populations is the limitations of field observations that many studies employ. Some limitations of field observations include accessibility to the animals as well as the availability of observers (Brookes et al., 2018). Field observations thus poses a problem if all individuals cannot be observed, creating an inaccurate description of the social network. Therefore, in animal populations that experiences both challenges, visualizing their social network could be problematic.

Some solutions to these challenges are the combined utilization of Social Network Analysis (SNA) and Global-Positioning System (GPS) telemetry to understand the social networks of animal populations (Brookes et al., 2018; Croft et al., 2008; Krause et al., 2007; Patzelt et al., 2014; VanderWaal et al., 2017; Wey et al., 2008). The major advantage of SNA is that it can predict social networks based on an individual's association indices with others (Krause et al., 2015; Shorrocks and Croft, 2009). SNA has also been used to determine the effect of multiple factors on social cohesion and association, such as age (Carter et al., 2013a; Guilhem et al., 2000; Manno, 2008), sex (Bouskila et al., 2015; Wolf et al., 2007), reproductive status (Bouskila et al., 2015; Manno, 2008; Sundaresan et al., 2007), morphological traits (Croft et al., 2005), sociability (Lusseau et al., 2006; Manno, 2008), behaviour (Pike et al., 2008), familiarity (Hansen et al., 2009; Pinter-Wollman et al., 2009), and kinship (Silk, 2002). The major advantage of GPS telemetry, on the other hand, is the ability for a more accurate identification and positioning of individuals. Therefore, GPS telemetry coupled with SNA would benefit social network studies by providing greater detail and precision in association and network data (Kraus et al., 2011; Kurvers et al., 2013).

Based on the advantages and benefits that GPS-telemetry and SNA provide, we used such methods to investigate the effects of genetic relatedness and age in the social organization of

female reindeer. The semi-domestic herd used in this study exhibits fission-fusion group dynamics (Body et al., 2015a, b) and has been part of a long-term study concerning behaviour during the breeding season (or "rut"). To investigate the social network and association patterns of reindeer, we addressed three aims: (1) define association patterns and test for non-randomness; (2) determine if genetic relatedness is a significant predictor of associations; and (3) determine if age is also a significant predictor of association.

Many ungulate species have been found to exhibit fission-fusion group dynamics along with having preferential associates, such as wild giraffes (*Giraffa camelopardalis*) (Bashaw et al., 2007; Bercovitch and Berry, 2012; Bercovitch and Berry, 2013a; Carter et al., 2013a; Carter et al., 2013b); Konik horses (*Equus ferus caballus*) (Bouskila et al., 2015); wild boar (*Sus scrofa*) (Podgorski et al., 2014); Grevy's zebra (*Equus grevyi*) and onager (*Equus hermionus khur*) (Sundaresan et al., 2007); and feral goats (*Capra hircus*) (Stanley and Dunbar, 2013). These non-random associations were often formed between closely-related individuals (Bashaw et al., 2007; Carter et al., 2013b; Podgorski et al., 2014), conspecifics of similar ages (Bercovitch and Berry, 2013a) and of the same sex (Bercovitch and Berry, 2013b; Bouskila et al., 2015; Carter et al., 2013a; Carter et al., 2013b; Podgorski et al., 2014). Other factors may include reproductive state (Bouskila et al., 2015), demography, phenotype and environmental factors (Sundaresan et al., 2007).

Kin selection theory predicts that individuals can obtain indirect fitness benefits by cooperating with kin (Hamilton, 1964a, b). Accordingly, multiple studies have observed that females tend to associate more with conspecifics of the same sex, for example, as seen in barnacle geese (*Branta leucopsis*) (Kurvers et al., 2013); primates (Silk, 2007); spotted hyenas (*Crocula crocula*) (Smith et al., 2010); and bottlenose dolphins (*Tursios aduncus*) (Wiszniewski

et al., 2010). Several studies on ungulates have also found a significant association between mothers and their offspring (Bashaw et al., 2007; Bercovitch and Berry, 2012; Clutton-Brock and Guinness, 1982; Festa-Bianchet, 1991; Nituch et al., 2008), including reindeer (*Rangifer tarandus*) (Djaković et al., 2012; Hirotani, 1989a, 1990). Therefore, we predict that spatial associations will be positively correlated with genetic relatedness among other ungulate populations exhibiting fission-fusion group dynamics.

Individuals may tend to associate with conspecifics with similar characteristics, also known as homophily (McPherson et al., 2001). Mutual and beneficial cooperation could drive such associations among similar-aged individuals due to similar needs and interests, such as food acquisition and protection from conspecifics (Guilhem et al., 2000; Mitani et al., 2002). Some ungulate species like mouflon sheep (*Ovis gmelini*) (Guilhem et al., 2000), Southdown and Dorset Horn sheep (*Ovis aries*) (Arnold et al., 1981), Thornicroft's giraffe (*Giraffa camelopardalis thornicroftii*) (Bercovitch and Berry, 2013a), Zebu cattle (*Bos indicus*) (Reinhardt and Reinhardt, 1981), as well as reindeer (Kojola and Nieminen, 1988) were found to associate significantly more with similar-aged conspecifics. Guilhem et al. (2000) suggested that yearling mouflon sheep associated significantly more with each other due to the harassment received from older and more dominant conspecifics, which was observed in reindeer by Kojola and Nieminen (1988). Immature female giraffes that matured into young adults also had more stable and numerous affiliations with other females, which Carter et al. (2013a) suggested was due to an increase in gregariousness. Therefore, it can be predicted that individuals associate more often depending on their age.

METHODS

Study Herd and GPS Data Collection

The study was conducted at the Kutuharju Field Reindeer Research Station in Kamaanen, Finland (69°N, 27°E). A semi-domestic herd of reindeer of known pedigree has been continuously monitored during the rut since 1996, where the age and sex structure has been manipulated every year. We collected data from the Sinioivi enclosure (13.4 km^2) with a portion of the reindeer population (53 out of 92 in 2009, and 44 out of 93 in 2011), and only analyzed data from females (42 females and 11 males in 2009; 34 females and 10 males in 2011). In the years 2009 and 2011, majority of individuals (40 of 42 females in 2009 and 33 of 34 females in 2011) were fixed with Tellus GPS collars (from Followit; URL: http://wildlife.followit.se/), and their movement was followed during the rutting season (September through October) using the "reality mining" approach described in Krause et al. (2013), which is the collection and analysis of animal social behaviour from animal-borne technologies with the goal of modelling their behaviour patterns. However, due to malfunctions in some of the GPS collars, only 35 females (out of 40) in 2009 and 32 females (out of 33) in 2011 were included in the analyses.

The rutting season was divided between periods for further analysis by following the method defined by Body et al. (2015a): Pre-rut (September 17-28, 2009; September 10-29, 2011); Peak-rut (September 29-October 4, 2009; September 30-October 6, 2011); and Post-rut (October 5-November 2, 2009; October 7-15, 2011). To ensure that all individuals were being analyzed for the same recording period, some GPS recordings in the beginning and end were removed for consistency. The GPS collars synchronously recorded reindeer positions every hour

in 2009 and every 15 minutes in 2011. Group composition was also verified by locating groups in the field where identification of individuals in the group was accomplished by unique collar identification numbers (Body et al., 2015b). Calves were not fixed with identification and GPS collars, and were thus excluded from this study. Females in 2009 were between the ages of 1 and 7, while females in 2011 were between ages 1 and 11.

Statistical Analyses

All statistical analyses were conducted using the program R (R Core Team, 2018).

Aim #1: Define Association Patterns and Test for Non-Randomness

Before investigating the effect of relatedness and age on the association patterns of female reindeer, communities must first be defined. Communities are clusters or social groups of well-connected individuals (James, 2015), and if a network is found to have a well-defined community structure, we can then determine if age and/or relatedness play a role in this organization.

Communities were based on the association patterns between female dyads, in which two individuals belong to the same group if their interindividual distance was below 89 meters (r_{max}, the intragroup maximal distance which represents the distance to the nearest neighbour and in which 95% of association patterns can be estimated from; see Body et al. (2015a) for further information). Using the R package SPATSOC (Robitaille et al., 2019), association between dyads (i.e. edges) was calculated using the simple ratio index (SRI), which is an unbiased estimate for the proportion of time individuals are seen together (Cairns and Schwager, 1987; Whitehead and Dufault, 1999). SRI can be calculated as follows:

$$\text{SRI} = \frac{x}{x+y_a+y_b+y_{ab}}$$

where x = the number of sampling periods with both reindeer **a** and **b** observed in the same group; y_a = the number of sampling periods with only reindeer **a** observed but not **b**; y_b = the number of sampling periods with only reindeer **b** observed but not **a**; and y_{ab} = the number of sampling periods reindeer **a** and **b** are observed but not in the same group. SRI can range between 0 (never seen together) to 1 (always seen together) (Cairns and Schwager, 1987; Whitehead and Dufault, 1999).

Females were then assigned to communities in each period (Pre-, Peak-, and Post-rut) based on the most parsimonious division of the network, which provides the most edges within communities and the least between, represented as the modularity coefficient, Q (Lusseau et al., 2008; Newman, 2006). Afterwards, communities were visualized as a social network using the R package 'igraph' (Csardi and Nepusz, 2006). A social network encompasses every individual in a specific population and consists of a set of n nodes representing each individual in the network and a set of E edges representing the social link between each individual (James, 2015).

After defining the communities in the network in each year, it needs to be determined whether females were not simply associating at random, and thus producing random communities. Null hypothesis significance testing (James, 2015) was used for this purpose and was done using a data-stream randomization technique in R using SPATSOC (Robitaille et al., 2019). Randomization of the data involved swapping individuals and group observations within or between temporal groups and individuals (Farine, 2017). Briefly, null hypothesis significance testing is done by comparing the observed data to a random set of data while keeping the number of individuals and associations the same (Whitehead, 2008b; Whitehead et al., 2005). The

coefficient of variation (CV) of the association index (i.e. SRI) was used as a test statistic, where significance was based on whether the observed SRI falls in the top or bottom 2.5% of the distribution of the random SRI data sets (>0.975 or <0.025, two tailed test), in which it can reject the hypothesis that the real value could have arisen by chance (Carter et al., 2013b; Djaković et al., 2012; Frere et al., 2010b; Whitehead et al., 2005).

Aim #2: Effect of Relatedness on Association Patterns

Blood samples were obtained from all reindeer and was analyzed for 12 DNA microsatellite loci to assess relatedness: Re03A, Re16A, Re31A, Re73A, Bm4513A, Re01A, Re48A, Re66A, FCB193A, Rt01A, RT7A, and Rt30A. Relatedness (*r*) was estimated for all female dyads with GPS collars for each year using the program GenAlEx v 6.5 (Peakall and Smouse, 2006, 2012). Unfortunately, all individuals in the population were not accounted for (2009: 53 genotyped out of 93; 2011: 44 genotyped out of 92); therefore, parentage and sibship of female dyads were estimated using the software COLONY v 2.0.6.5 (Jones and Wang, 2010). Probabilities of sibship was highly correlated with the Lynch & Ritland (1999) mean (LRM) relatedness estimator; therefore, LRM was used for the relatedness data.

General linear models (GLM) were initially used to evaluate the effect of relatedness, period (Pre-, Peak-, and Post-rut), and year (2009 and 2011) on female associations (SRI). However, due to non-normal and heteroscedastic residuals, generalized least squares (GLS) models were used with exponentially transformed SRI ($\lambda = 0.375$) based on the Tukey's Ladder of Powers where lambda (λ) represents the power coefficient to transform values (Mangiafico, 2016). The Akaike Information Criterion (AIC) score was then used to determine the best fitting

model. Afterwards, ANOVA was used to determine statistical significance of period and year on SRI.

A logistic regression with a binomial distribution was also used to determine if female associations (SRI) and relatedness differed between communities in each period and year. Due to non-normal and heteroscedastic residuals during the Peak-rut in both 2009 and 2011, GLS was used with exponentially transformed SRI ($\lambda_{2009} = 0.425$; $\lambda_{2011} = 0.375$) and followed by ANOVA to determine statistical significance. Relatedness was also exponentially transformed in both 2009 ($\lambda = -1.55$) and 2011 ($\lambda = -1.125$) to achieve normal residuals.

Aim #3: Effect of Age on Association Patterns

To investigate how age affects association levels, three individual-level network metrics (strength, affinity, and eigenvector centrality) were calculated using SRI in each year using the SPATSOC package in R (Robitaille et al., 2019). Strength is the weighted equivalent of degree (the number of edges a node is connected to), calculated as the sum of all weights of the edges connected to a node (Farine and Whitehead, 2015; James, 2015; Whitehead, 2008a). Strength represents gregariousness where individuals with high strength have strong associations with others and/or have many associates (Whitehead, 2008a). Affinity is the mean strength of an individual's associates (Whitehead, 2008a). A high affinity value either represents stronger relationships made by the individual's associates or an increase in the number of associates, whereas a low affinity value suggests the weakening of relationships with an individual's associates or a decrease in the number of associates (Whitehead, 2008a). Eigenvector centrality is the sum of the centralities (how well connected individuals are to others based on degree and strength) of an individual's connections (Farine and Whitehead, 2015). A high eigenvector centrality measure (either from a high degree or connections to individuals with high degrees)

would indicate that the individual is an important hub for sociality and/or transfer of information and disease in the network (Farine and Whitehead, 2015).

Preliminary analysis with GLM indicated heteroscedastic residuals; therefore, GLS models were also used such as in *Aim #2* to evaluate the effect of age, period, and year on female associations (strength, affinity, and eigenvector centrality). All individual-level metrics were exponentially transformed as well to achieve normality of residuals: $\lambda_{strength} = 0.675$; $\lambda_{affinity} = -0.675$; $\lambda_{eigenvector} = 2.35$. Afterwards, Kruskal-Wallis test or Welch's ANOVA was used to determine if female associations were statistically different between ages and age class ("Younger" females were between ages 1 and 7; "Older" females were between 9 and 11). "Younger" females may not necessarily be considered young, neither are "Older" females necessarily considered old; these are just classifications used in our analysis. Affinity was exponentially transformed ($\lambda = -0.675$), as well as eigenvector centrality ($\lambda = 2.35$) to achieve normal residuals.

Finally, to test if age affected community structure, ANOVA/Kruskal-Wallis test/Welch's ANOVA were used to determine if age was statistically different between communities in each period and year. Age was exponentially transformed ($\lambda = 0.45$) in 2009 for the Post-rut, as well as Affinity ($\lambda = -1.45$) in 2011 for the Post-rut to achieve normal residuals.

RESULTS

Aim #1: Define Association Patterns and Test for Non-Randomness

Females had distinct communities of varying sizes during all periods (Pre-, Peak-, and Post-rut) in both years (Fig. 1). In 2009, 35 females associated with each other to form three communities during the Pre-rut (communities consisted of 10, 12, and 13 females; Fig. 1A) and Peak-rut (communities consisted of 5, 14, and 16 females; Fig. 1B), and two communities during the Post-rut (communities consisted of 15 and 20 females; Fig. 1C). In 2011, 32 females formed four different communities during the Pre-rut (communities consisted of 5, 6, 8, and 13 females; Fig 1D) and three communities during the Peak-rut (two communities with 8 females and another with 16; Fig. 1E), and Post-rut (two communities with 10 females and another with 12; Fig. 1F).

These communities were also found to be formed by non-random associations based on comparing the CV between the observed and random data. The CV of the observed networks during Pre-, Peak-, and Post-rut in 2009 (Pre-rut: observed CV = 0.76, random CV = 0.22, $p <$ 0.001; Peak-rut: observed CV = 0.61, random CV = 0.21, $p < 0.001$; Post-rut: observed CV = 0.61, random CV = 0.21, $p < 0.001$) and 2011 (Pre-rut: observed CV = 1.06, random CV = 0.18, $p < 0.001$; Peak-rut: observed CV = 0.99, random CV = 0.18, $p < 0.001$; Post-rut: observed CV = 0.91, random CV = 0.18, $p < 0.001$) were all significantly higher than the random networks

Aim #2: Effect of Relatedness on Association Patterns

We found that relatedness was not a significant predictor of association strength between dyads (represented as SRI). The GLS model with the lowest AIC score was found to have a weight matrix with variance structure that changes according to period and year. The interaction

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between period and year was significant (ANOVA: $F_{1,3261} = 26.82$, $p < 0.001$), where mean SRI increased from Pre-rut to Peak-rut followed by a decrease from Peak-rut to Post-rut in both years. Mean SRI was significantly lower in the Pre-rut in comparison to the Peak-rut (post-hoc test, 2009: $p < 0.001$; 2011: $p < 0.001$) and Post-rut (post-hoc test, 2009: $p = 0.023$; 2011: $p < 0.0001$). Mean SRI was also higher in the Peak-rut in comparison to Post-rut in 2009 (post-hoc test, $p < 0.001$); however, was not significantly different in 2011 (post-hoc test, $p = 0.244$). Relatedness was not found to be a significant predictor (GLS: $t_{3273} = -0.93$, $p = 0.354$). If females preferred to spatially associate with relatives, then mean relatedness would have been significantly higher within communities in comparison to between communities; however, this was not the case (Fig. 2C and D).

In 2009, there was no significant difference in dyadic female association (SRI) between communities in the Pre-rut (ANOVA, $F_{3,591} = 0.32$, $p = 0.811$, Fig. 2A) and the Post-rut (ANOVA, $F_{2,592} = 2.82$, $p = 0.060$, Fig. 2A). However, mean SRI was significantly different between communities in the Peak-rut (ANOVA, $F_{3,591} = 552.58$, $p < 0.001$, Fig. 2A). On the other hand, there was no significant difference in mean relatedness between communities in all periods (ANOVA, Pre-rut: $F_{3,591} = 0.74$, $p = 0.529$; Peak-rut: $F_{3,591} = 0.74$, $p = 0.529$; Post-rut: $F_{2,592} = 1.29$; $p = 0.276$; Fig. 2C). Therefore, although females associated with each other more within communities in comparison to between communities, female preference may not be due to choosing relatives in 2009.

In 2011, mean SRI was not significantly different between communities in the Pre-rut (ANOVA, $F_{4,492=} = 1.63$, $p = 0.165$, Fig. 2B) and Post-rut (ANOVA, $F_{3,492} = 0.39$, $p = 0.764$, Fig. 2B); however, mean SRI was significantly different between communities in the Peak-rut (ANOVA, $F_{3,492} = 264.66$, $p < 0.001$, Fig. 2B). On the other hand, relatedness was not

significantly different between communities in all periods as well (ANOVA, Pre-rut: $F_{4,491}$ = 1.24, p = 0.293; Peak-rut: $F_{4,491}$ = 1.24, p = 0.293; Post-rut: $F_{3,492}$ = 0.76, p = 0.515; Fig. 2D). Much like in 2009, although females associated more within communities in comparison to between communities, females may not have necessarily preferred certain females based on relatedness.

Aim #3: Effect of Age on Association Patterns

The GLS model with the lowest AIC score was found to have a weight matrix with variance structure that changes according to year, period and age for Strength and Affinity, but only a variance structure that changes according to year and period for Eigenvector Centrality. ANOVA results found that the interaction between period and year was significant for Strength (ANOVA, $F_{2,189}$ = 24.47, p < 0.001) and Affinity (ANOVA, $F_{2,189}$ = 24.47, p < 0.001), but not for Eigenvector Centrality (ANOVA, $F_{2,189}$ = 0.38, p = 0.682). Mean Strength increased from Pre-rut to Peak-rut, followed by a decrease in Post-rut; whereas, mean Affinity had an opposite trend with a decrease from Pre-rut to Peak-rut, followed by an increase in Post-rut. This indicates that from Pre-rut to Peak-rut, individuals associated with other females more; however, their associates had weaker relationships with other females. A decrease in mean strength from Peak-rut to Post-rut indicates that females has weaker relationships with their associates, while a paralleled increase in affinity indicates said associates grew stronger bonds with other females.

On the other hand, mean Eigenvector Centrality was significantly different between years (ANOVA, $F_{1,189}$ = 22.22, p < 0.001) and periods (ANOVA, $F_{2,189}$ = 5.47, p = 0.005), in which Pre-rut was significantly lower in mean Eigenvector Centrality in comparison to Peak-rut (post-hoc test, p = 0.026) and Post-rut (post-hoc test, p = 0.033). This indicates that individuals were more central in their communities during Peak- and Post-rut in comparison to Pre-rut. A

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Pearson's correlation test also found that individual-level metrics (Strength, Affinity, Eigenvector Centrality) were highly correlated with each other: Strength and Affinity, r_{199} = -0.57, $p < 0.000$; Strength and Eigenvector Centrality, r_{199} = 0.75, $p < 0.000$; Affinity and Eigenvector Centrality, r_{199} = -0.58, $p < 0.000$.

ANOVA on GLS models also revealed that age was a significant variable for all individual-level metrics (Strength, $F_{1,189}$ = 34.86, $p < 0.0001$; Affinity, $F_{1,189}$ = 34.86, $p < 0.001$; Eigenvector Centrality, $F_{1,189}$ = 13.16, $p < 0.001$). Mean Strength was significantly lower in females at age 10 in comparison to females at the ages of 1, 3, and 5 (post-hoc test, $p < 0.05$, Fig. 3A). This means that females at ages 1, 3, and 5 had either more associates or stronger relationships in comparison to females at age 10. Mean Affinity was significantly higher in females at age 10 in comparison to females at age 1 (post-hoc test, $p = 0.047$, Fig. 3C), suggesting that females at age 1 were more close-knit with others of similar age in comparison to females at age 10. Mean Eigenvector Centrality was significantly higher in females at ages 1-5 and 7, in comparison to females at the ages of 9 to 11 (post-hoc test, $p < 0.005$, Fig. 3E), indicating that females at ages 1-5 and 7 were more central to the network in comparison to females at ages 9 to 11.

Females were then divided between two age classes: "Younger" (females 1-7 years old) and "Older" (females 9+ years old). In comparison to "Older" females, "Younger" females had significantly higher mean Strength (Kruskal-Wallis, chi-squared = 19.38, df = 1, $p < 0.000$, Fig. 2B), significantly lower mean Affinity (ANOVA, $F_{1,199}$ = 22.38, $p < 0.000$, Fig. 3D), and significantly higher mean Eigenvector Centrality (Kruskal-Wallis, chi-squared = 34.30, df = 1, $p < 0.000$, Fig. 3F). These results indicate that in comparison to "Older" females, "Younger"

females had stronger bonds with their associates, where said associates had weaker bonds with neighbouring females; however, focal animals were more central in their networks.

An ANOVA test found that Age was significantly different between communities during the Pre-rut in 2011 (ANOVA, $F_{3,28} = 3.151$, $p = 0.041$); however, a post hoc test determined that communities were not significantly different in mean Age ($p > 0.05$). Age was also not found to be significantly different across communities across all periods and years: 2009 (Pre-rut: ANOVA, $F_{2,32} = 1.49$, $p = 0.241$; Peak-rut: Kruskal-Wallis, chi-squared = 2.25, df = 2, $p = 0.324$; Post-rut: ANOVA, $F_{1,33} = 1.60$, $p = 0.215$; Fig. 2E); and 2011 (Peak-rut: ANOVA, $F_{2,29} = 1.47$, $p = 0.246$; Post-rut: ANOVA, $F_{2,29} = 2.16$, $p = 0.133$; Fig. 2F).

DISCUSSION

Aim #1: Defining Association Patterns and Test for Non-Randomness

Our results showed that the reindeer population in both years had distinct and non-random communities (Fig. 1). In support of our predictions, we found that female reindeer did not associate randomly, suggesting that they had preferred associations because the observed CV was well above the 97.5% of the distribution of the random data (Frere et al., 2010a). Our findings were similar to those by Djaković et al. (2012) on the same experimental population; however, in different years and based on field observations. Several authors in ungulate species exhibiting fission-fusion dynamics have reported non-random and preferred association patterns (Bashaw et al., 2007; Bercovitch and Berry, 2012; Bercovitch and Berry, 2013a; Bouskila et al., 2015; Carter et al., 2013a; Carter et al., 2013b; Podgorski et al., 2014; Stanley and Dunbar, 2013; Sundaresan et al., 2007).

We found differences in the number of communities between the years (Fig. 1), which may be due to the difference in the rate of location recording. In 2009, recordings were made every hour while recordings were made every 15 minutes in 2011. Therefore, the data from 2011 may give a more accurate description of the social network because of the higher rate of recording. However, the overall decrease in the number of communities from pre-rut to post-rut in both years is supported by the findings from Body et al. (2015a). Indeed, the number of groups decreased, and average size of groups increased right before the beginning of the peak-rut.

The cohesiveness observed in the peak-rut by Body et al. (2015a) as well as an increase in the association levels during peak-rut observed by Djaković et al. (2012) supports our findings as we observed female associations, represented by SRI and the individual-level metrics (strength and eigenvector centrality), to increase from pre-rut to peak-rut (Fig. 2). An increase in

strength usually results from stronger association levels or an increase in the number of associates (or "degree") (Whitehead, 2008a). However, degree did not change between periods (34 in 2009 and 31 in 2011. The decrease in affinity from pre-rut to peak-rut thus shows that the increase in mean strength during this time resulted from stronger association levels rather than an increase in number of associates, paralleling the cohesiveness of groups during the peak-rut observed by Body et al. (2015a). The increase in mean eigenvector centrality from pre-rut to peak-rut would then also be a consequence of the increased cohesiveness observed in the peak-rut by Body et al. (2015a).

The decrease in cohesiveness and thus higher fission rate (i.e. increase in group number and decrease in average group size) after the peak-rut is also supported by the observed results in SRI, strength, affinity, and eigenvector centrality. Mean SRI, strength and eigenvector centrality all decreased while mean affinity increased from peak-rut to post-rut. A decrease in SRI, strength, and eigenvector centrality suggests that after the peak-rut, focal animals are associating with their preferred associates less and becoming less central to their network; whereas an increase in affinity indicates that an individual's associates are spending more time with females outside their designated communities. However, the number of communities should have increased from peak-rut to post-rut based on the high fission rate, but the number of communities either decreased (in 2009) or remained the same (in 2011) from peak-rut to post-rut. This may be attributed to solitary females forming groups during this time (Body et al., 2015a), which is supported by a higher mean SRI, strength, and eigenvector centrality (and lower mean affinity) in the post-rut in comparison to the pre-rut. The non-random preferred associations between females could be attributed to several factors, including male herding as suggested by Djaković et al. (2012), or female preference for relatedness and/or age, which have been shown to

influence the social behaviours of other ungulate species (Bashaw et al., 2007; Bercovitch and Berry, 2013a; Carter et al., 2013b; Podgorski et al., 2014). However, we did not find supportive evidence that females are spatially assorting based on relatedness and/or age.

Aim #2: Effect of Relatedness on Association Patterns

We found that association strength (i.e. SRI) did not vary with relatedness, which is contrary to our predictions. We predicted female association levels would be positively correlated with increasing genetic relatedness among female reindeer based on multiple studies on ungulates (Bashaw et al., 2007; Bercovitch and Berry, 2012; Carter et al., 2013b; Clutton-Brock and Guinness, 1982; Festa-Bianchet, 1991; Nituch et al., 2008; Reinhardt and Reinhardt, 1981). Hirotani (1989a, 1990) and Djaković et al. (2012) also found that associations were significantly stronger between mother-offspring dyads in female reindeer.

This could be due to the inability to recognize kin; however, there is reason to believe that this is not the case in this reindeer population. Engelhardt et al. (2016b) found evidence to support the kin selection hypothesis during the calving period (May to June), where offspring were allonursed (nursing of non-offspring) more often by mothers who were closely related as opposed to if the mothers were distantly related to each other. This provides evidence that females can identify kin and show cooperative behaviour, which may have provided adaptive and nutritional benefits to closely related offspring (Engelhardt et al., 2016a). It would then be sensible to think that females are able to continue this cooperation between kin during other times of the year, including the rut (September to October). However, we found no evidence to support kin preference in spatial associations during this time.

According to the kin selection theory, although genetic relatedness could enhance the indirect benefits received by the social group, individuals should disperse to avoid imposing

costs on kin (Hamilton, 1964a, b). If reindeer choose not to spatially associate with kin despite the ability to recognize them during the rut, there is a possibility that the cost of staying with family is greater than the benefits associated with it. There are multiple studies providing evidence for the indirect benefits of kin association among females, such as higher reproductive success (Pope, 2000; Silk, 2007; Viblanc et al., 2010), increased foraging efficiency (Griffiths and Armstrong, 2002), decrease in aggressive encounters (Dobson et al., 2000; Konig, 1994; Rusu and Krackow, 2004), increased growth rates (Gerlach et al., 2007), reduction in resource competition (Silk, 2007), and increased offspring survival (Dobson et al., 2000; Silk, 2007). However, there are also costs to kin association such as lowered chance of survival and mating (Reyer, 1984), increase risk of inbreeding (Sugg et al., 1996), or costs of grouping unrelated to kin association, for example a decrease in foraging efficiency (Creel et al., 2014; Molvar and Bowyer, 1994; Uccheddu et al., 2015).

A study by Uccheddu et al. (2015) on reindeer during the rut found that an increase in group size led to a decrease in foraging efficiency in females. During the rut, a dominant male herds females into a group (or "harem") and drives off satellite/subdominant males that attempt to copulate with the females (Uccheddu et al., 2015). However, an increase of 6-7 females in the group negates any gains from harassment protection as foraging efficiency decreased. Therefore, females may not necessarily be spatially assorting with kin due to the costs that it could impose in the form of reduced foraging efficiency.

Another possible reason for our observed results could be that relatedness may not play a role in spatial association because most association studies look at amiable and agonistic behaviours within groups/communities, where relatedness may play a role. Djaković et al. (2012) and Hirotani (1989b; 1990) found that female reindeer, especially mother-daughter dyads,

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associated significantly more in comparison to less-related females during the rut. However, these results were based on the social behaviours obtained via field observations of groups, which do not take into consideration the fission-fusion dynamics of the population. A side analysis where I incorporated the relatedness categories Djaković et al. (2012) used ($r = 0$, $r = 0.0625$, $r = 0.125$, $r = 0.25$, $r = 0.50$) also showed no significant difference in mean SRI between relatedness categories per period (ANOVA on GLS, $F_{8,3213} = 0.617$, $p = 0.7643$). Although relatedness may play a role on the spatial association within communities, we found no evidence to suggest that female reindeer prefer to spatially associate with kin on a population-level.

Aim #3: Effect of Age on Association Patterns

We also predicted that younger and lower-ranking females would associate significantly more with each other due to the harassment from older and higher-ranking individuals. These predictions are based on the age-homophily observed in other ungulate species like mouflon sheep (Guilhem et al., 2000), Southdown and Dorset Horn sheep (Arnold et al., 1981), Thornicroft's giraffe (Bercovitch and Berry, 2013a), Zebu cattle (Reinhardt and Reinhardt, 1981), as well as reindeer (Kojola and Nieminen, 1988). Kojola and Nieminen (1988) also observed that older and higher-ranking females harassed younger and lower-ranking conspecifics, which led to younger females grouping together. However, we did not find evidence to support that females spatially assorted or grouped themselves into communities based on age.

If females preferred to be spatially approximate to similar-aged individuals, then we would have expected to see communities have significantly different mean ages. However, mean SRI was only significantly different between communities during the peak-rut in both 2009 and 2011 (Fig. 2A and B), and mean age was not significantly different between communities in all

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periods and years (Fig. 2E and F). Although we did not see females group together or spatially assort based on age, we did, however, find that age was still a significant factor in female association levels, represented by the individual-level metrics (strength, affinity, and eigenvector centrality) (Fig. 3A, C, and E). Significant differences in means were observed when comparing females below the age of 7 to those above this age; therefore, we wanted to see if association levels differed at this supposed age threshold.

We found that "Younger" females (ages 1 to 7) were significantly more social than "Older" females (ages 9 to 11) by showing higher mean strength, lower mean affinity, and higher mean eigenvector centrality (Fig. 3B, D, and F). These results are similar to the observed results found by Guilhem et al. (2000) in mouflon sheep, in which inter-individual distance increased with age. Our results may be attributed to the social ranks among female reindeer as well as the senescence effect. Like other ungulate species, dominance is linearly correlated to age in female reindeer (Holand et al., 2004); however, only in females under 8 years of age. No relationship between social rank and age was found in females 8 years or older when the senescent effect began to hinder reindeer performance (Weladji et al., 2002). Therefore, older females may not be associating with other females as much as younger females to decrease competition even though older females are still able to hold a high rank.

We may have also observed older females associating significantly less than younger females because of the disparity in sampling number – there were only 12 females above the age of 7 in total. There was high variance in the individual-level metrics across ages, where we do not often see a significant difference between females under the age of 7 and those above. Therefore, although we observed that females above the age of 7 were associating significantly

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less than females under the age of 7 in the years 2009 and 2011, we may observe different results

in other years with a more equal age distribution and thus needs to be validated by other studies.

CONCLUSION

We found that a semi-domestic population of reindeer formed non-random communities with preferred individuals during the rut; however, relatedness and age were not contributing factors in their spatial assortment or grouping behaviour. Despite the possible indirect benefits associated with kin association, relatedness may not play a role in spatial associations during the rut at the population-level due to the costs that individuals could impose on kin. Also, although age did not affect spatial assortment, females above the age of 7 socialized less with conspecifics, which could be due to the senescence effect and competition avoidance. These social patterns may be observed during the time outside of the rut; however, further analysis must be done specific to these time periods.

REFERENCES

Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC, 2012. Social networks predict patch discovery in a wild population of songbirds. Proceedings of the Royal Society B-Biological Sciences 279:4199-4205. doi: 10.1098/rspb.2012.1591.

Arnold GW, Wallace SR, Rea WA, 1981. Associations between individuals and home-range behavior in natural flocks of 3 breeds of domestic sheep. Applied Animal Ethology 7:239-257. doi: 10.1016/0304-3762(81)90081-x.

Aureli F, Schaffner Colleen M, Boesch C, Bearder Simon K, Call J, Chapman Colin A, Connor R, Fiore Anthony D, Dunbar Robin IM, Henzi SP, Holekamp K, Korstjens Amanda H, Layton R, Lee P, Lehmann J, Manson Joseph H, Ramos-Fernandez G, Strier Karen B, Schaik Carel Pv, 2008. Fission-Fusion Dynamics: New Research Frameworks. Current Anthropology 49:627-654. doi: 10.1086/586708.

Bashaw MJ, Bloomsmith MA, Maple TL, Bercovitch FB, 2007. Structure of social relationships among captive female giraffe (Giraffia camelopardalis). Journal of Comparative Psychology 121:46-53. doi: 10.1037/0735-7036.121.1.46.

Bercovitch FB, Berry PSM, 2012. Herd composition, kinship and fission-fission social dynamics among wild giraffe. African Journal of Ecology 51:206-216.

Bercovitch FB, Berry PSM, 2013a. Age proximity influences herd composition in wild giraffe. Journal of Zoology 290:281-286. doi: 10.1111/jzo.12039.

Bercovitch FB, Berry PSM, 2013b. Herd composition, kinship and fissionfusion social dynamics among wild giraffe. African Journal of Ecology 51:206-216. doi: 10.1111/aje.12024.

Body G, Weladji RB, Holand O, Nieminen M, 2015a. Fission-fusion group dynamics in reindeer reveal an increase of cohesiveness at the beginning of the peak rut. Acta Ethologica 18:101-110. doi: 10.1007/s10211-014-0190-8.

Body G, Weladji RB, Holand O, Nieminen M, 2015b. Measuring variation in the frequency of group fission and fusion from continuous monitoring of group sizes. Journal of Mammalogy 96:791-799. doi: 10.1093/jmammal/gyv084.

Bouskila A, Lourie E, Sommer S, de Vries H, Hermans ZM, van Dierendonck M, 2015. Similarity in sex and reproductive state, but not relatedness, influence the strength of association in the social network of feral horses in the Blauwe Kamer Nature Reserve. Israel Journal of Ecology & Evolution 61:106-113. doi: 10.1080/15659801.2016.1149921.

Brookes VJ, VanderWaal K, Ward MP, 2018. The social networks of free-roaming domestic dogs in island communities in the Torres Strait, Australia. Preventive Veterinary Medicine. doi: https://doi.org/10.1016/j.prevetmed.2018.09.008.

Cairns SJ, Schwager SJ, 1987. A Comparison of Association Indexes. Animal Behaviour 35:1454-1469. doi: 10.1016/s0003-3472(87)80018-0.

Carter KD, Brand R, Carter JK, Shorrocks B, Goldizen AW, 2013a. Social networks, long-term associations and age-related sociability of wild giraffes. Animal Behaviour 86:901-910. doi: 10.1016/j.anbehav.2013.08.002.

Carter KD, Seddon JM, Frere CH, Carter JK, Goldizen AW, 2013b. Fission-fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. Animal Behaviour 85:385-394. doi: 10.1016/j.anbehav.2012.11.011.

Chapman CA, White FJ, Wrangham RW, 1993. Defining subgroup size in fission-fusion societies. Folia Primatologica 61:31-34. doi: https://doi.org/10.1159/000156724.

Clutton-Brock TH, Guinness FE, 1982. Red Deer: Behavior and Ecology of Two Sexes: University of Chicago Press.

Couzin ID, Krause J, Franks NR, Levin SA, 2005. Effective leadership and decision-making in animal groups on the move. Nature 433:513-516. doi: 10.1038/nature03236.

Creel S, Schuette P, Christianson D, 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology 25:773-784. doi: 10.1093/beheco/aru050.

Croft DP, James R, Krause J, 2008. Exploring Animal Social Networks. Princeton, New Jersey: Princeton University Press.

Croft DP, James R, Thomas POR, Hathaway C, Mawdsley D, Laland KN, Krause J, 2006. Social structure and co-operative interactions in a wild population of guppies (Poecilia reticulata). Behavioral Ecology and Sociobiology 59:644-650. doi: 10.1007/s00265-005-0091-y.

Croft DP, James R, Ward AJW, Botham MS, Mawdsley D, Krause J, 2005. Assortative interactions and social networks in fish. Oecologia 143:211-219. doi: 10.1007/s00442-004-1796-8.

Cross PC, Lloyd-Smith JO, Bowers JA, Hay CT, Hofmeyr M, Getz WM, 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. Annales Zoologici Fennici 41:879-892.

Author. 2006. The igraph software package for complex network research. InterJournal.

Djakovic N, Holand O, Hovland AL, Roed KH, Weladji RB, Fjeldstad E, Nieminen M, 2012. Association patterns and kinship in female reindeer (Rangifer tarandus) during rut. Acta Ethologica 15:165-171. doi: 10.1007/s10211-011-0121-x.

Djaković N, Holand Ø, Hovland AL, Røed KH, Weladji RB, Fjeldstad E, Nieminen M, 2012. Association patterns and kinship in female reindeer (*Rangifer tarandus*) during rut. Acta Theologica 15:165-171.

Dobson FS, Jacquot C, Baudoin C, 2000. An experimental test of kin association in the house mouse. Canadian Journal of Zoology-Revue Canadienne De Zoologie 78:1806-1812. doi: 10.1139/cjz-78-10-1806.

Engelhardt SC, Weladji RB, Holand O, Nieminen M, 2016a. Allosuckling in reindeer (Rangifer tarandus): A test of the improved nutrition and compensation hypotheses. Mammalian Biology 81:146-152. doi: 10.1016/j.mambio.2015.10.003.

Engelhardt SC, Weladji RB, Holand O, Roed KH, Nieminen M, 2016b. Allonursing in reindeer, Rangifer tarandus: a test of the kin-selection hypothesis. Journal of Mammalogy 97:689-700. doi: 10.1093/jmammal/gyw027.

Farine DR, 2017. A guide to null models for animal social network analysis. Methods in Ecology and Evolution 8:1309-1320. doi: 10.1111/2041-210x.12772.

Farine DR, Whitehead H, 2015. Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology 84:1144-1163. doi: 10.1111/1365-2656.12418.

Festa-Bianchet M, 1991. The Social System of Bighorn Sheep - Grouping Patterns, Kinship and Female Dominance Rank. Animal Behaviour 42:71-82. doi: 10.1016/s0003-3472(05)80607-4.

Frere CH, Krutzen M, Mann J, Connor RC, Bejder L, Sherwin WB, 2010a. Social and genetic interactions drive fitness variation in a free-living dolphin population. Proceedings of the

National Academy of Sciences of the United States of America 107:19949-19954. doi: 10.1073/pnas.1007997107.

Frere CH, Krutzen M, Mann J, Watson-Capps JJ, Tsai YJ, Patterson EM, Connor R, Bejder L, Sherwin WB, 2010b. Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. Animal Behaviour 80:481-486. doi: 10.1016/j.anbehav.2010.06.007.

Gerlach G, Hodgins-Davis A, MacDonald B, Hannah RC, 2007. Benefits of kin association: related and familiar zebrafish larvae (Danio rerio) show improved growth. Behavioral Ecology and Sociobiology 61:1765-1770. doi: 10.1007/s00265-007-0409-z.

Griffiths SW, Armstrong JD, 2002. Kin-biased territory overlap and food sharing among Atlantic salmon juveniles. Journal of Animal Ecology 71:480-486. doi: 10.1046/j.1365-2656.2002.00614.x.

Guilhem C, Bideau E, Gerard JF, Maublanc ML, 2000. Agonistic and proximity patterns in enclosed mouflon (Ovis gmelini)ewes in relation to age, reproductive status and kinship. Behavioural Processes 50:101-112. doi: 10.1016/s0376-6357(00)00094-2.

Guttal V, Couzin ID, 2010. Social interactions, information use, and the evolution of collective migration. Proceedings of the National Academy of Sciences of the United States of America 107:16172-16177. doi: 10.1073/pnas.1006874107.

Hamilton WD, 1964a. Genetical evolution of social behavior. I. Journal of Theoretical Biology 7:1-16.

Hamilton WD, 1964b. Genetical evolution of social behaviour. II. Journal of Theoretical Biology 7:17-52. doi: https://doi.org/10.1016/0022-5193(64)90039-6.

Hansen H, McDonald DB, Groves P, Maier JAK, Ben-David M, 2009. Social Networks and the Formation and Maintenance of River Otter Groups. Ethology 115:384-396. doi: 10.1111/j.1439-0310.2009.01624.x.

Haydon DT, Morales JM, Yott A, Jenkins DA, Rosatte R, Fryxell JM, 2008. Socially informed random walks: incorporating group dynamics into models of population spread and growth. Proceedings of the Royal Society B-Biological Sciences 275:1101-1109. doi: 10.1098/rspb.2007.1688.

Hirotani A, 1989a. Social relationships of reindeer *Rangifer tarandus* during rut - implications for female choice. Applied Animal Behaviour Science 24:183-202.

Hirotani A, 1989b. Social relationships of reindeer Rangifer tarandus during rut: Implications for female choice. Applied Animal Behaviour Science 24:183-202.

Hirotani A, 1990. Social-organization of reindeer (rangifer-tarandus), with special reference to relationships among females. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68:743-749.

Holand Ø, Gjostein H, Losvar A, Kumpula J, Smith ME, Roed KH, Nieminen M, Weladji RB, 2004. Social rank in female reindeer (Rangifer tarandus): effects of body mass, antler size and age. Journal of Zoology 263:365-372.

James R, 2015. A networks primer. In: Krause J, James R, Franks DW, Croft DP, editors. Animal Social Networks New York, USA: Oxford University Press.

Jones O, Wang J, 2010. COLONY: A program for parentage and sibship inference from multilocus genotype data. Molecular ecology resources 10:551-555. doi: 10.1111/j.1755-0998.2009.02787.x.

Kojola I, Nieminen M, 1988. Aggression and Nearest Neighbour Distances in Female Reindeer During the Rut. Ethology 77:8.

Konig B, 1994. Components of Lifetime Reproductive Success in Communally and Solitarily Nursing House Mice - A Laboratory Study. Behavioral Ecology and Sociobiology 34:275-283. doi: 10.1007/s002650050043.

Kraus RHS, Kerstens HHD, Van Hooft P, Crooijmans R, Van der Poel JJ, Elmberg J, Vignal A, Huang YH, Li N, Prins HHT, Groenen MAM, 2011. Genome wide SNP discovery, analysis and evaluation in mallard (Anas platyrhynchos). Bmc Genomics 12:11. doi: 10.1186/1471-2164-12-150.

Krause J, Croft DP, James R, 2007. Social network theory in the behavioural sciences: potential applications. Behavioral Ecology and Sociobiology 62:15-27. doi: 10.1007/s00265-007-0445-8.

Krause J, James R, Franks DW, Croft DP, 2015. General Introduction. In: Krause J, James R, Franks DW, Croft DP, editors. Animal Social Networks New York, USA: Oxford University Press.

Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S, Rutz C, 2013. Reality mining of animal social systems. Trends in Ecology & Evolution 28:541-551. doi: 10.1016/j.tree.2013.06.002.

Kurvers R, Adamczyk V, Kraus RHS, Hoffman JI, van Wieren SE, van der Jeugd HP, Amos W, Prins HHT, Jonker RM, 2013. Contrasting context dependence of familiarity and kinship in animal social networks. Animal Behaviour 86:993-1001. doi: 10.1016/j.anbehav.2013.09.001.

Lusseau D, Whitehead H, Gero S, 2008. Incorporating uncertainty into the study of animal social networks. Animal Behaviour 75:1809-1815. doi: 10.1016/j.anbehav.2007.10.029.

Lusseau D, Wilson B, Hammond PS, Grellier K, Durban JW, Parsons KM, Barton TR, Thompson PM, 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75:14-24. doi: 10.1111/j.1365-2656.2005.01013.x.

Lynch M, Ritland K, 1999. Estimation of pairwise relatedness with molecular markers. Genetics 152:1753-1766.

Mangiafico SS, 2016. Summary and Analysis of Extension Program Evaluation in R, version 1.18.1. [accessed 2020Aug.30]. https://rcompanion.org/handbook/I_12.html.

Manno TG, 2008. Social networking in the Columbian ground squirrel, Spermophilus columbianus. Animal Behaviour 75:1221-1228. doi: 10.1016/j.anbehav.2007.09.025.

McPherson M, Smith-Lovin L, Cook JM, 2001. Birds of a feather: Homophily in social networks. Annual Review of Sociology 27:415-444. doi: 10.1146/annurev.soc.27.1.415.

Mitani JC, Watts DP, Pepper JW, Merriwether DA, 2002. Demographic and social constraints on male chimpanzee behaviour. Animal Behaviour 64:727-737. doi: 10.1006/anbe.2002.4014.

Molvar EM, Bowyer RT, 1994. Costs and Benefits of Group Living in a Recently Social Ungulate - The Alaskan Moose. Journal of Mammalogy 75:621-630. doi: 10.2307/1382509.

Newman MEJ, 2006. Modularity and community structure in networks. Proceedings of the National Academy of Sciences of the United States of America 103:8577-8582. doi: 10.1073/pnas.0601602103.

Nituch LA, Schaefer JA, Maxwell CD, 2008. Fine-scale spatial organization reflects genetic structure in sheep. Ethology 114:711-717. doi: 10.1111/j.1439-0310.2008.01522.x.

Patzelt A, Kopp GH, Ndao I, Kalbitzer U, Zinner D, Fischer J, 2014. Male tolerance and male-male bonds in a multilevel primate society. Proceedings of the National Academy of Sciences of the United States of America 111:14740-14745. doi: 10.1073/pnas.1405811111.

Peakall R, Smouse PE, 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288-295. doi: 10.1111/j.1471-8286.2005.01155.x.

Peakall R, Smouse PE, 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research-an update. Bioinformatics 28:2537-2539. doi: 10.1093/bioinformatics/bts460.

Pike TW, Samanta M, Lindstrom J, Royle NJ, 2008. Behavioural phenotype affects social interactions in an animal network. Proceedings of the Royal Society B-Biological Sciences 275:2515-2520. doi: 10.1098/rspb.2008.0744.

Pinter-Wollman N, Isbell LA, Hart LA, 2009. The relationship between social behaviour and habitat familiarity in African elephants (Loxodonta africana). Proceedings of the Royal Society B-Biological Sciences 276:1009-1014. doi: 10.1098/rspb.2008.1538.

Podgorski T, Lusseau D, Scandura M, Sonnichsen L, Jedrzejewska B, 2014. Long-Lasting, Kin-Directed Female Interactions in a Spatially Structured Wild Boar Social Network. Plos One 9:11. doi: 10.1371/journal.pone.0099875.

Pope TR, 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (Alouatta seniculus). Behavioral Ecology and Sociobiology 48:253-267. doi: 10.1007/s002650000236.

Proffitt KM, Gude JA, Shamhart J, King F, 2012. Variations in elk aggregation patterns across a range of elk population sizes at Wall Creek, Montana. Journal of Wildlife Management 76:847-856. doi: 10.1002/jwmg.310.

Author. 2018. R: A language and environment for statistical computing. Version 3.6.1. Vienna, Austria.

Reinhardt V, Reinhardt A, 1981. Cohesive Relationships in a Cattle Herd (*Bos Indicus*). Behaviour 77:121-151. doi: 10.1163/156853981x00194.

Reyer HU, 1984. Investment and Relatedness - a Cost-Benefit-Analysis of Breeding and Helping in the Pied Kingfisher (*Ceryle rudis*). Animal Behaviour 32:1163-1178. doi: 10.1016/s0003-3472(84)80233-x.

Robitaille AL, Webber QMR, Vander Wal E, 2019. Conducting social network analysis with animal telemetry data: Applications and methods using spatsoc. Methods in Ecology and Evolution 10:1203-1211. doi: 10.1111/2041-210x.13215.

Rusu AS, Krackow S, 2004. Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice. Behavioral Ecology and Sociobiology 56:298-305. doi: 10.1007/s00265-004-0787-4.

Shorrocks B, Croft DP, 2009. Necks and networks: a preliminary study of population structure in the reticulated giraffe (Giraffa camelopardalis reticulata de Winston). African Journal of Ecology 47:374-381. doi: 10.1111/j.1365-2028.2008.00984.x.

Silk JB, 2002. Kin selection in primate groups. International Journal of Primatology 23:849-875. doi: 10.1023/a:1015581016205.

Silk JB, 2007. Social components of fitness in primate groups. Science 317:1347-1351. doi: 10.1126/science.1140734.

Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE, Memenis SK, Holekamp KE, 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. Behavioral Ecology 21:284-303. doi: 10.1093/beheco/arp181.

Stanley CR, Dunbar RIM, 2013. Consistent social structure and optimal clique size revealed by social network analysis of feral goats, Capra hircus. Animal Behaviour 85:771-779. doi: 10.1016/j.anbehav.2013.01.020.

Sugg DW, Chesser RK, Dobson FS, Hoogland JL, 1996. Population genetics meets behavioral ecology. Trends in Ecology & Evolution 11:338-342. doi: 10.1016/0169-5347(96)20050-3.

Sundaresan SR, Fischhoff IR, Dushoff J, Rubenstein DI, 2007. Network metrics reveal differences in social organization between two fission-fusion species, Grevy's zebra and onager. Oecologia 151:140-149. doi: 10.1007/s00442-006-0553-6.

Uccheddu S, Body G, Weladji RB, Holand O, Nieminen M, 2015. Foraging competition in larger groups overrides harassment avoidance benefits in female reindeer (Rangifer tarandus). Oecologia 179:711-718. doi: 10.1007/s00442-015-3392-5.

VanderWaal K, Gilbertson M, Okanga S, Allan BF, Craft ME, 2017. Seasonality and pathogen transmission in pastoral cattle contact networks. Royal Society Open Science 4:11. doi: 10.1098/rsos.170808.

Viblanc VA, Arnaud CM, Dobson FS, Murie JO, 2010. Kin selection in Columbian ground squirrels (Urocitellus columbianus): littermate kin provide individual fitness benefits. Proceedings of the Royal Society B-Biological Sciences 277:989-994. doi: 10.1098/rspb.2009.1960.

Weladji RB, Mysterud A, Holand O, Lenvik D, 2002. Age-related reproductive effort in reindeer (Rangifer tarandus): evidence of senescence. Oecologia 131:79-82.

Wey T, Blumstein DT, Shen W, Jordan F, 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Animal Behaviour 75:333-344. doi: 10.1016/j.anbehav.2007.06.020.

Whitehead H, 1997. Analysing animal social structure. Animal Behaviour 53:1053-1067. doi: 10.1006/anbe.1996.0358.

Whitehead H, 2008a. Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis. Chicago, US: The University of Chicago Press.

Whitehead H, 2008b. Precision and power in the analysis of social structure using associations. Animal Behaviour 75:1093-1099. doi: 10.1016/j.anbehav.2007.08.022.

Whitehead H, Bejder L, Ottensmeyer CA, 2005. Testing association patterns: issues arising and extensions. Animal Behaviour.

Whitehead H, Dufault S, 1999. Techniques for analyzing vertebrate social structure using identified individuals: Review and recommendations. Advances in the Study of Behavior, Vol 28 28:33-74. doi: 10.1016/s0065-3454(08)60215-6.

Wiszniewski J, Lusseau D, Moller LM, 2010. Female bisexual kinship ties maintain social cohesion in a dolphin network. Animal Behaviour 80:895-904. doi: 10.1016/j.anbehav.2010.08.013.

Wolf JBW, Mawdsley D, Trillmich F, James R, 2007. Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. Animal Behaviour 74:1293-1302. doi: 10.1016/j.anbehav.2007.02.024.
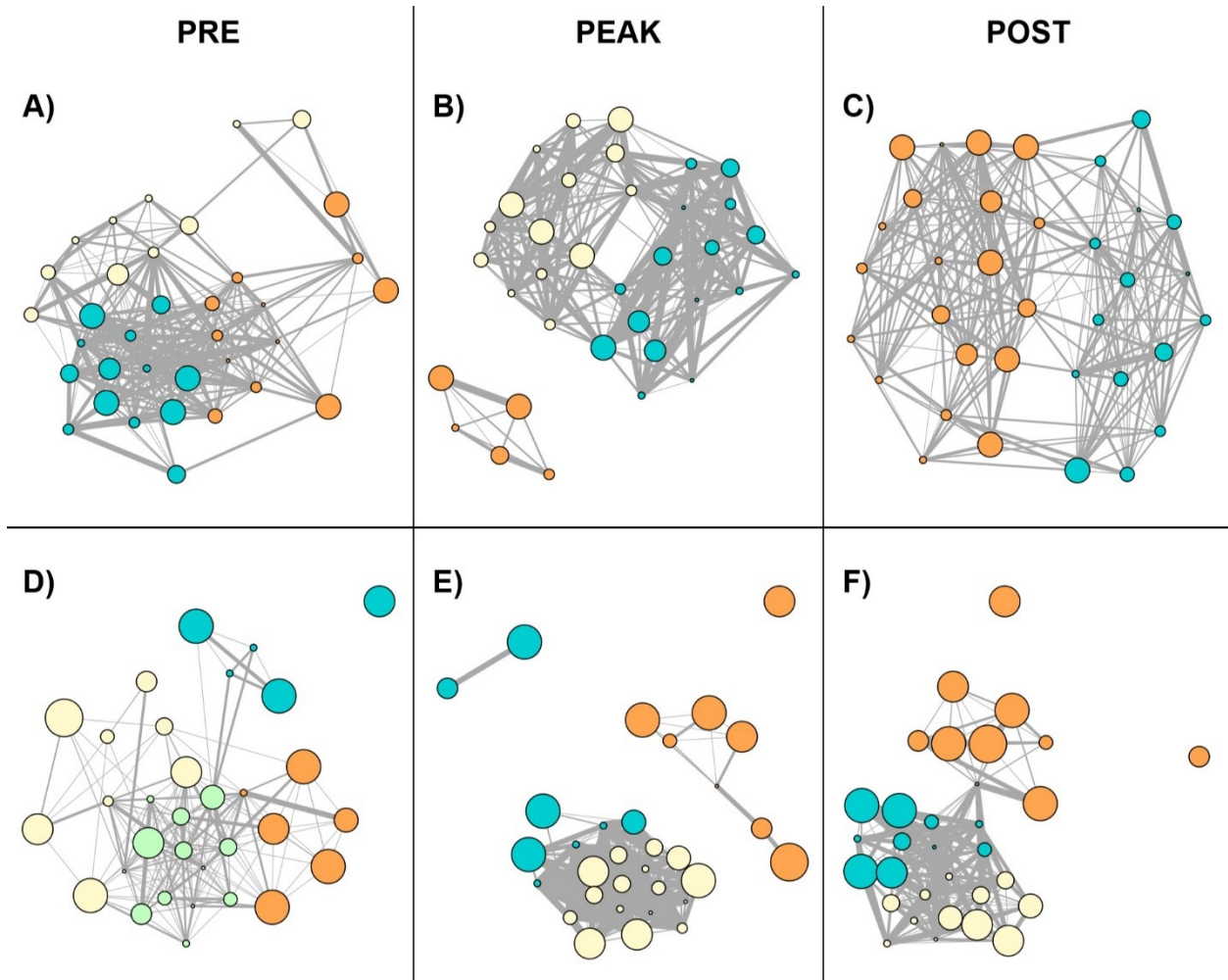
Figure 1. Visualization of social networks in the year 2009 A) to C) (N = 35), and 2011 D) to F) (N = 32) during the Pre-, Peak-, and Post-rut. Nodes represent individual females, size of nodes is relative to the age of the female, and edge width represents proportion of time dyads spent together (i.e. SRI). Optimal community assignment was based on the modularity coefficient, *Q*, differentiated by colors. Social networks were simplified by only showing edges above the mean SRI.
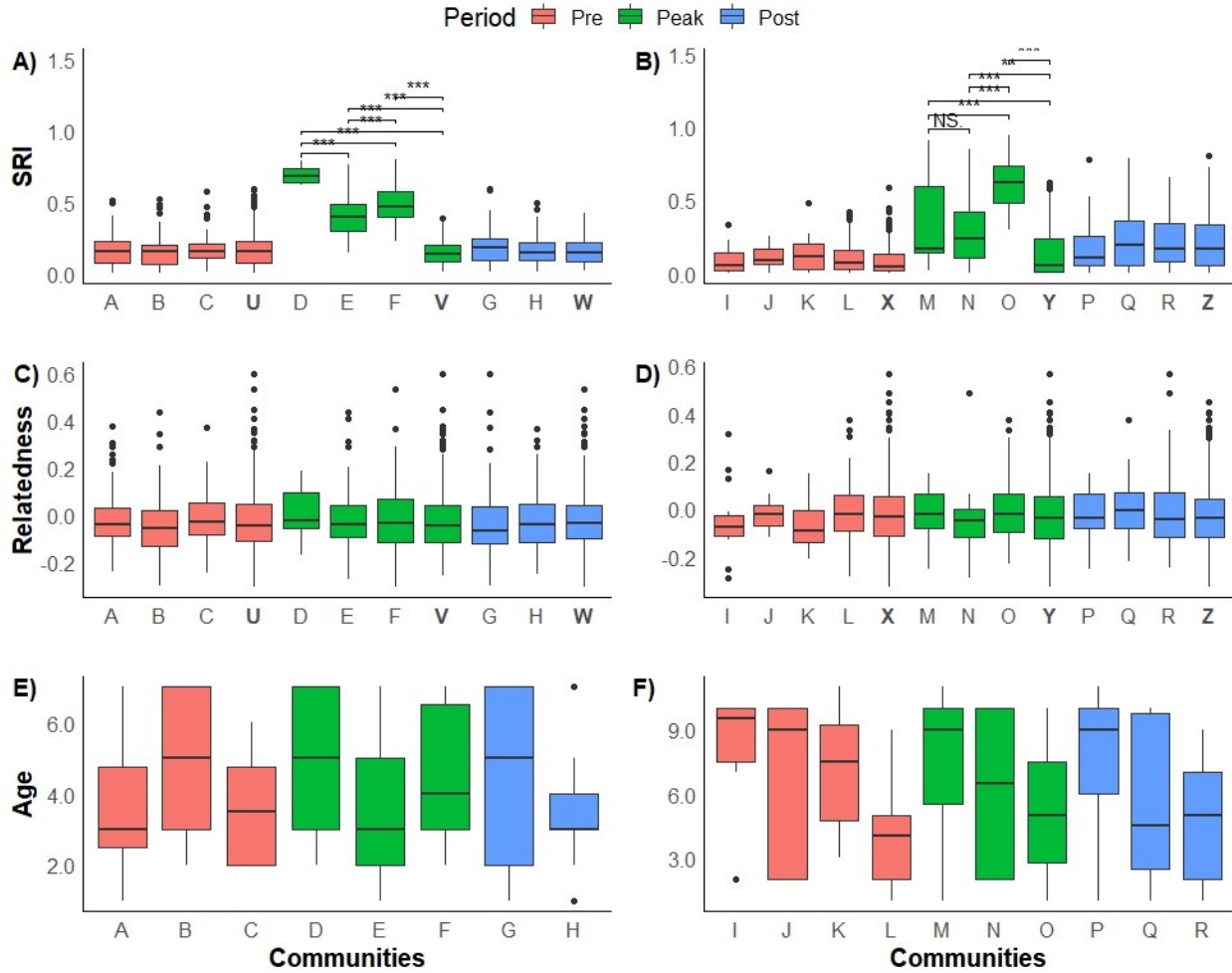
**Figure 2. Female association levels represented by the simple ratio index (SRI, A and C),
mean relatedness (B and D), and mean age (E and F) between communities in all periods
(Pre-, Peak-, and Post-rut) in the years 2009 (ACE, N = 35) and 2011 (BDF, N = 32).** Periods
are color-coded. Communities U, V, W, X, Y, and Z represent between-community values, while
communities A to R represent within-community values. Between-community values were
included in analysis to compare within-community data to between-community. Mean SRI was
only significantly different between communities during the peak-rut in both 2009 (ANOVA,
$F_{3,591} = 552.58$, $p < 0.001$) and 2011 (ANOVA, $F_{3,492} = 264.658$, $p < 0.001$).
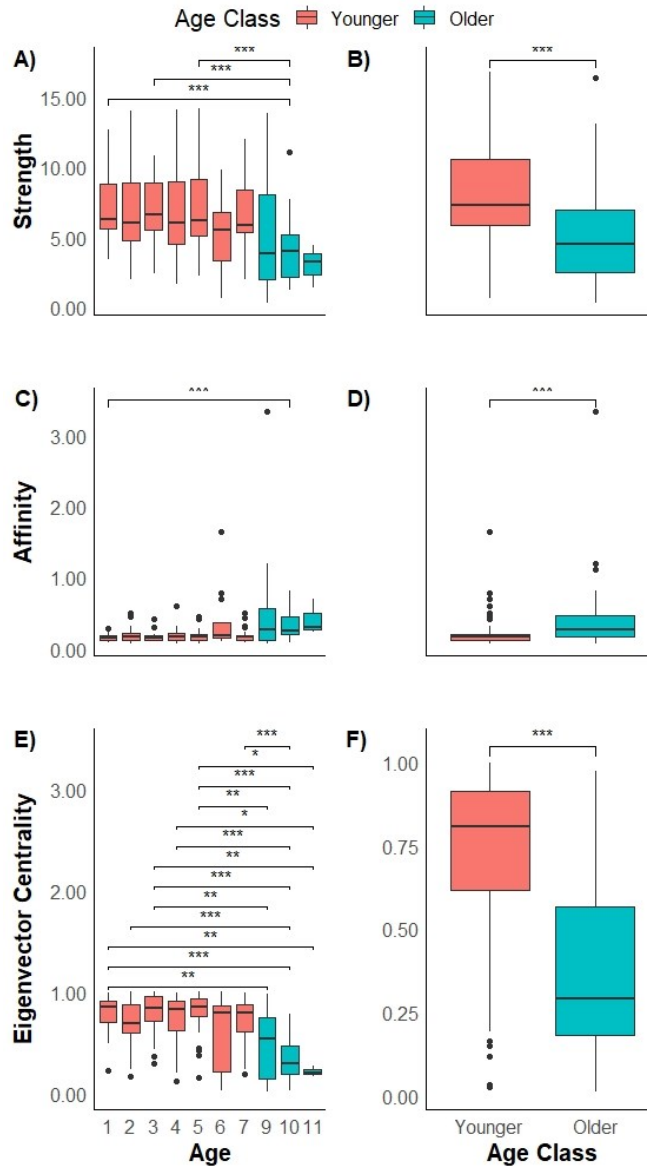
Figure 3. Female association strength represented by individual-level metrics (strength, affinity, and eigenvector centrality) as a function of female age (A, C, and E) and age class (B, D, and F) in the years 2009 and 2011, combined (N = 67). Strength is the number of edges a node is connected to; affinity is the mean strength of an individual's associates; and eigenvector centrality is how well connected an individual's connections are to others. Color represents the Age Class that the females are categorized under: Younger females (1-7 years of age) and Older females (9+ years of age).