



University of Exeter's Institutional Repository, ORE

<https://ore.exeter.ac.uk/repository/>

Article version: POST-PRINT

Author(s): J. Lewton and P.E. Rose

Article title: Evaluating the social structure of captive Rothschild's giraffes (*Giraffa camelopardalis rothschildi*): Relevance to animal management and animal welfare

Originally published in: Journal of Applied Animal Welfare Science

Source: doi.org/10.1080/10888705.2019.1573682

Link to published article (if available):

<https://www.tandfonline.com/doi/abs/10.1080/10888705.2019.1573682>

Publisher statement: This is an Author's Original Manuscript of an article submitted for consideration in JAAWS. JAAWS is available online from:

<https://www.tandfonline.com/toc/haaw20/current>

Usage guidelines

Before reusing this item please check the rights under which it has been made available.

Some items are restricted to non-commercial use. **Please cite the published version where applicable.**

Further information about usage policies can be found at:

Evaluating the social structure of captive Rothschild's giraffes (*Giraffa camelopardalis rothschildi*): Relevance to animal management and animal welfare

Social Network Analysis (SNA) is useful for evaluating management zoo regimes to ensure that any fitness benefits of sociality are preserved in captive-housed groups. This paper explores the association patterns of 13 giraffes housed at Longleat Safari Park, UK. Wild giraffes exhibit a fission-fusion social system with preferential bonding. As zoo-housed giraffe are common, they are excellent study subjects for using SNA to investigate key aspects of sociality within a managed social environment. Social bonds were assessed over different season and data from two study periods (2011 and 2015) were analyzed to see consistency of “social type” (i.e. more social or more solitary). Associations showed the occurrence of consistent preferential bonds between named individuals but time of year influenced the patterns of social bonds. Bonds between female giraffe, and their offspring, appeared to be strongest. For animals present in 2011 and 2015, differences in time spent socializing between years were apparent. Results suggest that giraffes may be flexible in their choice of social partner and zoo-managed herds should include a range of individuals from which each animal can choose a preferred associate.

Keywords: giraffe; social network analysis; zoo population management; partner preference; animal welfare

1: Introduction

Animal social systems have evolved from a trade-off between competition and cooperation (Koenig et al., 2013; Krause & Ruxton, 2002), where individuals may gain increased access to food, mates, shelter and other such valuable commodities at the expense of increased visibility to predation and elevated levels of competition with conspecifics (Krause & Ruxton, 2002; Majolo et al., 2008; Molvar & Bowyer, 1994). Such pressures have resulted in different strategies of social organization (group size and composition) and social structure (relationships between group members) being formed (Ebensperger et al., 2012; Jarman, 1974), and these have been shown to be important components of a species' life history strategy (i.e. to invest in preferential relationships or not).

There is growing evidence that social relationships formed within a group directly impact on the fitness of those associating, and fitness measures (such as infant survival to maturity) can be used to investigate the influence of social bonding on wild populations. Multiple studies have shown that social structure has an important influence on reproductive success of wild populations (Cameron et al., 2009; Gilby et al., 2013; Silk, 2007a, 2007b; Silk et al., 2003; Silk et al., 2010a, 2010b). Long-term research into the sociality of adult female baboons (*Papio cynocephalus*) shows that stable adult associations are positively correlated with infant survival (Silk et al., 2003); whilst similar research on chacma baboons (*Papio hamadryas ursinus*) shows significant increases in lifespan for females who maintain stronger social bonds with other female baboons (Silk et al., 2010a). Social interactions can also negatively impact fitness- for example, female spotted hyenas (*Crocuta crocuta*) with small cubs often avoid conspecifics during food shortages to reduce the risk of infanticide (Smith et al., 2007).

Whilst sociality has shown to be an important component of fitness in wild populations, there is limited evidence that shows the same for captive animals. One might expect social systems to differ between captive and wild populations, considering the differences in environmental factors. Social pressures such as limited food availability and increased predation risk are arguably non-existent for captive animals and social organization is managed- removing an animal's ability to relieve social tension (Price & Stoinski, 2007). Differences in the drivers for sociality may therefore cause disparity between the social structure of a wild and captive-housed species, which could negatively influence any fitness consequences of group living. Whilst SNA has had widespread application to zoo-housed primates, it has seen little use with other mammalian taxa within zoological collections.

We applied SNA methods to giraffe (*Giraffa camelopardalis*) to investigate the individuality of social bonding in a captive environment. The social organization of wild giraffe has been described as showing characteristics of a fission-fusion system, expressing daily turnover times for temporary groups (Bercovitch & Berry, 2013b; Carter, Brand, et al., 2013; Dagg, 2014). Despite previous confusions that suggested a loose, more random social system (Dagg & Foster, 1976), the social structure of wild giraffe is now agreeably described as social bonding in a structured network, with long-term relationships formed. Social bonding in wild individuals is strongest between mother-daughter dyads and female group members (Bercovitch & Berry, 2013b; Carter, Brand, et al., 2013; Shorrocks & Croft, 2009). Whilst wild individuals can maintain consistent associations with the same herd members, it is common that zoological collections will often control group sizes and composition of captive herds as part of population management goals. Such management practices may restrict opportunities for the formation of consistent social bonds (Price & Stoinski, 2007), which are noted as

occurring between (particularly female) giraffe in the wild (Bercovitch & Berry, 2013b; VanderWaal, Wang, et al., 2014). Increased performance of stereotypic behavior can be related to restricted access to conspecifics as well as the amount of space available when giraffes are socializing indoors (Bashaw et al., 2001), demonstrating the importance of social bonding to giraffe welfare. Studying long-term bonds within captive giraffe herds and evaluating how relationships mirror those documented in wild herds helps provide valuable data to evidence how to maintain a good quality of life for such social species in captivity. The relevance of SNA to determine a network's structure and bond stability, and to answer questions relating to changes in associations over time or differences between sexes (Rose & Croft, 2017, 2018) as well as identifying differences in types of social interaction performed around enclosure resources or the context for specific social behaviors (Frumkin et al., 2016; Hinton et al., 2013; Hughes & Driscoll, 2014) has been demonstrated in other gregarious captive species.

In this paper, we analyze the social network structure of a mixed-sex herd of 13 Rothschild's giraffes (*G.c. rothschildi*) at Longleat Safari Park, Wiltshire, UK to answer the following questions: i) Do group members express social preferences in their choice of associate? ii) What are the factors driving social network? iii) Is performance of social behavior consistent over time? We discuss the social structure of these giraffes in terms of research on free-living animals and evaluate our results against the wider field of zoo animal social behavior and husbandry research.

2: Methods

2.1: Study site and subjects

The herd of Rothschild's giraffe at Longleat Safari Park was observed from September 2015 to April 2016. The group were observed in two outdoor enclosures. The 'park' consists of a 24.3-hectare drive-through reserve, shared with plains zebra (*Equus quagga*) and helmeted guinea fowl (*Numida meleagris*). The park's terrain is grassed, with both flat and hilly topography, with multiple oak trees and a large pond. The second enclosure is a 75m² paddock for the giraffe only and used predominantly during winter conditions. The terrain in this smaller paddock is both grass and hard-standing.

During the main study period the group size varied (N=12-13). All giraffes were born at Longleat Safari Park, excluding one adult male who arrived from another UK zoo in 2014. Subjects were assigned to age classes in September 2015 and the group contained two adult males (one breeding bull and one young adult), five adult females, three juveniles and two calves (see Table 1 for population demographic information). Giraffe age classification was as follows: >6 years = adult, between 6 -1 years = subadult/juvenile, <1 year = calf (Dagg & Foster, 1976). During the study period one breeding female died and two female calves were born.

TABLE 1 GOES HERE

Table 1. Sex, birth dates and mother ID (only if mother is still present in group) for the study group. + indicates born during the study period, - indicates died during the study.

2.2: Study site and subjects

Giraffe behavior was recorded using instantaneous sampling (Martin & Bateson,

2007) of a focal individual for 10 minutes (with one minute sampling points) per animal. Each giraffe had ten behavior samples per observation session and the closest individual within two neck lengths of the subject was recorded as an associating dyad. Depending on daily husbandry regimes, one to three hours of data (collected in a continuous observation block) were recorded between 10:00 and 16:00 each day. The method of dyadic identification was based on Bashaw et al. (2007). Only one dyad was recorded associating per sample and associations were not directional. All observations were recorded from outside of the enclosure or from the inside of a jeep when the giraffes were out in the main park. The jeep was present at all times when the giraffes were in the park and its presence did not disturb the animals. Based on the location of the observer, not all giraffe were present in all observations.

2.2.1: Second study period

Data on overall time spent socializing compared to overall time spent alone from a previous unpublished study conducted in 2011 are compared with data from the 2015/2016 study. The second research period was carried out during a one-month period in summer 2011 and giraffes that were present in both studies were “Jemima”, “Ella”, “Dyan”, “Gerty”, “Kaiser” and “Kate”. Behavioral data in the 2011 study was collected by instantaneous sampling of focal individuals, with 5-minute sample points for six hours a day, for five days a week. Social associations were determined based on two individuals being in proximity within one-neck length of each other. The overall proportion of time a giraffe was recorded as socializing (compared to being seen alone) was calculated for comparison with the same measure of overall time socializing in the 2015/2016 study.

2.3: Data analysis

Data were analyzed in Socprog v. 2.8. (Whitehead, 2017) and in R (R Core Team, 2016) for t-tests. Networks were drawn in NetDraw v. 2.062 (Borgatti, 2002). Association indices (AI) were calculated in Socprog using the Simple Ratio Index, SRI (Cairns & Schwager, 1987). The formula for the SRI is $x / (x + y_{ab} + y_a + y_b)$. Where x = number of sample where a and b both occurred but not together; y_{ab} = sample were one or both were seen; y_a = samples of a only; y_b = samples of b only.

2.3.1: Analyzing network characteristics

Sampling periods were set to one day giving the animals the opportunity to change associates and reduce any chance of pseudoreplication of social choices. In total, 1146 giraffe dyadic bonds were recorded. A network of all associations within the herd was drawn in Netdraw and filtered to an association rate of >0.4 to identify the presence of strongest ties between animals. This network was spring embedded (Croft et al., 2008) to show tightly clustered nodes together in the center of the network and those with fewer connections positioned around the edge.

A Mantel test over 1000 permutations was run in Socprog to analyze any difference between and within sex classes for the distribution of association indices. To test if the mean overall time spent associating for non-related giraffe differed to the time spent associating for related giraffe, a one-sample t-test was run.

Five descriptive network measures were calculated in Socprog (Whitehead, 2008, 2017). These were: strength (the sum of the association indices of each individual with all others), eigenvector centrality based on Newman (2004)'s method (calculated as the first eigenvector from the association matrix), reach (as a measure of indirect

connections for each individual), clustering (how well the associates of each individual associate) and affinity (higher affinity individuals have high associations with individuals who have high strength).

Lagged (LAR) and Null Association Rates (NAR) were calculated and plotted in Socprog (Whitehead, 2009, 2017) to analyze the length of time giraffe dyads may remain associating. LAR is the probability that two individuals are associated given their association some time lag earlier (Whitehead, 2007) and therefore is a useful way of illustrating the type of social bond (permanent, temporary, long- or short-term) present within a network. Mathematical models available in Socprog (Whitehead, 2017) were fitted to the LAR /NAR plot to evaluate the pattern of associations present over time, based on the exponential decay in the probability of individuals associating over time (Whitehead, 1995). The candidate model was chosen from the lowest Quasi Akaike Information Criterion, QAIC (Whitehead, 2007) and in this case the best fit model was for two levels of casual acquaintances: $a_3 \cdot \exp(-a_1 \cdot t_d) + (1 - a_3) \cdot \exp(-a_2 \cdot t_d)$. With values of each parameter (a_1 - a_3 set at 0.5 association rate) and t_d representing the time lag (Whitehead, 2017).

2.3.2: Determining preferred and avoided associations

To identify the presence of preferred and avoided associations within the network permutation tests were run in Socprog over 1000 trials and up to 40000 permutations until coefficient of variation (CV) P values stabilized (Whitehead, 2009, 2017). The CV of the real network was compared to that of a random network (i.e. all there was equal degree of association between all individuals), and the number of observed versus expected significant dyads was identified.

Modularity of the network (i.e. how well the network divides into specific clusters of individuals with the same high association index) was calculated from permutations to identify the number of potential clusters present (Newman, 2006), and a cophenetic correlation coefficient to identify the reliability (CCC greater than 0.8) of clustering was also evaluated (Whitehead, 2017). Social differentiation (how varied is the network) was calculated in Socprog with values above 0.5 showing a differentiated rather than homogenous network apparent (Whitehead, 2008).

2.3.3: Determining predictors of social network structure

To compare association matrices for season, with data restricted to autumn/winter (September through to February) and spring (March to April), Mantel Z-test were run in Socprog. Dyadic plots of the number of dyads for each category of association index (for each season) were plotted in Socprog to visually show any influence of season on the distribution of dyadic association rates within the network.

To determine any influence of demographic characteristics on associations (age and sex), as well as calculated network measures (reach, strength, clustering coefficient, eigenvector centrality and affinity) on the association network, Multiple Regression Quadratic Assignment Procedures (MRQAP) tests were used (Dekker et al., 2007; Whitehead, 2017). MRQAP testing takes one association matrix as a dependent factor and the others as predictors, and analyses whether similarity in each predictor makes a significant contribution towards explaining the dependent matrix whilst controlling for the presence of the other predictors (Dekker et al., 2007). In this case the demographic characteristics and network measures listed above were considered as predictors and transformed into matrices for comparison with the association matrix in Socprog (Whitehead, 2017).

2.3.4: Analysing social type between years

The consistency of the social type (time spent being social compared to solitary) within the herd, for the six animals present in both the 2011 and 2015 studies was normally distributed and therefore to determine whether animals in 2011 were more social than in 2015/16 a paired t-test was applied to these data.

3: Results

3.1: Characteristics of this giraffe social network

Giraffe spent 47% of their time associating and nearly all giraffes were observed within a dyadic association- forming 78 directly connected pairs (Figure 1a). Subjects “Thorn” and “Piper” were the only giraffe not observed associating but were indirectly connected via conspecifics. Figure 1b shows a network of the strongest associations with the highest association indices being between similar-aged individuals and for mother-offspring dyads.

FIGURE 1 GOES HERE

Figure 1. Complete spring-embedded network for 13 giraffes (excluding the newest calf “Small”). a) All bonds, b) filtered to show bonds occurring for more than 40% of the time. Thicker edges denote stronger tie strength. Size of nodes equates to animal age. Female giraffe are white nodes, male giraffe are black nodes.

FIGURE 2 GOES HERE

Figure 2. Lagged Association Rate, LAR, (black line) plotted against a Null Association Rate, NAR, (hashed line) and both compared to a fitted model (grey line). The higher LAR is indicative of non-random association patterns showing these giraffes to consistently spend time

with selected conspecifics. The fitted model, association rate = $0.69897 * \exp(-2.5011 * td) + (1 - 0.69897) * \exp(-0.0017768 * td)$, indicates two levels of casual association; i.e. individuals who come together and preferentially socialize, but can disassociate and potentially reassociate in the future (Whitehead, 2017).

The existence of non-random bonding is supported by Figure 2 that shows giraffe dyads are remaining together over time. The output from the fitted model that best describes two levels of casual association (Whitehead, 2007, 2008) supports the results of seasonal changes to bonds shown in Figure 3; whilst bonds between giraffe can be preferential, these associations have a fluidity to them and can change with time of year.

TABLE 2 GOES HERE

Table 2. Distribution of association indices for all giraffe in the sample population

There are trends in the gregariousness (i.e. the likelihood of an individual to be seen associating) of individuals and those with highest or lowest typical group sizes (Table 2). Juvenile giraffes are some of the most gregarious within the group and show the largest typical group sizes, and apparent differences between the network metrics and association indices of juveniles compared to adult female giraffe are evident. Juveniles had a higher overall strength 4.43, compared to adult females 3.11 and higher eigenvector centrality 0.36 for juveniles, compared to 0.25 for adult females. Similar trends with juveniles and adult females are seen with values of reach, gregariousness and mean group size (See Table 2). Adult male giraffes are less gregarious. The calf, “Piper”, had the lowest mean association index and typical group size- with the highest association time spent with her mother (“Piper”- “Kate” 0.37 SRI). The adult that had

the highest association indices was the oldest female, “Jemima”, with a gregariousness score of 0.32 and typical group size of 4.9. “Jemima” also appeared to be the bull’s favorite female based on their association pattern (“Thorn”- “Jemima” 0.51, SRI).

Although these data suggest that female-female bonds may be slightly stronger than those between males and females, and compared to male-male bonds, there is no significant difference in the distribution of association indices between and within sex classes (Mantel test with 50000 permutations, $r= 0.168$; $P= 0.289$). When comparing overall time spent social for mother and offspring dyads, to time spent social for non-kin dyads, significantly more time is spent socializing between kin; the mean time social for non-kin is 12.39% and that for mother-offspring is 52% ($t= 4.03$; $df= 5$; $P= 0.010$).

3.2: Preferred and avoided relationships within the network

Permutation tests confirmed that the coefficient of variation of the real network (0.65245) was significantly higher than that of a random network (0.50111), $P< 0.01$. Permutation tests identified 19 significant dyads compared to an expected number of 3.9. Eight significant dyads were preferred partners (high association index) and 11 were avoided (low association index).

A cophenetic correlation coefficient of 0.740 approaches the critical value of 0.8 for confidence in clustering (Whitehead, 2017) however the modularity (0.09) of identified clusters (five) is below the critical value of 0.3 that indicates accurate division of these data (Newman, 2006). Therefore, with more data collection over a longer sample period, these giraffes may form themselves in stable, well-defined clusters. In spite of this, these giraffe do exist within a differentiated social network as the measure

of social differentiation calculated (0.574) is above the value of 0.5 that denotes a well-differentiated society and lack of homogeneity (Whitehead, 2017).

3.3: What predicts patterns of social choice within this giraffe network?

MRQAP tests analyzed the influence of similarity in age and sex and found neither to be a significant predictor of association preference in this group (age: $r = -0.213$; $P = 0.124$. Sex: $r = -0.185$; $P = 0.251$). Using the same method to test the combined effects of strength, reach, eigenvector centrality, affinity and clustering found that strength significantly predicts association patterns ($r = 0.418$; $P < 0.001$) and that eigenvector centrality tends towards significance ($r = -0.245$; $P = 0.08$). All other partial correlations were not significant (Reach: $r = 0.144$; $P = 0.293$. Clustering: $r = 0.134$; $P = 0.243$. Affinity: $r = 0.084$; $P = 0.588$).

Mantel Z-tests at 40000 permutations for data restricted to autumn/winter only and spring only show no significant correlation between association matrices ($r = 0.161$; $P = 0.422$). Therefore, dyadic relationships between these giraffes may be influenced by husbandry regimes changes at different times of the year (i.e. being indoors or restricted to hard-standing over winter may dilute strong attachments between individuals).

Testing for any differences between the association matrices between male and female giraffe, and between females only again shows a lack of consistency in association with season. Mantel Z-tests indicate no significant correlation between males and females ($r = 0.494$; $P = 0.126$) as well as for female-only bonds ($r = -0.022$; $P = 0.927$). The small number of male giraffes in the herd meant that r values of 1 were calculated for each season.

To illustrate any difference in the spread of association indices between different seasons, dyadic plots (Figure 3) were drawn. A wider range of female to male bonds is

seen in autumn, compared to spring. And stronger female to female bonds are noted in spring. Male to male bonds appear consistent with season. Physiological changes in the animals, as well as alterations to husbandry regime (based on housing and climatic factors) may influence female bonding within the herd.

FIGURE 3 GOES HERE

Figure 3. Dyadic plots showing the number of dyads in a specific category of association index (from 0 to 1) for spring 2016 and autumn 2015. Stronger female dyadic bonds are noted in spring (top).

3.4: Is there consistency in the social behavior of these giraffe across time?

Testing for consistency in behavioral traits (in this case solitary versus social) for six giraffe that were present in the original 2011 study as well as in 2015 showed that social behavior differed for all these individuals between the two studies. All giraffe spent more time associating in the 2011 study than in the 2015 study (Table 3). A significant difference in the mean time spent associating per individual is noted ($t=5.66$; $df=7.84$; $P<0.001$), which supports the suggestion that the herd is non-randomly associated.

TABLE 3 GOES HERE

Table 3. Time spent social and seen solitary for giraffe present in the studies in 2011 and 2015

4: Discussion

Our results show that these giraffes form a highly-connected network with a non-random distribution of associations. We find significant levels of preferred and avoided associations, with individuals discriminating in their choice of associates. This

is consistent with previous research that suggests both wild and captive giraffe form non-random social relationships within a structured network (Bashaw, 2011; Bashaw et al., 2007; Bercovitch & Berry, 2013b; Carter, Brand, et al., 2013; VanderWaal, Atwill, et al., 2014). The center of the network is dominated by closer ties between female giraffe (Figure 1), with males being more peripheral to the herd's network structure. This finding, together with results from published research into giraffe social bonds (Bashaw, 2011; Bashaw et al., 2007) supports the need for zoos to maintain groups of known adult females who clearly obtain benefits from long-term associations. These female giraffes initiate social contact less frequently with a male, preferring to invest time with other females (female-female maximum association time 58%, female-male maximum association time 43%). Giraffes are not consistent in the time that they will spend socializing (Table 3) indicating individual animal choices in partner can be fluid.

4.1: Sex differences and comparison to wild social behavior

Both the adult male giraffes score low on gregariousness and typical group size (see Table 2), which corresponds to the life history of bull giraffe documented in the literature (Dagg, 2014; Dagg & Foster, 1976; Pratt & Anderson, 1985). Male giraffes adopt a roaming reproductive strategy, to correspond with the estrous cycle of females (Bercovitch & Berry, 2010) meaning long-term relationships would not naturally occur between conspecifics. Herd leadership of a wild giraffe herd, influencing movement decision and direction of travel is most often the responsibility of the oldest female in the group (Berry & Bercovitch, 2015). The oldest female in this study herd "Jemima" also had the highest eigenvector centrality, indicating more potential influence over her associates. Future study on the influence of older female giraffes on the movement

patterns and choice of social assortment on other herd members in captivity would determine if such social-organizing behaviors are maintained in *ex situ* groups.

4.1.1: Bonds between mothers and offspring, and juvenile associations.

We found that juveniles overall had higher network metrics and association indices than adult female giraffe. Research on wild giraffes show that juveniles associate most with similarly-aged individuals (Saito & Idani, 2017), and an age-based preference for social assortment (leading to the maintenance of very strong social bonds within cohorts, even of non-kin calves) is clear (Bercovitch & Berry, 2013a). A high-level of juvenile dyadic interactions is observed in the wild (van der Jeugd & Prins, 2000) with juvenile-juvenile associations being sighted more than those for any other class combination. Bonds between juvenile giraffe may have an important anti-predatory role, as calves can be left together in crèches without parental supervision (Dagg, 2014; Langman, 1977)- an evolutionary mechanism that may explain preferential juvenile assortment in captivity.

A key characteristic of the social groups of wild giraffes is the strong associations between mother-offspring dyads (Bercovitch & Berry, 2013a, 2013b; Langman, 1977; Pratt & Anderson, 1979; Saito & Idani, 2018). In these captive giraffes a significant difference between average dyadic association time for mother-offspring dyads compared to all other dyadic class types is noted. Maternally-deprived giraffes can express different social behaviors (Siciliano- Martina & Martina, 2018) so maintaining bonds between related adult females may enhance calf development. As the strength of dyadic associations between female giraffe increases after calving (Saito & Idani, 2016) there is clearly a behavioral need for companionship during the birthing period and when a calf is newly-born. In other mammals, mother-daughter bonds are

important for infant survival (Fairbanks & McGuire, 1986; Moses & Millar, 1994; Silk et al., 2009) and, in some species, bonds between mothers and daughters that persist into adulthood can increase the reproductive success of the daughter (Fairbanks & McGuire, 1986; Moses & Millar, 1994). As cohort bonds between calves are strong and stable, and mother-daughter bonds are noted as the most stable noted in wild giraffe herds (Bercovitch & Berry, 2013a) there is clearly a need to provide the correct social environment for calves and mothers, during rearing, so all zoo-housed individuals experience good welfare and reduced stress.

We found no significant difference between the strength and persistence of female-female bonds and male-female bonds in these giraffes. This could be due to the permanent existence of males in this herd, as opposed to wild studies where male giraffe are transient and therefore female to female bonds are shown to be significantly stronger (Bercovitch & Berry, 2013b; Carter, Brand, et al., 2013). However, whilst results are not statistically significant, data in Table 2 clearly show higher maximum times spent associating for females compared to male giraffe and stronger ties with the overall network (Figure 1) are most apparent between female animals.

4.2: Changes over time, with season and between study periods.

Female-female association indices were higher in spring than in autumn, whilst female-male bonding appeared to be more diverse in autumn (Figure 3). Seasonal differences observed may have been caused by changes in husbandry methods and as we have no replication around years, we cannot determine the influence of other factors on any potential seasonal effects on the network. Giraffes spent considerably more time in a smaller enclosure during the autumn time, in response to poor weather conditions, which may have impacted group associations. However, variation in the patterning of

giraffe social bonds is supported by the output from the LAR (Figure 2) that illustrates two levels of casual associations between animals. Such an association pattern include animals that reassociate after a given period of time apart (Whitehead, 2017) so it is possible that giraffe bonds alter with management changes (individual choice become looser) over season but known companions will still seek out each other's company when given the opportunity. Longer-term study of this giraffe herd would be able to unpick any influence of husbandry change with time of year, compared to influences of environment and behavioral changes on the social bonds present between individual giraffe.

There were significant differences seen in the social preferences of giraffes present in both the 2011 and the 2015 study. Changes to herd structure and movement of individuals, as well changes to social choice as animals age, may have influenced social choices and therefore altered the amount of time each giraffe will spend socializing within a given year. Whilst these are limited data on a small number of animals, thus restricting wider conclusions, giraffes in captivity appear to alter their time spent socializing based on the social environment they are kept in. Fluidity in social behavior may have been caused by physiological changes and animals aging; increases in the sociability of female giraffes occurs with age (Carter, Brand, et al., 2013) and with the exception of "Jemima", all other female giraffe increase time spent socializing with age. As mature females are then courted by breeding males, lower socializing for "Jemima" in 2015 may be linked to reproductive influences over individual assortment choices. As female giraffe increase their time spent on vigilance when a bull is their nearest neighbor (Cameron & Du Toit, 2005), the presence of a breeding bull near a receptive female may explain differences in % time social to solitary. And interestingly, the male giraffe present in both study periods ("Kaiser")

increases time spent alone in 2015 compared to 2011- behavior which again mirrors observation of free-living giraffes (Bercovitch & Berry, 2010; Leuthold, 1979; VanderWaal, Wang, et al., 2014). As female preferences contribute to the variation in sociality amongst female giraffe (Carter, Seddon, et al., 2013) the differences required in times spent socializing may be a reflection of changing dynamics within the herd.

4.3: Implications for giraffe welfare

As SNA allows for strong bonds to be identified, management regimes can use these data to preserve dyadic bonds of biological importance to the species being kept (Rose & Croft, 2015). Maintaining mother-daughter bonds into adulthood may be important for infant survival rates in giraffe, and provide younger female giraffe with the experience of how to rear a calf. As research has identified behavioral and physiological indicators of stress in maternally-deprived giraffe (Siciliano- Martina & Martina, 2018), and that restricted access to group members causes stereotypic behavior (Bashaw et al., 2001), good quality of life in captive giraffe is clearly underpinned by a consistent and known social environment.

The design of enclosures may encourage proximity of giraffes by concentrating feeding stations or consistently feeding in the same location. This can cause the group to spend the majority of their time within the same area, contradictory to their natural behavior of wide-spread foraging movements (van der Jeugd & Prins, 2000). In our study, these giraffes spent 81% of their time within block A2 (Figure 4). This area contained shelter, feeding stations, salt licks and a public feeding area. Studies on captive species have shown resource access (e.g. to breeding and feeding locations) to be a predictor of social interactions (Hughes & Driscoll, 2014) and wild giraffes are shown to gather together around important resources (Young & Isbell, 1991); to

improve independence of data points we limited sampling periods to one day, as noted in VanderWaal, Wang, et al. (2014), to have confidence in our assessment of non-random assortment even though space usage was influenced by location of food and enrichment. To mirror the wandering behavior of giraffe between foraging areas (Leuthold & Leuthold, 1978), we recommend spreading browse (cut tree branches) and other food around the enclosure to allow giraffes the chance to move as a group between resources. As sex differences in foraging are noted (Mramba et al., 2017; Young & Isbell, 1991), and as female giraffe may reduce foraging time in place of vigilance when a bull is in close proximity (Cameron & Du Toit, 2005), increasing the diversity of feeding and browsing areas could also increase the variety of social relationships formed across the herd.

FIGURE 4 GOES HERE

Figure 4. Ariel view of the 24.3 hectare park (border is highlighted by the black line). Black circles symbolize areas used for public feeding. Copyright Google Maps.

5: Conclusions

These captive giraffes express social preferences and their herd contains a network of non-random associations. Bonds between female giraffes and their offspring were the strongest in the herd and males spent more time alone. Associations varied depending on time of year. The biological importance of such defined social structure may need to be considered more strictly in zoo management regimes for giraffe and other social taxa. SNA can assist in providing evidence for positive welfare by identifying important bonds that need to be preserved within a giraffe herd. As young giraffes possess a mechanism for forming and maintaining within-cohort, non-kin social

bonds, breeding groups should enable females to crèche calves of a similar age together. Moving male giraffe between herds and keeping females in stable herds appears best for long-term animal welfare and population management.

Conflict of Interest

We declare no conflict of interest

References

- Bashaw, M. J. (2011). Consistency of captive giraffe behavior under two different management regimes. *Zoo Biology*, 30(4), 371-378.
- Bashaw, M. J., Bloomsmith, M. A., Maple, T. L., & Bercovitch, F. B. (2007). The structure of social relationships among captive female giraffe (*Giraffa camelopardalis*). *Journal of Comparative Psychology*, 121(1), 46-53.
- Bashaw, M. J., Tarou, L. R., Maki, T. S., & Maple, T. L. (2001). A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science*, 73(3), 235-247.
- Bercovitch, F. B., & Berry, P. S. M. (2010). Ecological determinants of herd size in the Thornicroft's giraffe of Zambia. *African Journal of Ecology*, 48(4), 962-971.
- Bercovitch, F. B., & Berry, P. S. M. (2013a). Age proximity influences herd composition in wild giraffe. *Journal of Zoology*, 290(4), 281-286.
- Bercovitch, F. B., & Berry, P. S. M. (2013b). Herd composition, kinship and fission–fusion social dynamics among wild giraffe. *African Journal of Ecology*, 51(2), 206-216.
- Berry, P. S. M., & Bercovitch, F. B. (2015). Leadership of herd progressions in the Thornicroft's giraffe of Zambia. *African Journal of Ecology*, 53(2), 175-182.
- Borgatti, S. P. (2002). NetDraw: Graph visualization software. Harvard, USA: Analytic Technologies.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35(5), 1454-1469.
- Cameron, E. Z., & Du Toit, J. T. (2005). Social influences on vigilance behaviour in giraffes. *Animal Behaviour*, 69(6), 1337-1344.
- Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences*, 106(33), 13850-13853.
- Carter, K. D., Brand, R., Carter, J. K., Shorrocks, B., & Goldizen, A. W. (2013). Social networks, long-term associations and age-related sociability of wild giraffes. *Animal Behaviour*, 86(5), 901-910.
- Carter, K. D., Seddon, J. M., Frère, C. H., Carter, J. K., & Goldizen, A. W. (2013). Fission–fusion dynamics in wild giraffes may be driven by kinship, spatial overlap and individual social preferences. *Animal Behaviour*, 85(2), 385-394.
- Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton, USA: Princeton University Press.

- Dagg, A. I. (2014). *Giraffe: Biology, behaviour and conservation*. Cambridge, UK: Cambridge University Press.
- Dagg, A. I., & Foster, J. B. (1976). *The giraffe: Its biology, behaviour and ecology*. New York, USA: Van Nostrand Reinhold Company.
- Dekker, D., Krackhardt, D., & Snijders, T. A. B. (2007). Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika*, *72*(4), 563-581.
- Ebensperger, L. A., Rivera, D. S., & Hayes, L. D. (2012). Direct fitness of group living mammals varies with breeding strategy, climate and fitness estimates. *Journal of Animal Ecology*, *81*(5), 1013-1023.
- Fairbanks, L. A., & McGuire, M. T. (1986). Age, reproductive value, and dominance-related behaviour in vervet monkey females: cross-generational influences on social relationships and reproduction. *Animal Behaviour*, *34*(6), 1710-1721.
- Frumkin, N. B., Wey, T. W., Exnicios, M., Benham, C., Hinton, M. G., Lantz, S., Atherton, C., Forde, D., & Karubian, J. (2016). Inter-annual patterns of aggression and pair bonding in captive American flamingos (*Phoenicopterus ruber*). *Zoo Biology*, *35*(2), 111-119.
- Gilby, I. C., Brent, L. J. N., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, *67*(3), 373-381.
- Hinton, M. G., Bendelow, A., Lantz, S., Wey, T. M., Schoen, L., Brockett, R., & Karubian, J. (2013). Patterns of aggression among captive American flamingos (*Phoenicopterus ruber*). *Zoo Biology*, *32*(4), 445-453.
- Hughes, A. L., & Driscoll, C. (2014). Being in the thick of things: context-dependent network centrality in a captive flock of American flamingos. *Journal of Ethology*, *32*(2), 83-90.
- Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, *48*(3/4), 215-267.
- Koenig, A., Scarry, C. J., Wheeler, B. C., & Borries, C. (2013). Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. *Philosophical Transactions of the Royal Society B*, *368*(1618), 20120348.
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford, UK: Oxford University Press.
- Langman, V. A. (1977). Cow-calf relationships in giraffe (*Giraffa camelopardalis giraffa*). *Ethology*, *43*(3), 264-286.
- Leuthold, B. M. (1979). Social organization and behaviour of giraffe in Tsavo East National Park. *African Journal of Ecology*, *17*(1), 19-34.
- Leuthold, B. M., & Leuthold, W. (1978). Daytime activity patterns of gerenuk and giraffe in Tsavo National Park, Kenya. *African Journal of Ecology*, *16*(4), 231-243.
- Majolo, B., de Bortoli Vizioli, A., & Schino, G. (2008). Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour*, *76*(4), 1235-1247.
- Martin, P. R., & Bateson, P. P. G. (2007). *Measuring behaviour: an introductory guide* (3rd ed.). Cambridge, UK: Cambridge University Press.
- Molvar, E. M., & Bowyer, R. T. (1994). Costs and benefits of group living in a recently social ungulate: The Alaskan moose. *Journal of Mammalogy*, *75*(3), 621-630.
- Moses, R. A., & Millar, J. S. (1994). Philopatry and mother-daughter associations in bushy-tailed woodrats: space use and reproductive success. *Behavioral Ecology and Sociobiology*, *35*(2), 131-140.

- Mramba, R. P., Mahenya, O., Siyaya, A., Mathisen, K. M., Andreassen, H. P., & Skarpe, C. (2017). Sexual segregation in foraging giraffe. *Acta Oecologica*, *79*, 26-35.
- Newman, M. E. J. (2004). Analysis of weighted networks. *Physical review E*, *70*(5), 056131.
- Newman, M. E. J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences*, *103*(23), 8577-8582.
- Pratt, D. M., & Anderson, V. H. (1979). Giraffe cow- calf relationships and social development of the calf in the Serengeti. *Ethology*, *51*(3), 233-251.
- Pratt, D. M., & Anderson, V. H. (1985). Giraffe social behaviour. *Journal of Natural History*, *19*(4), 771-781.
- Price, E. E., & Stoinski, T. S. (2007). Group size: determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied Animal Behaviour Science*, *103*(3-4), 255-264.
- R Core Team. (2016). R: A language and environment for statistical computing. Vienna, Austria R Foundation for Statistical Computing.
- Rose, P. E., & Croft, D. P. (2015). The potential of Social Network Analysis as a tool for the management of zoo animals. *Animal Welfare*, *24*(2), 123-138.
- Rose, P. E., & Croft, D. P. (2017). Social bonds in a flock bird. Species differences and seasonality in social structure in captive flamingo flocks over a 12-month period. *Applied Animal Behaviour Science*, *193*, 87-97.
- Rose, P. E., & Croft, D. P. (2018). Quantifying the social structure of a large captive flock of greater flamingos (*Phoenicopterus roseus*): Potential implications for management in captivity. *Behavioural Processes*, *150*, 66-74.
- Saito, M., & Idani, G. (2016). How social relationships of female giraffe (*Giraffa camelopardalis tippelskirchi*) change after calving. *African Journal of Ecology*, *54*(2), 242-244.
- Saito, M., & Idani, G. (2017). Comparison of proximity and social behaviors between calves and juveniles in wild giraffe. *Proceedings of the Design Symposium on Conservation of Ecosystem*, *5*, 1-9.
- Saito, M., & Idani, G. (2018). Giraffe mother-calf relationships in the Miombo Woodland of Katavi National Park, Tanzania. *Mammal Study*, *43*(1), 11-17.
- Shorrocks, B., & Croft, D. P. (2009). Necks and networks: a preliminary study of population structure in the reticulated giraffe (*Giraffa camelopardalis reticulata* de Winston). *African Journal of Ecology*, *47*(3), 374-381.
- Siciliano- Martina, L., & Martina, J. P. (2018). Stress and social behaviors of maternally deprived captive giraffes (*Giraffa camelopardalis*). *Zoo Biology*, *37*(2), 80-89.
- Silk, J. B. (2007a). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1480), 539-559.
- Silk, J. B. (2007b). Social components of fitness in primate groups. *Science*, *317*(5843), 1347-1351.
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*(5648), 1231-1234.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3099-3104.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010a). Female chacma

- baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, 64(11), 1733-1747.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010b). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20(15), 1359-1361.
- Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2007). Rank-related partner choice in the fission–fusion society of the spotted hyena (*Crocuta crocuta*). *Behavioral Ecology and Sociobiology*, 61(5), 753-765.
- van der Jeugd, H. P., & Prins, H. H. T. (2000). Movements and group structure of giraffe (*Giraffa camelopardalis*) in Lake Manyara National Park, Tanzania. *Journal of Zoology*, 251(1), 15-21.
- VanderWaal, K. L., Atwill, E. R., Isbell, L. A., & McCowan, B. (2014). Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *Journal of Animal Ecology*, n/a-n/a.
- VanderWaal, K. L., Wang, H., McCowan, B., Fushing, H., & Isbell, L. A. (2014). Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*). *Behavioral Ecology*, 25(1), 17-26.
- Whitehead, H. (1995). Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology*, 6(2), 199-208.
- Whitehead, H. (2007). Selection of models of Lagged Identification Rates and Lagged Association Rates using AIC and QAIC. *Communications in Statistics - Simulation and Computation*, 36(6), 1233-1246.
- Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago, USA: University of Chicago Press.
- Whitehead, H. (2009). SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, 63(5), 765-778.
- Whitehead, H. (2017). Socprog: programming for analysing social structure (version 2.8). <http://myweb.dal.ca/hwhitehe/Manual.pdf>
- Young, T. P., & Isbell, L. A. (1991). Sex differences in giraffe feeding ecology: energetic and social constraints. *Ethology*, 87(1- 2), 79-89.

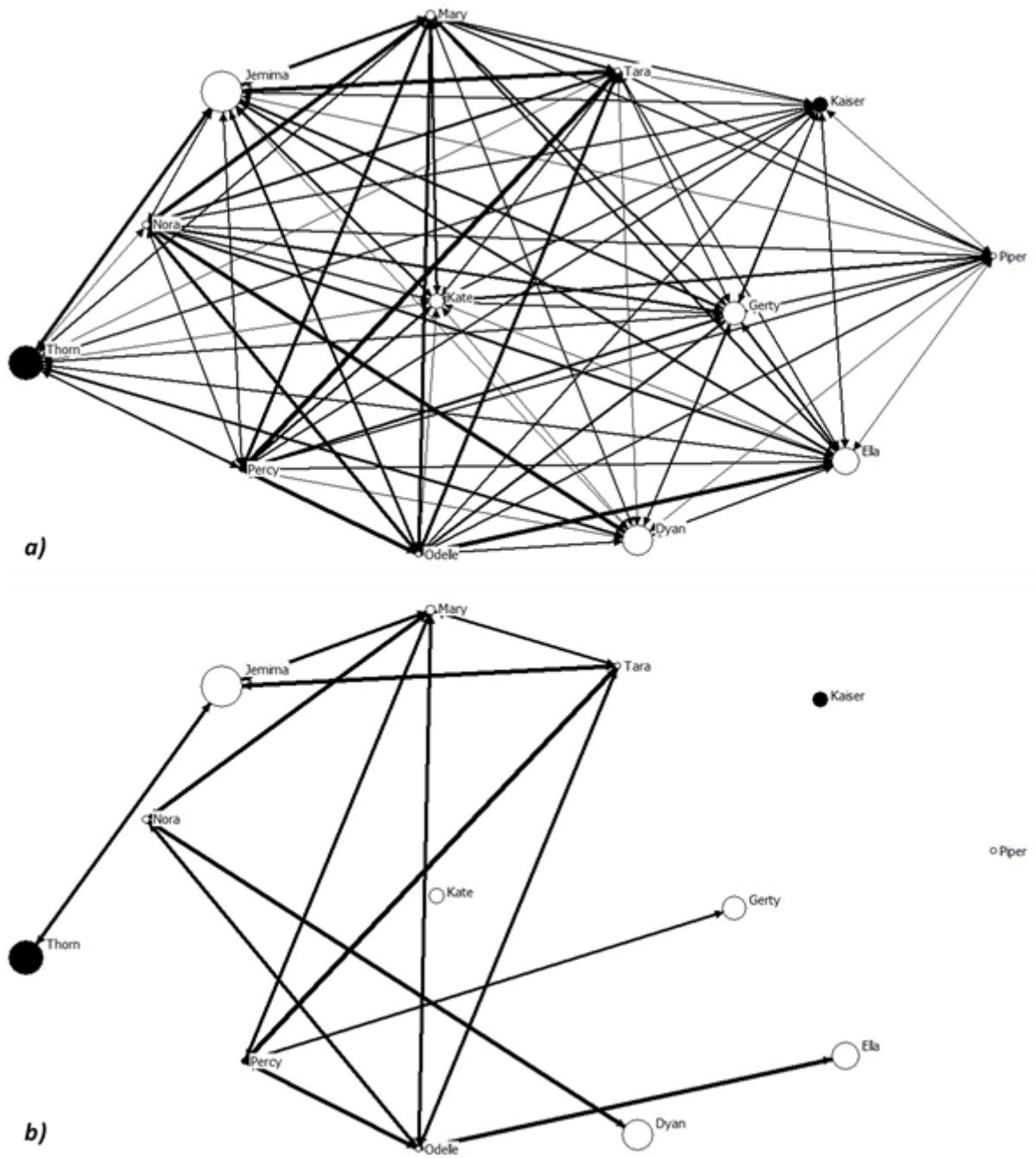


Figure 1. Complete spring-embedded network for 13 giraffes (excluding the newest calf “Small”). a) All bonds, b) filtered to show bonds occurring for more than 40% of the time. Thicker edges denote stronger tie strength. Size of nodes equates to animal age. Female giraffe are white nodes, male giraffe are black nodes.

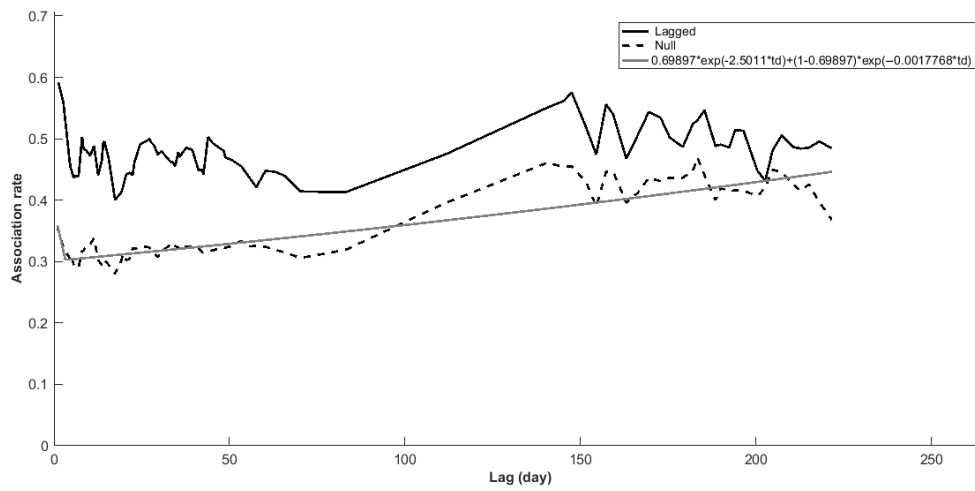


Figure 2. Lagged Association Rate, LAR, (black line) plotted against a Null Association Rate, NAR, (hashed line) and both compared to a fitted model (grey line). The higher LAR is indicative of non-random association patterns and show that these giraffes were consistently spending time with selected conspecifics. The fitted model, association rate $= 0.69897 \cdot \exp(-2.5011 \cdot td) + (1 - 0.69897) \cdot \exp(-0.0017768 \cdot td)$, indicates two levels of casual association.

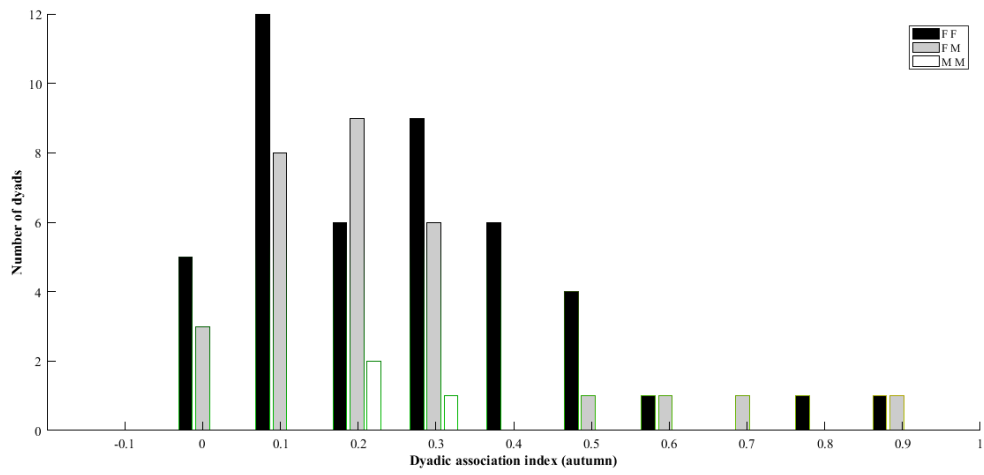
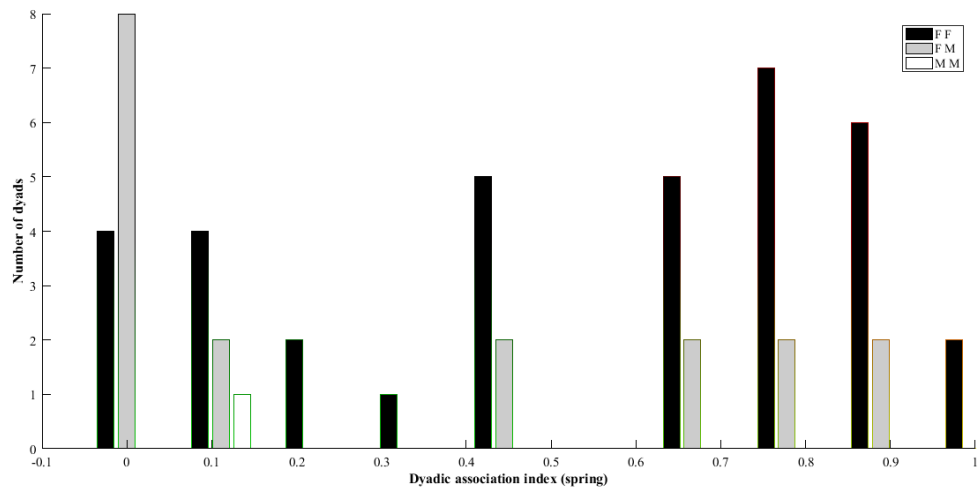


Figure 3. Dyadic plots showing the number of dyads in a specific category of association index (from 0 to 1) for spring 2016 and autumn 2015. Stronger female dyadic bonds are noted in spring (top).

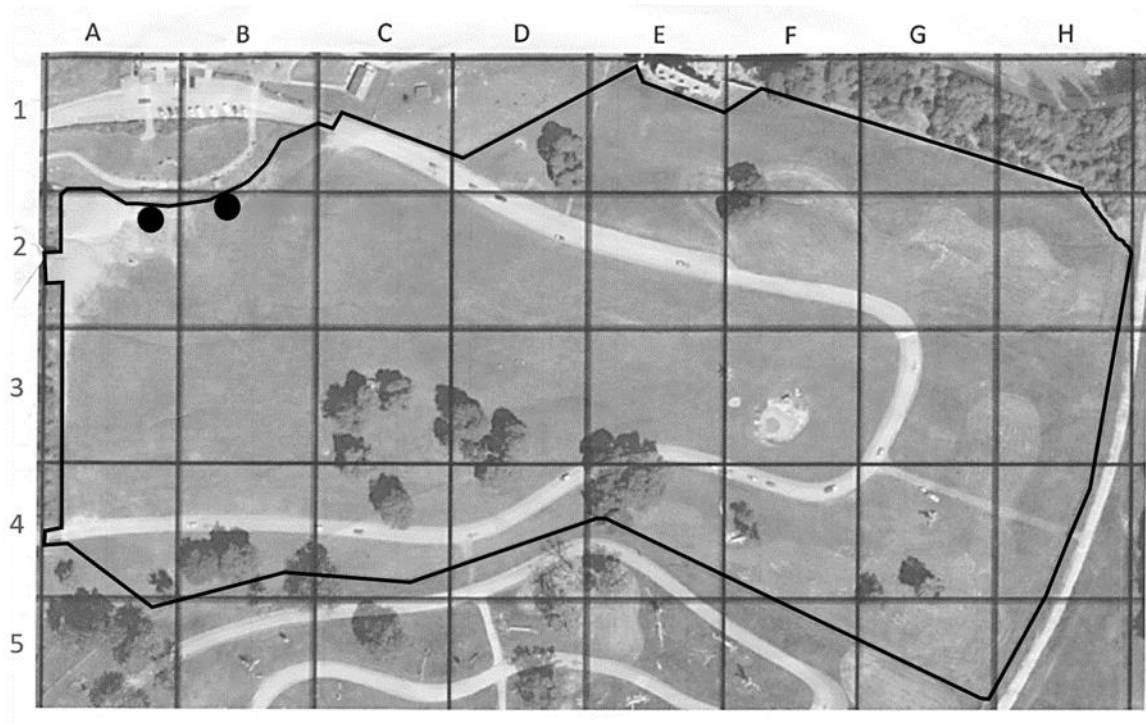


Figure 4. Ariel view of the 24.3 hectare park (border is highlighted by the black line).

Black circles symbolise areas used for public feeding. Copyright Google Maps.

Table 1. Sex, birth dates and mother ID (only if mother is still present in group) for the study group. + indicates born during the study period, - indicates died during the study.

Subject	Sex	Age Class	Date of Birth	Mother ID
Jemima	F	A	24/06/1998	
Thorn	M	A	19/02/2001	
Dyan -	F	A	06/03/2003	
Ella	F	A	28/07/2004	Jemima
Gerty	F	A	28/03/2006	
Kaiser	M	A	29/07/2010	
Kate	F	A	16/08/2010	
Mary	F	J	20/10/2012	
Nora	F	J	16/08/2013	Dyan
Odelle	F	J	27/03/2014	Ella
Percy	M	C	19/05/2015	Gerty
Tara	F	C	30/05/2015	Jemima
Piper +	F	C	04/11/2015	Kate
Small +	F	C	31/03/2016	Ella

Table 2. Distribution of association indices for all giraffe in the sample population

ID	Mean association index (gregariousness)	Sum of Association indices (typical group size)	Maximum association index
Dyan	0.22	3.65	0.69
Ella	0.26	4.06	0.68
Gerty	0.29	4.47	0.43
Jemima	0.32	4.9	0.62
Kaiser	0.18	3.17	0.27
Kate	0.21	3.47	0.38
Mary	0.39	5.65	0.68
Nora	0.34	5.06	0.69
Odelle	0.38	5.58	0.68
Percy	0.34	5.03	0.86
Piper	0.15	2.84	0.37
Tara	0.32	4.79	0.86
Thorn	0.18	3.16	0.51
Classed by sex			
Female	0.29	4.45	0.61
Male	0.23	3.79	0.55
Female-Female	0.3	3.74	0.58
Female-Male	0.24	0.71	0.43
Male-Female	0.24	2.37	0.55
Male-Male	0.21	1.42	0.23
Within classes	0.28	3.2	0.5
Between classes	0.24	1.09	0.45
Overall	0.27	4.29	0.59

Table 3. Time spent social and seen solitary for giraffe present in both 2011 and 2015

Giraffe	<i>2011</i>		<i>2015</i>	
	Alone (%)	Social (%)	Alone (%)	Social (%)
Dyan	28.54	71.46	35.16	64.84
Ella	25.46	74.54	46.00	54.00
Gerty	27.15	72.85	51.04	48.96
Jemima	36.03	63.97	50.20	49.80
Kaiser	27.00	73.00	44.76	55.24
Kate	28.04	71.96	63.90	36.10
Average (SEM)	28.70 (3.42)	71.30 (3.42)	48.51 (8.61)	51.49 (8.61)